Therya

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La Portada

Ejemplar de Berrendo (*Antilocapra mexicana peninsularis*), subespecie endemica de la peninsula de Baja California. Fotografia tomada en una de las áreas controladas de reproducción, previos a la liberación. Esta considerada como especie en peligro de extinción e incluida dentro de la Norma Oficial Mexicana (NOM-Ecol-059). Foto tomada por Sergio Ticul Álvarez Castañeda

Nuestro logo “Ozomatli”

El nombre de “Ozomatli” proviene del náhuatl se refiere al símbolo astrológico del mono en el calendario azteca, así como al dios de la danza y del fuego. Se relaciona con la alegría, la danza, el canto, las habilidades. Al signo decimoprimero en la cosmogonía mexica. “Ozomatli” es una representación pictórica de los mono arañas (*Ateles geoffroyi*). La especie de primate de más amplia distribución en México. “Es habitante de los bosques, sobre todo de los que están por donde sale el sol en Anáhuac. Tiene el dorso pequeño, es barrigudo y su cola, que a veces se enrosca, es larga. Sus manos y sus pies parecen de hombre; también sus uñas. Los Ozomatin gritan y silban y hacen visajes a la gente. Arrojan piedras y palos. Su cara es casi como la de una persona, pero tienen mucho pelo.”

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Contenido

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Conservación de mamíferos: fronteras científicas y trampas socio-políticas

Mammalian conservation: scientific frontiers and socio-political pitfalls

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Introduction: The frontiers of conservation biology are rapidly advancing. This is partly because of scientific achievements, but also it is because the human predicament continues to deteriorate in spite of heroic but inadequate efforts to make the human enterprise sustainable. Of greatest importance is the need to escape from the confrontational mode that pervades our social and political discussions. We must trade this conflict for a realization that there is only one objective for all of humanity, and that is the sustainability of human civilization. Mammalian conservation can play a major role in this struggle, but to do this we must take the initiative to promote meaningful dialogue with politicians, policy makers, economists, sociologists, and the public at large. At the same time, we must continue to be at the frontiers of our science while not neglecting the pursuit of much needed basic research on taxonomy, life history, and distribution of the world's mammals.

Some social, political, and strategic considerations: Themes suggested to enhance such communication are: non-confrontational cooperation, life support services, optimism, systems thinking, and adapting to various political regimes.

Frontiers of conservation science: Eight leading edge topics are suggested for the science component of conservation: 1) community tipping points, 2) trophic cascades, 3) landscape or ecoscape perspective, 4) role of common species in community dynamics, 5) climate change complications, 6) role of genetics, 6) social dynamics, 7) microorganism synergisms, and 8) translocations. Mammalian conservationists are poised to play a significant role in humanity's efforts to confront the myriad of intertwined problems that we face. Given that humans belong to the same taxonomic class that is the subject of our expertise, we have special responsibility to provide that leadership.

Key words: captive breeding, climate change, community tipping points, conservation genetics, cooperation, landscape perspective, life support services, microbiota synergisms, new conservation, optimism, social behavior, sustainable civilization, systems perspective, translocations, trophic cascades.

Introduction

The conservation of mammals on the world stage promises to be a major player as we struggle forward to save civilization from the ravages of population growth, accelerating per capita consumption, climate change, and inevitable social, economic, and political turmoil. In doing this, it will have to maintain a position of being at the frontiers of conservation science while at the same time being in a strong position to engage in necessary collaboration with social scientists, policy makers, economists, and political leaders. Such a synergism is essential if we are to succeed in this endeavor. Mammalogists have a special advantage in this undertaking in that the human species falls within the taxon (Class Mammalia) of their special expertise.

In this essay I will outline my thoughts on some major areas of conservation research that I feel will be at the leading edge of our efforts to improve our understanding of mammalian conservation, enhance our management tools for conservation, and facilitate cooperation with other disciplines and even with the public. I will also call attention to predictable difficulties on the political, policy, economic, and management side. While pursuing these major objectives, we need to remain cognizant that much remains to be discovered about the more than 5500 species of mammals with which we share the Earth. New species are being discovered every year, and for only a very small percentage of the known species do we have sufficient knowledge of their life histories, genetic structure, and adaptive potential to develop conservation strategies for them. Thus, the ongoing exploration of what species exist, what are their distributions, what are the details of their life histories, and what are their evolutionary histories and likely future adaptabilities, all must continue vigorously.

Some Social, Political, and Strategic Considerations

To be effective, conservation planning must be implemented, monitored, and continually revised. This means that while good conservation science is necessary, it is not sufficient. It is therefore imperative that we develop communication links with non-scientists who will be critically needed for implementation (Sörlin 2012). This cadre of potential collaborators includes politicians, policy makers, various types of social scientist, and, most importantly, the local citizenry where the conservation project is to be located. Communication must also be maintained with citizen environmentalists and NGO's that support conservation causes. This last group constitutes important allies in the cause of conservation, but for the most part they represent a different audience than do the politicians, etc. who are usually not, at least initially, mentally or emotionally involved in conservation. Our goals need to be: a) making sure that the importance of conservation to all of humanity is continually emphasized; b) passing on the results of the best scientific knowledge available to the environmentalist community so that they can be increasingly effective in their efforts; and c) developing communication bridges with the politician, etc. communities so that they are willing to listen to us, and then hopefully cooperate in implementation. A particularly intractable communication problem is found where ideological beliefs close off even the possibility of rational discussion on conservation issues (Feinberg and Willer 2011). Here are some suggested guidelines for pursuing these goals.

Non-environmentalists often view the conservation community as a special interest group, and therefore ignorable. We are considered to be obstructionists, fuzzy-minded idealists, anti-economic growth proponents, job destroyers, nature lovers, tree huggers, and generally opposed to progressive and healthy business activities. In fact, our special interest group is human civilization which we would like to see continue into the future in a sustainable way. Because this view is fortunately widely shared, even if not often articulated, it is important not to use language that implies that there are two antagonistic groups: conservationists and everyone else. For example, when conservationists say that they "want to save Nature" because they like it, it has intrinsic value, or because they want to save species from extinction, it drives a wedge between them and the rest of humanity who don't care about such things. An example of well-meaning language that needs to be avoided in the future, published recently (2014) by a supporter of the World Wildlife Fund in their newsletter, reads "I appreciate the WWF's global mission to balance the needs of nature and people." There is in fact no balance, but only a single common goal. This basic conceptual dichotomy is improved somewhat by the so-called "new conservation" (Marvier 2014) which involves advocating that human needs be incorporated explicitly into conservation so that conservation becomes more palatable to non-environmentalists, and therefore more successful. While this new emphasis does not diminish the importance of the traditional conservation approaches, it fails to fundamentally change the "us vs them" philosophy. It only says "let's talk" and by cooperation we will accomplish more. At this point in human history, we need a new paradigm, namely that there is only "us"; our common goal of sustainable human civilization requires both conservation of biodiversity and the support and participation of everyone else on the planet.

A powerful argument for conservation is the preservation of "ecosystem services" for the benefit of mankind. Our agriculture, weather, renewable resources, drug industry, flood control, disease control, invasive species control, etc. depend on such services. However, it is fair to surmise that a large majority of non-ecologists have minimal understanding of the word "ecosystem" even though it is increasingly being used in public discourse. I think we should instead use less esoteric expressions like "human services," "life support services," and "natural community services."

Given the deteriorating conditions on Earth, it is increasingly difficult to remain optimistic about humanity's resolve to effectively deal with our predicament. However, we must express optimism that improvements are actually possible without major catastrophes providing an incentive for action, and we must do this without losing a firm grasp of reality (Swaisgood and Sheppard 2010, Lidicker 2011, Redford *et al*. 2011). We must be ready to explain what things inspire hope for humanity, and conversely what things prompt despair. Pessimism alone leads to inaction and cynicism. Optimism on the other hand, can more readily recruit new adherents to conservation causes, as well as encourage positive actions, and thus encourage positive feedback loops. Conservation researchers should routinely make it clear what tangible benefits for humanity they anticipate from their projects and/or how the research might alleviate negative influences on our life support system (Lidicker 2011).

Although not appropriate for all audiences, where possible we should explain to non-scientists the essence of systems thinking. Life on Earth can be viewed as organized into living systems of varying complexity, such as cells, organisms, populations, and communities. Systems at one level of complexity can be grouped into larger more complex systems (for example, cells assembled to form an organism). Systems at all levels have a boundary and are composed of parts that interact with each other to produce new (emergent) properties. Reference to familiar non-living systems such as a car or computer can be constructive. Imagine a pile of all the disconnected parts that make up a car or computer and compare that to those parts assembled into a functioning system. The potential impacts of missing parts, such as resulting from extinctions or dispersal barriers, can thus be more easily conceptualized. In general, understanding the systems concept should make it easier to comprehend how successful conservation projects work as well as to appreciate why human interests and conservation are inseparable in the pursuit of survival for human civilization.

Conservation projects and regulations occur in the context of political systems that vary greatly across the Earth and over time. Successful implementation of conservation actions requires that this context be understood along with the associated cultural variations. Conservation actions can be accomplished in almost any political system, but are perhaps least likely to be successful where public participation and scientific input are impeded such as in authoritarian governments and corporate oligarchies.

Frontiers of Conservation Science

Consistent with its role as a major participant in conservation, mammal conservation takes its place at the leading edge of the research enterprise. To illustrate this, I have attempted to assemble a list of research areas that I believe are at the frontier of conservation science with an emphasis on mammals. The order of presentation carries no implication of priorities. At the outset, however, I would like to mention again the importance of three non-frontier areas that require ongoing attention. The first is the continuing search for undescribed species and for new distribution records. New species are being regularly discovered, and it is obviously critical to know details of the distribution of each species. Shifts in distribution range, and persistent declines in numbers are also essential information. The second area is that of life history knowledge. Only a very small fraction of known species have their life history parameters well documented. For widespread species, geographic uniformity in these features cannot be assumed, and information needs to be documented from across the species distribution. The third non-frontier area is that of population genetic structure and evolutionary potential. Although these are traditional research areas, there are many new techniques available that make it now much easier to follow movements such as dispersal or migratory pathways, to observe behavior of individuals, to determine social networks, to measure physiological and disease states, to determine food habits, vocalizations, genotypes, etc.

Community tipping points. Usually, when an ecological community is perturbed by a disturbance and the disturbance is subsequently removed, the community will return to something resembling its original state. Ecologists and conservationists depend on such resilience to restore damaged communities. It is now clear, however, that many if not most communities have an unstable equilibrium level of disturbance (sometimes called a tipping point) such that disturbances more severe than those typically experienced do not allow recovery even when the disturbance is removed. Instead, a new type of stable community is formed. As restoration of communities becomes more and more common in conservation, we need to learn more about the nature of these tipping points. Can we someday predict if and when they will occur? Dai *et al*. (2012) and Fung *et al*. (2013) suggest possible methods for this. Sometimes there may be the loss of a keystone or dominant species from the community that forces major reorganization. Perhaps there may be a role for species diversity to be an important factor influencing the nature of this potential disequilibrium. Groups of mutualists (cooperons; Levchenko and Kotolupov 2010) are another possible agent of such disequilibrium. The phenomenon seems analogous to the Allee effect (anti-regulation) in population dynamics (Lidicker 2010). It is now widely accepted that positive species interactions (coactions) are as important in structuring ecological communities as are negative interactions (Boucher 1985, Dugatkin 1997, White and Torres 2009, and Kozo-Polansky *et al*. 2010), and this fact provides clues in the search for and prediction of possible drivers of community tipping points.

Trophic cascades. Aside from the important community adjustments that occur when a top predator is lost from a community, there is much current interest in conservation of the top carnivores themselves (Estes *et al*. 2011, Ripple *et al*. 2014a, 2014b). Since they occur in relatively small numbers and generally require very large home ranges, they are often highly sensitive to habitat loss and degradation. Moreover, nature reserves are generally too small to support populations of top carnivores that are large enough to be sustainable. Also, to avoid genetic inbreeding or stochastic reductions in numbers to non-viable levels, it is often imperative to connect multiple small reserves with appropriate corridors for these carnivores to use at least occasionally. The required features of such corridors then need to be determined. Further complications arise if these top predators are killed for trophies or to protect livestock (Chapron and López-Bao 2014). Two newly discovered reasons for conserving top predators are their possible role in the storage and flux of atmospheric carbon (Wilmers *et al*. (2012), and in countering the negative effects of anthropogenic nutrient loading. Hughes *et al*. (2013) provide an example of this unanticipated benefit of top predators involving a 4-level trophic cascade.

Landscape perspective. As ecologists have learned to think in systems contexts, they have tackled analyses of larger and larger chunks of real estate, and even explicitly included man-modified habitats. This revolution in thinking occurred in the mid-1980s (Lidicker 1995, 2007, Wiens *et al*. 2007), and has rejuvenated the concept of landscape ecology. This term, however, is currently applied to any study area that is large in size from a human perspective. Because of this, the designation of landscape has become disconnected from the traditional hierarchy of systems familiar to ecologists. Steps in hierarchical systems are based on major changes in system complexity, not on size, and they are characterized by new emergent properties. Cell systems are organized into organism systems, which in turn are grouped into population systems (more than one individual organism of the same kind or species). Populations of different kinds of organisms are organized into community systems. The next logical higher level would be systems composed of more than one kind of community. Although landscapes would often contain more than one community-type, this feature is not built into the landscape definition. To fill this need, I have suggested the term "ecoscape" for this (Lidicker 2008). Ecoscapes have novel emergent properties such as edge effects (Lidicker 1999, Lidicker and Peterson 1999), community fragmentation properties, meta-population dynamics, connectedness, inter-patch fluxes of energy, nutrients, organisms, and information, temporal stability, and resilience. Research in mammalian conservation will contribute to and profit from ecoscape level approaches.

Role of Common Species. There is a natural tendency to ignore common species in a conservation context. After all, if a species is abundant it should not be of much conservation interest. Instead, focus tends to be on trying to prevent the extinction of rare species. However, species that are common because they are abundant in their communities, as opposed to species considered common because they have a widespread distribution, often are keystone components of their communities. This means that if they should disappear or even just be significantly reduced in numbers, there will likely be cascading effects on other members of the community. Many local extinctions are probable, and these in turn may reduce the number of trophic levels with top carnivores being particularly vulnerable. The community may deteriorate to the point of a tipping point that will drastically change the nature of the community and prevent restoration efforts. Imagine a redwood forest (*Sequoia sempervirens*) suddenly deprived of its redwoods or a western North American prairie with prairie-dogs (*Cynomys* spp.) extirpated or a European beech forest (*Fagus sylvatica*) without its beeches. Delibes-Mateos *et al*. (2011) and Gaston (2011) draw attention to this easily overlooked issue.

Climate Change Complications. Of unknown, but surely over-riding importance, is the role that climate change will make in complicating our conservation efforts. Research that enlightens how species respond in diverse ways (both genetically and non-genetically) to these threats will be most helpful in reserve planning. It might well be instructive if these responses could be predicted based on species characteristics. Intentional translocations of species across dispersal barriers may be part of the strategy. Pioneering research that documents distributional changes over the past nearly 100 years have been insightful (Moritz *et al*. 2008). Camacho *et al*. (2010) outline the challenges and suggest future research directions, while Mazziotta *et al*. (2014) provide a method for improving our ability to measure the response of organisms to future climate changes. Sgrò *et al. (*2011) discuss ways to build evolutionary resilience with climate change.

Role of Genetics. Not long ago, genetics and evolution were considered to be irrelevant for ecological investigations by most ecologists and conservationists, because of different time frames in which they were assumed to operate. Now, we know better (Allendorf *et al.* 2014, Frankham *et al.* 2009, Weeks *et al.* 2011). Population density bottlenecks, for example, can greatly reduce genetic variation in populations and result in deleterious inbreeding for long periods (Haig 1998). Lohr *et al*. (2014) have shown experimentally that one aspect of this decline in viability, namely accumulated genetic load, can lead to significant reductions in life spans. Low genetic diversity can also lead to increased susceptibility to infectious diseases (Morris *et al.*2012) as well as reduced potential for evolutionary adaptation. Fragmentation of communities can have similar effects depending on the level of connectivity among the fragments (metapopulation genetics). Loss of polymorphisms can affect social behavior, effective population size, demographic machinery on a seasonal or multiannual scale, and possibly symbiotic coactions with other species. New techniques are becoming available for using molecular markers (Haig 1998) to estimate demographic parameters such as dispersal rates and distances (vagility), invasiveness, resistance to pathogens, demic extinction rates, and aspects of social dynamics. Genetic polymorphisms may reveal insights into the spatial scale of local adaptation, temporal variations in selection pressures, mate selection, prospects for future adaptation to changing conditions, resistance to anti-regulating local extinctions (Allee effects), and the extent to which these genetic attributes vary among individuals and between neighboring demes.

Social dynamics. Mammalian social behavior varies tremendously across taxa, and can also be responsive to density, season, and local habitat conditions, and is therefore susceptible to anthropogenic changes. Understanding the dynamics of sociality in taxa and local populations of conservation interest is important as social behavior influences demographic phenomena as well as genetic composition. For these reasons, social behavior and its dynamics can be useful in understanding local extinction risks, the potential for future adaptation to change, and the likelihood that a species will be able to shift its distribution in response to climate changes. Dispersal dynamics can be strongly influenced by social behavior. Emigration, for example, can be encouraged by social cohesiveness of a group of individuals or by group aggression against excluded former members. It can also be inhibited if individuals are unwilling to leave their social environment. Laurance (1990) for example found that dispersal of a social marsupial living in large blocks of Queensland (Australia) rain forest was not possible among forest fragments even when seemingly adequate corridors were present. The chances of successful immigration into an already inhabited habitat fragment can also be strongly dependent on social interactions. As mentioned, social behavior also has numerous possible feedbacks with genetic structure.

Microorganism synergisms. The role of parasitic microorganisms as mortality agents has long held the attention of mammal ecologists. New emerging diseases are regularly being described, and with increasing globalization pathogens are being introduced around the world, often with disastrous consequences. There is also the potential for pandemics among humans based on new transfers of bacterial and viral pathogens from other species (zoonoses). Recent examples are HIV and Ebola viruses. But, what is new and exciting is the recent findings that the huge variety of micro-organisms that live on or in mammal hosts (microbiomes) can have numerous unanticipated non-pathogenic impacts on those hosts, and this includes humans (Dorit 2014). Many species are mutualistic and can influence digestion, development of immune systems, and even behavior. Moreover, the effects are not the sum of individual micro-organism/host interactions, but a product of the particular mix of symbionts present, as well as, of course, the genome of the host. Hanski *et al.* (2012) have discovered that humans growing up in relatively clean urban environments are much more prone to develop allergies than those experiencing rural areas with concomitant contact with a much greater diversity of microorganisms. As discussed by Dunn (2012), Hanski's research has implications also for an additional role of maintaining biodiversity, namely improving the health of mammalian inhabitants. Kohl *et al*. (2014) report that certain gut microbes allow woodrats (*Neotoma*) to feed extensively on toxic plants. Ezenwa *et al*. (2012) review mutual interactions between animal behavior and an individual's microbiome, and conclude that "Given the importance of chemical communication throughout the animal kingdom, symbiont alteration of host chemistry can be a potent force that shapes many fundamental animal behaviors." For example, Bravo *et al*. (2011) have shown experimentally that in mice (*Mus musculus*) the gut microbiome can influence stress, anxiety, and depression-related behavior through the host's neuroendocrine system. Theis *et al*. (2012) report that symbiotic bacteria in hyenas appear to mediate their social pheromones. Verhulst *et al*. (2011) have found that humans with higher microbial diversity on their skins are less attractive to the malaria mosquito (*Anopheles gambiae*). It is apparent that microbiome/host interactions will be found to be major influences on host behavior, health, and social interactions. Influences on mate choice may even be implicated in demic differentiation and speciation. These new insights on the diverse roles of microbiota clearly have implications for using captive breeding to save rare species, especially when reintroductions of individuals back into natural habitats are contemplated.

Translocations. As we move slowly away from the comfortable paradigm of using the past as our vision for conservation actions, we are increasingly faced with the reality that historically-based restorations and reserve management tactics are in many cases becoming irrelevant. Rampant extinctions continue in spite of our not insignificant conservation efforts (Dirzo *et al*. 2014), climate change that now seems very likely irreversible in human time frames, and the debut of novel communities with which we have no experience, all suggest that translocations, including reintroductions, will become increasingly important conservation tools (Seddon *et al*. 2014). The intentional movement of living organisms by humans to places where they currently are not present or present only in low numbers will require new skills and much new knowledge (Weeks *et al.* 2011).

Motivations for translocations will include: 1) saving a species from extinction, 2) helping a species cross a barrier in order to accommodate climate changes, 3) restoring genetic diversity, and hence lost vitality and improved adaptive potential to a dangerously inbred deme (Weeks *et al.* 2011, Whiteley *et al.* 2015), 4) helping a species cope with pathogens, 5) restoration of lost ecosystem services, 6) enhancing a community's defense against invasive species, 7) restoring a lost genetic polymorphism to an isolated deme, 8) helping to prevent a community suffering from cascading extinctions from descending toward a different equilibrium structure, and undoubtedly there are other reasons we do not yet know about.

If a translocation originates from captive breeding stock, we will need to worry about: a) whether the introduced individuals have a suitable microbiota for their new home, b) whether the captive breeding episode has selected against genes that might be important for successful introduction, c) whether sufficient genetic diversity will be present in the new deme for long-term future success, d) whether the social structure of the introduced cohort will be compatible to the new physical and social situation, and e) whether the new location is a novel community in which the success of our target species is untested.

Conclusions

Conservation of mammals must play a commanding role in humanity's efforts to confront the serious and complexly intertwined problems that we face. Success will depend on our abilities to work with the public and non-scientist decision makers. Five guidelines have been suggested to facilitate this required cooperation. Fundamentally important will be our success in shifting the conservation stage from a confrontational one to a situation where all of humanity recognizes that conservationists and everyone else share a single endangered planet and a common goal of sustaining human life. Simultaneously, we must pursue the scientific understanding that supports conservation. Over the past half a century, ecological research in this area has confronted a continually changing array of frontiers (Lidicker 1994, 2002). These can be roughly characterized as the progressive tackling of increasingly complex study objects. That is, there has been a shift toward focusing on successive layers of systems complexity. "Autecology" gave way to population dynamics, populations were soon seen in a community context, and then interactions between adjacent communities were acknowledged in an ecoscape context. Eight research arenas are outlined here that represent current challenging and exciting frontier subjects for our attention. Mammalogists have the advantage that our own species is within the taxon (Class Mammalia) with which we have special expertise. With this comes special responsibility to provide the best possible leadership that we can muster.

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Resumen

Introducción: Las fronteras de la biología de la conservación están avanzando rápidamente. Esto es parcialmente debido a los logros científicos, pero también se debe a que la condición humana sigue deteriorándose a pesar de los esfuerzos heroicos, pero insuficientes, para conseguir que la actividad humana sea sostenible. Es de mayor importancia la necesidad de salir del modo de confrontación que impregna nuestras discusiones sociales y políticas. Se debe de manejar este conflicto para que se comprenda que sólo hay un objetivo para toda la humanidad, y que es la sostenibilidad de la civilización humana. La conservación de mamíferos puede jugar un papel mayor en esta lucha, pero para conseguirlo, debemos tomar la iniciativa de promover un dialogo serio y activo con los políticos, economistas, sociólogos, y el público en general. Al mismo tiempo, debemos continuar con nuestros esfuerzos por alcanzar los límites de nuestra ciencia sin descuidar la búsqueda de la tan necesaria investigación básica como son la taxonomía, historia natural, y la distribución de los mamíferos del mundo.

Algunas consideraciones sociales, políticas y estratégicas: Los temas sugeridos para mejorar la comunicación son: la cooperación no conflictiva, el optimismo, los servicios de soporte de vida, sistemas de pensamiento jerárquico enfocado a los ecosistemas, y la adaptación a diferentes regímenes políticos.

Fronteras de la ciencia de la conservación: Ocho temas de vanguardia que se sugieren para el componente de la ciencia de la conservación: 1) puntos de inflexión de la comunidad, 2) las cascadas tróficas, 3) la ecología del paisaje o "ecoscapes", 4) el papel de las especies comunes en la dinámica de la comunidad, 5) complicaciones del cambio climático, 6) papel de la genética, 6) la dinámica social, 7) sinergias de microorganismos, y 8) translocaciones. Conservacionistas de mamíferos están preparados para desempeñar un papel significativo en los esfuerzos de la humanidad para enfrentar la miríada de problemas entrelazados que nos enfrentamos. Dado que los seres humanos pertenecen a la misma clase taxonómica que es objeto de nuestra experiencia, tenemos la responsabilidad especial de proporcionar ese liderazgo.

Palabras clave: cambio climático, cascadas tróficas, civilización sostenible, cooperación, comportamiento social, cría en cautiverio, genética de conservación, nueva conservación, optimismo, perspectiva del paisaje, perspectiva sistémica, puntos de inflexión de la comunidad, servicios de apoyo a la vida, sinergismos de microbiota, translocaciones.

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Estado del conocimiento y conservación de lagomorfos en peligro y críticamente en peligro a nivel mundial

State of knowledge and conservation of endangered and critically endangered lagomorphs worldwide

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Introduction: Lagomorphs (rabbits, hares, and pikas) are widely distributed in every continent of the world, except Antarctica. They include 91 species: 31 rabbits of the genera *Brachylagus*, *Bunolagus*, *Caprolagus*, *Nesolagus*, *Pentalagus*, *Poelagus*, *Prolagus*, *Pronolagus*, *Romerolagus,* and *Sylvilagus*; 32 hares of the genus *Lepus* and 28 pikas of the genus *Ochotona*. According to the International Union for Conservation of Nature (IUCN 2014), the list of threatened species of lagomorphs includes one extinct, three critically endangered, ten endangered, five near threatened, five vulnerable, 61 of least concern, and six with deficient data. Although a rich diversity of lagomorphs and endemic species exists, some of the wild populations have been declining at an accelerated rate, product of human activities and climate change. In order to evaluate specific conservation actions for species at risk in the near future, the aim of this study is to determine the state of knowledge of endangered and critically endangered species and conservation proposals based on recent studies. This work should serve as a starting point for proposing management and habitat conservation plans for these species and filling the information gaps to address them as soon as possible.

Methods: We performed an analysis of the recent trends in the state of knowledge of worldwide endangered and critically endangered lagomorphs, based on the compilation of the recent bibliographic citations in the IUCN list of endangered species (2014), the Lagomorphs Specialist Group of the IUCN web page, and on published studies focusing on these species. Each study was divided into various topics to know those that need to be addressed. We show detailed information for species that are at risk of extinction in the near future (critically endangered and endangered categories), describing the threats to their populations and existing conservation proposals.

Results: A total of 13 endangered and critically endangered species of lagomorphs have been the subject of study with a total of 78 contributions, of which the most frequently represented (25) refer to phylogeny, systematics, taxonomy, and evolution, followed by conservation (18), and ecology (14); the least represented are studies of reproduction and morphology with only one each. The critically endangered and endangered species have restricted distributions and in general, their threat factors are introduction of exotic species; habitat loss due to development of human settlements and productive activities; induced fires for the growth of new grass shoots for livestock; poaching; and the presence of predators and feral dogs.

Discussion and Conclusions: Worldwide human activities have affected the survival of species of lagomorphs, especially those with restricted distributions. Less than 55 % (7 species) of the total number of species of endangered and critically endangered lagomorphs has been subject of specific study in recent works (2011 to date); moreover, in some cases only one publication was found. Although recent efforts have generated knowledge about the state of conservation and threat factors of some species of endemic lagomorphs, more detailed and long-term studies are needed to propose management and conservation of their habitats in collaboration with society and different academic and institutional sectors.

Key words: Conservation, endemism, hares, lagomorphs, pikas, rabbits, risk category.

Introduction

Lagomorphs (Order Lagomorpha) are comprised by the families Ochotonidae (pikas) and Leporidae (rabbits and hares). Approximately 91 species, including 31 rabbits of the genera *Brachylagus*, *Bunolagus*, *Caprolagus*, *Nesolagus*, *Oryctolagus*, *Pentalagus*, *Poelagus*, *Prolagus*, *Pronolagus*, *Romerolagus*, and *Sylvilagus*; 32 hares of the genus *Lepus* and 28 pikas of the genus *Ochotona* (Chapman and Flux 2008; Table 1) have been described. They are widely distributed with native and introduced species in all continents of the world except Antarctica, and occur from sea level to 5,000 m from 83° N (*L. arcticus*) to 45° S (*L. europaeus*; Chapman and Ceballos 1990; Flux and Angermann 1990).

Lagomorphs are associated with fertility since some species are very prolific; they give birth to numerous litters, reproduce almost all year round, and have short gestation periods. Ecologically, they are an essential part of the food chain. Their size and abundance supports a community of predators from small to medium size. Lagomorph populations maintain weasels, foxes, coyotes, cats, snakes, and many birds of prey (Chapman and Flux 1990).

The order is ancient, with fossil records dating back to more than 50 million years ago. They are adapted to a wide variety of environments, including scrub, grassland, temperate, cloud and rain forests, deserts, and agricultural areas. Despite the importance of hares and rabbits in many places, they are considered pests in some regions because they affect agriculture. Therefore, they are subject to control programs, with the hares *Lepus alleni*, *L. californicus*, *L. americanus*, *L. europaeus*, *L. nigricollis*, *L. townsendii*, and *L. yarkandensis*, and the common rabbit or European rabbit *Oryctolagus cuniculus*, included in the list of the 100-most damaging invasive alien species of the world by the International Union for the Conservation of Nature (IUCN). Their distribution is quite wide and in some countries, such as Australia, they have become a plague due to the lack of natural predators or competitors (Flux *et al*. 1990).

In spite of the high species diversity and numerous endemic species, some of the wild populations of lagomorphs have been declining at an accelerated rate. The causes have been attributed to different risk factors, such as habitat alteration, deforestation or clearing of natural habitats for agriculture, which have increased the degree of isolation of populations, and global climate change. These factors have affect several species of pikas, such as *O. hyperborea*, *O. nubrica*, *O. thibetana*, and *O. pusilla* (Smith *et al*. 1990). Threats to hares and rabbits include hunting for food and trade of their meat and skin, which have affected populations of *L. timidus, L. capensis,* and *S. cunicularius*. However, other species remain abundant and are considered as game animals, such as *S. aquaticus*, *S. audubonii*, *S. floridanus*, and *S. nuttallii* (Chapman and Ceballos 1990).

Productive human activities such as plant cover transformation and intensive land use changes (*e. g*. increasing human settlements, induced fires, and deforestation for agricultural and development activities) have also had negative effects on populations of lagomorphs. In insular populations of hares and rabbits the introduction of exotic species (rodents and domestic cats) that compete for space and resources, and wild predators (birds, reptiles and carnivorous mammals) that prey on them, could have caused them a serious risk of extinction in the medium term (Lorenzo *et al*. 2014).

Although a great number of species of lagomorphs exists, knowledge of different aspects of their basic biology and natural history (behavior, use of habitat, home range size, population size, reproduction, feeding) is scarce for many threatened and endangered species with very restricted ranges (insular species: *e. g. L. insularis*, *S. mansuetus*, *S. graysoni*). Moreover, dynamic populations studies should be performed considering other widespread species, subjected to different natural pressures (competition, predation); population displacements due to sharing their range with other aggressive lagomorph species (*S. transitionalis*-*S. floridanus*; *L. alleni*-*L. californicus*, *californicus*), and by human activities that have caused habitat transformation, as in *Brachylagus idahoensis*, *Bunolagus monticularis*, and *Poelagus majorita* (Chapman and Ceballos 1990; Dobler and Dixon 1990; Duthie and Robinson 1990; Flux and Angermann 1990).

The objective of our study is to determine the state of knowledge and conservation status of lagomorph species worldwide at risk of extinction in the near future based on recent studies considering the tendencies of the topic areas dealt with at present and detailing data and existing conservation proposals up to date. This study should serve as a starting point to propose plans for habitat management and conservation of these species and identify the information gaps to address them as soon as possible.

Material and methods

State of knowledge. To evaluate current trends in the state of knowledge of lagomorphs under endangered and critically endangered status, we considered the citations of the IUCN Lagomorphs Specialist Group (2014), and compiled citations of recent published studies focusing on these lagomorphs.

Conservation. We detailed information about the conservation proposals for lagomorphs, taking into consideration the conservation actions according to the IUCN list of endangered species (2014), and compiled citations of published studies on the current situation of these species.

Results

Of all the species of lagomorphs worldwide, one (*Prolagus sardus*) is extinct, three are critically endangered, 10 endangered, five near threatened, five vulnerable, 61 species of least concern, and six with deficient data. It is a concern that in a recent analysis, Leach *et al.* (2014) predict a significant reduction in the distribution area of the majority of the species when considering the effect of climate change on them. We detail the existing information of the species critically endangered and endangered according to the IUCN (2014). Their approximate distributions are shown in Figure 1.

A total of 13 endangered and critically endangered species of lagomorphs have been the subject of recent studies with a total of 78 contributions, of which the most frequently represented (25) refer to phylogeny, systematics, taxonomy and evolution, followed by conservation (18), and ecology (14); the least represented are studies of reproduction and morphology with only one each (Table 1). Topic areas required to attend conservation issues and existing conservation proposals by species are show in Table 2.

Critically endangered species

Bunolagus monticularis. This species distributed in South Africa is endemic to central Karoo and located in an area < 500 km^2. The riverine rabbit inhabits riparian vegetation on alluvial soils adjacent to seasonal rivers, but its habitat has been highly fragmented and transformed (60 %).

Its population has declined drastically; the few subpopulations have less than 50 individuals, and they are isolated due to anthropogenic barriers; therefore, today this lagomorph is critically endangered (South African Mammal CAMP Workshop 2013, IUCN 2014). According to Leach *et al*. (2014), the bioclimatic envelope of the riverine rabbit is predicted to have declined 85 % by 2080.

Conservation proposals. Currently, the riverine rabbit work groups have been performing surveys, monitoring, outreach, and education (Collins *et al*. 2004). They suggest that the preservation of suitable habitat of the riparian rabbit must receive the highest priority for restoration and breeding programs; translocations and reintroductions are inappropriate at this time. On the other hand, Hughes *et al*. (2008) developed a habitat model to assist in identifying isolated populations, which would contribute to different conservation efforts related to introduction or reintroduction of the species, taking into account the possible effects of global change; according to their results, they considered current breeding programs in captivity should be reevaluated. No data have been published about its habitat, ecology, genetics or population status since 2008, so we recommend evaluating this species to update information.

Ochotona argentata. The silver pika is critically endangered (Smith and Johnston 2008), and occupies a very restricted area (2 x 1.5 km) in the isolated Helan Shan Mountains in central China (Erbajeva and Ma 2006). Formerly included as subspecies of *O. alpina* and of *O. pallasi*, the silver pika is unique in morphology, number of chromosomes, molecular characteristics and vocalizations (Smith and Xie 2008). However, there is confusion whether *O. argentata* and *O. helanshanensis* are separate species (Hoffmann and Smith 2005). A detailed comparative study of *Ochotona argentata*, *O. pallasi* and *O. alpina* showed conclusively that silver pikas differ significantly from the latter species by several characters and features, thus confirming *O. argentata* as an independent species inhabiting Central Asia (Erbajeva and Ma 2006). Additionally, *O. argentata* is a well-defined taxon within the "*pallasi*" group (Lissovsky *et al*. 2007).

Figure 1. Approximate distributional locations of the endangered (open circles) and critically endangered (closed circles) lagomorph species. (1) *Lepus flavigularis*; (2) *Bunolagus monticularis*; (3) *Ochotona argentata*; (4) *Sylvilagus mansuetus*; (5) *Caprolagus hispidus*; (6) *Ochotona hoffmanni*; (7) *Ochotona iliensis*; (8) *Ochotona koslowi*; (9) Pentalagus *furnessi*; (10) *Romerolagus diazi*; (11) *Sylvilagus graysoni*; (12) *Sylvilagus insonus*; (13) *Sylvilagus robustus*.

Conservation proposals. Information regarding its life history remains unknown (Chung 2008) and apparently, its range of occurrence and area of occupancy have declined dramatically in

Table 1. Topics of published studies of endangered and critically endangered lagomorphs worldwide. Citations obtained from the website of the Lagomorph Specialist Group of the International Union for Conservation of Nature (IUCN 2014).

Species/Topics	Reproduction	Genetic	Ecology	Physiology	Morphology	Conservation	Phylogeny/ Systematic/ Taxonomy/ Evolution	Climatic change/ Biogeography/ Distribution	Management	Total
Bunolagus monticularis						20, 87		37, 44		4
Caprolagus hispidus			4, 5, 93			57	79	44		6
Lepus flavigularis	71		9, 72, 81		77	13, 54, 73				8
Ochotona argentata						18, 85	24, 31, 33, 34, 36, 51	86		9
Ochotona hoffmanni						18	30, 31, 32, 33, 34, 36, 51	44		9
Ochotona iliensis			45			18, 47, 48	34, 42, 43, 67, 68, 88, 102			11
Ochotona koslowi			31, 101			46, 49, 103	42, 50, 68, 102	44		10
Pentalagus furnessi		1, 66	41			92		44	95	6
Romerolagus diazi		66	59, 74, 80, 96	2, 75					60	8
Sylvilagus graysoni								44		1
Sylvilagus insonus								44		1
Sylvilagus mansuetus						7, 52		44		3
Sylvilagus robustus		63, 64								2
Total	1	5	14	2	1	18	25	10	2	78

recent years. The abundance and biology of the silver pika are poorly understood (Chung 2008). *Ochotona argentata* is under the threat of range contraction due to continuing global warming (Ge *et al*. 2012). Conservation proposals are to perform necessary observations and follow recommendations about their conservation status (Formozov 1997; Formozov *et al*. 2004).

Sylvilagus mansuetus. The San Jose brush rabbit is endemic to the San Jose Island (194 km^2) in the Gulf of California, Baja California Sur. This island is a protected natural area since 1978 (Semarnat 2010), where it is possible to find exotic mammals (cats, goats, and donkeys; Wood *et al*. 2002, Álvarez-Castañeda and Ortega-Rubio 2003). The rabbit's habitat (xeric) has been altered only slightly, without human settlements and infrastructure; xeric vegetation cover is the adequate for the species activities since they were detected in two breeding sites under the base of a cardon cactus (*Pachycereus pringley*) near a desert thorn (*Lycium* sp.) patch in November 2008 (Lorenzo *et al*. 2011). However, the possible development of a resort with a golf course, private airport, and a small marina, as well as the re-opening of a salt mine that was intensively exploited and which would result in workers accompanied by dogs and cats, would contribute substantially to predation of rabbits on the island (Lorenzo *et al*. 2014).

Table 2. Research areas required to address conservation issues and actions proposed for species of critically endangered (CE), and endangered (E) lagomorphs worldwide.

Species	Research areas required to address conservation issues	Conservation actions proposed
Bunolagus monticularis (CE)	Natural history, ecology, evolution, management	Performing surveys; monitoring populations; outreach, and education; preservation of suitable habitat; restoration; breeding programs, translocations; and reintroductions.
Caprolagus hispidus (E)	Natural history, conservation, evolution, biogeography, distribution, management	Local education; adequate grassland management; monitoring populations; captive breeding program; management plan.
Lepus flavigularis (E)	Natural history, evolution, biogeography, distribution, management	Monitor populations; use and manage rangelands in the paddocks; handle induced grassland fires properly; avoid hare hunting pressure; environmental education programs; translocation program.
Ochotona argentata (CE)	Natural history, ecology, biogeography, distribution, management	Perform necessary observations to know their conservation status.
Ochotona hoffmanni (E)	Natural history, ecology, conservation, biogeography, distribution, management	Establish objectives for its conservation, and a monitoring program with more studies.
Ochotona iliensis (E)	Natural history, ecology, biogeography, distribution, management	Establish conservation action objectives and a monitoring program with more studies.
Ochotona koslowi (E)	Natural history, biogeography, distribution, management	More fieldwork to develop and implement conservation action plans.
Pentalagus furnessi (E)	All	Restriction of extensive grazing in mature forests; control of predators and cessation of road construction that may be favoring predator expansion.
Romerolagus diazi (E)	Natural history, conservation, evolution, biogeography, distribution, management	Protect their habitat through appropriate management and rational exploitation of the forests; hunting control and its regulation; education campaigns; population management in captive colonies.
Sylvilagus graysoni (E)	All	A detailed long-term study to identify the current state of conservation and the basic biological characteristics.
Sylvilagus insonus (E)	All	Intensive studies to determine whether this species still survives and confirm its current local distribution, habitat requirements and a risk assessment study on their survival.
Sylvilagus mansuetus (CE)	All	Assess pressures caused by the destruction of the habitat and illegal hunting; management programs to eradicate exotic fauna and control hunting.
Sylvilagus robustus (E)	All	Monitoring populations; detailed studies to determine the best actions for its conservation; establishment of protected areas and appropriate management plans.

In addition, various animals are predators of *S. mansuetus*, including feral cats (*Felis sylvestris*; Bonnaud *et al.* 2011) and ringtails (*Bassariscus astutus*) although the latter are opportunistic (Lorenzo *et al*. 2011). Reptiles include vipers as rattlesnakes (*Crotalus enyo*, *C. mitchelli*, *C. ruber lucanensis*) and bull snakes (*Pituophis melanoleucus bimaris* and *P. vertebralis*; Espinosa-Gayosso and Álvarez-Castañeda 2006; Lorenzo *et al*. 2014). Avian predators include Osprey (*Pandion haliaetus*), Red-tailed hawk (*Buteo jamaicensis*), Peregrine falcon (*Falco peregrinus*), and American kestrel (*F. sparverius*; Cody and Velarde 2002).

The greatest impact on the rabbit population on this island is the presence of wild cats in high density, which may be preying on both young and adult rabbits. In addition, some fishermen have admitted to hunting rabbits occasionally (Lorenzo *et al*. 2011), which may be factors that result in the low population densities on this island. If the pressure from feral cats is not reduced and hunting pressure continues, the rabbit population could be at risk of extinction in the medium term (Lorenzo *et al*. 2014). According to Leach *et al*. (2014) the bioclimatic envelope of the San Jose brush rabbit is predicted to have decreased 25 % by 2080.

Conservation proposals. Although *S. mansuetus* is entirely distributed within a protected area, it is urgent to assess pressures caused by the destruction of the habitat and illegal hunting (sport or subsistence) which have been previously reported (Gómez-Nisino 2006; Lorenzo *et al*. 2011) and considered within its management programs to eradicate exotic fauna and control hunting. It is necessary to develop research projects to determine population dynamics, reproduction, ethology, and other aspects of its biology and ecology that have been ignored.

Endangered species

Caprolagus hispidus. This species is distributed in South Asia; it is located in Bangladesh, India, Nepal and Bhutan, possibly covering an area from 11 to 500 km^2 of tall grasslands with very fragmented populations. It is currently listed as endangered because its habitat has been reduced dramatically by anthropogenic activity, such as agriculture, urban development, and the burning of grasslands. Studies show that the species ecology is subject to the spatial and temporal dynamics of these grasslands (Maheswaran and Smith 2008; Aryal *et al*. 2012; Tandan *et al*. 2013; IUCN 2014). According to Leach *et al*. (2014), the bioclimatic envelope of the hispid hare is predicted to have increased 21 % by 2080.

Conservation proposals. The hispid hare appears not only in Appendix I of CITES but in Schedule I of the Act on Protection of Wildlife in India and in Schedule I of the National Parks and Conservation Measures Wildlife Nepal. In addition, *C. hispidus* occurs in several protected areas along India. However, further studies on its biology and ecology, such as presence/absence, distribution, movement patterns, behavior, reproduction, and studies of the possible long-term effects of activities such as the burning of grasslands, harvesting, and livestock grazing are needed. A return to the natural system would help prevent the extirpation of *C. hispidus*, as well as other native species. Local education regarding the status of *C. hispidus* is necessary, including educating staff of reserves where *C. hispidus* occurs (Maheswaran and Smith 2008; Aryal and Kumar 2010; IUCN 2014).

Aryal *et al*. (2012) recommend a change to the timing of grass burning to either before or after the hispid hare breeding season to reduce the direct (burning, destruction of nests) and indirect (increased risk of predation) negative effects of such grassland management on hare populations. Population management strategies and a field-based conservation captive breeding program should be implemented immediately to maintain a viable population of the hispid hare in certain protected areas. Finally, Tandan *et al*. (2013) recommend that management authorities should prepare a species-focused management plan to conserve and monitor the hispid hare population and other small mammals of the region.

Lepus flavigularis. The Tehuantepec hare is located only in four disjunct populations in the surroundings of Laguna Inferior and Laguna Superior in the Tehuantepec Isthmus, Oaxaca in an approximate area of 673 km^2 (Cervantes *et al*. 2008; Lorenzo *et al*. 2014). This lagomorph inhabits open grasslands with nanche (*Byrsonima crassifolia*), morro (*Crescentia alata*), and xeric shrub with the presence of tree species and it is threatened by physical conditions (Carrillo-Reyes *et al*. 2012; Lorenzo *et al*. 2014). Change in land use, ranging from the increase of human settlements to bad management and lack of control of production activities, such as ranching and burning of pastures for seasonal agriculture, has resulted in habitat fragmentation of the Tehuantepec hare. Therefore, existing populations are almost completely isolated and most have little genetic viability within them, aggravating their situation (Rioja *et al*. 2011; Lorenzo *et al*. 2014). Excessive hunting is another anthropogenic factor that has caused the decrease of population densities of this species, contributing to its current situation (Lorenzo *et al*. 2014). A recent modelling analysis concluded that the Tehuantepec jackrabbit population of Santa Maria del Mar, Oaxaca is at high risk of extinction (Rioja *et al*. 2012). In this analysis, the population survived over the 500 years of simulation only in the model that involved hunting, besides the base model. The effects of three catastrophic scenarios in combination, as well as inbreeding, increased the risk of extinction up to 100 % in an average of 41.60 ± 25.88 years.

Conservation proposals. Monitoring the Tehuantepec jackrabbit's populations continuously in the study area is recommended, as well as undertaking collaborative activities among academic, governmental, and social sectors proposing actions to use and manage rangelands in the paddocks; handle induced grassland fires properly; avoid hare hunting pressure; implement mitigation actions for the establishment of wind farms in one of the populations; and carry out environmental education programs for residents of the study area starting from the basic level (Lorenzo *et al*. 2014; Rioja and Carrillo-Reyes 2014). Rioja *et al*. (2012) also proposed assessing the relevance of a translocation program to the Santa Maria del Mar population, with individuals from other populations.

Ochotona hoffmanni. Hoffmann's pika occupies a limited area in Mongolia (Bayan-Ulaan Mountains) and Russia (province of Chita, Crest of Erman; area of 600 km^2; Formozov 1997; Formozov and Baklushinskaya 1999). This species was previously included as subspecies of *O. alpina* and subsequently elevated to a specific rank (Formozov *et al*. 1996; Formozov and Baklushinskaya 1999; Formozov *et al*. 2004; Hoffmann and Smith 2005). According to Leach *et al*. (2014), the silver pika's bioclimatic envelope is predicted to have declined 90 % by 2080.

Conservation proposals. No further information is available on other aspects of this species (Chung 2008). More studies are needed to establish objectives for its conservation and a monitoring program.

Ochotona iliensis. Only 27 records of the Ili pika are known, in addition to ten sightings confirmed by local shepherds. This species is distributed exclusively in the mountain ranges of north Tian Shan (Mt. Poluokenu, Mt. Yilianhabierduo, Mt. Tiangeer) and south Tian Shan (Mt. Tieersiketaniao, Mt. Keketiegaitaniao) of China. Populations of Ili pika are fragmentally distributed and its population estimation could be of 2,000 mature individuals existed in the early 1990's (Li 2004; Li and Smith 2005). Recent studies on this pika have reported that no existing populations have been found in more than half (57 %) of the sites where the species was originally recorded 10–20 years ago, which indicate that may be undergoing a rapid extinction (Li and Smith 2005). The possible population decline might have been due to: 1) plague, 2) expansion of human population and pastoral activities in higher elevations; and 3) global climate change forcing Ili pika to retreat to higher elevations for suitable habitat. This combination of factors has contributed to their reduction (Li and Smith 2005).

Conservation proposals. Low population density and fragmented distribution of Ili pika could led to low gene flow. An *ex situ* study conducted by Li *et al*. (1994) was able to demonstrate that Ili pika was suitable to be kept in an artificial environment with high adaptability to lower elevation and types of vegetation, which opened up possibilities for an artificial breeding program for rescue (Chung 2008). More studies are needed to establish objectives of conservation action and a monitoring program for this species.

Ochotona koslowi. Koslov's pika occupies the high isolated mountains near the junction of the Qinghai province, Xinjiang Uygur and Xizang autonomous regions in central China. According to Li *et al*. (2000) Kozlov's Pika was distributed in central, west Mt. Kunlun, south Mt. Kongka and Aerjin Mountain Nature Reserve (Aqikekule Lake, Tuzi Lake and Yueya River). Kozlovi's pika was rediscovered in 1984 after it was described nearly a century ago (Zheng 1986). A recent expedition led by Li *et al*. (2000) in Aerjin Mountain Nature Reserve concluded that it had a very restricted and fragmented distribution (800 km between subpopulation). Evidence has shown that the range of this species could be extended further to the west of what was previously thought (Smith 2008). In addition, its population dynamics remains uncertain. The limited distribution area and ancestral skull properties suggest that Kozlov's pika may be an ancestral species in decline (Li *et al*. 2006). According to the bioclimatic envelope modeled by Leach *et al.* (2014), Kozlov's pika is predicted to decrease to total extinction.

Conservation proposals. More fieldwork is necessary to develop and implement conservation action plans for this species. It is likely a sister species of *O. ladacensis* (Yu *et al*. 2000). Current distribution and status in two of the three distributed locations (*e. g*. central, west Mt. Kunlun and S Mt. Kongka) are unknown. Since 1998, there has been little new information on Kozlov's pika. Collection of this preliminary information was made possible only during a field survey of chiru (*Pantholops hodgsonii*). Strengthened cooperation is needed to protect this rare and unique animal (Li *et al*. 2006).

Pentalagus furnessi. The Amami rabbit occupies only two small islands in the Ryukyu Islands South of Japan within an area of 335 km^2. The habitat of the only black rabbit consists of evergreen forest and areas where perennial grasses dominate. In 2003 the size of its population was estimated from 2,000 to 4,800 individuals in four habitat fragments in Amami Island in addition to a small town in Tokuno Island. The species is threatened by invasive mongooses, feral cats and dogs, as well as by deforestation and development projects (Sugimura *et al*. 2000; Sugimura *et al*. 2003; Sugimura and Yamada 2004; Yamada 2008; Sugimura *et al.* 2014). Recently Abrantes *et al*. (2011) reported that *P. furnessi* has a particular genetic alteration which in exposure to the *Myxoma* virus (MV) it can potentially cause an epizootic disease with particularly high mortality rates. Kubo *et al*. (2014) reported dermatitis associated with a parasite. In contrast to other species, the Amami rabbit's bioclimatic envelope is predicted to increase 150 % by 2080 (Leach *et al.* 2014).

Conservation proposals. Restriction of extensive grazing in mature forests, control of predators, and cessation of road construction that may be favoring predator expansion in the forests, are all indicated (Sugimura *et al*. 2000).

Romerolagus diazi. The volcano rabbit is located in the Transverse Neovolcanic Belt and restricted to three discontinuous areas with a total of 280 km^2 covering the slopes of the Popocatepetl, Iztaccihuatl (Sierra Nevada), El Pelado, and Tlaloc (Sierra Chichinautzin) volcanoes in central Mexico. The species is located from 2,800 to 4,250 m in pine forests (*Pinus*) with grasses (zacatón, mainly *Muhlenbergia macroura*, *Festuca rosei*, *F. amplissima* and *Stipa ichu*) and rocky substrate (Fa and Bell 1990; Sánchez-Trocino *et al.* 2013). Its predators are weasels (*Mustela frenata*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), rattlesnakes (*Crotalus* spp.), and the Red-tailed hawk (*Buteo jamaicensis*; Fa and Bell 1990).

Its habitat has been threatened by forest destruction by burning, invasive agriculture, overgrazing by cattle and sheep, over-exploitation of wood and cutting of zacatón for brush, manufacturing, housing development, and poaching. A substantial area of its original habitat has disappeared due to the expansion of Mexico City and a rapid increase of rural settlements around its habitat (Fa and Bell 1990; Romero and Velazquez 1994; Velázquez *et al*. 1996; Portales *et al*. 2004). Studies, as that of Martínez-García (2011), show that in certain areas as Altzomoni, in sites as El Arco and El Pinar population density of this rabbit is very close to its carrying capacity. Moreover, Rizo-Aguilar *et al.* (2014) found faecal cortisol metabolites levels significantly higher in animals from the disturbed sites indicating potentially higher physiological stress intensities.

Conservation proposals. It is necessary to protect *R. diazi*'s habitat through appropriate management and rational exploitation of the forests where it lives, both by governmental and social sectors. Hunting control and its regulation must be compatible with the recovery of other areas and wildlife conservation. Education campaigns at different levels and spreading the impact of land use on wildlife conservation are necessary, as many locals are unaware of the protected status of *R. diazi*. The species requires a proper population management in captive colonies in zoological parks as in Mexico City (Fa and Bell 1990).

Sylvilagus graysoni. The Tres Marias rabbit is endemic of the Tres Marias Islands, Nayarit, Mexico with two recognized subspecies. *S. g. graysoni* in the Maria Madre (the largest with 145 km^2), Maria Magdalena, and Maria Cleofas islands and *S. g. badistes* in San Juanito Island. The species is located in dry deciduous and moist forests, characterized by dense cover with many tree species (Chapman and Ceballos 1990).

The islands have been a high security prison of the Mexican Government, so the presence of a large number of people has resulted in extensive ecological disturbances. Although Maria Magdalena Island has been designated an ecological reserve by the Mexican Government, a large extension of natural vegetation areas has been destroyed in Maria Madre and Maria Cleofas islands by local inhabitants. According to Leach *et al*. (2014), the Tres Marias cottontail's bioclimatic envelope is predicted to have declined 20 % by 2080.

In addition, the rats *Rattus rattus* were accidentally introduced in all the islands, and the White-tailed deer (*Odocoileus virginianus*) and domestic goats were purposely introduced to the Maria Magdalena Island. These introduced species have caused profound changes in the ecological conditions of the islands and have caused great impact on native wildlife (Chapman and Ceballos 1990). The greatest threats to the species are introduced species that compete for food, alter native vegetation, and prey on rabbits, causing habitat destruction in addition to that one caused by the human inhabitants (Chapman and Ceballos 1990).

Conservation proposals. A detailed long-term study strongly recommended to identify the current state of conservation and the basic biological characteristics of the species (Chapman and Ceballos 1990).

Sylvilagus insonus. The Omiltemi rabbit is restricted to a highly fragmented area less than 500 km^2 in a natural reserve area, Omiltemi State Park in the Sierra Madre del Sur, Guerrero, Mexico at an elevational range from 2,133 to 3,048 m (Chapman and Ceballos 1990; Cervantes and Lorenzo 1997). This species is the rarest and least understood of all lagomorphs, definitely known from only three specimens with questionable diagnosis (Nelson 1904; Wilson 1991; Cervantes and Lorenzo 1997). Prior to recovering of a skin of a hunted specimen donated by local residents in 1998 (Cervantes *et al*. 2004), many sources had considered this species among rabbits the most threatened in the world (Chapman *et al*. 1990) and possibly extinct (Caughley and Gunn 1996; MacPhee and Fleming 1997, 1999; Cervantes *et al*. 2004). The consequences of deforestation and excessive hunting may be important factors that have threatened this species and prevented its observation in field (Jiménez-Almaráz *et al*. 1993). According to Leach *et al.* (2014), the Omiltemi rabbit's bioclimatic envelope is predicted to have decreased 80 % by 2080.

Conservation proposals. It is of utmost importance to take measures to ensure the survival of all Omiltemi State Park fauna and their habitats. Intensive studies are necessary to determine whether *S. insonus* still survives and confirm its current local distribution. Studies should focus on habitat requirements and a risk assessment study on the survival of this threatened species. Until such information is available, a comprehensive conservation strategy of this species and its habitat cannot be developed.

Sylvilagus robustus. The Robust cottontail rabbit is found in isolated mountains in western Texas, eastern New Mexico (U. S. A.) and northern Mexico, with a total extent of occurrence in this range of approximately 1,815 km^2 and with an estimated area of occupancy of 730 km^2, commonly over 1,800 m (Ruedas 1998). For a long time it was considered as a subspecies of *Sylvilagus floridanus*. It occurs in small population densities, which increases its sensitivity to threats. It is likely sensitive to drought since it occurs less frequently in dry years. The destruction of its habitat due to urbanization, development, grazing cattle, and cutting of shrubs is reducing the available habitat for the species (Ruedas 1998).

Conservation proposals. Detailed studies are required to determine the best actions for its conservation, including population genetics, life history, population status, and the effects of its threats, followed by the establishment of protected areas and appropriate management plans. Monitoring of this species is necessary because it also experiences extreme fluctuations in number of mature individuals because of drought and other threats (Ruedas 1998).

Discussion

State of knowledge. Less than 55 % (7/13 species) of the total number of endangered and critically endangered lagomorph species has been subject of specific study in recent works (2011 to date), and in some cases only one publication was found. The lack of recent knowledge for many of the species of lagomorphs worldwide may be due to several factors that have limited their study. For example, lack of institutional support or funding sources; reduced academic staff to perform studies (only 66 members in the Lagomorph Specialist Group of the IUCN); lack of security conditions in the areas where these species are distributed; and/or difficulty involved in capture and taxonomic identification of some taxa. For species with restricted distribution, endemic, and in the categories of critically endangered and endangered, these factors are compounded even more; they are potentially vulnerable to the effects of the changes associated with the destruction of their habitats induced by humans and climate change, hindering their observation and thus their study.

The current trends in the state of knowledge of endangered and critically endangered lagomorphs worldwide indicate that the research areas of phylogeny, systematics, taxonomy and evolution are the most represented, followed by conservation and ecology. For *P. furnessi* and all the species of *Sylvilagus* more studies are necessary in all research areas in biology to know the current conservation status and propose specific conservation actions. The species with the largest number of studies is *O. iliensis* with 11 studies on ecology, conservation, phylogeny, systematics, taxonomy and evolution, followed by *O. koslowi* with 10 studies in the same areas. The species that have very few studies are *S. graysoni* and *S. insonus*.

The regions where endangered and critically endangered lagomorph species are most numerous (Central America and East Central Asia) are generally recognized as biodiversity hotspots, places with their own biogeographic history, and with ecosystems (such as cloud and temperate forest) which support biological diversity,have high numbers of endemic species, and are often severely threatened (Myers *et al*. 2000). Thus they must be priority sites for conservation. Moreover, it is very important to generate proposals for conservation for the species of lagomorphs in critical risk categories, from a biogeographical perspective. Prioritizing areas for conservation and reincorporating these relevant and under-represented species in the system of natural protected areas should play a very important role in the decision-making process.

Conservation. Human activities in the world have directly and indirectly affected the survival of lagomorph species, especially those with restricted distributions. Changes in agricultural practices, including the use of fertilizers and pesticides, as well as increase of monocultivation and the burning of pastures for livestock, have an impact on the declining populations of lagomorphs. Decisions regarding land use should consider the impact of other factors, such as conservation, hunting, fur industry, and the increase in human settlements.

Similarly, it is of great importance to propose management alternatives and urgent actions of protection, conservation, and recovery of subspecies considered historically widely distributed, for example, *S. bachmani peninsularis* and *S. b. exiguus* in the Baja California Peninsula, whose populations are considered threatened and require immediate conservation actions, including their habitats. *Sylvilagus b. peninsularis* could be considered as extinct by anthropogenic activities (Lorenzo *et al*. 2013). *Sylvilagus b. riparius* is a candidate to be recorded as critically endangered on the red list of the IUCN; it is found along streams of the lower reaches of the San Joaquin River in California, U.S.A. It occupies approximately 225 hectares in two separate areas, one of which is highly fragmented. One population has been reduced to about 25 % of its size based on population censuses in the past 11 years. Part of its habitat is intended for urban development in the coming decade. A third population has recently been established in a historic habitat, but it is too early to determine if the restored population will be viable (Kelly *et al*. 2004; Williams *et al*. 2008). Field studies are necessary to determine the current status of *S. floridanus yucatanicus* in the Yucatan Peninsula (Escobedo-Cabrera and Lorenzo 2011), *S. brasiliensis truei* in southeastern Mexico, and *S. cunicularius cunicularius* in central and western Mexico, which share the threat of habitat fragmentation.

Populations of *L. callotis callotis* and *L. callotis gaillardi* in northwestern, central, and southern Mexico have shown a drastic decline mainly due to the loss and degradation of their habitat (NMDGF 1988) by sport hunting, habitat disturbance and fragmentation, provoked fires (Martínez-Villeda 2006), and tending to be displaced by more generalist species such as *L. californicus* or *Sylvilagus* spp. (Bednarz and Cook 1984; Desmond 2004; Brown *et al*. in press). Although recent efforts have generated knowledge about the state of conservation and threat factors of some species of endemic lagomorphs, it is still necessary to carry out more detailed and long-term studies to propose management plans and conservation of their habitats in collaboration with society and academic and institutional sectors.

To protect populations of lagomorphs from disappearing, it is necessary to perform simultaneous actions of conservation and controlled use, as well as to increase life quality for local residents to reduce pressure on the species and their habitats through improving production activities (fishing and livestock). For some of the species of insular rabbits and hares their future seems uncertain; although there are conservation schemes in operation, and some are in protected areas, some threats to their populations still remain. Local protected natural areas may represent a viable alternative for the conservation of lagomorphs and improvement in life quality of residents in other areas. Unfortunately, in many countries, efforts on research and protection on rabbits and wild hares are scarce. It is very important to increase studies of poorly known lagomorphs for their proper utilization and conservation.

In addition, there are substantial gaps in information regarding biology of several species (eight species have deficient data in the IUCN), which becomes relevant considering that without this information, it would not be possible to make an adequate assessment of the conservation status and threats they face, and any species management plan and their habitats would likely be unsuccessful. More than 40 % (6 species) of endangered and critically endangered species have no recent studies. It is necessary to know the current state of the populations of the lagomorphs in depth, carry out long-term studies on population dynamics including their relationship with other species of native fauna and flora as well as the effects of exotic species present.

Control of exotic species is a conservation priority for insular lagomorphs, including control and management of feral animals (dogs and cats) that directly attack their young. Surveillance carried out by elements of the local authorities is recommended to prevent poaching.

For some species, breeding programs are recommended in certified semi-captivity units, for management and use of wildlife to ensure sustainable consumption by generating extra income to its inhabitants. In addition, environmental education campaigns that promote the conservation and controlled use of plants and animals should be established permanently at different levels. These programs must have the objective of disseminating the results of investigations and the role played by the lagomorphs in their ecosystems, as well as the impacts that affect them with human activities. It is essential to include local authorities and population in the strategies developed, because any conservation program would be a failure without their support.

Resumen

Introducción: Los lagomorfos (conejos, liebres y pikas) están ampliamente distribuidos en todos los continentes, excepto Antártica. Comprenden 91 especies: 31 conejos de los géneros *Brachylagus*, *Bunolagus*, *Caprolagus*, *Nesolagus*, *Pentalagus*, *Poelagus*, *Prolagus*, *Pronolagus*, *Romerolagus* y *Sylvilagus*; 32 liebres del género *Lepus* y 28 pikas del género *Ochotona*. De acuerdo a la lista de especies amenazadas de la IUCN (2014), una está extinta, tres están críticamente en peligro, 10 en peligro, cinco cercanas a la amenaza, cinco vulnerables, 61 en preocupación menor y seis con datos deficientes. Algunas de sus poblaciones están declinando a ritmo acelerado por actividades humanas y el cambio climático. Con el fin de determinar acciones específicas de conservación para las especies en riesgo en un futuro cercano, el objetivo de este estudio es presentar el estado de conocimiento para las especies en peligro y críticamente en peligro y ofrecer propuestas de conservación basadas en estudios recientes. Este estudio puede servir como un punto de partida para proponer planes de manejo y conservación del hábitat para estas especies y conocer los huecos de información para atenderlos lo más pronto posible.

Metodología: Presentamos un análisis de las recientes tendencias del estado del conocimiento de las especies de lagomorfos en peligro y críticamente en peligro a nivel mundial, con base en la recopilación de citas bibliográficas recientes, obtenidas de la lista roja de la IUCN (2014), la página de la red mundial del Grupo Especialista de los Lagomorfos de la IUCN y de estudios focales de sus especies. Cada estudio fue separado por varios temas para conocer cuáles necesitan atención. Presentamos información detallada para las especies en riesgo de extinción en un futuro cercano (en peligro y críticamente en peligro), describiendo las amenazas a sus poblaciones y propuestas de conservación existentes.

Resultados: Un total de 13 especies de lagomorfos en peligro y críticamente en peligro han sido sujetos de estudio, con un total de 78 artículos; los más representados (25) se refieren al tema de filogenia, sistemática, taxonomía y evolución, seguidos por el tema de conservación (18) y ecología (14); y los menos representados son los estudios de reproducción y morfología con un estudio cada uno. Las especies críticamente en peligro y en peligro tienen distribuciones restringidas y en general, sus factores de amenaza son: la introducción de especies exóticas; la pérdida de su hábitat por el desarrollo de asentamientos humanos y actividades productivas; los incendios inducidos para el crecimiento de nuevo pasto para el ganado; la cacería furtiva; la presencia de perros ferales y depredadores silvestres.

Discusión y conclusiones: Las actividades humanas en el mundo han afectado la supervivencia de las especies de lagomorfos, especialmente aquellas con distribuciones restringidas. Menos del 55 % (7 especies) del total de las especies de lagomorfos en peligro y críticamente en peligro han sido sujeto de estudio en trabajos recientes (2011 a la fecha); además, en algunos casos se encontró solo una publicación. Aunque los esfuerzos recientes han generado conocimiento sobre el estado de conservación y factores de amenaza de algunas especies de lagomorfos endémicos, es necesario llevar a cabo estudios más detallados y a largo plazo y para proponer planes de manejo y conservación de su hábitat en colaboración con la sociedad y los diferentes sectores académicos e institucionales.

Palabras clave: categoría de riesgo, conejos, conservación, endemismo, lagomorfos, liebres, pikas.

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El ecoturismo multidisciplinario como un enfoque para la conservación en África

Ecotourism as a multidisciplinary conservation approach in Africa

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Introduction: Conservation biology addresses complex issues that require multidisciplinary solutions capable of addresing various ecological, social, cultural, economic, political and legal aspects. Compromises between biodiversity conservation and human development are inevitable given societal demands and funding constraints. Ecotourism has the potential to provide local stakeholders with socioeconomic benefits while achieving conservation objectives. Reported here is an expansion to a cost-benefit analysis of tourism in Kenya's national parks that explored issues and potential improvements to maximize benefits and minimize costs. Issues raised in this analysis are explored in the wider context of conservation in Africa. In particular, conservation in Africa would benefit from a greater involvement of local community stakeholders in ecotourism decision-making, the development of tourist interest in a wider range of wildlife, and a wider application of adaptive management principles.

Discussion and conclusions: *Local communities as major conservation stakeholders.* This section explores and emphasizes the importance of local communities as major stakeholders in conservation. In order for ecotourism to balance conservation and development objectives, local community stakeholders must be able to equitably share in socioeconomic benefits. Their engagement, involvement and empowerment is critical to the success of ecotourism as a multidisciplinary conservation approach.

Conservation prioritization and ecotourism diversification. This section discusses the need for ecotourism across the African continent to diversify beyond the traditional "Big Five". Expanding the viewing preferences and interests of different visitors can help draw attention and funding to less iconic species to achieve greater overall biodiversity conservation.

Monitoring and adaptive management. This section stresses the importance of scientific research and understanding to conservation objectives. Data need to be gathered systematically in ongoing monitoring and evaluation to facilitate adaptive management.

Key words: Adaptive management, Africa, conservation, cost-benefit analysis, ecotourism, local community, monitoring, stakeholder engagement, tourism diversification.

Introduction

As anthropogenic impacts on the natural world continue to mount, the importance of conservation efforts to protect biodiversity grows. Conservation is a field that transcends the traditional boundaries of pure sciences; it must produce solutions that address ecological concerns alongside human dimensions, including sociopolitical, economic, legal, cultural, aesthetic and spiritual considerations (McNeely 2006; Sanderson *et al*. 2008). The greatest challenge in conservation is translating a plan into action through implementation, which requires access to adequate resources (Hoeksta *et al*. 2002; Stephenson and Ntiamoa-Baidu 2010). Assessing the expected costs and benefits of conservation strategies can maximize ecological and socioeconomic returns and cost-effectiveness (Di Minin *et al*. 2013b). Prioritizing goals and actions can help make the most of limited resources in producing positive impacts for species and their habitats (Dietz 2010; Brown and Swaminathan 2010; Game *et al*. 2013).

The realities of modern society coupled with resource constraints in conservation render trade-offs between biodiversity conservation and human development unavoidable (Di Minin *et al*. 2013b). Where applicable, accounting for potential economic benefits in decision-making can produce solutions that combine conservation and sustainable development objectives (Di Minin *et al*. 2013b). Conservation-based business, such as ecotourism, can provide socioeconomic benefits for local communities, representing a mutually beneficial approach to achieving conservation and economic development goals simultaneously (Di Minin *et al*. 2013b). Through the economic incentivizing of species conservation, ecotourism may hold a critical role in the ability of species to thrive in the natural world (Lindsey *et al*. 2007).

Ecotourism is defined as "responsible travel to natural areas that conserves the environment and improves the wellbeing of local people" by The International Ecotourism Society (TIES), representing a pragmatic compromise in balancing conservation objectives with human development in a sustainable manner (Sekercioğlu 2002; Eshun 2014; Frempong and Adjei 2014; TIES 2014). This form of tourism has the capacity to effect environmental, social, cultural and economic impacts at great scales; whether such potential is used for positive impacts or negative impacts depends on how it is carried out (Okech and Bob 2009). When applied in a fair and equitable manner, it offers conservationists an alternative approach to strict protectionism by allowing for the usually non-consumptive use of precious natural resources (Brooks 2012; Waylen and Mulder 2012). To maximize social and ecological benefits, ecotourism needs to be complemented with other suitable approaches and tools and may not be universally applicable due to constraints of geography, landscape, inadequate local ecological information, or sociocultural norms specific to each region or country (Coria and Calfucura 2012).

In Kenya, ecotourism contributes significantly to the economy and revolves around its 65 national parks and reserves (Ikiara and Okech 2002; Ramser 2007; Akama, Maingi and Camargo 2011). Through a process of monetary valuation, Cheung (2012) quantified the socioeconomic and environmental impacts of tourism in Kenya's national parks and found that the overall benefits outweigh the costs. Cheung (2012) estimated that the collective benefits range between Kenyan Shillings (KES) 47,328,086,850 and KES 67,052,853,000 annually, while evaluating all socioeconomic and environmental costs between KES 3,864,954,704 and KES 4,624,588,710 per year. This means that tourism in Kenya's protected areas brings a net benefit ranging from KES 21,531,098,140 to KES 42,015,498,296 per annum once socioeconomic and environmental impacts are accounted for (Cheung 2012). Noting the assumptions and inherent difficulties in assigning monetary values to impacts, the author highlighted the overall trend that the socioeconomic and environmental benefits outweigh the costs as broadly representative of the impacts of tourism in Kenya's national parks (Cheung 2012). However, although the cost-benefit ratio is favorable to having tourism in Kenya's protected areas, there are stakeholders who benefit more than others, who in conttrast may directly and disproportionately bear more of the costs while receiving little benefit (Cheung 2012). The analysis by Cheung (2012) identified and discussed areas of the industry where improvements could further maximize benefits and minimize costs. The purpose of this paper is to expand on some of the issues discussed in Cheung's (2012) cost-benefit analysis, and place them into a wider context of taking an interdisciplinary approach to conservation on the African continent.

Discussion

Local communities as major conservation stakeholders

Conservation must take into account local contexts in planning and implementation, as local peoples and communities are inherently significant stakeholders (Hodgman 2005; Waylen *et al*.

2010). Conservation efforts are most effective when all parties agree to common goals and how to achieve them; obstacles may emerge when these are unclear or poorly communicated (Hodgman 2005; Ahebwa 2012; van der Duim and Sandbrook 2012). Cheung (2012) echoed the sentiments of other researchers in noting that local communities were disempowered by an established neo-colonial structure present in the ecotourism industry in Kenya that hinders local participation in decision-making (Scheyvens 1999; Coast 2002; Akama 2004; Manyara and Jones 2007). While it is the intention of governments and NGOs to improve the economic welfare of local and indigenous peoples, their paternalistic role in ecotourism development and management have effectively disengaged local stakeholders from the decision-making process (Coria and Calfucura 2012).

In spite of the favorable cost-benefit ratio, ecotourism has been unable to improve the livelihoods of local communities in Kenya. The description of benefits from revenue-sharing by local stakeholders as being "very minimal" reflects existing administrative inefficiencies and weaknesses in addition to the disempowerment of these communities (Beh and Lelengula 2009; Bruyere 2009; Cheung 2012). Given the widespread poverty that persists in the country, there is a need for ecotourism opportunities and revenue to be equitably and efficiently distributed (Sindiga 1995; Beh and Lelengula 2009; Bruyere 2009; Gusset *et al*. 2009; Hazzah2009; Mulder and Frank 2009). The employment of outside labor has also led to imbalances in local representation on tourism workforces (Manyara and Jones 2007; Beh and Lelengula 2009; Bruyere 2009). Okech and Bob (2009) found that involvement in tourism-related work was common among local communities adjacent to the Maasai Mara National Reserve and Amboseli National Park, and this included direct employment, receiving money from camping concessions, earning fees from manyatta (family settlement) visits, and from the sale of souvenir handicrafts. However, for local communities, these benefits were determined to be insufficient to offset the negative impacts of tourism in their local areas (Okech and Bob 2009). These problems are not unique to ecotourism in Kenya. Ecotourism has largely failed to deliver adequate socioeconomic benefits to local stakeholders in many other African nations (Bruyere 2009; Beh and Lelengula 2009; Coria and Calfucura 2012). Many researchers have stressed the importance of ensuring that local communities are able to share meaningfully in the socioeconomic benefits brought by ecotourism (Snyder and Sulle 2011; Ahebwa 2012; Tumusiime and Vedeld 2012; van der Duim and Sandbrook 2012; Shoo and Songorwa 2013; Yitbarek *et al*. 2013).

Conservation that is stakeholder-driven can both account for the needs of local peoples while helping to balance conservation and socioeconomic priorities and objectives (Klein *et al*. 2008). Community-based ecotourism is more likely to draw suitable compromises between conservation objectives, income generation, and community development (Kiss 2004). Local empowerment can be improved through a greater focus on local community leadership, independence and priorities, as well as by actively discouraging foreign elitism (Thompson and Homewood 2002; Manyara and Jones 2007). Increasing emphasis on partnerships between foreign tour operators and local communities can help unlock the industry's potential to aid economic development and reduce poverty in Kenya and across the continent (Manyara and Jones 2007). However, the decentralization of control over natural resources must be carefully conducted to prevent unfairness. For instance, Snyder and Sulle (2011) found in Tanzania that community members who are literate may take advantage of others who are not, and are thus unable to read contracts or revenue reports. Women and the elderly are other stakeholder groups that may become marginalized as decision-making powers are decentralized (Snyder and Sulle 2011).

Ecotourism can only act as a significant contributor to local livelihoods when benefits are shared in a mutually beneficial manner (Snyder and Sulle 2011). Ensuring that benefits are shared equitably has direct implications for conservation objectives, as many communities living in and around areas of high biodiversity simply have no economic incentives to conserve biodiversity otherwise (Okech and Bob 2009). Government and political commitment can be a critical factor in ensuring that opportunities and benefits are equitably shared. As a point of comparison, Maasai locals hold a large percentage of hotel and park positions in Kenya's Maasai Mara Game Reserve, whereas local communities have found it difficult to find employment related to ecotourism in Tanzania's Ngorongoro Conservation Area (Charnley 2005). In the latter case, capacity building in local communities through training and education can help local people improve their skills and employability. Many individuals do not have education beyond primary levels, even though they may possess in-depth knowledge of the local landscapes and natural history (Charnley 2005). The dependence of ecotourism on political stability, sufficient infrastructure, and tourism-associated development further highlights the need for increased community involvement in decision-making (Linsey *et al*. 2007). Longstanding issues involving corruption, bureaucratic bloat, and overarching government policies that conflict with conservation efforts have been discussed (Ferreira 2004; Parker and Khare 2005; Smith and Walpole 2005). Not only do such problems hinder economic development and exacerbate the cycle of poverty, they can also create hurdles for conservation efforts and hasten biodiversity loss (Smith and Walpole 2005). While this essay is unable to address these issues in further detail, they are fundamentally serious and require further investigation to ensure that conservation efforts, including ecotourism, can be effectively implemented without such hindrances.

Clearly, community-based ecotourism does not automatically guarantee conservation results or economic development for local stakeholders (Snyder and Sulle 2011; Coria and Calfucura 2012). However, the long-term cultural and social sustainability of ecotourism can be improved by empowering local communities, which can be achieved through direct participation, management, and ownership of conservation businesses (Akama 2011; Maingi and Camargo 2011; Di Minin *et al*. 2013b; Yitbarek *et al*. 2013). The development of cultural tourism experiences for tourists can help local communities conserve their cultural identity and can create opportunities for such stakeholders (Charnley 2005). For instance, the development of cultural boma settlement tours and walking safaris are able to provide local Maasai in Tanzania's Ngorongoro Conservation Area with opportunities for direct tourism involvement (Charnley 2005). These tourist experiences can operate with a relatively flexible schedule, allowing local community participants to maintain their traditional lifestyle as pastoralists and agriculturalists (Charnley 2005). These activities are also constructed on the unique skill set of local community members, where existing knowledge and familiarity with culture, local wildlife and landscape can be utilized to generate direct tourism income (Charnley 2005).

The growth of ecotourism can also help to address human-wildlife conflict, a significant challenge for the conservation of mammalian predators. Encounters between humans and predators are frequent in many parts of Africa, which inevitably leads to conflict. In multiple land-use areas, livestock depredation by carnivores causes economic losses for livestock owners and fuels retaliatory killings (Kolowski and Holekamp 2005; Kissui 2008; Hazzah 2009; Mulder and Frank 2009; Hemson *et al*. 2009). Despite hyenas being the most frequent raiders of livestock, lions are the most common targets in retaliatory killings because they are comparatively easier to track and kill, especially since they are more likely to defend carcasses against humans; other predators like cheetahs and hyenas are more likely to run away (Kissui 2008; Hazzah 2009; Mulder and Frank 2009). For local stakeholders, the economic incentive against conducting retaliatory killings and to protect other wildlife exists only when ecotourism revenues are large enough and if they are able to equitably share in these benefits (Romañach 2007; Lindsey and Woodroffe 2007; Bruyere 2009; Beh and Lelengula 2009; Hemson *et al*. 2009; Coria and Calfucura 2012). Equitably shared benefits from ecotourism can also provide pastoral and agricultural communities with an incentive to limit herd size, which can help prevent overgrazing and competition with wildlife (Snyder and Sulle 2011). Where other business interests may be present, such as commercial forestry and mining, socioeconomic considerations in conservation planning can help reduce potential policy conflicts (Di Minim *et al*. 2013). By accounting for both economic benefits and lost opportunity costs, conservation businesses like ecotourism can reduce conflicts between alternative development plans and facilitate conservation actions in a sustainable manner (Di Minin *et al*. 2013b).

Conservation prioritization and ecotourism diversification. Ecotourism is the fastest-growing sector in tourism, which happens to be the fastest growing industry in the world (Parker and Khare 2005; Lindsey *et al*. 2007; Coria and Calfucura 2012). It is able to generate funds for conservation while allowing wealth to be redistributed from developed to developing nations (Lindsey *et al*. 2007). However, its scope in Africa is limited by the viewing preferences of tourists, especially inexperienced safari-goers who are largely focused on the flagship "Big Five" of lions, elephants, buffaloes, leopards and rhinoceros (Lindsey *et al*. 2007; Di Minin *et al*. 2013a). Although responsible for attracting most foreign tourists to protected areas, these species are expensive to conserve. Lions, leopards and elephants can damage the livelihoods of their human neighbors while rhinos require costly anti-poaching strategies to be protected (Lindsey *et al*. 2007; Di Minin *et al*. 2013a). The limited nature of funding renders the prioritization of conservation efforts- deciding how and where to protect what- imperative (Carwadine *et al*. 2008; Joseph, Maloney and Possingham 2009).

Funding is of the utmost importance in conservation as it largely dictates the feasibility and implementation of plans (Hoeksta *et al*. 2002; Stephenson and Ntiamoa-Baidu 2010). Conservation projects devoted to charismatic megafauna, often large, iconic mammal species, tend to receive more attention and funding than taxa that are not as well-known or appealing to the general public, such as native grasses or invertebrates (Bottrill *et al*. 2011; Buckeridge 2014). The viewing preferences of tourists in protected areas directly relate to the generation of conservation funds, as donor funding may be skewed towards areas or projects that contain these iconic species (Lindsey *et al*. 2007).

In South Africa, Di Minin *et al*. (2013a) echoed the findings of Lindsey *et al*. (2007) that visitors with lower income levels are willing to visit several protected areas to search for less observable, less iconic species, as opposed to wealthier tourists who are most interested in seeing charismatic megafauna without having to visit multiple protected areas to observe them. Similar trends can be observed in Kenya, where despite having 65 national parks and reserves, the majority of tourists choose to congregate in a few specific parks; the top five parks accounted for 54 % of all visitor arrivals in 2009, while the top ten accounted for 80 % (Republic of Kenya Ministry of Tourism and Wildlife 2010). Areas without the charismatic "Big Five" but where less iconic species are present should consider marketing specifically to domestic and African regional tourists as well as to those who may have more safari experience. This demographic tends to hold an interest in a greater diversity of wildlife and less easily observable species (Lindsey *et al.* 2007; Di Minin *et al*. 2013a). The development of less-visited parks may prevent or at least alleviate over-utilization of the most popular protected areas (Lindsey *et al*. 2007; Cheung 2012). Financial mechanisms, such as a "safari tax", can be considered for subsidizing the conservation of less iconic species, for developing consumer interest in a broader biodiversity base, and for raising general environmental awareness (Di Minin *et al*. 2013a). The development of public and tourist interest in a wider range of wildlife may ultimately increase and diversify donor funding to biodiversity conservation projects (Lindsey *et al*. 2007; Di Minin *et al*. 2013a).

Monitoring and adaptive management. Poor ecological and socioeconomic understanding of the situation, especially when exacerbated by inadequate stakeholder engagement, can create counterproductively negative attitudes among local communities towards conservationists (Jepson2001; Brickle and Chayadin 2001). There is no disagreement among conservation biologists that to be effective, conservation efforts must be built upon a foundation of strong scientific knowledge (Gordon2004; Hester and Festa-Bianchet 2004; Cardillo and Meijaard 2012). Cheung (2012) emphasized the need for relevant scientific data, such as population dynamics, habitat requirements, migration patterns, and behavioral responses to changing conditions, to be systematically recorded. This is necessary to facilitate the ongoing assessment of tourism impacts in Kenya's national parks.

Ongoing monitoring of such information should be used to develop appropriate regulatory policies and to effectively mitigate impacts and prevent ecological damage (Cheung 2012).

Despite being widely promoted as important for improving conservation effectiveness, adaptive management, monitoring, and evaluation of conservation efforts have rarely been carried out (Kleimann *et al*. 2000; Regan *et al*. 2008; Swaisgood *et al*. 2011). Much of this comes down to the insufficiencies in funding for ongoing monitoring and review (Kleimann *et al*. 2000; Swaisgood *et al*. 2011). The impetus behind taking adaptive management approaches in conservation is clear. Plans and actions must evolve as knowledge and conditions change (Sanderson *et al*. 2008). Considerations for flexibility and feasibility when setting targets enable conservation efforts to cope with continually changing ecological conditions, social acceptance of conservation, and biological knowledge (Carwadine *et al*. 2008).

Cheung (2012) recommended that to ensure the long-term sustainability of tourism in Kenya's national parks, a system for systematically reviewing and evaluating tourism operations and programs is needed, starting with a structure for ongoing monitoring. The idea for a tourism-specific environmental impact assessment process was proposed to assess the appropriateness of tourism operations, evaluate impacts and ensure that local communities are able to participate equitably (Cheung 2012). It was further stipulated that such a process must take a multidisciplinary approach, in which moral, ethical, cultural and socioeconomic issues are addressed alongside ecological aspects. Ongoing monitoring is needed to inform such reviews and evaluations (Cheung 2012). Additionally, where the neo-colonial structure of the tourism industry persists, public participation mandated by an environmental impact assessment process should be able to draw some level of public participation (O'Faircheallaigh 2010). It is recommended that legislation and standards be established to implement a tourism-specific environmental impact assessment process.

While it is impossible for tourism to eliminate all negative impacts, the specific actions that are damaging can be reduced with proper training, certification, and regulatory enforcement (Akama2011; Maingi and Camargo 2011; Cheung 2012). For instance, many safari drivers do not avoid practices that excessively interfere with wildlife or damage the environment, such as driving too close to the animals, crowding around wildlife, and driving over delicate habitats (Cheung 2012). Standardized training and licensing by government authorities may help reduce the prevalence of such practices, especially when coupled with adequate enforcement. This could be by a government agency or by tour drivers themselves in the form of community policing (Ikiara and Okech 2002; Cheung 2012). The recent development of sustainability certification programs in the tourism industry has been driven by consumer behavior and increased awareness of sustainability in more affluent nations (Strambach and Surmeier 2013). Tourism certification schemes in Africa have traditionally focused on environmental issues in hospitality and accommodation. An example is Ecotourism Kenya's certification scheme for the country's tourist accommodations (Akama, Maingi and Camargo 2011). The incorporation of social and cultural dimensions in sustainability certification for ecotourism has been stressed, with some efforts now being made to develop appropriate indicators and standards (Akama 2011; Maingi and Camargo 2011; Stramback and Surmeier 2013). Measures to assess local community empowerment and participation in the industry should also be explored (Akama 2011; Maingi and Camargo 2011).

Conclusions

Conservation businesses, including ecotourism, have the potential to simultaneously protect endangered biodiversity while providing financial and social benefits to local stakeholders (Di Minin *et al*. 2013). To reiterate Cheung's (2012) findings, tourism in Kenya's protected areas brings an annual net benefit ranging from KES 21,531,098,140 to KES 42,015,498,296. Local stakeholders must be able to equitably share in these socioeconomic benefits for tourism to be able to achieve both conservation and development objectives. This can be done through the empowerment of local communities through direct participation in decision-making, management and ownership of conservation businesses (Akama 2011; Maingi and Camargo 2011; Di Minin *et al*. 2013b; Yitbarek *et al*. 2013).

Ecotourism holds significant value to conservationists, as it is an approach that can provide local stakeholders with an economic incentive to protect species for conservation (Lindsey *et al*. 2007). Diversifying current market interest in a greater variety of wildlife may increase donor funding for a wider range of conservation efforts (Lindsey *et al*. 2007; Di Minin *et al*. 2013a). Conducting ongoing monitoring enables conservation actions to evolve as knowledge and conditions change through a systematic process of reviews and evaluation (Sanderson *et al*. 2008; Cheung 2012). Capacity building to enhance local employment, adequate training, sustainability certification schemes, and regulatory enforcement can help reduce the negative impacts of tourism (Akama 2011; Maingi and Camargo 2011; Cheung 2012).

Understanding the costs and benefits of different conservation approaches can ensure that effective and efficient ecological and socioeconomic results are achieved with limited funds (Di Minin *et al*. 2013b). Conservation requires multidisciplinary solutions to tackle complex problems involving ecological, social, cultural, economic, political and legal aspects (McNeely 2006; Sanderson *et al*. 2008). Community-based ecotourism has the potential to establish a symbiotic relationship between tourism, local stakeholders and the natural world (Coria and Calfucura 2012). The potential of ecotourism in Africa to produce both positive ecological and socioeconomic results are inextricably linked and requires further development and improvement.

Resumen

Introducción: La biología de la conservación se ocupa de cuestiones complejas que requieren soluciones multidisciplinares capaces de enfrentarse a diversos aspectos ecológicos, sociales, culturales, económicos, políticos y jurídicos. Los compromisos entre la conservación de la biodiversidad y el desarrollo humano son las ineludibles demandas sociales y las limitaciones de financiación. El ecoturismo tiene el potencial de proporcionar a los interesados locales beneficios socioeconómicos, mientras se logran los objetivos de conservación. El presente escrito es una expansión al análisis de costo-beneficio del turismo en los parques nacionales de Kenia que explora cuestiones y las posibles mejoras para maximizar los beneficios y minimizar los costos. Las cuestiones planteadas en este análisis se exploran en el contexto más amplio de la conservación en África. En particular, la conservación en África, con el ecoturismo se beneficiaría de una mayor participación de las partes interesadas de la comunidad local toma de decisiones, el desarrollo de interés turístico en una gama más amplia de la vida silvestre, y una aplicación profunda en los principios de gestión adaptativa.

Discusión y conclusiones: *Comunidades locales como principales grupos de interés de conservación.* Esta sección explora y pone de relieve la importancia de las comunidades locales como principales interesados en la conservación. Para que en el ecoturismo se puedan equilibrar los objetivos de conservación y desarrollo, las partes interesadas de la comunidad local deben ser capaces de compartir equitativamente los beneficios socioeconómicos. Su compromiso, la participación y el empoderamiento es parte fundamental para el éxito del ecoturismo como un método de conservación multidisciplinario.

Conservación priorización y diversificación ecoturismo. En esta sección se discute la necesidad de ecoturismo en todo el continente africano para diversificar más allá del tradicional "Cinco Grandes". Ampliando las preferencias e intereses de los diferentes visitantes, esta visión puede ayudar a llamar la atención y financiación a las especies menos icónicas para lograr una mayor conservación de la biodiversidad en general.

Monitoreo y manejo adaptativo. En esta sección se hace hincapié en la importancia de la investigación científica y la comprensión de los objetivos de conservación. Los datos deben ser recogidos de forma sistemática en el seguimiento y la evaluación continua para facilitar la gestión adaptativa.

Palabras Clave: África, análisis, comunidad local, costo-beneficio de diversificación del turismo, conservación, ecoturismo, manejo adaptativo, seguimiento, grupos de interés.

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Species richness, distribution, and conservation of moles and shrews (Mammalia, Eulipotyphla) from Mexico

Riqueza, distribución y conservación de los topos y las musarañas (Mammalia, Eulipotyphla) de México

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Introduction: Moles (Talpidae) and shrews (Soricidae) are the only representatives of the order Eulipotyphla in Mexico and they account for 7 % of mammals in the country. Despite their richness, even basic aspects such as their species-level taxonomic knowledge and geographical distribution are still uncertain. The scarcity of such information implies that the biology and conservation status of eulipotyphlans are also unclear or unevaluated, which involves a serious impediment to the design of management strategies for a group that tends to be susceptible to climate change and impacts of anthropogenic habitat transformation. Here, we performed a comprehensive assessment of the current state of knowledge and threats to the survival of Mexican moles and shrews using information from natural history collections and spatial environmental data.

Methods: We reviewed the available information in biological collections, databases, and literature records of Mexican eulipotyphlans, and evaluated the bias road in the collection of specimens. The current distribution was estimated for nearly all moles and shrews recorded in Mexico, using ecological niche modeling and retaining the remnant vegetation areas. Finally, we calculated the extent of distribution for each species within protected areas and within the most threatened ecosystems in Mexico to identify the most vulnerable taxa.

Results: The eulipotyphlan diversity of Mexico is represented by three species of moles and 36 of shrews. Of all these, 26 species (67 %) are endemic to the country and 27 (69 %) are listed in a risk category by Mexican government or global assessments. Eleven taxa are known only from no more ten specimens or from very few collecting sites. The shrew *Sorex stizodon* has not been recorded for more than a century. Current distributions of twelve species were not estimated because they are represented by just a few locality records (< 5). The region that could contain most taxonomic richness is the highlands of central and southern Mexico. The species with the highest percentage of transformed habitat are the mole *Scalopus latimanus* and the shrews *Cryptotis merriami*, *C. mexicanus*, *C. obscurus*, and *Sorex ornatus*. Based on the current distribution, the number of records, the current protection within AP and /or potential threats, *Cryptotis griseoventris* and the recently described *C. lacandonensis* should be protected by the Mexican government.

Discussion and Conclusions: This paper provides the first detailed documentation of available information on the taxonomy, nomenclature, current distribution, and threats of moles and shrews in Mexico. Information from natural history collections corroborates the sparse and biased knowledge about the distribution of eulipotyphlans (Ramírez-Pulido *et al*. 2005; Carraway 2007). Our spatial analyses provide evidence that several species may be more endangered than suggested by global approaches (IUCN) and Mexican government legislation. Several species of moles and shrews may be represented sparsely in collections because of insufficient collecting. Our niche models projected onto a map to identify the distribution should be used in directing field survey efforts and scientific collecting in order to increase the information regarding the current population status of moles and shrews.

Key words: bias road, current distribution, field surveys, Insectivora, natural history collections, small mammals.

Introducción

El orden Eulipotyphla es un grupo monofilético que incluye a los erizos del Viejo Mundo (Erinaceidae), a los solenodontes (Solenodontidae) de las Antillas Mayores, a las musarañas (Soricidae) y a los topos (Talpidae; Stanhope *et al*. 1998; Douady *et al*. 2002). Anteriormente se agrupaban en el orden Insectivora junto a los topos dorados del sur de África (Chrysochloridae) y a los tenrecs originarios de Madagascar (Tenrecidae); actualmente, estas dos últimas familias pertenecen a un clado africano denominado Afrotheria (Stanhope *et al*. 1998). Otros esquemas alternativos de clasificación han agrupado a todas estas familias en diversos órdenes, como Soricomorpha, Erinaceomorpha y Lipotyphla (Simpson 1945; Hutterer 2005; Ramírez-Pulido *et al*. 2008; Asher y Helgen 2010; Wilson y Redder 2011). Lo cual refleja que la taxonomía y sistemática de estos mamíferos pequeños han sido un reto constante dentro del estudio evolutivo de los mamíferos (Simpson 1945; Stanhope *et al*. 1998; Douady *et al*. 2002; Douady y Douzery 2003; Nikaido *et al*. 2003; Symonds 2005).

El linaje que dio origen al orden Eulipotyphla es tan antiguo en la historia de los mamíferos que incluso precede a la extinción de los dinosaurios, hace cerca de 66 millones de años (Douady y Douzery 2003; Roca *et al*. 2004). El tiempo trascurrido desde su origen ha producido un grupo con más de 450 especies que se distribuyen en casi todo el planeta y con una gran diversidad de formas y estrategias de vida (Symonds 2005). En México, los eulipotiflos están representados por los topos y las musarañas (Maldonado 1999; Carraway 2007), con más de 35 especies que, en general, se caracterizan por su tamaño relativamente pequeño y por alimentarse principalmente de insectos y artrópodos. La mayoría de los topos son fosoriales, es decir, están adaptados a una vida debajo de la tierra, tienen forma de torpedo, poseen ojos y orejas diminutas y los sentidos olfativo, auditivo y táctil están bien desarrollados (Symonds 2005; Merritt 2010). Los topos mexicanos habitan marginalmente en el extremo norte del país (Maldonado 1999). Por su parte, las musarañas se encuentran entre los mamíferos terrestres de menor tamaño en el planeta, poseen ojos diminutos, cabeza alargada y hocico particularmente puntiagudo y, debido a su apetito voraz, se mantienen activas tanto en el día como en la noche (Churchfield 2002). Las musarañas están distribuidas en casi todo el territorio mexicano (Carraway 2007). Los eulipotiflos integran uno de los componentes mastozoológicos de la biodiversidad en México más importantes en cuanto a su número de especies, apenas por detrás de los roedores, murciélagos, carnívoros y artiodáctilos (incluyendo cetáceos, Asher y Helgen 2010).

El común denominador para ambas familias es que son poco estudiadas y se encuentran entre los mamíferos menos conocidos del país (Carraway 2007; Cervantes *et al*. 2008). Quizá la dificultad que implica, tanto su captura como la identificación taxonómica de los taxones, son factores que han limitado su estudio (Ramírez-Pulido *et al*. 2005; Carraway 2007; Woodman *et al*. 2012). Como consecuencia, el número de especies reconocidas podría ser incierto, sus distribuciones geográficas parcialmente conocidas y su estado de conservación poco evaluado (Cervantes *et al*. 2008; Guevara *et al*. 2014a; Guevara *et al*. 2014b). El notable vacío de información en el conocimiento de su riqueza taxonómica y distribución geográfica no ha permitido realizar una adecuada valoración del estado de conservación y las amenazas que enfrentan en México. Los topos y las musarañas son potencialmente vulnerables a los efectos de los cambios asociados con la destrucción del hábitat inducida por el humano y por el cambio climático (Schloss *et al*. 2012; Woodman *et al*. 2012).

Los estudios recientes sobre eulipotiflos mexicanos incluyen la revalidación y descripción de especies (Yates y Salazar-Bravo 2005; Carraway 2007; Guevara *et al*. 2014b) y estudios sobre taxonomía y sistemática filogenética (Ramírez-Pulido *et al*. 2004, 2005; Esteva *et al*. 2010; Woodman 2010; Guevara y Cervantes 2014). Estos esfuerzos han marcado el inicio de la utilización integral de los datos obtenidos en acervos biológicos con información geográfica que están siendo manejados para incrementar nuestro conocimiento sobre taxonomía y aspectos ecológicos y evolutivos, que repercuten en la planeación de estrategias de conservación (Graham *et al*. 2004; Sánchez-Cordero *et al*. 2001, 2005).

En este sentido, en las últimas décadas se ha desarrollado el modelado del nicho ecológico (MNE), una herramienta que brinda la opción de combinar la información geográfica relacionada a los ejemplares de museo con variables bioclimáticas que caractericen los requerimientos ambientales de las especies para mantener poblaciones viables (Soberón y Peterson 2005). De esta forma, el MNE permite identificar regiones en el espacio geográfico donde una especie no ha sido registrada, pero es probable que ocurra (Sánchez-Cordero *et al*. 2001, 2005). Por esto, los MNE se han aplicado ampliamente en muchos estudios relacionados con la delimitación de las distribuciones de especies y la planeación de estrategias de conservación (Peterson *et al*. 2011), incluso para taxones con un número reducido de registros (Pearson *et al*. 2007; Jackson y Robertson 2011). Por lo anterior, los objetivos de la presente contribución son explorar y dar a conocer la información disponible en colecciones biológicas y bases de datos en torno al orden Eulipotyphla en México, integrar los cambios nomenclaturales y de clasificación taxonómica recientes y, finalmente, modelar el nicho ecológico de las especies para estimar sus distribuciones actuales e identificar a los linajes más vulnerables en el país.

Material y Métodos

Información taxonómica y geográfica. La actualización taxonómica y nomenclatural se basó en las evaluaciones del estado taxonómico, descripción de taxones nuevos y en propuestas nomenclaturales recientes (Matson y McCarthy 2005; Yates y Salazar-Bravo 2005; Carraway 2007; Esteva *et al*. 2010; Woodman 2012; Woodman *et al*. 2012; Guevara *et al*. 2014a, 2014b; Ramírez-Pulido *et al*. 2014). Para la obtención de los datos geográficos se solicitaron los registros contenidos en el Sistema Nacional de Información sobre Biodiversidad (SNIB) de la Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) y se consultaron las bases de datos del Mammal Networked Information System (MaNIS; http://www.manisnet.org) y el Global Biodiversity Information Facility (GBIF; http://www.gbif.org) para un registro inicial de 15,732 ejemplares. Una vez teniendo las localidades en grados decimales (*n* = 7,778), se realizó la validación geográfica de los registros de cada especie sobreponiendo la capa de localidades de cada una de las especies sobre el polígono estimado por la Unión Internacional para la Conservación de la Naturaleza (IUCN 2013). A la vez, se consultaron las siguientes colecciones biológicas para validar la información taxonómica y geográfica: Colección Zoológica Regional (Mammalia) del Instituto de Historia Natural y Ecología, Tuxtla Gutiérrez, Chiapas (CZRMA); Colección Nacional de Mamíferos, Distrito Federal (CNMA); Colección Mastozoológica El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas (ECO-SC-M); The University of Kansas, Natural History Museum, Lawrence (KU); Museo de Zoología "Alfonso L. Herrera", Distrito Federal (MZFC); Universidad Autónoma Metropolitana Unidad Iztapalapa, Distrito Federal (UAMI); Universidad Autónoma de Yucatán, Mérida, Yucatán (UADY); Colección Osteológica del Laboratorio de Arqueozoología "M. en C. Ticul Álvarez Solórzano", Distrito Federal (INAH); Colección de Mamíferos del Centro de Educación Ambiental e Investigación Sierra de Huautla, UAEM, Cuernavaca, Morelos (CIByC); Colección Regional Mastozoológica del CIIDIR-Oaxaca, Oaxaca de Juárez (OAXMA) y el National Museum of Natural History, Smithsonian Institution,Washington (USNM). Se puso especial atención en el número de ejemplares depositados en colecciones biológicas por cada especie como indicativo del conocimiento de las especies.

Modelado de nicho ecológico. La estimación del nicho ecológico se realizó con el método de máxima entropía en el programa Maxent v. 3.3 (Phillips *et al*. 2006), ya que proporciona información útil y establece una aproximación de la distribución de múltiples taxones (Sánchez-Cordero *et al*. 2005). Al estimar la distribución de las especies se requiere definir el área de estudio en la cual se calibra el modelo (ver Peterson *et al*. 2011) y debe hacerse en función del área accesible que tiene la especie para expandir su distribución (región 'M' en diagrama BAM de Soberón y Peterson 2005). La selección de las áreas de estudio por especie se realizó al intersectar los registros validados con la regionalización biogeográfica de las Ecorregiones Terrestres del Mundo a Nivel III (*Commission for Environmental Cooperation*; http://www.cec.org), más un *buffer* adicional de 40 kilómetros para permitir la inclusión de áreas con registro fósil, en los casos en los que existen (Choate 1970; Carraway 2007). Ante la falta de un mayor conocimiento biogeográfico de las especies, consideramos que esta selección de áreas de calibración es un supuesto explícito que puede ser puesto a prueba conforme se obtenga mayor evidencia.

Las coberturas bioclimáticas seleccionadas como predictores de la distribución fueron 19 variables bioclimáticas (http://www. worldclim.org): temperatura promedio anual (bio01), oscilación diurna de la temperatura (bio02), isotermalidad (bio03), estacionalidad de la temperatura (bio04), temperatura máxima promedio del periodo más cálido (bio05), temperatura mínima promedio del periodo más frío (bio06), oscilación anual de la temperatura (bio07), temperatura promedio del trimestre más lluvioso (bio08), temperatura promedio del trimestre más seco (bio09), temperatura promedio del trimestre más cálido (bio10), temperatura promedio del trimestre más frío (bio11), precipitación anual (bio12), precipitación del periodo más lluvioso (bio13), precipitación del periodo más seco (bio14), estacionalidad de la precipitación (bio15), precipitación del trimestre más lluvioso (bio16), precipitación del trimestre más seco (bio17), precipitación del trimestre más cálido (18), precipitación del trimestre más frío (bio19) y la variable topográfica que indica la pendiente del terreno (pen; http://edc.usgs. gov/products/ elevation/gtopo30/hydro), cada una con resolución de 30 segundos (≈ 1 km^2). Todas las capas fueron recortadas para su análisis de acuerdo al área seleccionada de cada especie. Con la intención de evitar el problema de la multicolinealidad entre variables, se usó el coeficiente de correlación de Pearson para eliminar a las variables bioclimáticas correlacionadas para cada especie en el programa ENMTools (Warren *et al*. 2010; Tablas 1 y 2).

No se generaron modelos de distribución para las especies en las que los registros son insuficientes ($n \leq 4$). Para el caso de las especies con ≥ 5 y ≤ 25 registros utilizamos el método de *Jackknife* (Pearson *et al*. 2007; Tabla 1). En este enfoque, el modelo se calibra usando n-1 registros y se evalúa la capacidad de predecir el registro faltante en la etapa de calibración, repitiendo el proceso hasta que todos los registros se han utilizado para la evaluación. Este método requiere la aplicación de un umbral (Pearson *et al*. 2007; Jackson y Robertson 2011). Se eligió el valor más bajo predicho que está asociado con cualquiera de los registros de presencia observados (umbral de presencia más bajo, Pearson *et al*. 2007; *Minimum training presence* en Maxent). Este umbral puede interpretarse como el reconocimiento de píxeles que son al menos tan adecuados para la especie, como aquellos en los que se ha confirmado su presencia. Dicho umbral se eligió debido al control estricto sobre la presencia para estas especies y a que la intención es detectar regiones que potencialmente podrían albergar poblaciones aún no descubiertas (Peterson *et al*. 2011). Se usó el software desarrollado por Pearson *et al*. (2007) para calcular el porcentaje de registros predichos correctamente y el *P*-valor para evaluar la significancia de las predicciones.

Para el caso de las especies con ≥ 26 registros (Tabla 2), se utilizó el método de validación cruzada (*k*-fold) para evaluar la consistencia de los modelos por cada especie usando diferentes subconjuntos de datos para la calibración, permitiendo un máximo de 50 réplicas. Debido a la incertidumbre en el límite taxonómico entre las musarañas *Cryptotis mexicanus* y *C. obscurus* (Choate 1970; Guevara y Cervantes 2014), se utilizaron los registros por arriba de los 20° 30′ para *C. obscurus* y por debajo de los 20° para *C. mexicanus* (ver Choate 1970). La validación independiente del umbral de estos modelos se determinó mediante el área bajo la curva (AUC) del análisis *Receiver Operating Characteristic* (ROC). Se incluye la diferencia entre los datos de calibración y los de evaluación (AUC_{di}). Entre menor sea la diferencia entre los datos de calibración y evaluación, menor es el riesgo de que los modelos estén sobre ajustados, es decir, que sean específicos a los datos de calibración (Warren y Seifter 2011). Los valores de AUC_{ev} (de evaluación) y AUC_{di} son apropiados para las comparaciones de modelos producidos para la misma especie, en el mismo sitio de estudio o área de calibración y bajo diferentes parámetros (Anderson y González Jr. 2011). Para la evaluación dependiente del umbral, se permitió error de comisión al incluir el 90 % de los datos de calibración (*10 percentile training presence* en Maxent).

Sesgo de muestreo. Maxent compara los valores ambientales en los registros de presencia de las especies con puntos generados a través del área de estudio conocidos como *background*, los cuales son generados bajo el supuesto de que toda el área ha sido muestreada sin sesgo (Phillips *et al*. 2006). Aquí se evaluó si existe un sesgo en el muestreo dirigido hacia las carreteras, ya que este sesgo geográfico podría estar acompañado de sesgo ambiental que afectaría a los modelos (Phillips *et al*. 2009). Debido a la escasez de registros de la familia Talpidae para México, este análisis solo se realizó para la familia Soricidae. Para ello, se utilizó la ruta de caminos en formato *shapefile* disponible a través del *Digital Chart of the World* (http://www.princeton.edu). Se importaron los puntos de colecta para la familia en formato *shapefile* (datos observados; 651 localidades únicas) y calculamos la distancia de cada punto al camino más cercano. Después, se generó el mismo número de puntos al azar y se calcularon las distancias a los caminos con el fin de evaluar si ambas distribuciones de puntos son diferentes mediante una prueba no-paramétrica para dos muestras independientes (prueba de Mann-Whitney) en el paquete estadístico Statistica (STATSOFT INC. 2005).

Con base en este cálculo, se creó un *buffer* hacia los caminos igual a la media más 1 desviación estándar del valor observado en los registros y se generó un archivo en formato ASCII para poder ingresarlo al programa Maxent. Al usar este archivo de sesgo, se espera que los datos de *background* posean el mismo sesgo que los datos de presencia (Phillips *et al*. 2009). Con fines de comparación, todos los MNE se realizaron con y sin información sobre el sesgo en el muestreo. Los mapas presentados por especie (Apéndice 1) se seleccionaron de acuerdo a los resultados de la evaluación del modelo y a la inspección visual en el espacio geográfico.

Distribución actual y análisis de amenazas. Se convirtió la distribución estimada a la distribución actual al contabilizar y excluir zonas transformadas por el hombre que reducen la posibilidad de encontrar poblaciones viables de las especies (zonas urbanas, desprovisto de vegetación, asentamientos humanos, sin vegetación aparente; Serie V; INEGI 2014). Con la finalidad de conocer la vulnerabilidad de las especies en México, se calculó el área de distribución actual por especie que se encuentra dentro de las áreas protegidas (AP) de cualquier categoría (IUCN y UNEP 2014) y dentro de los dos ecosistemas más amenazados de México: el bosque mesófilo de montaña y bosque tropical perennifolio (Challenger y Soberón 2008; selvas altas y medianas perennifolias y subperennifolias según INEGI 2014). Se incluyeron las categorías de riesgo de extinción para cada especie de acuerdo a los estándares del gobierno mexicano (SEMARNART 2010) e internacionales (IUCN 2013). Las distribuciones por especie se sumaron para presentar la riqueza taxonómica en México; debido al número de especies, esto solo se hizo para la familia Soricidae (Figura 1). Con la finalidad de mostrar el control de calidad sobre los datos de presencia con los que se construyeron los modelos, se muestra el intervalo altitudinal de los registros (Tabla 3) y sus valores de temperatura promedio anual y la precipitación anual (bio01, bio12; http://www. worldclim.org) representados en una gráfica de dispersión, junto con los valores climáticos para México y para el área en la que se calibró el modelo (Apéndice 1).

Resultados

Taxonomía y nomenclatura. Se presenta una lista con tres especies de topos y 36 de musarañas registradas en México, lo que representa el 8 % y 9 % de la diversidad mundial para cada grupo, respectivamente. Nuestra propuesta de las 39 especies alistadas es similar a las listas recientes (Ceballos y Arroyo-Cabrales 2013; Ramírez-Pulido *et al*. 2014), más la inclusión de una especie nueva de musaraña descrita recientemente (Guevara *et al*. 2014b). En contraste con Ceballos y Arroyo-Cabrales (2013) y de acuerdo con Ramírez-Pulido *et al*. (2014), consideramos a *Cryptotis griseoventris* y a *Sorex saussurei* como endémicas de México y a *C. tropicalis* con distribución hasta Guatemala (Woodman *et al*. 2012). El 67 % de las especies son endémicas de México (Tabla 3). Para la familia Talpidae se sigue la propuesta de Yates y Salazar-Bravo (2005) que reconocen como especie válida a *Scapanus anthonyi*, anteriormente considerada como una subespecie de *S. latimanus*. Con esto, *S. latimanus* está representado en México por la subespecie *S. l. ocultus*. Por su parte, *Scalopus aquaticus* posee a las subespecies *S. a. inflatus* y *S. a. montanus*. En cuanto a la familia Soricidae, se trata al género *Cryptotis* como masculino (ICZN 2006), por lo que los nombres válidos para *C. magna*, *C. mexicana*, *C. obscura* y *C. parva* son: *C. magnus*, *C. mexicanus*, *C. obscurus* y *C. parvus*, respectivamente. Se integra al listado a *Cryptotis lacandonensis*, una especie nueva descrita de la Selva Lacandona en el sureste tropical mexicano (Guevara *et al*. 2014b). Mantenemos a *C. parvus pueblensis* como una subespecie (Choate 1970; Carraway 2007; Ceballos y Arroyo-Cabrales 2013), aunque existen menciones para ser reconocida a nivel específico (Woodman y Croft 2005; Guevara y Cervantes 2014). Con base en el artículo 31.2.1 del ICZN (1999), la terminación *cola* como parte de un sustantivo es retenida sin importar que el género con el que combina sea femenino o masculino; por lo anterior, los nombres válidos son *C. alticola* y *S. monticola* (ver Woodman 2012). Para el género *Sorex* se consideran las propuestas de Matson y McCarthy (2005), Carraway (2007) y Woodman *et al*. (2012).

Información geográfica y ejemplares de museo. El análisis del sesgo en el muestreo para las musarañas indicó que existe una tendencia significativa a colectarlas cerca de los caminos más cercanos ($X = 3.78$ km, $Z = 4.38$, $P < 0.001$). En este sentido, en las regiones en donde disminuye la red de carreteras como en el Istmo de Tehuantepec o en la Península de Baja California se observa una menor densidad de puntos de colecta. En cuanto al número de ejemplares, algunas especies del orden se conocen por tres o menos ejemplares colectados en México, como es el caso del topo *Scalopus aquaticus* y de las musarañas *C. lacandonensis*, *C. merriami*, *Notiosorex cockrumi*, *N. villai*, *Sorex arizonae* y *S. stizodon* (Tabla 3). Cabe destacar que para *Scalopus aquaticus* solo se recopilaron dos registros en México, siendo el ejemplar más reciente uno obtenido en 1950. En el caso de las musarañas, los registros más recientes para *C. merriami* y *Sorex sclateri* en México son de 1965, para *N. cockrumi* y *S. macrodon* de 1975 y para *S. stizodon* el único registro fue obtenido en 1895. Las especies con el menor número de localidades (≤ 5 localidades) son *Scapanus anthonyi*, *C. lacandonensis*, C. *nelsoni*, *N. cockrumi*, *N. villai*, *Sorex emarginatus*, *S. macrodon*, *S. orizabae*, *S. sclateri* y *S. stizodon*. En el otro extremo están los taxones que han sido ampliamente colectados en el país, encabezando la lista las musarañas *C. mexicanus*, *C. parvus*, *S. salvini*, *C. obscurus*, *S. saussurei*, *C. goldmani, S. veraepacis* y *C. magnus*.

Tabla 1. Prueba de *Jackknife* para los modelos de nicho de 17 especies de musarañas de México de los géneros *Cryptotis*, *Megasorex Notiosorex* y *Sorex* con y sin información del sesgo en el muestreo.

	n	Con sesgo		Sin sesgo		
		éxito	P-valor	éxito	P-valor	Variables ambientales
C. alticola	19	91.7	0.000*	94.7	0.000*	bio01, bio02, bio03, bio04, bio07, bio12, bio15, bio18, pen
C. goodwini	16	84.6	0.000*	93.3	0.000*	bio01, bio03, bio04, bio05, bio12, bio15, bio17, bio18, bio19, pen
C. griseoventris	5	80.0	0.000*	80.0	0.000*	bio01, bio03, bio04, bio05, bio07, bio12, bio15, bio18, bio19, pen
C. magnus	25	94.1	0.000*	96.0	0.000*	bio01, bio04, bio05, bio07, bio12, bio15, pen
C. mayensis	25	82.6	0.000*	83.3	0.000*	bio01, bio03, bio04, bio05, bio12, bio15, bio18, pen
C. merriami	16	85.7	0.000*	85.7	0.000*	bio01, bio02, bio03, bio04, bio06, bio12, bio15, bio18, bio19, pen
C. peregrina	5	75.0	0.000*	80.0	0.000*	bio01, bio02, bio03, bio04, bio05, bio12, bio14, bio15, bio18, bio19, pen
C. phillipsii	21	81.3	0.000*	88.9	0.000*	bio01, bio02, bio03, bio04, bio05, bio12, bio14, bio15, bio18, bio19, pen
C. tropicalis	8	87.5	0.225	87.5	0.396	bio01, bio02, bio03, bio05, bio07, bio12, bio14, bio15, bio18, bio19, pen
M. gigas	23	76.2	0.000*	87.0	0.000*	bio01, bio02, bio03, bio04, bio05, bio12, bio14, bio15, bio18, bio19, pen
N. evotis	19	66.7	0.015*	63.1	0.000*	bio01, bio02, bio03, bio05, bio07, bio12, bio15, bio17, bio18, bio19, pen
S. arizonae	18	94.1	0.000*	94.1	0.000*	bio01, bio02, bio03, bio07, bio10, bio12, bio14, bio15, bio19, pen
S. ixtlanensis	10	90.0	0.000*	60.0	0.002*	bio01, bio02, bio03, bio05, bio12, bio14, bio15, bio18, pen
S. mediopua	6	75.0	0.114	83.3	0.155	bio01, bio02, bio03, bio04, bio06, bio12, bio14, bio15, bio18, pen
S. milleri	6	50.0	0.000*	50.0	0.000*	bio01, bio02, bio03, bio10, bio11, bio12, bio14, bio15, bio16, pen
S oreopolus	11	88.9	0.000*	90.0	0.000*	bio01, bio02, bio03, bio04, bio05, bio12, bio14, bio15, bio18, pen
S. ventralis	22	91.0	0.000*	93.8	0.000*	bio01, bio02, bio03, bio04, bio06, bio12, bio14, bio15, bio18, pen

n = número de localidades; éxito de predicción representado en porcentaje. *Especies con significancia estadística durante la evaluación (Pearson et al. 2007). Se muestran las variables ambientales utilizadas por especie (ver Materiales y Métodos)

Modelos de nicho ecológico. En 15 de las 17 especies analizadas bajo el método de *Jackknife* por su pequeño número de muestra (Pearson *et al*. 2007), los resultados predictivos fueron significativos (Tabla 1). En todos los casos el porcentaje de registros correctamente predichos fue mayor al 75%, excepto para *Sorex milleri* y *Notiosorex evotis* (Tabla 1). Las especies con predicciones no diferentes a lo esperado al azar fueron *C. tropicalis* y *S. mediopua*, por lo que no se propone una estimación de su distribución actual. Una posible explicación a este resultado, además del tamaño de muestra, es que en ambas especies los datos de colecta muestran una notable variación en el espacio ambiental, dificultando la estimación del nicho ecológico (Figura 2). Para el caso de las especies con ≥ 26 registros (Tabla 2), todos los modelos mostraron valores relativamente altos de AUC_{ev} (> 0.87), excepto para el caso del topo *Scalopus aquaticus* (AUC_{ev} = 0.821) y valores de AUC_{di} fueron bajos (0.014 – 0.041), lo cual sugiere que los modelos no están sobre ajustados a los datos de calibración (Warren y Seifter 2011). Cuando comparamos los modelos realizados con y sin el archivo del sesgo en el muestreo, no encontramos tendencia hacia la mejora en la evaluación de los modelos para alguno de ellos (Tablas 1 y 2). Lo mismo ocurrió al inspeccionar los MNE proyectados en el espacio geográfico.

Tabla 2. Evaluación de modelos de nicho de dos especies de topos de los géneros *Scalopus* y *Scapanus* y 10 especies de musarañas de los géneros *Cryptotis*, *Notiosorex* y *Sorex* de México con y sin información del sesgo en el muestreo.

	n	Con sesgo		Sin sesgo		
		AUC_{ev}	AUC_{di}	AUC_{ev}	AUC_{di}	Variables ambientales
Talpidae						
S. aquaticus	804			0.821 ± 0.043	0.034	bio01, bio02, bio05, bio11, bio12, bio14, bio15, bio19, pen
S. latimanus	595			0.904 ± 0.039	0.018	bio01, bio05, bio07, bio11, bio12, bio14, bio17, bio19, pen
Soricidae						
C. goldmani	30	0.978 ± 0.052	0.006	0.961 ± 0.059	0.012	bio01, bio05, bio07, bio12, bio15, bio18, pen
C. mexicanus	93	0.889 ± 0.107	0.028	0.908 ± 0.101	0.031	bio01, bio02, bio05, bio07, bio12, bio14, bio15, bio18, pen
C. obscurus	42	0.948 ± 0.118	0.021	0.953 ± 0.091	0.015	bio01, bio02, bio03, bio05, bio06, bio07, bio12, bio15, pen
C. parvus	660	0.875 ± 0.057	0.021	0.87 ± 0.066	0.021	bio01, bio02, bio03, bio05, bio08, bio12, bio15, bio17, bio18, pen
N. crawfordi	260	0.871 ± 0.126	0.041	0.874 ± 0.123	0.035	bio01, bio02, bio03, bio07, bio08, bio09, bio12, bio13, bio17, bio19, pen
S. monticola	764	0.906 ± 0.036	0.014	0.911 ± 0.031	0.010	bio01, bio02, bio03, bio07, bio08, bio12, bio14, bio15, bio18, pen
S. ornatus	212	0.942 ± 0.045	0.018	0.944 ± 0.042	0.017	bio01, bio02, bio03, bio07, bio08, bio09, bio10, bio12, bio15, bio18, pen
S. saussurei	38	0.917 ± 0.1	0.028	0.931 ± 0.096	0.021	bio01, bio02, bio03, bio04, bio07, bio12, bio15, bio18, pen
S. salvini	64	0.948 ± 0.084	0.014	0.946 ± 0.094	0.015	bio01, bio02, bio03, bio05, bio12, bio14, bio15, bio18, bio19, pen
S. veraepacis	50	0.935 ± 0.076	0.014	0.945 ± 0.065	0.017	bio01, bio02, bio03, bio05, bio12, bio14, bio18, bio19, pen

n = número de localidades; AUC_{ev}: AUC de datos de evaluación; AUC_{di}: diferencia de AUC entre datos de calibración y de evaluación. Se muestran las variables ambientales utilizadas por especie (ver Materiales y Métodos)

La suma de los modelos de distribución encontró 11,305 km^2 predichos como habitables para la familia Talpidae y 1,012,197 km^2 para la familia Soricidae dentro de México (Tabla 3, Apéndice 1). Las especies con la mayor superficie de distribución actual son las musarañas *Notiosorex crawfordi*, *Cryptotis parvus*, *N. evotis*, *Sorex ventralis* y *C. mayensis* (> 125,000 km^2), mientras que las especies endémicas de México que poseen distribución más restringida son *S. milleri*, *C peregrina*, *C. griseoventris* y *C. magnus* (< 5,000 km^2, Tabla 3). El 75.6 % de la superficie estimada para la familia Soricidae es adecuada para al menos una especie, localizándose principalmente en las zonas desérticas del norte de México y en la Península de Yucatán, en donde se extienden las distribuciones de *N. crawfordi*, *C. parvus* y *C. mayensis*, principalmente. Mientras tanto, la región que podría albergar a la mayor riqueza taxonómica se encuentra en las zonas altas del centro y sur del país al estimar que el 5.89 % de la superficie es habitable incluso para cinco a nueve especies de los géneros *Cryptotis* y *Sorex* (Figura 1), como las especies endémicas de México *C. alticola*, *C. goldmani*, *C. griseoventris*, *C. magnus*, *C. mexicanus*, *C. peregrina*, *C. phillipsii*, *Sorex ixtlanensis*, *S. oreopolus*, *S. saussureri* y *S. ventralis*; además de *S. macrodon*, *S. mediopua*, *S. orizabae*, *S. sclateri* y *S. ventralis* que a pesar de no haber estimado su distribución, también habitan esas zonas.

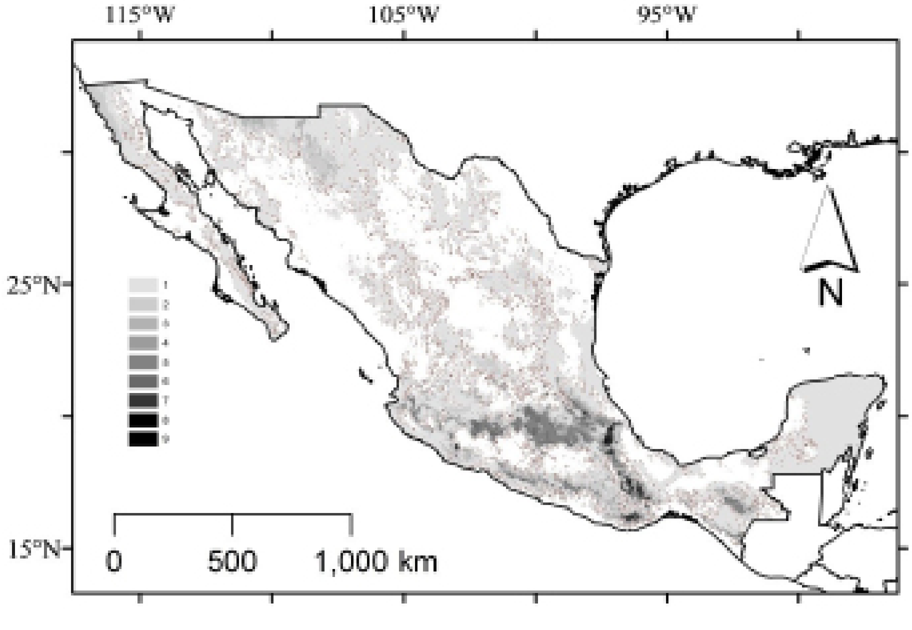

Figura 1. Riqueza de especies de musarañas (orden Eulipotyphla) en México. Las zonas más oscuras muestran la distribución actual estimada para un mayor número de especies (1 a 9 especies).

Al contabilizar el hábitat transformado por el hombre dentro de la distribución predicha como habitable, las especies con el mayor porcentaje de afectación son el topo *Scalopus latimanus* y las musarañas *Cryptotis merriami*, *C. mexicanus*, *Sorex ornatus* y *C. obscurus* (Tabla 3). Por otro lado, las especies con menor proporción de suelo transformado son las musarañas *S. milleri*, *C. peregrina*, *S. arizonae*, *S. montícola*, *C. magnus* y *C. goldmani*. Cabe mencionar que el cálculo del hábitat transformado fue conservador, ya que no se consideró el rubro de áreas de uso en agricultura, debido a que algunas especies pueden tolerar esta transformación (Cervantes *et al*. 2008; Guevara *et al*. 2011). De ser incluidas, el área de distribución actual de las especies podría ser menor.

Tabla 3. Número de ejemplares de topos y musarañas colectados en México (*n*), superficie de la distribución actual y porcentaje dentro de hábitat transformado, en áreas protegidas (AP) y en ecosistemas terrestres más amenazados de México (BMM, Bosque Mesófilo de Montaña; BTP, Bosque Tropical Perennifolio). Se presenta la categoría de riesgo de extinción (SEMARNAT 2010 y IUCN 2013) y el intervalo altitudinal de los registros (msnm). El fondo gris señala a las especies endémicas del país.

	n	Cobertura (km2)	Transformado (%)	Dentro de AP (%)	BMM y BTP (%)	IUCN	SEMARNAT	Altitud (m)
FAMILIA TALPIDAE (topos)								
Scalopus aquaticus (Linnaeus, 1758)	2	4,761	3.9	14.2	0.0	LC	P	0 - 1333
Scapanus anthonyi J. A. Allen, 1893	12	-	-	-	-	-	A	1712 - 2389
Scapanus latimanus (Bachman, 1842)	7	6,544	8.4	0.4	0.0	LC	P	0 - 2801
FAMILIA SORICIDAE (musarañas)								
Cryptotis alticola (Merriam, 1895)	60	63,170	3.6	19.3	1	-	PR	2242 - 4134
Cryptotis goldmani (Merriam, 1895)	116	41,824	0.9	1.6	6.3	LC	PR	961 - 3433
Cryptotis goodwini Jackson, 1933	4	1,546	5.0	52.1	32.5	LC	-	1464 - 3085
Cryptotis griseoventris Jackson, 1933	21	3,067	1.5	1.6	0.2	V	-	1912 - 2775
Cryptotis lacandonensis Guevara *et al.*, 2014	2	-	-	-	-	-	-	90
Cryptotis magnus (Merriam, 1895)	105	3,610	0.6	8.0	20.6	V	PR	1300 - 3109
Cryptotis mayensis (Merriam, 1901)	82	125,079	2.3	19.9	11.2	LC	PR	0 - 600
Cryptotis merriami Choate, 1970	1	16,431	7.9	15.9	15.6	LC	-	438 - 1659
Cryptotis mexicanus (Coues, 1877)	461	41,509	6.9	7.2	10.3	LC	-	435 - 3150
Cryptotis nelsoni (Merriam, 1895)	56	-	-	-	-	CE	PR	932 - 1426
Cryptotis obscurus (Merriam, 1895)	160	6,326	6.3	19.2	10.2	V	PR	790 - 2615
Cryptotis parvus (Say, 1823)	396	332,387	4.6	10.4	3.3	LC	PR	0 - 2532
Cryptotis peregrina (Merriam, 1895)	44	2,205	0.2	4.1	4.3	-	PR	2559 - 3056
Cryptotis phillipsii (Schaldach, 1966)	53	5,780	2.0	0.8	4.7	V	-	885 - 2417
Cryptotis tropicalis (Merriam, 1895)	14	-	-	-	-	-	-	444 - 1594
Megasorex gigas (Merriam, 1897)	59	61,335	3.1	8.3	0.9	LC	A	706 - 1412
Notiosorex cockrumi Baker et al., 2003	2	-	-	-	-	LC	A	888 - 1475
Notiosorex crawfordi (Coues, 1877)	86	388,464	1.3	13.4	0.02	LC	A	15 - 2323
Notiosorex evotis (Coues, 1877)	38	143,899	2.9	8.8	0.3	LC	A	2 - 1856
Notiosorex villai Carraway y Timm, 2000	3	-	-	-	-	V	A	750 - 1258
Sorex arizonae Diersing y Hoffmeister, 1977	1	42,061	0.5	14.7	0.0	LC	P	1470 - 2435
Sorex emarginatus Jackson, 1925	8	-		-	-	LC	-	1757 - 2496
Sorex ixtlanensis Carraway, 2007	38	16,905	4.4	3.4	23.3	-		1185 - 2886
Sorex macrodon Merriam, 1895	11	-	-	-	-	V	A	752 - 1697
Sorex mediopua Carraway, 2007	39	-	-	-	-	LC	-	1480 - 2973
Sorex milleri Jackson, 1947	51	611	0.0	22.6	0.0	V	PR	2521 - 3573
Sorex monticola Merriam, 1890	15	22,794	0.5	9.3	0.0	LC	A	495 - 4027
Sorex oreopolus Merriam, 1892	17	52,222	5.6	19.3	0.9	LC	-	2243 - 3823
Sorex orizabae Merriam 1895	30	-	-	-	-	LC	-	2103 - 3557
Sorex ornatus Merriam, 1895	50	14,259	6.7	9.9	0.0	LC	A	0 - 2659
Sorex saussurei Merriam, 1892	136	53,042	4.3	21.4	1.4	LC	-	1733 - 3941
Sorex sclateri Merriam, 1897	5	-	-	-	-	CE	A	1341 - 1483
Sorex stizodon Merriam, 1895	1	-	-	-	-	CE	A	2130
Sorex ventralis Merriam, 1895	86	131,738	3.6	12.4	1.7	LC	-	1571 - 4129
Sorex salvini Merriam, 1897	234	95,791	1.5	13.2	4.1	LC	A	1403 - 3941
Sorex veraepacis Alston, 1877	109	29,980	4.5	8.9	16.4	LC	A	907 - 3162

El 63 % de las especies del orden poseen registros confirmados dentro de las Áreas Protegidas (AP), mientras que los modelos sugieren que todas las especies en las que se estimó su distribución actual habitan dentro de las AP. Del total de la superficie estimada, el topo *Scapanus latimanus* y las musarañas *C. goldmani*, *C. griseoventris* y *C. phillipsii* tienen menos del 2 % de sus distribuciones dentro de las AP; por el otro lado, la especie con la mayor proporción en AP es *C. goodwini* (52.1 %), aunque su distribución en México es relativamente pequeña (< 1,546 km^2). En referencia a los dos ecosistemas terrestres más amenazados del país (Challenger y Soberón 2008), *C. goodwini* (32.5 %), *Sorex ixtlanensis* (23.3 %) y *C. magnus* (20.6 %), son las especies que poseen la mayor distribución actual dentro de los bosques mesófilos de montaña y los bosques tropicales perennifolios. A estas especies habrá que sumar otras más para las que no se estimó su distribución, pero sus registros se ubican en estos ecosistemas, como las musarañas *C. lacandonensis*, *C. nelsoni, S. sclateri* y *S. stizodon*.

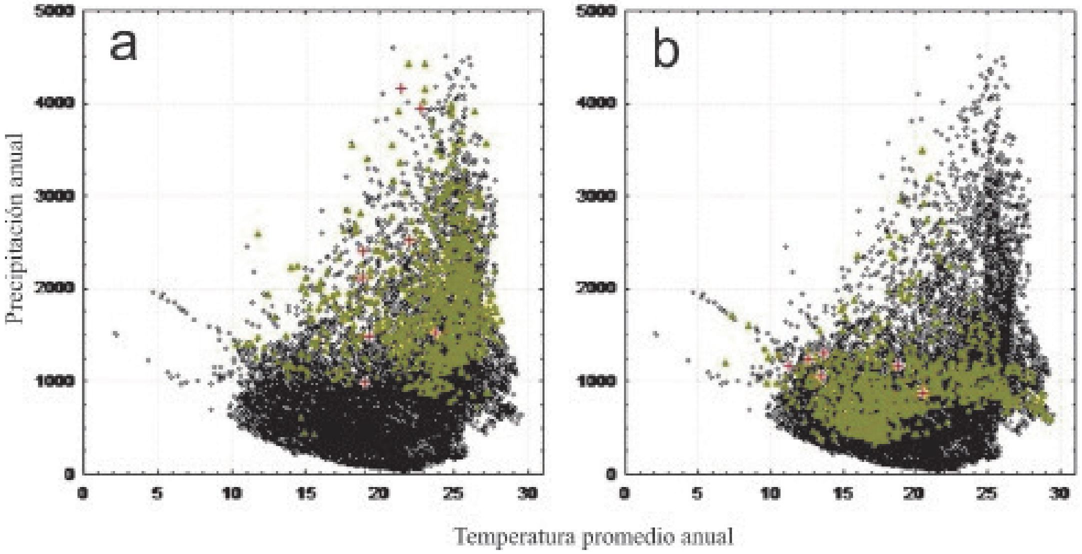

Figura 2. Gráfica de dispersión de las localidades de colecta (cruces rojas) de *Cryptotis tropicalis* (a) y *Sorex mediopua* (b) en el espacio ambiental. Los puntos negros son los valores para México y los puntos verdes los valores para el área de calibración del modelo.

Discusion

Sumado a las revisiones de Maldonado (1999) y Carraway (2007), los resultados de este estudio representan el mayor esfuerzo integral por dar a conocer el estado del conocimiento sobre el orden Eulipotyphla en México. Actualmente, 11 de las 39 especies del orden poseen menos de 10 ejemplares de museo colectados dentro del país. Si bien es cierto que esto puede deberse a la dificultad que implica la captura de topos y musarañas, la cantidad de registros también podría indicar el estado de riesgo de las especies (Escalante-Espinosa 2003). Cualquiera que fuese el caso, la colecta científica sigue siendo un aspecto esencial para la adquisición y validación de datos que van desde la taxonomía alfa hasta el manejo y la toma de decisiones en conservación (Sánchez-Cordero *et al*. 2001; Patterson 2002; Rocha *et al*. 2014). Al menos antes del inicio del presente siglo, la colecta de topos y musarañas en México podría definirse como contingente, ya que era un resultado circunstancial al tratar de colectar diversas especies de roedores (Ramírez-Pulido *et al*. 2004; Carraway 2007).

En el caso de las musarañas, sólo los esfuerzos más recientes han explotado el uso de técnicas de bajo precio para colectarlas, como las trampas de caída o tipo "*pitfall*", aunque sólo se ha realizado en contadas regiones del país (Cervantes *et al*. 2008; Guevara *et al*. 2011).

Es posible que algunas especies de eulipotiflos que no han sido colectadas durante las últimas décadas en México, ya se encuentren extirpadas o extintas (Ceballos y Navarro 1991). El caso más alarmante es la musaraña de San Cristóbal de Las Casas, *Sorex stizodon* que sólo se conoce del holotipo colectado en 1895 (Goldman 1951; Naranjo y Espinoza 2001). Otro caso ejemplar es el del topo *Scalopus aquaticus*, ya que el último registro confirmado dentro del país tiene más de medio siglo y el estado de conservación de sus poblaciones es desconocido (Ceballos y Navarro 1991). Un caso diferente, donde se ha redescubierto a una especie, lo representa la musaraña *Cryptotis nelsoni*, ya que sólo se conocía de la serie tipo colectada en 1894, pero más de un siglo después se obtuvieron nuevos ejemplares y más localidades de colecta en la Sierra de Los Tuxtlas, en la costa este de México (Cervantes y Guevara 2010).

Con base en la distribución actual, el número de registros, la protección actual dentro de AP y/o las amenazas potenciales, consideramos que las musarañas *Cryptotis griseoventris* y la recientemente descrita *C. lacandonensis* deberían estar protegidas por el gobierno mexicano. Actualmente, *C. griseoventris* se encuentra catalogada como vulnerable por las normas internacionales, debido a su distribución restringida y a que su área de distribución está severamente fragmentada debido a la extensa deforestación (IUCN 2013; Guevara *et al*. 2014a). Otras especies también enfrentan elevadas tasas de deforestación dentro de sus áreas históricas como *S. macrodon*, en la que se ha estimado que solo permanece alrededor del 15 % de la cobertura forestal original en su distribución (Sánchez-Cordero *et al*. 2005). Las zonas con mayor riqueza taxonómica y mayor número de endemismos del orden coincide con regiones de particular importancia en la conservación de los mamíferos en México como la Faja Volcánica Transmexicana, la Sierra Madre del Sur y Los Altos de Chiapas (Escalante-Espinosa 2003; Vázquez *et al*. 2009). Estas regiones poseen actualmente extensas áreas que han sido transformadas para su uso en la agricultura y el urbanismo (Sánchez-Cordero *et al*. 2005, 2009; PACC 2011). Las especies endémicas que se distribuyen en estas regiones serían las más vulnerables, como las musarañas *Cryptotis alticola*, *C. goldmani*, *C. griseoventris*, *C. phillipsii*, *Sorex oreopolus*, *S. saussurei*, *S. sclateri*, *S. stizodon* y *S. ventralis*. Todas las especies del género *Cryptotis* de estas zonas se encuentran en alguna categoría de riesgo federal o internacional (Tabla 3), mientras que para el género *Sorex*, solo *S. sclateri*, y *S. stizodon* están bajo alguna categoría de riesgo (Semarnat 2010; IUCN 2013).

El cambio climático también podría ser una amenaza para los topos y las musarañas en México, sin olvidar que cada especie reacciona de manera particular (Peterson *et al*. 2001; Trejo *et al*. 2011; Schloss *et al*. 2012). Estimaciones recientes sugieren que cerca del 68 % de la extensión de los bosques mesófilos en México se perderán durante el presente siglo como una consecuencia del cambio climático (Ponce-Reyes *et al*. 2012); de cumplirse este escenario, al menos 24 de las 36 especies de musarañas perderán el hábitat adecuado para su sobrevivencia. Para el caso de los boques tropicales perennifolios, el cambio climático será responsable de una pérdida cercana al 80 % en la distribución para la musaraña *Megasorex gigas* (Trejo *et al*. 2011), representante de un género monotípico y uno de los 12 géneros de mamíferos endémicos de México.

Es importante mencionar que, los estudios recientes en torno a la familia Soricidae en México han contribuido a actualizar el conocimiento sobre la riqueza y distribución actual de las especies (Carraway 2007; Cervantes *et al*. 2008; Cervantes y Guevara 2010; Guevara *et al*. 2014b) y a incrementar el conocimiento sobre su variación morfológica intra e interespecífica (Ramírez-Pulido *et al*. 2004, 2005; Carraway 2007). Como lo indican estudios previos y como lo sugiere la distribución fragmentada en diversas especies de los géneros *Cryptotis* y *Sorex* (Apéndice 1), aún se requieren evaluaciones taxonómicas para esclarecer el límite taxonómico entre algunas especies (Esteva *et al*. 2010; Guevara y Cervantes 2014). Para el caso de la familia Talpidae ha habido un escaso conocimiento generado durante las últimas décadas y se conoce poco sobre el estado de las poblaciones (Ceballos y Navarro 1991), por lo que el paso inmediato a seguir es poner en claro la situación actual de las poblaciones de las tres especies de topo.

A pesar del sesgo significativo de colecta a lo largo de los caminos como en el caso de las musarañas, la comparación entre los MNE que consideran el sesgo contra los que no lo consideran, muestran que los resultados son similares. Esto podría indicar que el sesgo geográfico en el muestreo de este grupo de mamíferos no ha arrastrado un sesgo ambiental. No obstante, otras aproximaciones que evalúan el sesgo geográfico para ser incorporado en el MNE podrían ser exploradas en el futuro (Phillips *et al*. 2009; Anderson y González Jr. 2011). En cuanto al número de muestra, infortunadamente la mayoría de la especies de eulipotiflos en México poseen un número reducido de localidades, por lo que en esos casos las estimaciones deberían tomarse con mayor cautela, a pesar de haber elegido el método más apropiado (Pearson *et al*. 2007). Conforme se incremente el número de localidades, será posible validar y robustecer los resultados para especies con tamaños de muestra reducidos (Jackson y Robertson 2011). Consideramos que los esfuerzos de colecta deberían enfocarse a los taxones menos representados en las colecciones biológicas y en aquellos que no han sido registrados en décadas. Un paso inicial podría ser el impulso de inventarios dirigido a estas especies, particularmente dentro de las AP (Sánchez-Cordero *et al*. 2005, 2009; Ceballos 2007; Rocha *et al*. 2014). Además, es importante utilizar métodos adecuados de colecta y dar prioridad a las regiones actualmente adecuadas para las especies (Apéndice 1; Raxworthy *et al*. 2003; Woodman *et al*. 2012). A medida que se obtengan más datos y se actualicen sobre los topos y las musarañas en México, las evaluaciones y los análisis subsecuentes podrán redefinir las prioridades de conservación dentro de uno de los grupos de mamíferos más diversos del país.

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Resumen

Introducción. Los topos (Talpidae) y las musarañas (Soricidae) son los únicos representantes del orden Eulipotyphla en México, conformando cerca del 7 % de la mastofauna del país. A pesar de su riqueza, algunos aspectos básicos como la taxonomía alfa y el conocimiento de su distribución geográfica permanecen incompletos. La falta de esta información implica que el estado de conservación de los eulipotiflos también permanezca sin ser evaluado, lo que implica un serio impedimento para el diseño de estrategias de manejo para un grupo que tiende a ser especialmente susceptible al cambio climático y a los impactos en la transformación del hábitat. Por tal motivo, con base en la información de colecciones de historia natural y datos ambientales espaciales se realizó una evaluación del estado actual del conocimiento y las posibles amenazas a la supervivencia de los topos y musarañas mexicanos.

Metodología. Revisamos la información disponible en las colecciones biológicas, bases de datos y registros de la literatura. Evaluamos el sesgo geográfico de colecta y estimamos la distribución actual de casi todas las especies de topos y musarañas registrados en México mediante el modelado de sus nichos ecológicos, reteniendo áreas con hábitat natural remanente. Por último, calculamos la extensión de la distribución de cada especie dentro de las Áreas Protegidas y dentro de los ecosistemas más amenazados en México con la finalidad de identificar a los taxones más vulnerables.

Resultados. La diversidad mexicana de eulipotiflos está representada por tres especies de topos y 36 de musarañas. 26 de estas especies (67 %) son endémicas del país y 27 (69 %) se encuentran bajo alguna categoría de riesgo de acuerdo al gobierno mexicano o por instancias internacionales. Once taxones se conocen por no más de 10 ejemplares o por muy pocas localidades en el país. Una musaraña en particular (*Sorex stizodon*) no ha sido registrada desde hace más de un siglo. Debido al escaso número de localidades (< 5), no se estimó la distribución actual de 12 especies. La región que podría albergar a la mayor riqueza taxonómica se encuentra en las zonas altas del centro y sur del país. Las especies con el mayor porcentaje de hábitat transformado son el topo *Scalopus latimanus* y las musarañas *Cryptotis merriami*, *C. mexicanus*, *C. obscurus* y *Sorex ornatus*. Con base en la distribución actual, el número de registros, la protección actual dentro de AP y/o las amenazas potenciales, las musarañas *Cryptotis griseoventris* y la recientemente descrita *C. lacandonensis* deberían estar protegidas por el gobierno mexicano.

Discusión y conclusiones. Este trabajo proporciona la primera documentación detallada de la información disponible sobre la taxonomía, nomenclatura, distribución y amenazas de los topos y musarañas en México. La información obtenida en colecciones de historia natural corrobora el escaso y sesgado conocimiento sobre la distribución actual de los eulipotiflos (Ramírez-Pulido *et al.* 2005; Carraway 2007). Nuestro análisis espacial proporciona evidencia de que algunas especies podrían estar más amenazadas de lo que actualmente se reconoce por criterios globales (UICN) y por el gobierno mexicano. El bajo número de ejemplares (< 10) de algunos eulipotiflos podría ser consecuencia de la falta de muestreo. Conforme se incremente el número de localidades, será posible validar y robustecer los resultados de modelado de nicho ecológico para especies con tamaños de muestra reducidos. Nuestros modelos de nicho convertidos a distribución actual deberían ser utilizados para dirigir esfuerzos de estudios de campo y colecta científica, con el fin de incrementar la información sobre el estado actual de las poblaciones de topos y musarañas.

Palabras clave: colecciones biológicas, distribución actual, Insectivora, inventarios, mamíferos pequeños, sesgo a caminos.

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Apéndice 1

Distribución actual de 2 especies de topos de los géneros *Scalopus* y *Scapanus* y 25 de musarañas de los géneros *Cryptotis*, *Megasorex*, *Notiosorex* y *Sorex* dentro de México. De izquierda a derecha se muestra el nombre científico, la distribución actual (azul) con las localidades registradas para México (puntos en rojo) y la ubicación de las localidades con las que se generaron los modelos (cruces en rojo) en el espacio ambiental: temperatura promedio anual (TMA, eje x) y precipitación anual (PA, eje y). También se muestran los valores para ambas variables para México (puntos negros) y para el área de calibración del modelo (puntos verdes). Al final, se presentan las localidades para las especies para las cuales no se generaron modelos de nicho ecológico.

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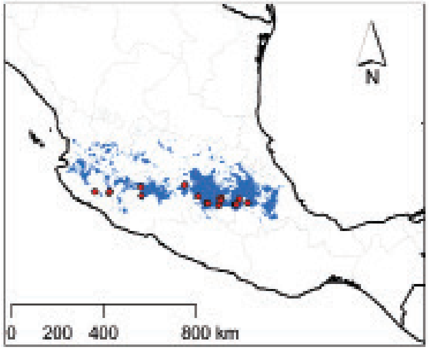

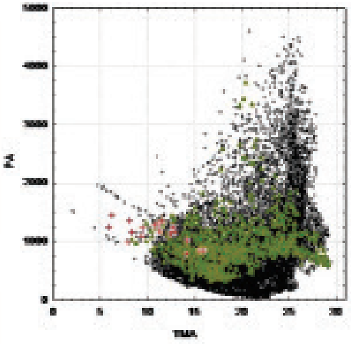

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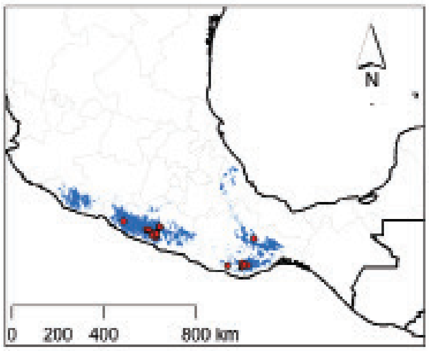

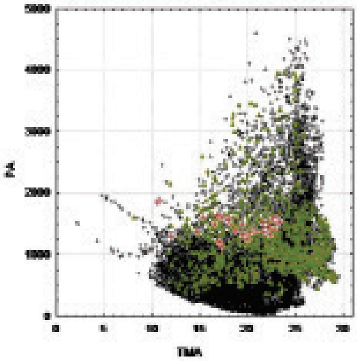

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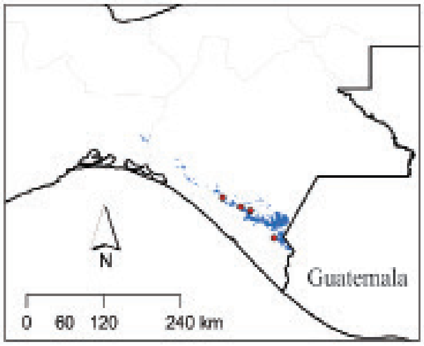

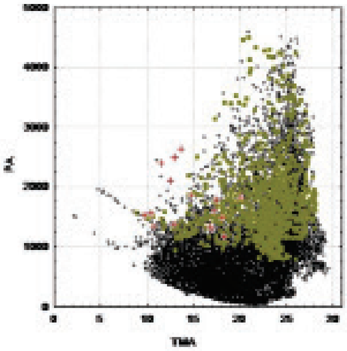

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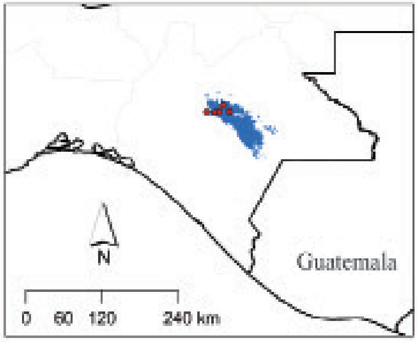

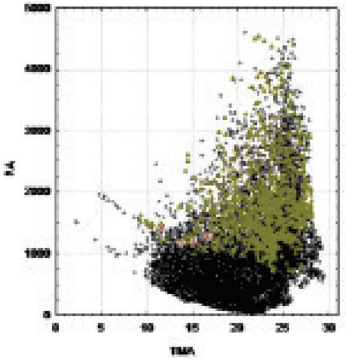

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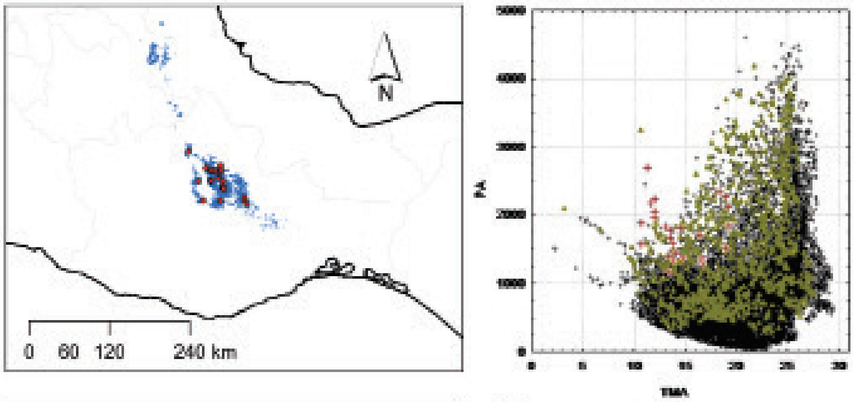

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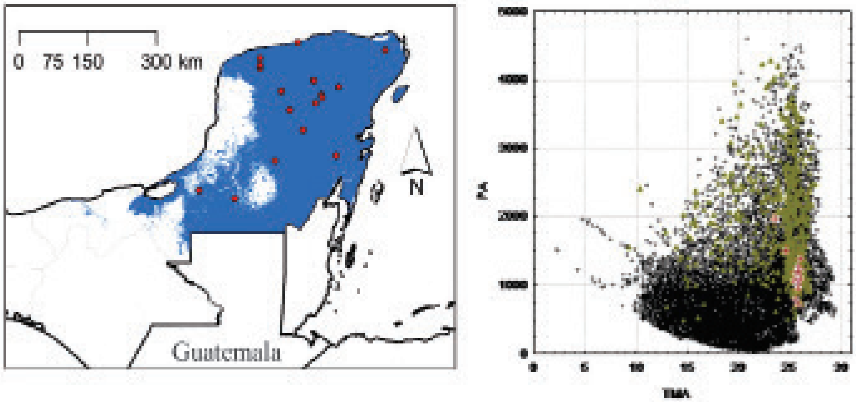

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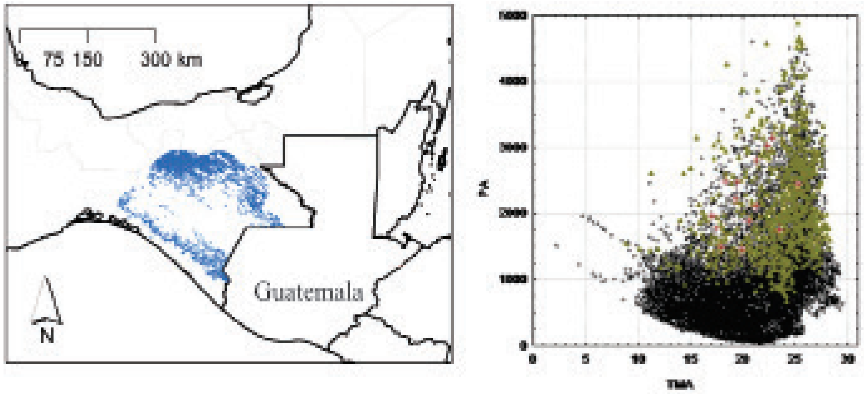

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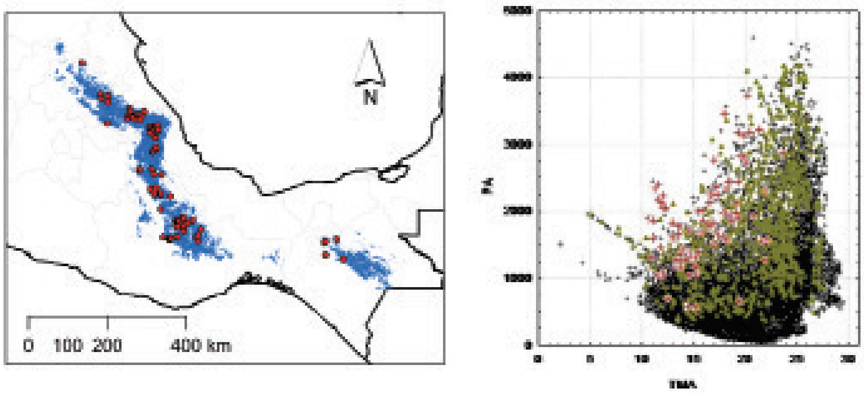

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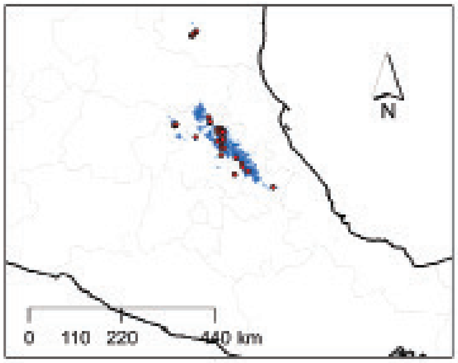

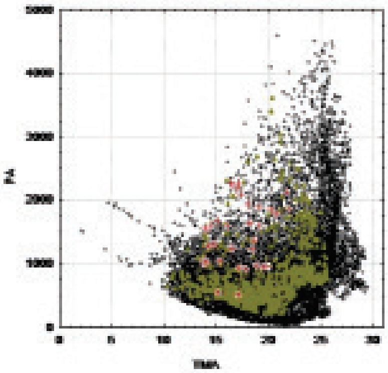

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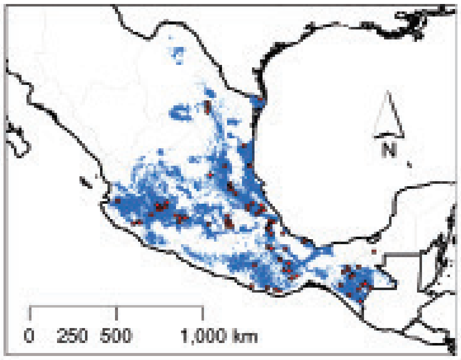

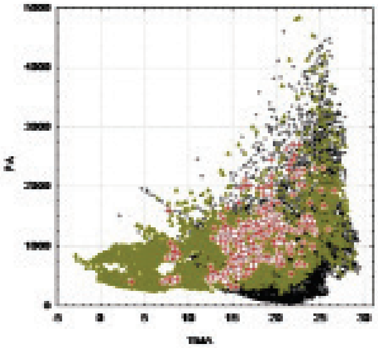

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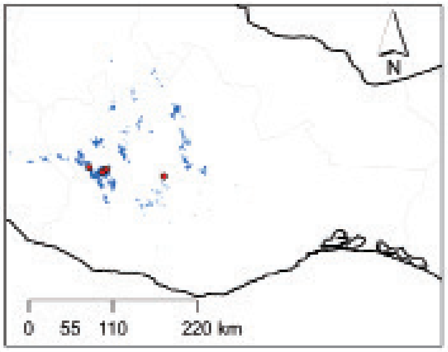

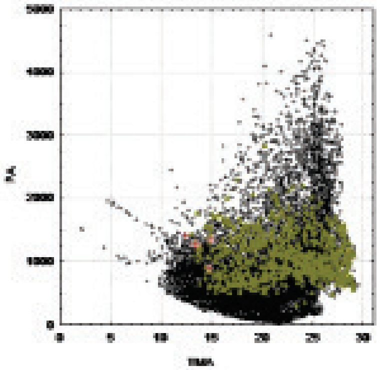

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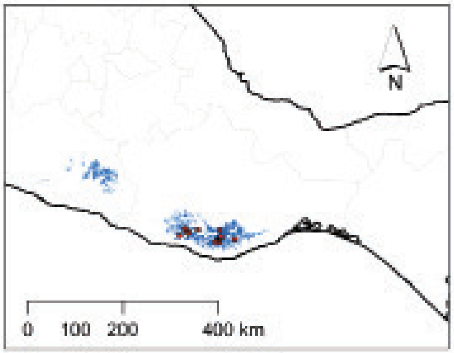

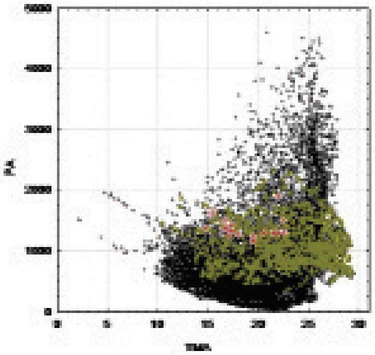

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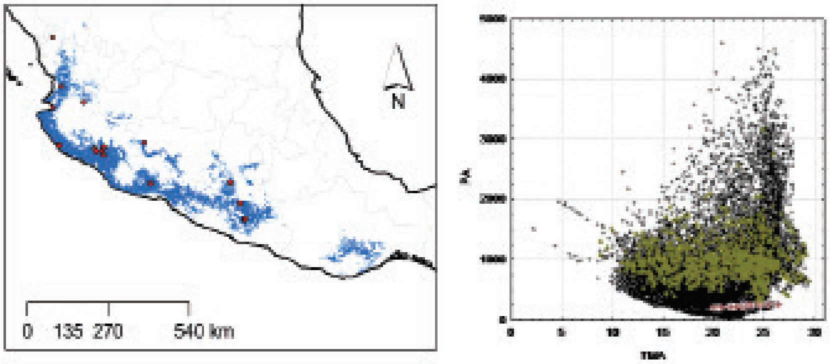

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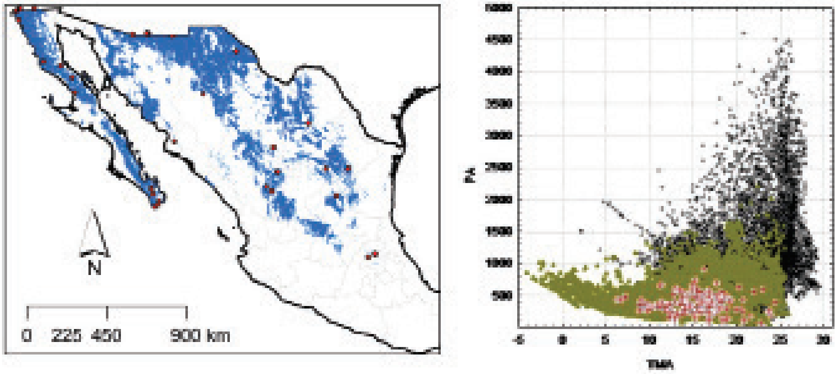

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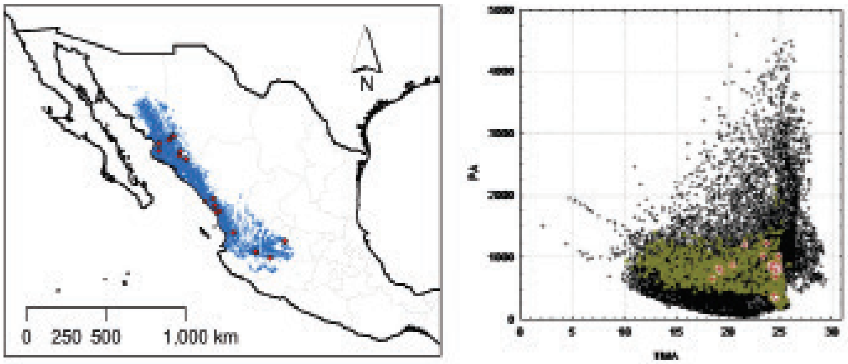

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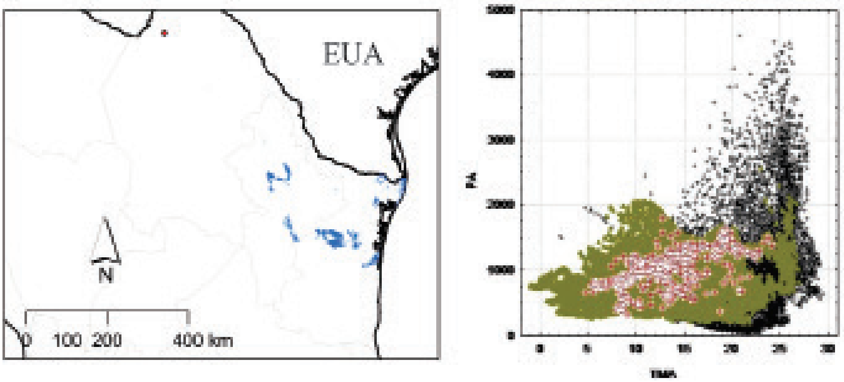

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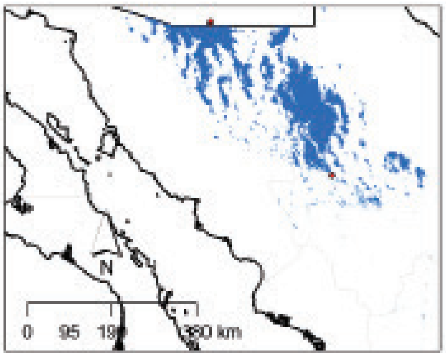

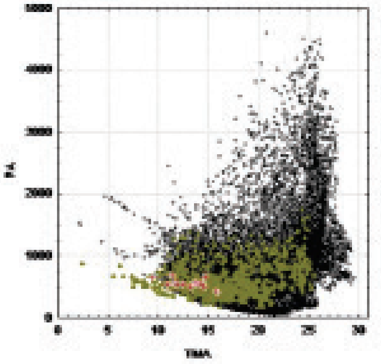

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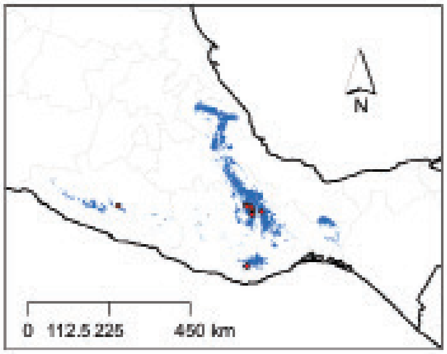

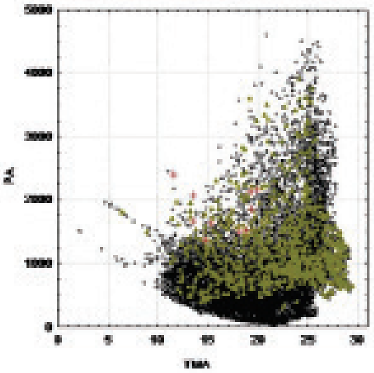

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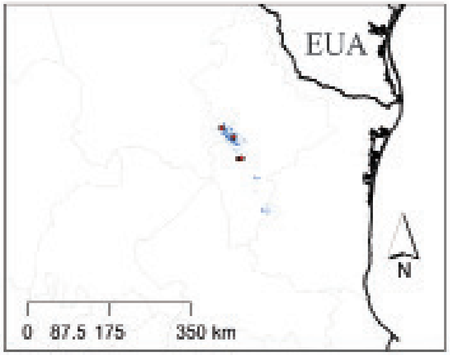

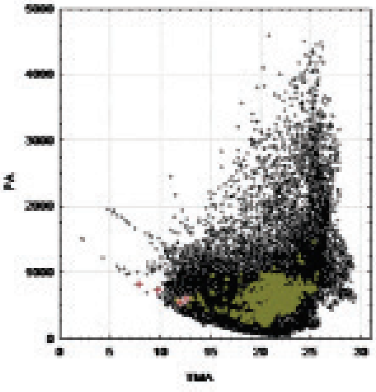

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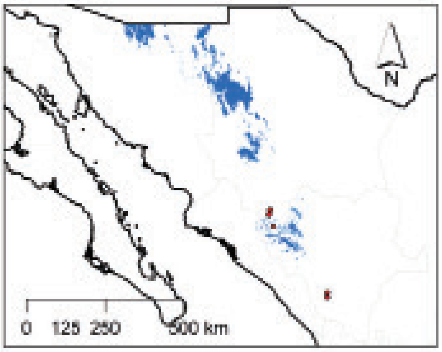

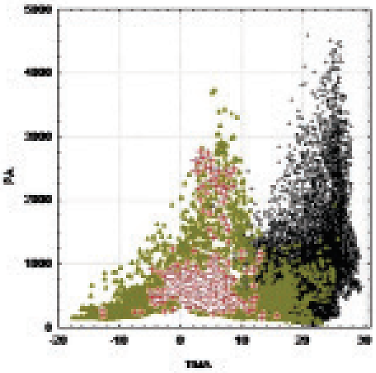

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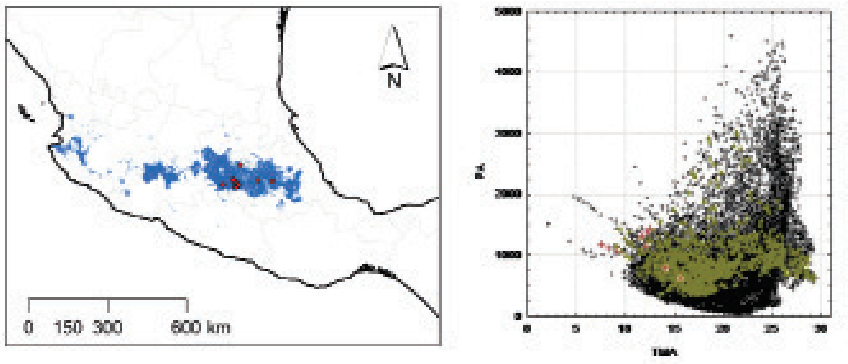

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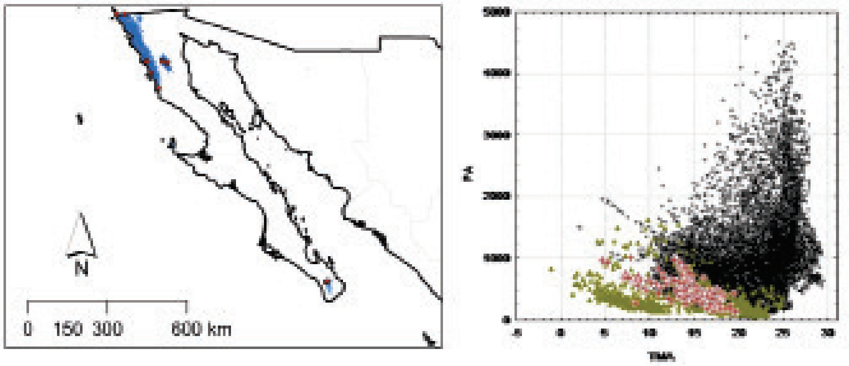

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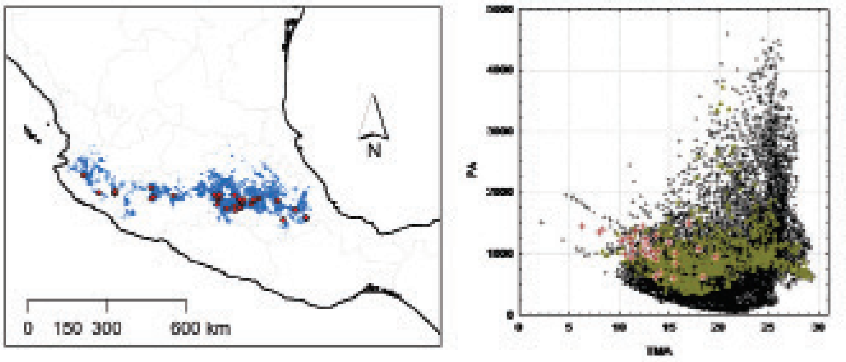

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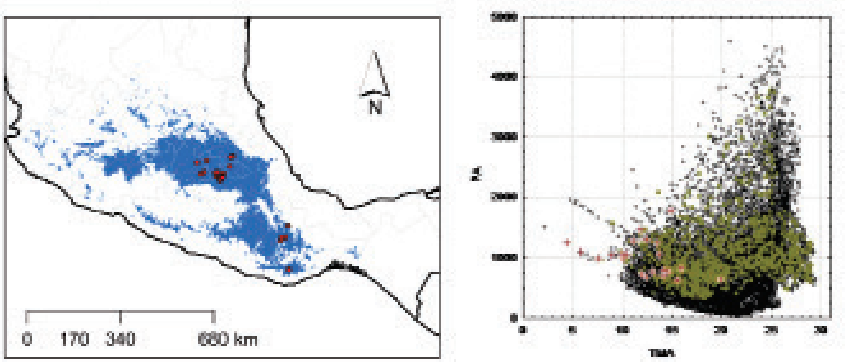

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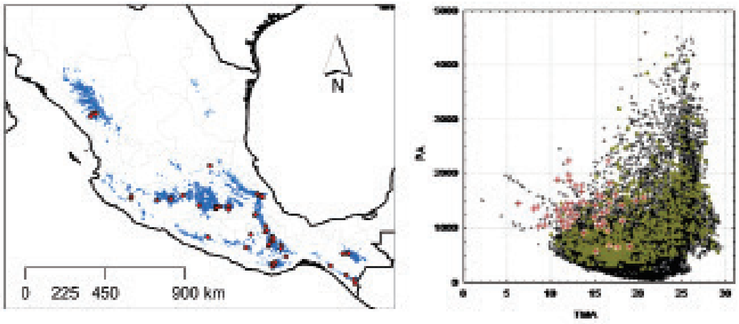

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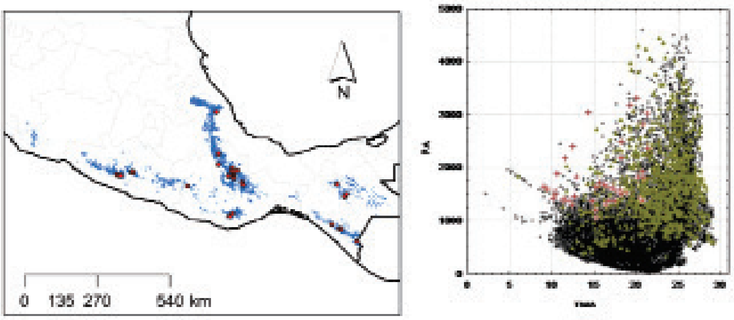
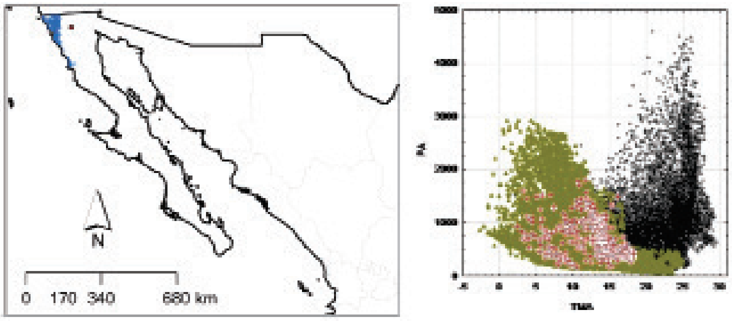
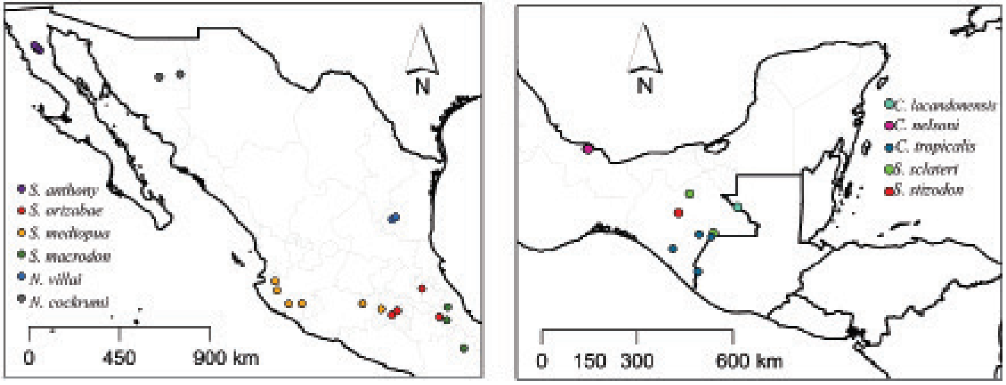


Scapanus latimanus



Especies sin modelo de nicho ecológico (ver Materiales y métodos)



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Los murciélagos de África: Conservación en tiempos del Ébola

African bats: Conservation in the time of Ebola

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*Corresponding author

Introduction: Bats are among the most poorly studied mammals, despite their diversity and important ecological services. The ongoing Ebola epidemic in western Africa underscores the increasingly recognized role of bats as reservoirs for emerging human diseases. An understanding of the mechanisms supporting pathogen maintenance in bat hosts is essential to informing future public health measures, as well as conservation efforts for wild bat populations. This is crucial in Africa, where the human population is burgeoning, increasing habitat loss and human contact with wildlife.

The importance of natural history. The natural history and ecology of bats, especially in Africa, is poorly understood, making responsible management decisions difficult. Metrics for guiding management of pathogens and their host populations, such as critical community size and minimum viable population size, often require more natural history knowledge than we currently have available. We argue that management action without adequate research can lead to counterproductive results. In the past, fear-based management responses such as culling campaigns have counterintuitively increased the prevalence of pathogens in the target host population, as has been observed in the vampire bat-rabies system and the Egyptian fruit bat-Marburg system.

Bat conservation in the time of Ebola. Many of the same anthropogenic stressors that are threatening bat populations, such as habitat loss and hunting, are also likely drivers of zoonotic pathogen emergence. Given this, and given that reducing bat populations can increase rather than decrease pathogen prevalence, we argue that conservation measures for bats should be strengthened in this time of Ebola. We offer a few potential first steps.

Conclusions and Future Directions: We advocate the precautionary principle, and encourage significant and urgent increases in natural history studies, education, and conservation measures for African bats.

Key words: bat conservation, Chiroptera, culling, Ebola, natural history, zoonotic pathogens

Introduction

Most emerging infectious diseases of humans are zoonotic in origin (Taylor *et al*. 2001), and the ongoing Ebola crisis highlights the increasingly-publicized role of bats as important reservoirs for zoonotic disease (Leroy *et al*. 2014). Though not the most represented mammalian order among zoonotic hosts (Woolhouse and Gowtage-Sequiera 2005), bats appear to host more viruses *per species* than rodent reservoirs for zoonotic disease (Luis *et al*. 2013), and bat-borne zoonoses are notable for their striking human pathogenicity (Dobson 2005). Indeed, bats are now the acknowledged reservoir hosts for rabies and related lyssaviruses, Hendra and Nipah henipaviruses, Marburg virus, and SARS- and MERS- coronaviruses, all known zoonotic agents causing severe pathology in humans (Calisher *et al*. 2006; Memish *et al*. 2013; Amman *et al*. 2014). Additionally, bats are a likely, though as yet unconfirmed, reservoir for Ebola virus (Olival and Hayman 2014).

Despite this incriminating evidence, bats also play a critical role in ecosystems on all continents except Antarctica. Bats provide a wide range of ecosystem services, from seed dispersal and forest regeneration to control of invertebrate agricultural pests. Their loss in any system is likely to have cascading consequences for ecosystem health and human wellbeing (Kunz *et al.* 2011). In fact, one study estimated that bat control of agricultural pests could be worth up to $53 billion per year in the US alone (Boyles *et al*. 2011).

Bat populations across the globe are threatened by anthropogenic stressors to ecosystems, including habitat loss, roost disturbance, hunting, and climate change (Mickleburgh *et al*. 2002 and 2009, Welbergen *et al*. 2008). As of 2002, almost a quarter of known bat species were globally threatened (Mickleburgh *et al*. 2002), and threats to bat populations are only increasing as the human population continues to grow. Efforts to conserve bats are non-existent in most of Africa (Racey 2013), despite the major challenges that arise from widespread human consumption of fruit bats (Pteropodidae; Mickleburgh *et al*. 2009). In fact, pteropodids, which serve as reservoirs for the majority of known bat-borne emerging zoonoses, are significantly more threatened than other bat families (Schipper *et al*. 2008). Habitat loss and hunting of pteropodids could play a major role in spillover of zoonotic disease, underscoring the importance of understanding and mitigating these threats.

Careful management will be necessary to promote peaceful coexistence of humans and wildlife, including bats, into the future. This will be especially challenging in Africa, where bat-human contact rates are high and where at least three bat-borne zoonotic viruses have emerged in the last half-century (Ebola and Marburg filoviruses and Duvenhage lyssavirus; Gear *et al*. 1975; Pourrut *et al*. 2005; Paweska *et al*. 2006). Challenges will only escalate as human populations continue to increase; the African continent is projected to double its existing human population and take the lead in world population growth by 2050 (UN Department of Economic and Social Affairs 2013, Haub and Kaneda 2014; Zinkina and Korotayev 2014). The continent is expected to harbor around 40 % of the world's human population by the end of this century (You *et al*. 2014).

The most deadly of the bat-borne diseases that have arisen on the African continent are the Ebola filoviruses, which caused nearly 1,600 documented human deaths prior to 2013 (Pourrut *et al*. 2005; Leroy *et al*. 2009; Albariño *et al*. 2013; Olival and Hayman 2014) and have so far resulted in over 8,600 (as of late January 2015, CDC documented human deaths during the current outbreak). Although the current crisis is driven by human-to-human transmission and has not been confirmed to be linked to bats, the ongoing outbreak has raised questions among local populations in multiple countries and in the popular media about control of possible reservoir hosts (*e. g*. Lee 2014; Konan 2014; Odemwingie and Tsan 2014), in this case, several fruit bat species such as *Hypsignathus monstrosus, Epomops franqueti,* and *Myonycteris torquata* (Leroy *et al*. 2005). Culling in the face of zoonotic disease is not unprecedented among bats. It has been used since the 1960's in an attempt to control rabies virus in Peru (Arellano-Sota 1988), has been advocated as a method for controlling Hendra virus among flying foxes in Australia (Martin and McIlwee 2002), and was used in 2008 in an effort to combat Marburg virus in Uganda (Amman *et al*. 2014). At present, localized culling and eviction efforts are occurring in Africa as a response to the Ebola outbreak in Cameroon (J. Fahr, pers. comm. November 20, 2014) and Nigeria (The Rainbow 2014). However, as we will discuss, bat culling for pathogen control has proven ineffective, and, in fact, has counterintuitively increased rabies prevalence in vampire bats and Marburg virus prevalence in Egyptian fruit bats.

We contend that dramatic management action against zoonotic disease reservoirs, such as a culling campaign, should be avoided in the absence of knowledge-based predictive models. However, our present understanding of the natural history, population dynamics, and disease dynamics of bat species, especially in Africa, is gravely inadequate for generating the models necessary to guide management action. Though we are beginning to unravel physiological mechanisms permitting bats to host pathogens at the individual level (Baker 2013; O'Shea *et al*. 2014; Brook and Dobson 2015), an understanding of the mechanisms enabling pathogen persistence at the population level remains elusive. Management action such as culling could have unforeseen and counterintuitive effects on pathogen dynamics, while also placing understudied African bat populations at risk of extinction. Thus, we strongly advocate the precautionary principle: our tenuous grasp on many aspects of bat ecology and natural history could lead to a counterintuitive increase in infection rates or extinction of ecologically important species if management action is attempted. Instead, we recommend: 1) improving our understanding of bats and their pathogens via detailed natural history studies, 2) promoting understanding and caution via educational campaigns, and 3) mitigating human-bat contact through habitat conservation measures for bats.

The Importance of Natural History

The practice and esteem of natural history, defined as "the observation and description of the natural world, with the study of organisms and their linkages to the environment being central", has dramatically declined over the past 40 years (Tewksbury *et al*. 2014). However, knowledge gleaned through natural history studies of pathogen reservoir species (Figure 1)—in particular, population size and distribution, frequency of intra- and interspecific interaction, movement dynamics, and life history traits—will be critical to parameterizing predictive models for enzootic

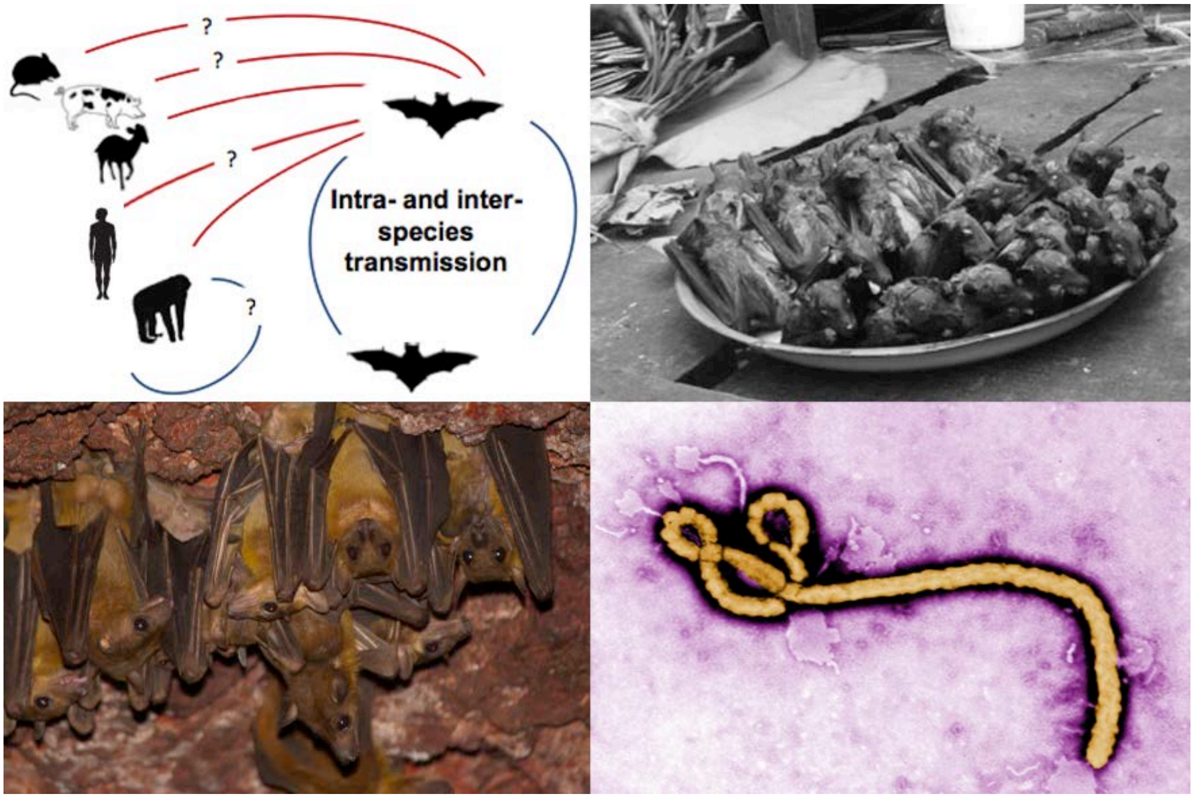

Figure 1. Natural history information is critical for making management decisions. Clockwise from top left: 1) The natural history and behavior that drives intra- and inter-species transmission of Ebola is not well understood (figure adapted from Olival and Hayman 2014). 2) the bushmeat trade is widespread on the African continent. Here, a number of straw-colored fruit bats (*Eidolon helvum*) and one hammer-headed fruit bat (*Hypsignathus monstrosus*), in both of which Ebola antibodies have been detected, for sale as bushmeat in Kisangani, Democratic Republic of the Congo. Knowledge of the human-wildlife interface is crucial (Photo by Guy-Crispin Gembu Tungaluna, Mickleburgh *et al*. 2009). 3) The Ebola filovirus. We must learn more about pathogen dynamics and what behavioral and ecological traits drive intra- and inter-species pathogen transmission (Photo source: Wikimedia Commons). 4) Egyptian fruit bats (*Rousettus aegyptiacus*) roosting in a cave in West Africa. Our knowledge of colony and population sizes and dynamics is poor for many species (Photo by Piotr Naskrecki).

pathogen dynamics in the reservoir host and to making assessments of potential risk for zoonotic epidemics.

Though recognition of bats' roles in zoonotic disease is growing, information supporting the basic ecology of bat reservoirs, especially in Africa, is lacking (Monadjem *et al*. 2010a). In the case of Ebola, many critical natural history questions for possible reservoir hosts are still outstanding. How many bats, and of which species, are infected? How do the various fruit bat species transmit the pathogen to one another? Are males and females and bats of all age classes equally likely to transmit the pathogen? Why do outbreaks occur sporadically? Are there seasonal behavioral or physiological changes important to viral shedding among hosts? Without answers to these basic questions, our capacity for intervention is limited.

Management action in the face of a pathogen outbreak often involves changing the population dynamics of a pathogen or its host, either by reducing numbers, inoculating host individuals, or moving host individuals. Consequently, two of the most important metrics for making management decisions regarding pathogens and their hosts are critical community size and minimum viable population size.

Critical community size

The crucial role of host population size in the transmission and maintenance of pathogens is a core principle in disease dynamics (Kermack and McKendrick 1927). Typically, a pathogen will invade a naïve, or uninfected, host population when the pathogen's "basic reproduction number" is greater than one (*i. e.*, $R_0 > 1$), meaning that an average infected individual passes the pathogen to more than one conspecific. This allows the pathogen to reproduce infections at a rate sufficient to maintain transmission. The required number of hosts for invasion and persistence of a disease in the population varies based on the transmissibility of the pathogen and the rate of recovery from infection in the host. During early work on human measles in UK cities, Bartlett (1957) coined the term "critical community size" (CCS), which refers to the threshold host population size necessary for long-term maintenance of a given pathogen. (Note that because the concept of CCS was devised for human systems, "community" in this context does not refer to the ecological concept of multiple associated species; rather, it refers to all individuals, associated in space and time, of all species susceptible to infection by the pathogen in question). CCS is not well characterized in most wildlife populations and its applicability has been debated. Certain pathogens, chiefly those transmitted in a frequency-dependent manner, including vector-borne pathogens but also certain behaviorally-mediated directly-transmitted pathogens (i.e. bite-transmitted lyssaviruses), will not be limited by host CCS (Lloyd-Smith *et al*. 2005). The relevance of CCS has only recently come under discussion in relation to zoonotic pathogens in bat reservoirs (Peel *et al*. 2012, 2013). By definition, "reservoir species" enable pathogens to persist; thus, understanding the mechanisms supporting pathogen persistence in bat populations will be critical to efforts to mitigate human public health risk for zoonoses.

In theory, a pathogen can be controlled and a host population downgraded from "reservoir" status by bringing the host population size below the CCS. In order to consider such measures, detailed knowledge of both pathogen dynamics and host population dynamics, locally and within a metapopulation context, is essential. However, such complementary knowledge of both host and pathogen dynamics is difficult to obtain. In a literature review examining correlates of viral richness in bat hosts, Turmelle and Olival (2009) identified only 33 of approximately 1,200 extant bat species globally for which both an estimate of host viral richness and host population structure, indicative of some awareness of host population dynamics, were available.

Minimum viable population size

The smaller a population is, the more susceptible it is to extinction by chance events and/or by deterministic anti-regulating forces (Allee effect; Lidicker 2010). The Minimum Viable Population Size concept was formalized by Shaffer (1981), who defined a "minimum viable population" (MVP) of a given species in a given habitat as any population size supporting a 99 % chance of surviving at least 1,000 years into the future. To estimate MVP in Yellowstone grizzly bears, he then developed a model that simulates population trajectories by incorporating demographic and environmental stochasticity to generate extinction probabilities for any given starting population size (Shaffer 1983; Shaffer and Samson 1985). This was the first true population viability analysis (PVA) using mathematical modeling to assess extinction risk, and to determine MVP in a given population (Beissinger and McCullough 2002). Since its origins, the MVP theory has grown in complexity and PVA has evolved into precise modeling efforts, with recognition that species survival is context-specific and that there is no rule of thumb for a viable minimum population size (Traill *et al*. 2007; Flather *et al*. 2011a, b). Though PVA in its various iterations has been applied to numerous organisms and systems the world over, the concept has never been formally applied to bats. The simulations at the core of PVA require accurate, long-term census data and knowledge of effective population size, or the number of individuals that contribute to reproduction. These basic natural history data are lacking for most bat species, especially on the vastly understudied African continent.

Estimating population size in bats

CCS and MVP are closely related concepts that have the same threshold: $R_0 = 1$. For a pathogen to persist, a host community must be large enough (the "critical community size") that each individual passes the pathogen to at least one other on average. For a population of hosts to persist, it must be large enough (the "minimum viable population") that each individual is at least on average able to replace itself over its lifetime, and the population must exceed in numbers any minimum threshold density that may be imposed by Allee effects (Lidicker 2010).

The calculation of CCS and MVP are critical for making management decisions for controlling a pathogen or for conserving a threatened species, and they rely on some knowledge of the population size and dynamics for the species in question. However, bat population sizes are inherently difficult to estimate because of bats' high mobility, nocturnal habits, and roosting sites that are difficult to locate and access. Traditional methods such as mark-recapture are rarely successful in estimating bat population sizes, due to low recapture rates and failure to meet the method's assumptions of equal survival and capture probability for marked and unmarked individuals (Kunz *et al*. 2009; Schorr *et al*. 2014). Changes in population size can be especially difficult to detect in bats, particularly among species that do not roost in large colonies: one recent study showed that more than 25,000 individuals would need to be captured and marked each year to detect a 33 % decline in the annual survival of solitary, migratory tree-roosting bats in North America (Schorr *et al*. 2014). In fruit bats, local abundance can be highly variable based on fruit and flower availability, and many species are migratory (Happold and Happold 2013), further complicating assessments of population change. In fact, since seasonal fluctuations are known to play a role in pathogen dynamics (Altizer *et al*. 2006), seasonal fluxes in range and in colony size may be more important, though potentially even more challenging to quantify, than overall population size or average colony size (Turmelle and Olival 2009).

Much work remains to be done, and modern technologies are advancing our ability to address these challenges. For example, for colony-roosting species, the power of mark-recapture studies is improved by using pit-tag readers installed at the entry and exit points of roosts to increase the recapture rate. For cave-roosting bats, colony size can be extrapolated to population size using models based on cave density (Peuchmaille *et al*. 2009), which can be readily mapped using GIS. Recently, microsatellite analysis using fecal DNA has been adopted to estimate local colony size from genetic diversity in a given sample (Peuchmaille and Petit 2007). It is imperative that we take advantage of cutting-edge technologies to improve our natural history knowledge of bats and their pathogens.

Distribution and connectivity of bat populations

Recent work has shown that the shape of a host's geographical distribution, in addition to its population size, can have profound implications for pathogen dynamics (Figure 2). Maganga *et al*. (2014) showed that bats with a larger and more fragmented geographic range were more likely to harbor greater viral richness. This may occur because of cross-species pathogen transmission at the edges of a host species' distribution (Maganga *et al*. 2014), or be due to the greater genetic structure present in a fragmented population, with moderate levels of genetic structure leading to the highest viral richness (Turmelle and Olival 2009). Greater viral richness and genetic diversity promote evolutionary flexibility in these pathogens, resulting in a higher likelihood that one of those viruses has the capacity to spill over into human populations (Morse 1993). Conversely, however, high host population connectivity can have important implications for the spread of a single pathogen.

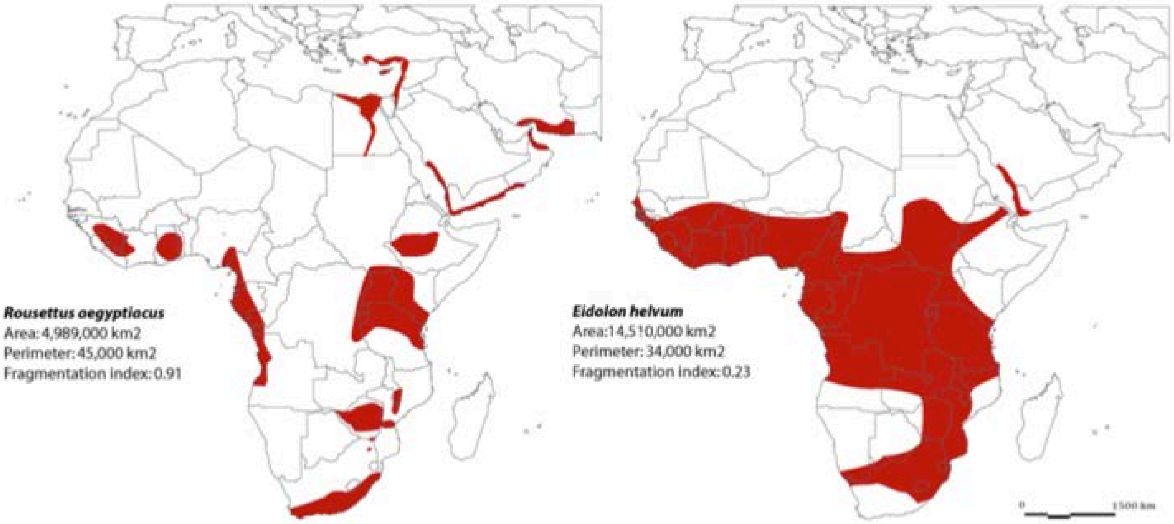

Figure 2. Range maps for *Rousettus aegyptiacus* (left) and *Eidolon helvum* (right), in both of which Ebola antibodies have been detected. Fragmented species ranges in Africa may be range gaps or knowledge gaps. If the latter, they must be filled (Maps from Maganga *et al*. 2014).

The unusually well-studied straw-colored fruit bat (*Eidolon helvum*), for example, exhibits an extraordinary genetic panmixia across its vast continental range (Peel *et al*. 2013). No genetic isolation is evident among African populations separated by more than 4,500 km, making *E. helvum* the largest ever documented panmictic unit of any mammal. This high connectivity among many millions of individuals could have serious implications for the transmission and maintenance of emerging zoonotic pathogens (Peel *et al*. 2013). With a migratory route that can span more than 2,500 km (Richter and Cumming 2008), *E. helvum* could be an effective cross-continental African viral emissary that also comes into contact with human populations via urban roost sites and bushmeat consumption (Hayman *et al*. 2008).

Though not linked directly to the current Ebola epidemic, nor implicated as an important Ebola reservoir, *E. helvum* has demonstrated seropositivity for Ebola (Hayman *et al*. 2010) and is known to share foraging and roost sites with *Epomops franqueti* (Jones 1972), a likely reservoir for the virus (Leroy 2005). Bat species with overlapping geographic ranges are known to share viruses between species extensively (Luis *et al*. 2013). Because many fruit bats and some microbats migrate in response to local rainfall patterns and hence food availability (Happold and Happold 2013), some bats may be sequentially sympatric with multiple other species, possibly increasing the extent of viral mixing. Pathogen control measures are thus further complicated by possible alternative reservoirs. Even if one species is extirpated, a pathogen can persist in a sympatric species. Ebola antibodies and/or RNA have been detected in at least nine fruit bat species (Leroy 2005; Hayman *et al*. 2008; Pourrut *et al*. 2009; Hayman *et al*. 2012; Reed 2012) and one microbat species (Pourrut *et al*. 2009; Table 1) with combined ranges spanning most of sub-Saharan Africa (Figure 3). Consequently, efforts to control a pathogen with significant cross-species behavior (such as Ebola) via population control of one or even multiple hosts would approach impossibility.

These recent insights into the effects of host distribution on pathogen transmission underscore the importance of conducting abundance and diversity surveys in poorly known geographic areas. Gaps are apparent in the distributions of many African bat species (Monadjem *et al*. 2010a). However, because many areas of Africa lack survey data for bats, discriminating knowledge gaps from true species absence is challenging. Additionally, many distribution maps currently rely on surveys conducted 30-40 years ago or more (Happold and Happold 2013), although anthropogenic influence has surely led to more recent changes. In particular, habitats are becoming increasingly fragmented as deforestation progresses, which may have substantial effects on population range and connectivity and hence on viral richness and spread. It is crucial that our natural history knowledge keeps pace with these changes.

Lessons from the past: applying population knowledge to interventions

In the past, culling has been used or proposed as a primary management tool for controlling pathogen prevalence in wild mammalian host species. Culling operations rely on two assumptions: 1) R_0 for a pathogen increases with the host population size (N), and, in turn, fadeout of the pathogen becomes more likely as the population shrinks; and 2) culling directly affects N in a predictably negative way.

Table 1. African bat species in which evidence of Ebola infection has been found, and the location of the study. The geographic ranges of these species have been given in Figure 3.

Family	Species	Location	References
Pteropodidae	*Eidolon helvum*	Ghana	Hayman *et al*. 2010; Hayman *et al*. 2012
Pteropodidae	*Epomops franqueti*	Gabon/Republic of Congo; Ghana	Leroy 2005; Pourrut *et al*. 2007; Pourrut *et al*. 2009; Hayman *et al*. 2012
Pteropodidae	*Epomophorus gambianus*	Ghana	Hayman *et al*. 2012
Pteropodidae	*Epomophorus labiatus*	Sudan, Uganda	Reed 2012
Pteropodidae	*Hypsignathus monstrosus*	Gabon/Republic of Congo; Ghana	Leroy 2005; Pourrut *et al*. 2009; Hayman *et al*. 2012
Pteropodidae	*Micropteropus pusillus*	Gabon/Republic of Congo	Pourrut *et al*. 2009
Pteropodidae	*Myonycteris torquata*	Gabon/Republic of Congo	Leroy *et al*. 2005; Pourrut *et al*. 2007; Pourrut *et al*. 2009
Pteropodidae	*Nanonycteris veldkampii*	Ghana	Hayman *et al*. 2012
Pteropodidae	*Rousettus aegyptiacus*	Gabon/Republic of Congo	Pourrut *et al*. 2009
Molossidae	*Mops condylurus (Tadarida condylura)*	Gabon/Republic of Congo	Pourrut *et al*. 2009

Under these assumptions, N and R_0 are not affected by reactionary processes such as immigration of susceptible individuals, compensatory reproduction (Choisy and Rohani 2006), or confounding evolutionary factors (Bolzoni and De Leo 2013). Conceivably, if the CCS for the pathogen in question is larger than the MVP for the host, managers could maintain bat populations while eradicating disease. This, however, would require a much more detailed understanding of population size, CCS, and MVP in bats than we currently possess.

Thus far, efforts to control zoonotic events by reducing reservoir populations below CCS have had unpredictable results (Donnelly *et al*. 2003; Streicker *et al*. 2012; Blackwood *et al*. 2013). The consequences of attempting pathogen management without adequate knowledge are especially evident in the cases of vampire bat control in Peru and Egyptian fruit bat control in Uganda. Management authorities have attempted culling as a means of controlling the transmission of rabies virus from vampire bats (*Desmodus rotundus*) to livestock and humans. Managers have employed "vampiricide," a paste applied to the fur of captured vampire bats, which kills conspecifics as they groom treated individuals (Arellano-Sota 1988). Vampire bat culling efforts are based on assumptions of density-dependent viral transmission; the bats must reach a critical community size before the virus can gain a foothold and become persistent, or "enzootic", in the population. However, Streicker *et al*. (2012) found that rabies virus prevalence was unrelated to colony size, and was actually higher in bat colonies that were subjected to culling. In fact, rabies appears to be transmitted in a frequency-dependent manner based on behavioral biting patterns of bat hosts. Since frequency-dependent transmission is independent of population size, culling is ineffective. In addition, vampire bat culling practices appear to have variable demographic effects: adults, which have already gained immunity due to exposure, may be disproportionately culled, which could increase R_0 by opening niche space for susceptible juveniles to proliferate (Streicker *et al*. 2012).

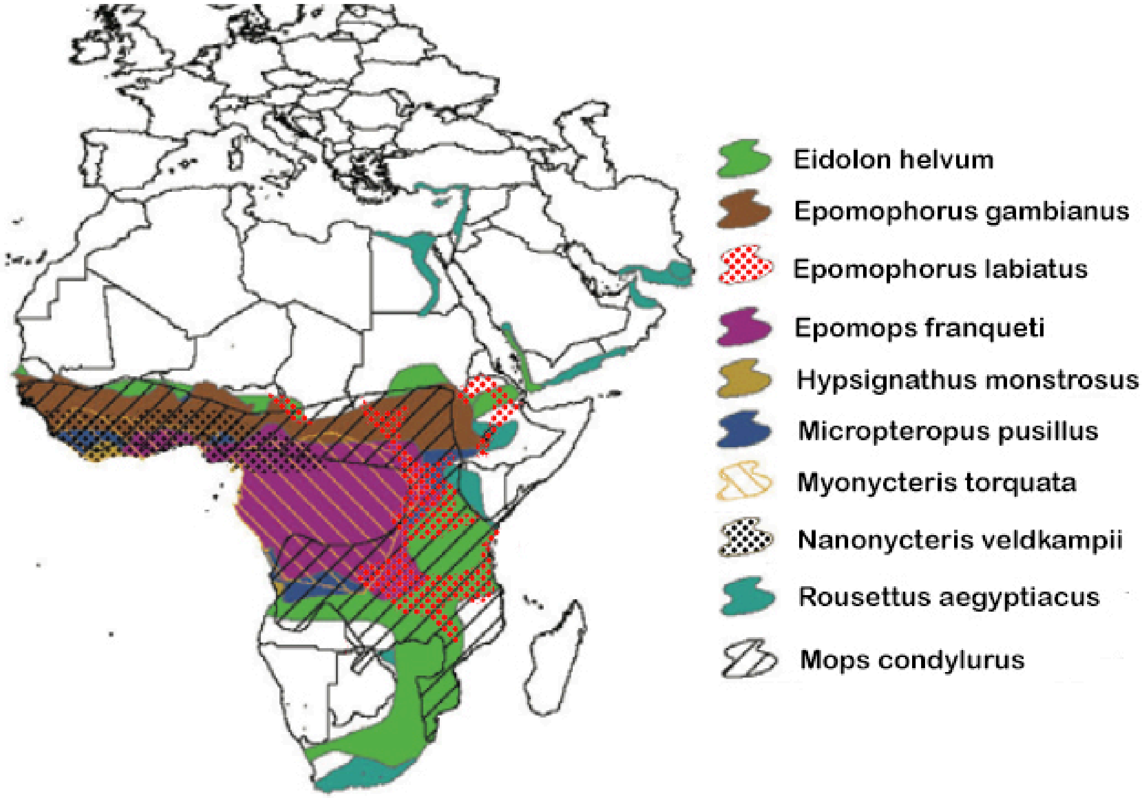

Figure 3. Range maps of the 10 African species of bat in which Ebola antibodies and/or DNA have been detected, showing their highly sympatric and cross-continental distributions (adapted from Olival and Hayman 2014).

In Uganda, six human cases (two fatal) of Marburg Hemorrhagic Fever (MHF) occurred in 2007 and 2008. All cases were linked to Kitaka Mine or a nearby cave, each location containing 40,000-100,000 Egyptian fruit bats (*Rousettus aegyptiacus*). These bats were confirmed to be Marburg reservoirs. In response, miners at Kitaka exterminated the fruit bat colony by blocking off the mine entrance with fishing nets, in which the bats became entangled. The entrances were then sealed. In 2012, a larger outbreak of MHF occurred in Ibanda, about 20 km from Kitaka Mine, resulting in 15 human cases of the disease. Amman *et al*. (2014) found that *R. aegyptiacus* had recolonized the mine, with a new colony that was 1 to 5 % of the original size. Phylogenetic analysis showed that Marburg virus strains in the new colony were nearly identical to those isolated from patients in Ibanda, making the Kitaka bats a likely source of the outbreak. Tests indicated that Marburg virus prevalence in the new fruit bat colony was significantly higher than before the culling efforts, with an increase from 5.1 % in 2007/2008 to 13.3 % in 2012. Moreover, this prevalence was significantly higher than in unculled Egyptian fruit bat populations in Uganda (2.5 %) and Gabon (4.8 %). It is possible that after the colony was culled, Kitaka was reinhabited by a pool of susceptible individuals, leading to higher transmission rates and thus a greater risk of spillover (Amman *et al*. 2014).

Unintended consequences of culling such as these described for vampire bats and Egyptian fruit bats may not be unique. In a rare case where sufficient data supports efforts to model the effects of bat culling on pathogen prevalence, a similar result is predicted: recent models demonstrate the inefficacy of culling infected individuals as a control method for White Nose Syndrome in North American bats (Hallam and McCracken 2010). To reduce R_0 for any pathogen, it is not strictly necessary to reduce the number of individuals, but to reduce the rate of transmission among those individuals (Carter *et al*. 2009). This transmission is often dependent on host density but can be independent of host population size in the case of pathogens transmitted via frequency-dependent mechanisms. Modeling efforts suggest that, due to the highly communal nature of the bat species affected by WNS, even a greatly reduced population would maintain dispersal between roost sites and high contact between individuals, thus still allowing for high transmission rates in hibernacula and maternity colonies (Hallam and McCracken 2010).

Other efforts to model culling effects demonstrate how, in cases of superinfection, or the coexistence of multiple viral strains within a given host, culling could impart a strong selective pressure for establishment of the less virulent strain (Bolzoni and De Leo 2013). Typically, viral strains that are less virulent in hosts will have fewer negative impacts on host fitness. Thus, they result in less frequent host mortality and are able to persist at lower population sizes, reducing the CCS and making their eradication more difficult. As many viral pathogens that show mild virulence in bats exhibit extreme virulence in other mammalian hosts (O'Shea *et al*. 2014; Brook and Dobson *in press*), such culling practices have important implications for zoonotic risk: culling may support the persistence, and sometimes higher prevalence, of pathogens within bat reservoirs, eventually enabling spillover to humans (Bolzoni and De Leo 2013).

As a side effect, culling may also endanger non-target species. Vampire bat culling threatens the population viability of a sympatric, endemic bat species, Dekeyser's nectar bat (*Lonchophylla dekeyseri*), which shares roosts with vampire bats. The nectar bats experience high mortality via incidental poisoning and roost destruction intended to kill vampire bats (Aguiar *et al*. 2010). Such unintended consequences for non-target species could be a particularly important concern in bats, since multi-species roosting and feeding groups are common. For example, during a campaign to eradicate Egyptian fruit bats (*R. aegyptiacus*) in Israel during the 1950s in an effort to reduce damage to fruit crops, approximately 90 % of insectivorous bats, which roosted in the same caves, were lost as unintended casualties. This resulted in an explosion in the population of noctuid moths, causing substantial crop damage (Makin and Mendelssohn 1985).

Thus, culling operations can have a number of counterintuitive effects on pathogen prevalence and species dynamics. Any such management action consequently requires the use of PVA, the quantification of CCS, knowledge of host and pathogen dynamics, and knowledge of the natural history of potentially impacted, non-target species to carefully model the impacts of intervention. Although predicting thresholds for pathogen persistence is difficult in most wildlife species (Lloyd-Smith *et al*. 2005), it is especially challenging in bats because of our poor understanding of bat ecology and natural history, which is particularly lacking among African bats. Hence, even if the fine balance between CCS and MVP were attempted, culling may worsen our disease crisis and lead to the endangerment or extinction of target and non-target bat species.

Looking to the future – Mozambique as case study

A study of bat communities by J. Guyton in Mozambique, where data on Chiroptera are scarce, is currently in progress. Before 2010, the most recent species inventory was compiled in 1976 (Smithers and Lobão Tello 1976), and it largely ignored the northern half of the country (Monadjem *et al*. 2010b). Though an inventory was published in 2010 (Monadjem *et al*. 2010a), many areas of Mozambique remain under-surveyed, and some of the northern parts continue to lack data entirely (Van Cakenberghe 2013). Before this survey, Gorongosa National Park was only surveyed for small mammals twice, and with limited scope, since the beginning of the civil war in 1977: two localities were surveyed as part of a countrywide effort in 2010 (Monadjem *et al*. 2010b), and a rapid assessment was conducted on Mount Gorongosa in 2011, with only opportunistic records of bats.

Working in this dramatically understudied country is rapidly yielding much new information on the distribution and natural history of African bats. As one example, Lander's horseshoe bat (*Rhinolophus landeri*) is commonly cited in the literature as roosting in colonies no larger than a dozen individuals in southern Africa (Smithers 1983; Taylor 2000; Monadjem *et al*. 2010a). However, an *R. landeri* colony of over 200 individuals has been documented in central Mozambique that is stable both within and between years. This colony is in a defunct well near the park's headquarters (Guyton, *in prep*). Thus, some assessments of bat colony and total population size may be off by an order of magnitude or more due to geographical gaps in knowledge, posing serious challenges for any effort to model pathogen dynamics among bat hosts or extinction estimates for threatened populations.

Additionally, the fruit bat *Epomophorus crypturus* was not recorded in this region since recorded by Smithers and Lobão Tello (1976). It was feared that this species may have been extirpated due to direct persecution for its role as a crop pest as well as widespread conversion of its forest habitat. However, several individuals of *E. crypturus* were captured in the park buffer zone earlier this year (Guyton, unpublished data). Additionally, dramatic morphological differences have been noted among bats that have been placed in the same *Epomophorus* species, indicating that there may be more species diversity within that genus than currently thought (Figure 4; Guyton, unpublished data). Natural history observations such as these are important for assessments of human disease risk in the region, especially when concerning fruit bat species, which harbor the bulk of bat-borne zoonotic diseases. Knowledge gaps such as those existing in Mozambique will be crucial to fill as we strive to preempt zoonotic public health crises. Placing emphasis on shifting funding toward natural history studies while training local biologists to tackle such questions can help to fill these gaps.

Bat conservation in the time of Ebola

Presumably, bat populations have served as reservoirs for pathogens highly virulent to other mammalian hosts since their origins. Indeed, bats demonstrate deep phylogenetic relationships with lyssaviruses (Badrane 2001), filoviruses (Taylor *et al*. 2010), paramyxoviruses (Drexler *et al*. 2012), coronaviruses (Cui *et al*. 2007), hepadnaviruses (Drexler *et al*. 2013), hepaciviruses (Quan

2012), influenza A virus (Tong *et al*. 2012), and simplexviruses (Sasaki 2014), as well as with certain non-viral pathogens including malarial protozoa (Schaer *et al*. 2013), trypanosomes (Barnabe *et al*. 2003; Ramírez *et al*. 2014) and *Bartonella* spp. bacteria (Kosoy *et al*. 2010). In spite of this ancient history, however, most high profile bat-borne zoonotic events have occurred within the last two decades (Dobson 2005). This begs the question: what is different about today's ecosystems that has led to so many recent spillover events?

Anthropogenic pressures and pathogen spillover

Various lines of evidence suggest that anthropogenic disturbance of bat populations and their habitats is likely responsible for the recent upsurge in bat-borne emerging diseases. Most bat-related zoonotic events have stemmed from Old World fruit bat reservoirs, which have experienced hunting-attributed declines of up to a quarter of their original population sizes over the past fifty years (Mickleburgh *et al*. 2009). Rates of fruit bat harvest appear to be unsustainable globally (Epstein *et al*. 2009; Divljan 2011; Kamins *et al*. 2011), often with the greatest harvest effort concentrated on reproductive female bats (Mickleburgh 2002; Brook unpublished data). Additionally, the reduction of bat numbers by hunting can, like culling, have counterintuitive effects on disease dynamics. This is especially true since human hunters target adult individuals that may have already gained immunity to the pathogen (Mickleburgh 2002), leaving niche space for susceptible juveniles (Streicker *et al*. 2012). In addition, hunting appears to be linked to spillover events: there is evidence of intensive hunting of relevant bat populations in the regions of zoonotic emergence for

Figure 4. Two species of Epomophorus from Gorongosa National Park, Mozambique. Left: An unusual individual that keys out to *E. wahlbergi*. Right: *E. crypturus* (Photos by Piotr Naskrecki).

Hendra virus (Divljan 2006), Nipah virus (Epstein *et al*. 2009), SARS-CoV (Mickleburgh *et al*. 2009), and Ebola virus (Leroy *et al*. 2009). Ebola outbreaks have been directly linked to contact with bushmeat, with cases arising from handling of primate carcasses (Formenty *et al*. 1999; Leroy *et al*. 2004), as well as, potentially, hunting and consumption of fruit bats (Leroy *et al*. 2009). Elevated contact with animals will always make hunters potential conduits for pathogens, even in the absence of other indirect effects of hunting on pathogen prevalence.

Human encroachment into natural habitats may also play a role in recent spillover events. In the case of Nipah virus, agricultural intensification may have heightened contact between bat reservoirs and secondary pig hosts. This may have allowed for repeated reintroductions of Nipah virus into swine populations, from which the virus was subsequently transferred to the human population (Pulliam *et al*. 2012). In the case of Hendra virus, anthropogenic habitat fragmentation is posited to have resulted in a loss of immunity in isolated flying fox populations, thus leading to epidemic spikes in flying fox infection upon pathogen introduction via a rare migratory individual. These epidemics, in turn, are thought to drive emergence into secondary horse hosts and eventual spillover into humans (Plowright *et al*. 2011).

Additionally, habitat loss and resource provisioning can go hand-in-hand to create a push-pull dynamic that draws potential reservoir species into human settlements. For example, a boom in the Latin American livestock industry has provided a ballooning food source for vampire bats, thus drawing the reservoir into closer contact with humans and exacerbating zoonotic disease (Streicker *et al*. 2012). In Australia, ornamental plants in urban and suburban environments provide pteropodids with year-round access to fruiting and flowering trees (Parry-Jones and Augee 2001; Markus and Hall 2004; Plowright *et al*. 2011), attracting bats into areas of high human population density and increasing the risk of zoonotic pathogen transmission through indirect contact. Indeed, in Mozambique, pteropodid bats of the genus *Epomophorus* are more frequently captured in human communities than in natural habitats, as the former provide access to high concentrations of cultivated fruit (Guyton unpublished data). It is crucial to understand how the behavioral drivers of this phenomenon in bats could be exploited to improve conservation measures and relieve the pressures that are driving bats into situations that put humans at risk of spillover.

Bat conservation and community education

The above evidence indicates that anthropogenic pressure may be contributing to increased emergence of bat-borne zoonotic pathogens. Increased conservation measures, such as protection of remaining forested habitat, habitat restoration, and hunting restrictions can help relieve this pressure and reduce the potential for spillover. The establishment of a zoonotic pathogen in human populations able to maintain independent transmission is thought to usually follow multiple, dead-end spillover events from wildlife populations—a phenomenon termed "viral chatter" (Wolfe *et al*. 2005). Reducing contact frequency between humans and wildlife hosts would reduce the intensity of this viral chatter, thus mitigating the likelihood of a zoonotic pathogen adapting (either behaviorally or genetically) to sustain human-to-human transmission, as has occurred with Nipah virus in Bangladesh (Luby *et al*. 2009) and, recently, with Ebola in West Africa (Leroy *et al*. 2014).

Creative solutions can be devised to reduce human contact with bats without resorting to population control measures. For example, exclusion netting over crops can reduce damage by fruit bats while simultaneously reducing provisions that attract bats to human communities (Fleming and Robinson 1987). In an effort to minimize wildlife-human contact and combat Ebola, the governments of Guinea (Bausch and Schwarz 2014) and Sierra Leone (Ansumana *et al*. 2014) have recently banned all harvesting and sale of bushmeat. These laws, however, are poorly enforced, and the sale of bushmeat continues in the region (Gyasiwaa 2014; UN Office for Coordination of Humanitarian Affairs 2014). This is an unsurprisingly common phenomenon, given that deeply entrenched cultural practices can be difficult to change, and people often rely on bushmeat for nutrients that are difficult to attain elsewhere (Golden *et al*. 2011).

Although quashing the bushmeat trade thoroughly and immediately is unrealistic, efforts can be made to shift human behavior and educate the public in a way that reduces the risk of zoonotic transmission. One potential compromise, if seasonal dynamics are found to be important in viral infection prevalence among bats, might be to impose a hunting season accompanied by awareness campaigns. Additionally, discouraging people from hunting or scavenging notable pathogen reservoirs, such as particular fruit bat species and great apes, could reduce exposure to the riskiest situations. Encouraging safer slaughter and handling practices of wildlife and domestic stock may also help. Ultimately, however, for human safety and for the preservation of biodiversity, human development efforts should aim to provide communities with safe, sustainable sources of animal protein.

Finally, our burgeoning zoonotic disease crisis has yielded an influx of North American and European biologists spearheading bat-related research projects in Africa, projects that need to be accompanied by more earnest educational outreach efforts. Within the U. S., Lubee Bat Conservancy, founded in Gainseville, Florida in 1989, offers a quality model for bat education and conservation that we believe has the potential for application in the developing world. At Lubee, captive breeding for fruit bat conservation takes place side-by-side with active research efforts, educational outreach, and tourism. Researchers sincere in their desires to educate Africans about bats should look to centers like Lubee as a model for how to carry out public health and disease-related science in conjunction with outreach promoting bat conservation in the developing world.

Conclusions and future directions

While ongoing research into the internal structure of emerging pathogens such as Ebola virus (Gire *et al*. 2014) and efforts to develop treatments (Mupapa *et al*. 1999) and vaccines (Fausther-Bovendo *et al*. 2012) are of undeniable importance, quarantine of infected humans and mitigation of spillover from wild reservoir populations may be the most effective public health measures in controlling epidemics in regions, like Africa, with limited medical services (Leroy *et al*. 2014). Thus, we should aim to understand bats and their pathogens sufficiently to know at which point to intervene in the cycle of transmission. Our current knowledge of the basic natural history of bats, especially in Africa, is woefully inadequate to attempt any accurate prediction of the impact of management interventions on the population dynamics of wild bats and the pathogens they host. However, as bat-borne zoonoses are increasing in frequency and severity (Leroy *et al*. 2014), it is paramount that we undertake natural history studies informing models of pathogen and host population dynamics and their responses to proposed interventions.

Bat natural history research was once limited by how difficult bats are to observe, but modern technology is changing that. In particular, much-needed assessments of population size and connectivity for bat species across the globe are becoming increasingly possible with the help of modern molecular and remote sensing technologies. Population assessments for bats will be particularly important in understudied regions, such as Africa, where human-bat contact rates are high and risk for zoonotic emergence is substantial. Such assessments will be important for efforts to explain both pathogen persistence in reservoir communities of varying sizes and structures, as well as to assess the vulnerability of reservoir species to extinction risk in the face of proposed interventions, such as culling.

Previous research indicates that bushmeat hunting, anthropogenic land conversion, and human encroachment into natural habitats have played key roles in the heightened emergence of bat-borne zoonotic diseases during the past half-century. Though we are still disentangling the mechanisms producing the majority of spillover events, evidence is sufficient to merit our strong support of the precautionary principle: handicapped as we are by a dearth of basic ecological knowledge, drastic population-level interventions could have dire consequences for at-risk bats globally, as well as unintended, sometimes counterproductive, consequences for pathogen control. Rather than risk exacerbating our present health crisis and initiating a conservation dilemma with hasty intervention measures, we instead advocate for detailed natural history studies combined with serious efforts to minimize human-bat contact through education and conservation campaigns. In the time of cholera epidemics, Gabriel García Márquez wrote (1988), "wisdom comes to us when it can no longer do any good." In the time of Ebola, let's seek that wisdom while it may still be of use.

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Resumen

Introducción: Los murciélagos son algunos de los mamíferos más pobremente estudiados, a pesar de su diversidad y los importantes servicios ecológicos que prestan. La epidemia actual de Ébola en el occidente de África subraya el papel cada vez más reconocido de los murciélagos como reservorios de enfermedades humanas emergentes. La comprensión de los mecanismos que permitan el mantenimiento de patógenos en los murciélagos como hospederos es fundamental para diseñar las futuras medidas en salud pública, así como los esfuerzos de conservación de las poblaciones de murciélagos silvestres. Esto es crucial en África, donde la población humana está creciendo y aumentando la pérdida de hábitat además del contacto humano con la vida silvestre.

La importancia de la historia natural: La historia natural y la ecología de los murciélagos, especialmente en África, son poco conocidas, por lo que la toma de decisiones de gestión por parte de los responsables es difícil. Las medidas para la gestión de los patógenos y sus reservorios, como el tamaño crítico de la comunidad y el mínimo viable de población, a menudo requieren más conocimientos de la historia natural que el existente actualmente. Sostenemos que una acción de gestión sin una investigación adecuada puede conducir a resultados contraproducentes. En el pasado, las respuestas de gestión basados en el miedo, como el de las campañas de sacrificio de ejemplares han aumentado la prevalencia de patógenos en la población destino principalmente, como se ha observado en el sistema de murciélago-vampiro de la rabia y el sistema fruto del palo-Marburg egipcio.

Conservación de murciélagos en los tiempos del Ébola: Muchos de los mismos factores de estrés antropogénicos que amenazan las poblaciones de murciélagos, como la pérdida de hábitat y la caza, son también las causas probables de la aparición de patógenos zoonóticos. Ante esto y dado que la reducción de las poblaciones de murciélagos puede aumentar la prevalencia de patógenos en lugar de disminuirla, sostenemos que las medidas de conservación de los murciélagos deben fortalecerse en esta época del Ébola. Se presentan los primeros pasos potenciales.

Clonclusiones y direcciones futuras: Evocamos al principio de precaución, y animan a los aumentos significativos y urgentes en estudios de historia natural, la educación, y las medidas de conservación de los murciélagos africanos.

Palabras clave: : Chiroptera, conservación de murciélagos, Ébola, historia natural, sacrificio, zoonosis patógena

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Conservation nectar bats (Phyllostomidae: Glossophagini) at risk in Coahuila and Nuevo Leon

Conservación de murciélagos nectarívoros (Phyllostomidae: Glossophagini) en riesgo en Coahuila y Nuevo León

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Introduction: Cave-dwelling nectar-feeding bats (Phyllostomidae: Glossophagini) face greater danger of extinction compared to other bats due to their restricted diet and the limited availability of suitable caves. Recent conservation biology literature suggests that successful conservation strategies should consider both biological and social perspectives. This paper presents the biological and social perspectives considered to implement conservation efforts for the threatened species *Leptonycteris nivalis* and *Choeronycteris mexicana* in the states of Coahuila and Nuevo Leon. Our objectives were to: 1) document caves used by these species, 2) describe community-based conservation strategies that link key actors (local communities, scientists, educators, government entities) resulting in a network, and 3) propose strategies to strengthen the links between key actors in the bat conservation network in order to maintain it in the long term.

Material and methods: To document caves used by *L. nivalis* and *C. mexicana* in Coahuila and Nuevo Leon, we combined searching available literature for known roosting sites and field surveys to confirm sites not previously reported. We implemented community-based conservation strategies with targeted local communities through workshops and used surveys to obtain indicators of knowledge and perception of bats by members of the communities.

Results: We report six caves used by nectar-feeding bats, which together house 12 species of bats (Table 1). The community-based conservation strategies that we implemented with local communities are described in four phases: information, communication, education, and training. A total of 574 residents from 52 communities participated in the study area. Surveys indicate that 60 % of the participants do not have knowledge of bat biology, 80 % are not aware of bats' ecological functions, and 71 % mention that bats are animals that cause fear.

Conclusions: We propose a conservation network consisting of key actors (local communities, scientists, non-governmental organizations, government entities, and financial institutions) with links that are strengthened by bi-directional communication (Figure 2). Flow of resources and information through networks such as this will facilitate the integration of social and biological perspectives for successful conservation actions.

Key words: environmental education, conservation planning, community-based conservation, *Leptonycteris nivalis, Choeronycteris mexicana*

Introducción

Los murciélagos son el segundo grupo más diverso de mamíferos con más de 1,116 especies en el mundo (Simmons 2005). México se posiciona como el quinto país con mayor riqueza de especies de murciélagos en el mundo con 138 especies (Medellin *et al.* 2008). Por su parte, los estados de Coahuila y Nuevo León albergan el 31 % de la quiropterofauna mexicana (43 especies en total; Baker 1956; Easterla y Baccus 1973; Wilson *et al.* 1985; Moreno-Valdez 1996; Jiménez-Guzmán *et al.* 1999; Contreras-Balderas *et al.* 2007).

A nivel mundial, los quirópteros representan uno de los grupos de mamíferos más amenazados (Mickleburgh *et al.* 2002). En la misma tendencia, más de la cuarta parte de las especies de murciélagos presentes en México se encuentran en alguna categoría de riesgo bajo la norma oficial mexicana de protección de especies nativas del país (NOM-059-SEMARNAT-2010; SEMARNAT 2010). Entre la quiropterofauna mexicana, la tribu Glossophagini (Phyllostomidae: Glossophaginae) son particularmente vulnerables al riesgo de extinción, dado que presentan hábitos alimenticios muy específicos (nectarívoros-polinívoros), además de que son sensibles a disturbios en las cuevas donde se refugian (Arita y Santos-del-Prado 1999). Entre los murciélagos cavernícolas del norte de México incluidos en la NOM-059-SEMARNAT con categoría de amenazados se encuentran las especies nectarívoras *Leptonycteris nivalis* y *Choeronycteris mexicana*. Estas dos especies presentan un amplio rango de distribución que abarca una porción considerable del territorio de México y parte del sur de Estados Unidos. Globalmente, *L. nivalis* es clasificado como en peligro (Arroyo-Cabrales *et al.* 2008) y *C. mexicana* como casi amenazado (Arroyo-Cabrales y Perez 2008) por la Unión Internacional para la Conservación de la Naturaleza (UICN) debido a que se estima una disminucion en sus poblaciones del 50 y 30 por ciento respectivamente, en los últimos diez años. Estas especies de murciélagos nectarívoros juegan un rol ecológico muy importante para los ecosistemas áridos y semiáridos de México al polinizar plantas clave como los agaves y las cactáceas.

La presencia de refugios y el hábitat disponible en el norte de México son de especial relevancia para ambas especies. Para el caso de *C. mexicana*, se han documentado hembras con crías durante los meses de verano en varios sitios de Coahuila y Nuevo León. A pesar de que *C. mexicana* presenta una amplia distribución, parece ser una constante la baja abundancia de individuos en los refugios donde ha sido reportada (Baker 1956; Jiménez-Guzmán *et al.* 1999). En el caso de *L. nivalis*, dentro de su amplio rango de distribución (*i. e.* desde el centro de México hasta el Sur de Estados Unidos de América) solamente se reconocen dos cuevas de maternidad (*i. e.* donde se han encontrado hembras preñadas o con crías) ubicadas en la parte norte de su distribución; una en el estado de Nuevo León, México y la otra en el estado de Texas, Estados Unidos (Easterla 1972; Medellín 1994). Además hay evidencia que sugiere que las hembras preñadas migran al norte cada primavera siguiendo los eventos de floración de plantas del género *Agave* (Moreno-Valdez *et al.* 2000). Lo anterior hace resaltar la importancia de proteger refugios y el hábitat de estas especies de filostómidos en riesgo de extinción, particularmente en los estados de Coahuila y Nuevo León.

A pesar de que los quirópteros se distinguen como uno de los grupos de mamíferos más amenazados en el mundo y en nuestro país, pocas publicaciones hablan de los esfuerzos de conservación para favorecer a las especies de murciélagos cavernícolas en riesgo. Ejemplos concretos son las acciones realizadas por el Programa de Conservación de Murciélagos de México (PCMM) en cuevas de los estados de Morelos y Campeche (López-Segurajauregui *et al.* 2006; Vargas-Contreras *et al.* 2012). Particularmente para el noreste de México, destacan los esfuerzos desarrollados por Arnulfo Moreno Valdez en el monitoreo, educación y conservación de los murciélagos cavernícolas de esta región (Tuttle y Moreno 2005), así como los esfuerzos para la protección como Santuario Natural a la Cueva de la Boca, Nuevo León, por parte de Pronatura Noreste (Pronatura Noreste 2006).

Una de las limitantes para definir acciones de conservación es la escasa disponibilidad de información sobre la biología y ecología de las especies en riesgo. En el caso de los murciélagos nectarívoros *L. nivalis* y *C. mexicana*, su sobrevivencia depende de la disponibilidad de alimento (*i. e.* principalmente néctar de flores para ambas especies), y de sitios de refugio (*i. e.* cuevas) que reúnen las características requeridas por cada especie. Además del conocimiento ecológico, la adecuada implementación de estrategias de conservación requiere considerar el componente social e incluir a las comunidades locales (Brosius *et al.* 1998). La educación ambiental puede ser un elemento clave para fortalecer la comunicación entre las partes locales interesadas con profesionales de conservación y permitir que se aplique la información científica en acciones de conservación (Bizerril *et al.* 2011; Vargas-Contreras *et al.* 2012).

Los programas de posgrado diseñados para integrar perspectivas sociales y biológicas pueden servir de catalizadores al reforzar redes de actores claves requeridas para acciones de conservación (Packard y Schmidly 1991; Fitzgerald y Stronza 2009). En este artículo, describimos un caso de estudio en el que las alianzas entre una organización no gubernamental local y científicos académicos (estudiantes de licenciatura y posgrado) reforzaron la participación de comunidades locales en la protección de cuevas usadas por murciélagos en riesgo.

Con la intención de contribuir a la generación de información ecológica de murciélagos nectarívoros amenazados, a partir del 2012 se iniciaron actividades de monitoreo para identificar sitios prioritarios para su conservación en los estados de Coahuila y Nuevo León (EPGR y TEL datos no publicados). Posteriormente, en 2013 se realizaron actividades de educación ambiental y talleres participativos con las comunidades que residen en la cercanía a las cuevas identificadas como refugio de *L. nivalis* y/o *C. mexicana*, con el fin de informarlas sobre la importancia del rol ecológico de estos mamíferos e involucrarlas en acciones de conservación (CJ y JMP datos no publicados; ESHAC-CONANP 2013). Los objetivos del presente artículo son: 1) documentar los refugios identificados para *L. nivalis* y *C. mexicana,* 2) diseñar estrategias sociales que vinculen a actores clave (comunidades locales, científicos, educadores, organizaciones no gubernamentales, entidades gubernamentales), resultando en una red de conservación, y 3) proponer estrategias para reforzar los vínculos entre los actores clave de la red de conservación de murciélagos de manera que se mantenga a largo plazo.

Métodos

Para documentar cuevas usadas por *L. nivalis* y *C. mexicana* en Coahuila y Nuevo León, combinamos la búsqueda de refugios conocidos para ambas especies en la literatura disponible (Baker 1956; Easterla y Baccus 1973; Wilson *et al.* 1985; Arroyo-Cabrales *et al.* 1987; Arita y Humphrey 1988; Hensley y Wilkins 1988; Moreno-Valdez 1996; Jimenéz-Guzmán *et al.* 1999; Moreno-Valdez *et al.* 2000; Contreras-Balderas *et al.* 2007) y trabajo de campo para identificar sitios no documentados previamente, el cuál consistió en contactar a comunidades locales en zonas previamente identificadas como hábitat potencial (EPGR y TEL datos no publicados) y obtener información sobre cuevas mediante entrevistas, a manera de diálogo semi-estructurado con informantes clave (residentes de la comunidad con conocimiento de cuevas en la zona; Geilfus 2002). Visitamos las cuevas identificadas entre los meses de mayo y agosto del 2012 y 2013, en al menos dos ocasiones cada año. En cada visita se colocaron redes de niebla cerca de la entrada a las cuevas para capturar murciélagos y documentar las especies que utilizan el sitio. Finalmente, consolidamos un listado de especies de murciélagos reportados para cada cueva en la literatura y como resultado de nuestros muestreos.

Posteriormente, implementamos estrategias de conservación basadas en la comunidad con las poblaciones ubicadas en la cercanía de las cuevas identificadas a través de talleres participativos. Además aplicamos encuestas cerradas para obtener indicadores del conocimiento y percepción de los murciélagos por parte de los miembros de las comunidades. Las preguntas de las encuestas desarrolladas buscaron identificar aspectos sobre el conocimiento previo de los participantes sobre qué son los murciélagos y cuál es su función, asimismo cuál es la percepción social sobre este grupo de mamíferos. Finalmente, se indagó sobre eventos previos de capacitación y sensibilización sobre murciélagos.

Resultados

Los refugios identificados corresponden a un total de seis cuevas que se ubican dentro de tres áreas naturales protegidas a nivel nacional (en Nuevo León, el Parque Nacional Cumbres de Monterrey, y en Coahuila, el Área de Protección de los Recursos Naturales CADNR004 Cuenca Don Martín y el Área de Protección de los Recursos Naturales CADNR026 Sierra de Arteaga; Figura 1). Estos refugios, albergan poblaciones de por lo menos 12 especies de murciélagos, de las cuales solo dos especies (*L. nivalis* y *C. mexicana*) están consideradas en riesgo (Tabla 1).

Al hablar de la riqueza de murciélagos para cada refugio, las cuevas El Infierno y Rosillo 1 resultaron ser las más diversas con un total de nueve y siete especies, respectivamente. En contraparte, la menor riqueza fue observada para la Cueva del Guano en Rayones, Nuevo León, con solo una especie, *C. mexicana*; sin embargo en esta cueva se observó la mayor abundancia de

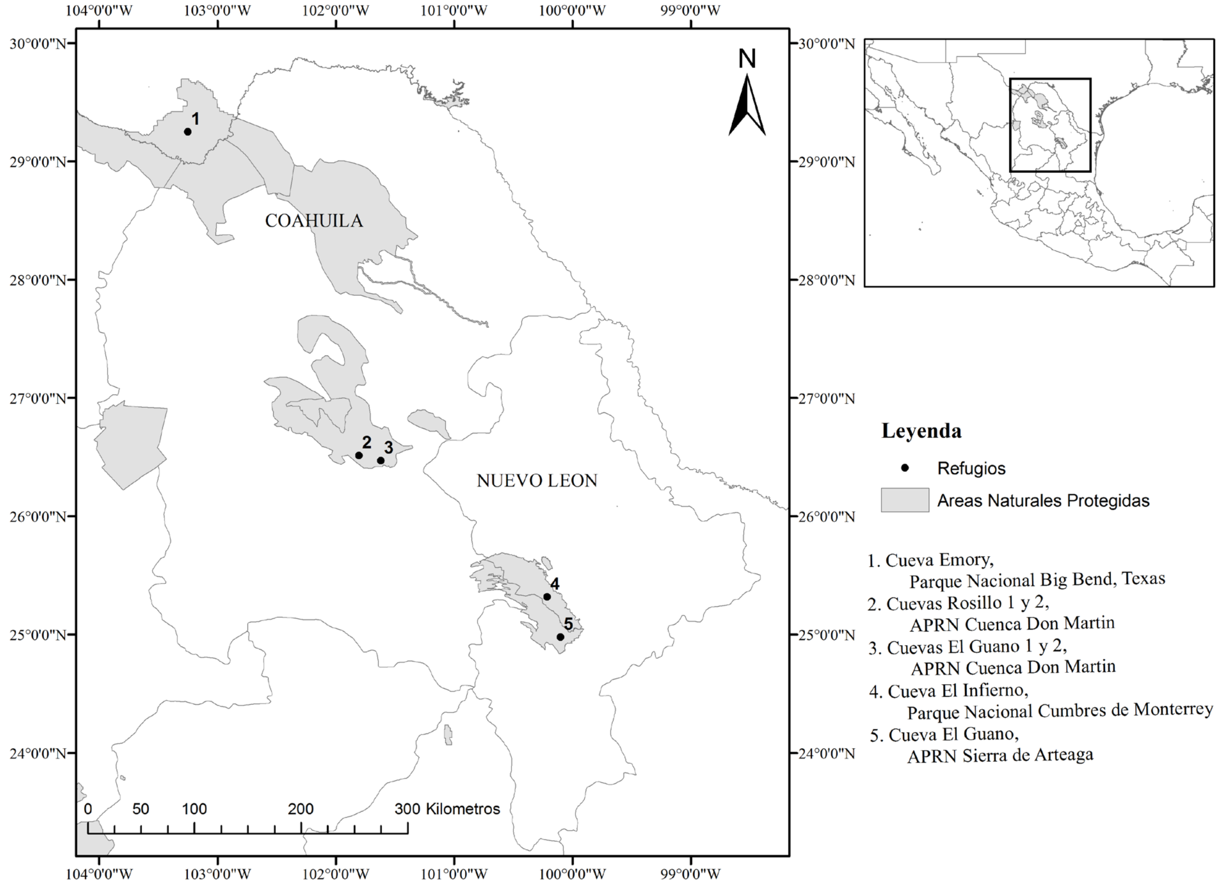

Figura 1. Ubicación de los refugios identificados para *Leptonycteris nivalis* y *Choeronycteris mexicana*

esta especie amenazada (siete individuos). De acuerdo con Arita (1993), el 80 % de las 215 cuevas incluidas en su estudio cuentan con una baja riqueza de especies de murciélagos (tres o menos) mientras que solo el 10 % sirve de refugio para seis especies o más, y concluye que un adecuado plan de conservación de cuevas de murciélagos no debe basarse solamente en el criterio de riqueza pues muy pocas de las especies vulnerables se refugian en cuevas con alta diversidad taxonómica. En el caso de las cuevas más diversas (El Infierno y Rosillo 1), combinan tanto una alta riqueza específica con la presencia de especies vulnerables. La diversidad relativamente alta encontrada en estas dos cuevas puede deberse a que son los refugios de mayor tamaño dentro de los sitios estudiados; Rosillo 1 mide cerca de un kilómetro de profundidad horizontal con techos de hasta 40.0 m, mientras que El Infierno es una cueva vertical que mide 80 m de profundidad, con una entrada de 43.0 m de largo por 20.5 m de ancho. Finalmente, la especie mejor representada dentro de este grupo de cuevas fue *C. mexicana*, especie común pero con abundancias bajas.

Hasta la fecha, solo en dos de los seis refugios mencionados se ha registrado al murciélago magueyero mayor (*L. nivalis*), en la cueva El Infierno y la cueva El Rosillo 1. La cueva El Infierno ha sido reportada como una de las dos cuevas de maternidad conocidas para esta especie, por lo que es un refugio prioritario (Moreno-Valdez *et al.* 2004; Ammerman *et al.* 2009). En la cueva El Rosillo 1, se ha registrado la presencia de hembras de *L. nivalis*, lo que sugiere que este refugio pudiera fungir como otro sitio de maternidad para la especie dentro de su ámbito de distribución. Por otra parte, la cueva El Rosillo 1 es utilizada como refugio por poblaciones del murciélago migratorio *e. g. Tadarida brasiliensis*.

Las estrategias de conservación basada en la comunidad que implementamos se describen en la siguiente sección, en cuatro fases: información, comunicación, educación, y capacitación. En suma se ha trabajado con 52 comunidades con un total de 574 participantes en los talleres de educación ambiental. Como parte de los talleres, realizamos encuestas a los participantes encuestas a los participantes para obtener indicadores de las diferencias en el conocimiento de murciélagos previo y posterior al taller, así como diferencia en la percepción hacia los murciélagos y documentar el interés en conocer más sobre estos mamíferos. Los resultados de las encuestas previas al taller indican que más del 60 % de los encuestados, respondieron no saber a qué grupo pertenecen los murciélagos (considerándolos principalmente como ratones con alas). Por su parte, el 80 % de los encuestados, respondió no conocer las funciones ecológicas de los murciélagos y un 71 %, consideraron que los murciélagos son animales que generan miedo. Esto denota el grado de desconocimiento de la población de estudio hacia este grupo de mamíferos.

Red de Conservación de Murciélagos. La integración de aspectos ecológicos y sociales es fundamental en la implementación de cualquier estrategia de conservación (Mascia *et al.* 2003; Knight *et al.* 2010; Ardoin y Heimlich 2013). Diversos trabajos argumentan que las estrategias sociales que se enfocan en promover la conexión de las personas con la naturaleza, construir conocimiento y promover el cuidado del ambiente, pueden y deben jugar un papel central en los programas de conservación (Jacobson y McDuff 1998; Mascia *et al.* 2003). A su vez, se ha descrito un continuo de estrategias sociales necesarias para la conservación (Ardoin y Heimlich 2013). A continuación describimos dichas estrategias presentándolas a manera de fases en el desarrollo de una red de conservación de murciélagos, la cual vincula a comunidades locales con científicos, educadores, y entidades gubernamentales.

Fase 1 Información: Esta fase se refiere a la información ecológica que poseen tanto las comunidades locales como los científicos. La apropiada difusión de dicha información conlleva a aumentar el entendimiento de las especies en riesgo y su hábitat, y así se concientiza a la sociedad sobre su entorno ambiental. En la primera sección de este artículo presentamos la información sobre los refugios que se identificaron para las especies de murciélagos en riesgo en el área de estudio. Esto fue resultado de análisis de hábitat y muestreos de campo llevados a cabo por

Tabla 1. Listado de especies de murciélagos encontradas en los refugios estudiados. Arreglo taxonómico según Simmons (2005).

	Categoría de riesgo según NOM-059-SEMARNAT-2010	Categoría de riesgo según la IUCN	Cueva El Infierno, La Camotera, Nuevo León	Cueva del Guano 1, Cuatro Ciénegas, Coahuila	Cueva del Guano 2, Cuatro Ciénegas, Coahuila	Cueva El Rosillo 1, Cuatro Ciénegas, Coahuila	Cueva El Rosillo 2, Cuatro Ciénegas, Coahuila	Cueva del Guano, Rayones, Nuevo León
Familia Phyllostomidae								
Choeronycteris mexicana	A	NT	X	X	X	X	X	X
Leptonycteris nivalis	A	EN	X			X		
Familia Vespertilionidae								
Corynorhinus townsendii		LC		X	X	X	X	
Eptesicus fuscus		LC				X		
Lasiurus cinereus		LC	X					
Myotis auriculus		LC	X					
Myotis californicus		LC	X					
Myotis thysanodes		LC	X			X	X	
Myotis yumanensis		LC	X					
Pipistrellus hesperus		LC	X					
Antrozous pallidus		LC	X			X		
Familia Molossidae								
Tadarida brasiliensis		LC				X		
Total de especies			9	2	2	7	3	1

IUCN= Unión Internacional para la Conservación de la Naturaleza; A=Amenazada, NT= Casi amenazado (Near threatened), EN= En peligro (Endangered), LC= Preocupación menor (Least concern)

científicos académicos y de información proporcionada por residentes locales sobre ubicación de cuevas potenciales. Particularmente, esta información recopilada, se obtuvo mediante diálogos semi-estructurados (Geilfus 2002), y posteriormente el recorrido hacia las áreas con guías locales.

Fase 2 Comunicación: La fase de comunicación implica establecer un diálogo entre las audiencias clave del programa de conservación. A través del desarrollo de proyectos en los que se benefician las comunidades, las organizaciones no gubernamentales (ONG) locales desarrollan un vínculo con los residentes locales. De esta manera, las ONG funcionan como facilitadoras en el establecimiento del diálogo entre los diferentes actores clave en la red de conservación.

La organización no gubernamental Especies, Sociedad y Hábitat, A. C. (ESHAC) ha venido trabajando con las comunidades de Coahuila y Nuevo León desde 2011 en diversos proyectos de manejo sustentable de los recursos naturales. ESHAC facilitó el contacto de los investigadores académicos con las comunidades para obtener información sobre ubicación de cuevas y sitios potenciales de forrajeo (*i. e.* zonas con agaves paniculados en floración). Asimismo, la información resultante de los muestreos de murciélagos y su hábitat, regresó a la comunidad a través de talleres coordinados por ESHAC (descritos en la fase 3 y 4).

Fase 3 Educación: La fase de educación se refiere a promover conocimientos que motiven a actuar en beneficio a la conservación. Primeramente investigadores académicos desarrollaron un estudio piloto de educación ambiental en donde se evaluó la pertinencia de actividades y materiales educativos de diversas características comunicativas (videos, manualidades, obras de teatro). Considerando como parámetros de evaluación: 1) con qué eficacia los materiales existentes de conservación de murciélagos abordan los conocimientos y habilidades consideradas esenciales por los educadores, 2) cuál de las estrategias interactivas es más asequible: videos, manualidades, u obras y, 3) el nivel de participación de los estudiantes dentro de cada actividad. Como primer paso para recopilar los materiales se contactó una red de organizaciones con conocimientos sobre educación ambiental, empezando con actores clave de Bat Conservation International (BCI), siguiendo con otros recomendados por efecto domino (*e. g.* Bat World Sanctuary, Organization for Bat Conservation, Texas Parks and Wildlife, el Programa para la Conservación de Murciélagos de México, etc.). Posteriormente, se estructuró un taller educativo con el siguiente formato: (1) la presentación de material videográfico, (2) el desarrollo de manualidades, y (3) la presentación de obras de teatro y cuentos. Los resultados de este estudio piloto, obtenidos por medio de cuestionarios y observaciones realizadas por el educador, muestran que los estudiantes retuvieron los conocimientos presentados dentro del formato de este taller, y las actividades que tuvieron mayor participación fueron los videos y manualidades. Al utilizar diversos métodos de enseñanza interactivos se incrementa la retención y recolección de información, y facilita la transmisión de conocimientos hacia los estudiantes, ya que participan no solo mentalmente, sino también físicamente en el proceso (Haury y Rillero 1994; Johnson *et al.* 1997).

Finalmente, estos materiales fueron compartidos con la organización no gubernamental ESHAC, la cual llev*ó* a cabo talleres de educación ambiental dirigidos a niños de 6 a 12 años. Además ESHAC trabajó directamente con personal del Consejo Nacional para el Fomento Educativo (CONAFE) en el estado de Nuevo León, para iniciar una red de educadores locales, la cual inicialmente incluye un poco más de 45 comunidades rurales dentro del rango de distribución de los murciélagos nectarívoros *C. mexicana y L. nivalis*. Por otra parte, el proyecto de conservación de las especies de murciélagos y sus refugios fue socializado con los pobladores locales a través del desarrollo de talleres de información donde se habló de la importancia, el rol ecológico y aspectos de conservación de los murciélagos en riesgo.

Fase 4 Capacitación: La fase de capacitación conlleva formar capacidades de la sociedad civil para apoyar y trabajar en beneficio de la conservación. Como parte de esta estrategia social, ESHAC coordinó reuniones con residentes de las comunidades locales para conformar comités de vigilancia certificados por la Procuraduría Federal de Protección al Ambiente (PROFEPA). El rol de los comités de vigilancia es procurar la protección de los refugios de murciélagos amenazados. Adicionalmente, considerando el marco de estos comités comunitarios formalizados, se pretende como siguiente paso fortalecer las capacidades comunitarias en el desarrollo de acciones concretas de caracterización y monitoreo de hábitat (*e. g.* documentar el estado fenológico de agaves), además de documentar la presencia de murciélagos nectarívoros utilizando métodos que no requieran su captura (*e. g.* uso de trampas-cámaras e inventarios con detectores acústicos). Al involucrar a las comunidades locales en el monitoreo se refuerza el conocimiento ecológico local y se enriquece el conocimiento científico con lo que se favorece una mejor planificación de los esfuerzos de conservación.

La implementación de estas cuatro fases tiene como resultado la vinculación de comunidades locales con científicos, educadores y entidades gubernamentales, lo que conforma una red de conservación de murciélagos. En la figura 2 presentamos un modelo que resume los componentes de la red de conservación. El modelo se basa en un enfoque multidisciplinario mencionado en diversas publicaciones sobre biología de la conservación (Meffe *et al.* 2006; Primack 2010). Los actores participantes se representan en diferentes círculos. En la parte superior colocamos a los organismos que son fuentes de financiamiento para las actividades de conservación. Esto es un aspecto fundamental para que tanto la academia como las organizaciones no gubernamentales

(ONG) desarrollen acciones de educación, conservación e investigación y este sea utilizado como parte de programas de conservación colaborando con comunidades locales. El siguiente grupo de actores es la academia, en donde consideramos a las universidades y centros de investigación como generadores del conocimiento científico de diversas disciplinas, desde biológico (Ecología, Botánica, Zoología, Genética, Evolución, etc.) hasta social (Antropología, Economía, Psicología, Pedagogía, etc.). Los académicos pueden interactuar directamente con las comunidades locales, a quienes se contacta para acceder al conocimiento ecológico local (*e. g.* preguntar sobre ubicación de cuevas con murciélagos, y de zonas con presencia de magueyes como recurso de forrajeo para los murciélagos nectarívoros). Asimismo, los académicos pueden interactuar con las ONG locales quienes, por lo general, tienen una relación más cercana con las comunidades. Las ONG funcionan como facilitadores y coordinadores de las actividades de conservación (*e. g.* capacitación de miembros de la comunidad para realizar monitoreo biológico, coordinar talleres de educación ambiental y sobre uso sustentable de los recursos naturales). Finalmente las comunidades se benefician de los proyectos de conservación al recibir capacitación sobre el manejo sustentable de los recursos naturales en sus terrenos que les permitirá garantizar el mantenimiento de dichos recursos para el futuro de su comunidad.

Estrategias para reforzar los vínculos de la red de conservación de murciélagos. La red de conservación que describimos se mantiene a través de los vínculos entre los diversos actores clave, en donde el conocimiento ecológico de las especies proviene tanto de los científicos como de las comunidades locales. Este conocimiento se comparte entre los actores a través de vínculos y una estrategia para reforzarlos es procurar la comunicación bidireccional. Es decir, al implementar estrategias que involucran a las comunidades en el monitoreo de las especies amenazadas y su hábitat, los científicos obtienen datos de manera continua y con mayor

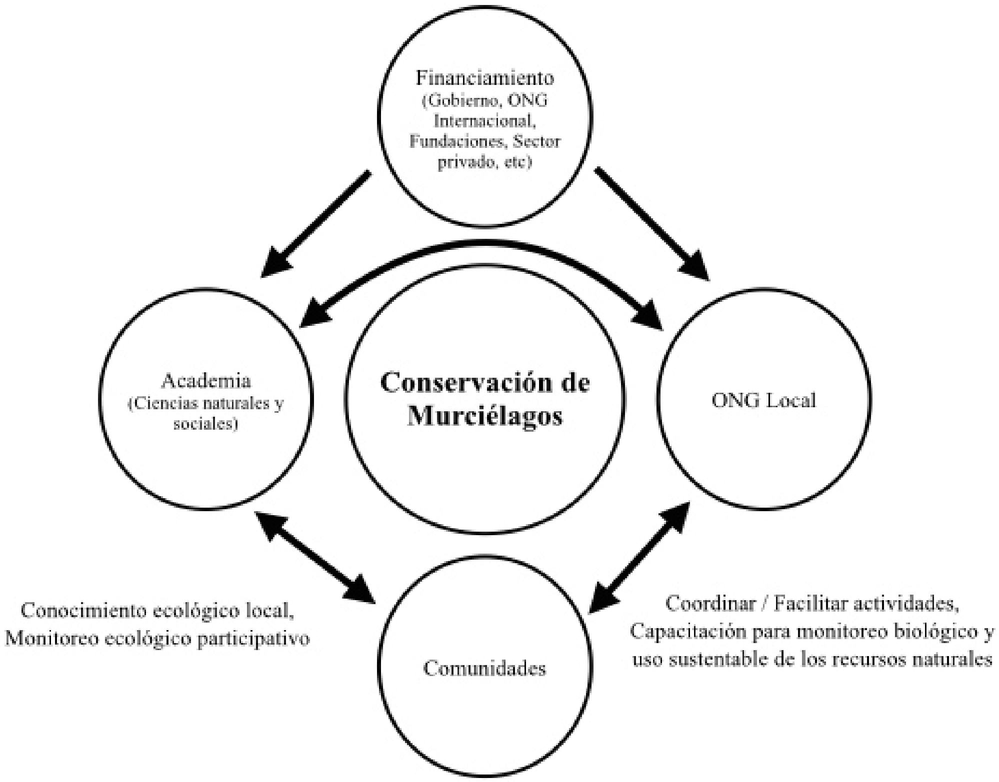

Figura 2 . Modelo representando la red de conservación de murciélagos.

frecuencia de lo habitual dadas las restricciones logísticas de trasladarse a los sitios de monitoreo. La obtención de estos datos permite analizar e identificar tendencias de cambio que afectan a las especies de interés. A su vez, las conclusiones a las que lleguen los científicos con los datos recabados por los residentes locales deben regresar a la comunidad para motivarlos a continuar participando en el monitoreo. Las ONG llevan a cabo un papel muy importante al tener mayor cercanía con las comunidades y ser gestores que refuerzan los vínculos entre los académicos y las comunidades. Finalmente, el recabar datos que documentan el éxito de las acciones de conservación puede favorecer a que las instituciones financiadoras continúen invirtiendo en estos proyectos. De esta forma, el involucramiento social puede repercutir de manera positiva en las actividades de monitoreo y conservación de las especies y su *hábitat*.

Conclusiones

Los esfuerzos de conservación que presentamos en este documento se fundamentan en aspectos ecológicos de las especies de murciélagos amenazadas para los estados de Coahuila y Nuevo León al identificar refugios y sitios de forrajeo prioritarios. Además, se consideran aspectos sociales que involucran a las comunidades que tienen influencia directa en el hábitat de estos murciélagos. La red de conservación que describimos, identificando a los actores clave y sus vínculos, es un modelo que puede ser transferible a otras áreas y otras especies de interés a conservar. Por otra parte, dada la carencia de ejercicios similares al contexto ecológico y social al presente estudio, sugerimos considerar éste modelo como un ejercicio de planificación para la conservación de estas especies y puede ser tomado como una línea base que permita evaluar el éxito del mismo en el mediano y largo plazo. La adecuada planificación de estrategias de conservación que integren aspectos ecológicos y sociales puede resultar en beneficios para las especies en riesgo y las comunidades humanas.

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Resumen

Introducción: Los murciélagos nectarívoros cavernícolas enfrentan mayor riesgo de extinción comparado con otros murciélagos debido a sus hábitos alimenticios restringidos y la limitada disponibilidad de cuevas con las características requeridas por estas especies. Literatura reciente de biología de la conservación sugiere que las estrategias de conservación exitosas deben incluir fundamentos biológicos y sociales. Este artículo presenta las perspectivas biológicas y sociales consideradas para implementar esfuerzos de conservación de las especies amenazadas *Leptonycteris nivalis* y *Choeronycteris mexicana* en los estados de Coahuila y Nuevo León. Nuestros objetivos fueron: 1) documentar las cuevas usadas por estas especies, 2) describir estrategias de conservación basadas en la comunidad que vinculan a actores clave (comunidades locales, científicos, educadores, organizaciones no gubernamentales, entidades gubernamentales) resultando en una red de conservación, y 3) proponer estrategias para reforzar los vínculos entre los actores clave de la red de conservación de murciélagos de manera que se mantenga a largo plazo.

Métodos: Para documentar cuevas usadas por *L. nivalis* y *C. mexicana* en Coahuila y Nuevo León, combinamos la búsqueda de sitios conocidos como refugios en literatura disponible, y muestreos de campo para documentar sitios de refugio no reportados previo a este artículo. Implementamos las estrategias sociales con comunidades locales objetivo por medio de talleres y aplicamos encuestas para obtener indicadores del conocimiento y percepción de los murciélagos por parte de los miembros de las comunidades.

Resultados: Reportamos seis cuevas refugios de las especies nectarívoras y que en conjunto albergan un total de 12 especies de murciélagos (Tabla 1). Las estrategias de conservación basadas en la comunidad que implementamos se describen en cuatro fases: información, comunicación, educación, y capacitación. Participaron 574 residentes de 52 comunidades en la zona de estudio. Las encuestas indican que el 60 % de los participantes no tienen conocimiento de la biología de los murciélagos, el 80 % desconoce sus funciones ecológicas, y el 71 % menciona que son animales que generan miedo.

Conclusiones: Proponemos una red de conservación conformada por actores clave (comunidades locales, científicas, organizaciones no gubernamentales, entidades gubernamentales, e instituciones financiadoras) en donde los vínculos se refuerzan por medio de una comunicación bidireccional (Figura 2). El flujo de recursos e información a través de redes como la aquí propuesta facilita la integración de perspectivas sociales y biológicas esenciales para lograr acciones de conservación exitosas.

Palabras clave: educación ambiental, planeamiento para la conservación, conservación basada en la comunidad, *Leptonycteris nivalis*, *Choeronycteris mexicana*

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Apéndice I

Preguntas que conformaron las encuestas cerradas para obtener indicadores del conocimiento y percepción de los murciélagos por parte de los miembros de las comunidades.

1. ¿Qué son los murciélagos?

Respuestas

- a). Mamíferos voladores
- b). No sé
- c). Ratones voladores
- d). Otro: ¿Cuál?

2. ¿Conoces la función de los murciélagos?

- Si
  - a): Control de plagas
  - b). Polinizadores
  - c). Se alimentan de sangre
  - d). Son depredadores
  - e). Otra: ¿Cuál?
- No

3. ¿Qué te provocan los murciélagos?

- a). Indiferencia
- b). Interés
- c). Miedo
- d). Repulsión
- e). No determinado

4. ¿Ha recibido alguna plática o capacitación a cerca de los murciélagos?

- a) Si.
  - ¿Cuándo?
  - ¿Quién la impartió?
- b) No.

5. ¿Te interesaría conocer más sobre ellos?

- a) Si.
- b) No.

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¿Cómo pueden cambiar las investigaciones científicas las prioridades de conservación? Una revisión de una década de investigación con ratas topo ciegas (Rodentia: Spalacinae) en la Cuenca de los Cárpatos

How can scientific researches change conservation priorities? A review of decade-long research on blind mole-rats (Rodentia: Spalacinae) in the Carpathian Basin

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Introduction: From time to time, it could be useful to revise and re-assess the results of long-term programs in conservation and research. This paper overviews an ongoing research program that started 10 years ago in Central Europe and focuses on blind mole-rats, a scarcely investigated and consequently enigmatic group of rodents.

Results: *Systematics and Taxonomy*. By means of molecular biological methods targeting the sequences of mitochondrial genes we conclude that five species of blind mole-rats, representatives of genera *Spalax* and *Nannospalax*, occur in the Carpathian Basin. Based on our present knowledge they are the only terrestrial vertebrate species endemic to the region.

Mapping of distributions. As recently as one hundred years ago blind mole-rats were widespread and common all over the Carpathian Basin. In the last decade, all the regions in Hungary, the Transylvanian Basin and Vojvodina where previous genuine records were known, were checked systematically. Maps and aerial photography provided information on the exact location of habitat patches that are supposed to be suitable for blind mole-rats even today. In recent years (from 2008 onwards) the survey area was extended to all locations where residents reported on the occurrence of mole-rats.

Threatening factors. The main cause of population decline is agricultural development which brought about significant changes in cultivation and land use. The following specific threatening factors were defined: cultivation, tree plantations, natural reafforestation, invasive plants, overgrazing, site developement, genetic bottlenecks, extreme weather conditions, and inadequate legal protection.

Risk assessment. Red List categories for all species of Carpathian Basin blind mole-rats were assessed according to the 2001 criteria. Accordingly, one species is proposed to be ranked as Vulnerable, two as Endangered, one as Critically Endangered, and one as Data Deficient (probably extinct).

Conclusions: Results from molecular biological and systematic studies, distribution mapping and determination of threatening factors, have had profound effects on practical conservation. These include action plans, wide international co-operations, establishment of a new protected area, updated protected species' list, species-level risk assessment, and the first-ever relocation program of a subterranean mammal.

Key words: *Nannospalax*, protected species, recent distribution, risk assessment, Spalacinae, *Spalax*, threatening factors

Introduction

There are many conservation programs all over the world seeking solutions for a diverse array of problems ranging from global challenges to grassroots issues. The main priority of many long-term scientific research projects is to provide information that could aid decision-makers and experts in their line of work. From time to time, it could be useful to revise and re-assess the results of long-term programs in conservation and research. Such reviews are valuable resources of information for future guidelines in science and planning as well as for the evaluation of current conservation status quos (*e. g*. Ostrowski *et al*. 1998; Amori and Gippoliti 2000; Towns *et al*. 2001). In our case study, we review the results of an ongoing research program that started 10 years ago in Central Europe and focuses on a scarcely investigated and consequentially enigmatic group of rodents. Our results so far had dramatically changed the group's stance in conservation and had completely re-designed the regional priorities in mammal conservation. In addition, they taught us a memorable lesson about the importance of scientific research both for practical nature conservation and in decision-making processes. On the down side, our research has also shed light on a phenomenon that may well be common in all cryptic and little known creatures. The lack of research coupled with obscure taxonomy often escorts a species hand-in-hand towards extinction while the whole process remains unnoticed even for experts and responsible decision-makers.

Eurasian blind mole-rats (subfamily Spalacinae) are adapted to exclusively underground life (Méhely 1909; Topachevskii 1969; Savić and Nevo 1990). These small mammals have cylindrically shaped bodies with no external ears and a vestigial tail, and are completely blind spending their entire life in their tunnel system built underground (Topachevskii 1969; Figure 1). Species of the subfamily can be found in the Balkan Peninsula, in steppe grasslands in Central and Eastern Europe, in the Middle East (Asia Minor and the coastline of the Levant), and in a narrow coastal strip in north-east Africa (Musser and Carleton 2005). Because of their rather uniform external appearance and gross cranial morphology, the systematics of blind mole-rats has been hotly debated over the last century. Compared to other rodent groups, the conditions resulting from their lifestyle created a decreased morphological variability and all species are very similar both externally and osteologically (Nevo 2000). The first comprehensive work, a milestone in blind mole-rat systematics, was published by Méhely (1909) who, based on his study of subtle differences in cranial and dental structures, recognized one genus with three subgenera and eight species with 14 additional subspecies. His opinion was later regarded as overly 'splitting', whereas at the other extreme, Ellerman and Morrison-Scott (1951) accepted only three species in one genus. The next baseline work in Spalacinae systematics was published by the outstanding Ukrainian morphotaxonomist, Topachevskii (1969), who, after studying hundreds of specimens, basically came to the same conclusions as Méhely (1909) as regards the genus-group systematics. However, his concept of a basic taxonomic divide between 'small' and 'large' blind mole-rats, although supported by craniodental differences, was not always followed in the literature published in English (*e. g*. Savić and Nevo 1990; Nevo *et al*. 2001; Musser and Carleton 2005). Nevertheless, as cytogenetic (Lyapunova *et al*. 1971) and molecular genetic (Hadid *et al*. 2012) investigations provided further support of deep taxonomic divergences within the subfamily, and support of the presence of two genera (*Spalax* and *Nannospalax*), this old established classification scheme has finally been accepted in the most recent publications (Németh *et al*. 2009; Arslan *et al*. 2011; Kryštufek *et al*. 2012; Chisamera *et al*. 2013). Putting aside the lineage of large blind mole-rats (genus *Spalax*), taxa belonging to *Nannospalax* present a long-standing source of dispute and disagreement over their systematics (Savić and Nevo 1990; Musser and Carleton 2005). Within the latter genus, one of the recognised species groups (regarded as superspecies) that includes a large number of karyologically different taxa (for the list of these see Savić and Soldatović 1984) is the

Lesser blind mole-rat, *Nannospalax* (superspecies *leucodon;* Musser and Carleton 2005). Although the species status of taxa differentiated solely on chromosomal grounds has not been widely accepted (Sözen *et al*. 2006; Ivanitskaya *et al*. 2008; Kryštufek *et al*. 2012), the results of the until now fairly limited molecular genetic investigations of this superspecies (Hadid *et al*. 2012; Németh *et al*. 2013a) and the results of breeding experiments with several Central European and Balkan chromosomal forms (Savić and Soldatović 1984) raises the necessity of species level separation at least of some of them. Alongside with taxonomic uncertainty the determination of conservation status of different mole-rat taxa is further hampered by their exclusively subterranean lifestyle which makes it difficult to evaluate their population size. While the *leucodon*-superspecies itself was categorised for a long time as Least Concern (Temple and Terry 2007, 2009), and changed recently to "Data Deficient" (Kryštufek and Amori 2008) to express the systematic problems within the group, while populations and habitats of many different European chromosomal taxa are disappearing at an alarming rate, a phenomenon which has just recently been realized (Kryštufek 1999; Kryštufek and Amori 2008; Németh *et al*. 2009).

Figure 1. *Spalax antiquus* (Aiton, Romania) in its natural habitat.

At the onset of the second millenium, all the available taxonomic and other scientific data as well as information related to the conservation of Central European blind mole-rats come from decades earlier (Németh 2011). While the whole region underwent a grand-scale and substantial change in land-use, blind mole-rats slowly sank into obscurity. Basically nothing was known about the actual distribution, population sizes or, due to the lack of modern taxonomic investigations, the sytematic position of the populations (Csorba 1998). Even though several authors throughout the region tried to raise awareness concerning the potentially threathened status of certain populations or even of the Lesser blind mole-rat in general (Báldi *et al*. 1995; Mikes *et al*. 1982; Habijan-Mikes *et al*. 1986; Savić *et al*. 1984), no comprehensive study was carried out. In Hungary for example, where blind mole-rats are strictly protected, data were only available on the monotonous and very likely unescapable demise of the extremely isolated and small population fragments. Due to the lack of practically applicable information, no plan was implemented to stop these processes. In 2003, in order to bridge the above-mentioned gaps in our knowledge, we started a research project on the Hungarian blind mole-rats. However, the scope of our investigation soon overstepped political boundaries and embraced the entire Carpathian Basin as a topographically well-defined unit of the European landscape.

Results

Systematics and taxonomy

Early taxonomy. Nehring (1897, 1898a, b, c) was the first to separate the single recognized species of blind mole-rats into several distinct species. He considered all the populations within the Carpathian Basin belonging to a single species that he described as *Spalax hungaricus* (Nehring 1898b). A few years later, Méhely (1909) recognised three dinstinct blind mole-rat taxa within the Carpathian Basin: *S. hungaricus hungaricus* (Central part of the Carpathian Basin), *S. hungaricus transsylvanicus* (Transylvania), and *S. monticola syrmiensis* (western part of the Carpathian Basin). He also made mention of an extinct taxon, *S. graecus antiquus,* only known from paleontological records. Almost three decades later, based on his review of Transylvanian specimens in the collection of the Hungarian Natural History Museum, Szunyoghy (1937) described an extant subspecies of *S. graecus* as *S. graecus mezösegiensis.* Ellerman and Morrison-Scott (1951) did not find Méhely's arguments convincing and saw the distinction of only three species justified for the entire distribution area of blind mole-rats. According to them, blind mole-rats in the Carpathian Basin belong to two species: *S. leucodon* and *S. microphthalmus.* In the monograph by Topachevskii (1969), all small European blind mole-rats (including *S. hungaricus* and *S. monticola*) were uniformly classified as Nordmann's *S. leucodon* (1840); he also agreed to the existence of a separate species, *S. graecus,* into which he assigned the larger blind mole-rats of Transylvania.

The 60's and the 70's were the golden age for cytogenetics. These investigations contributed significant information to the ongoing dispute on blind mole-rat taxonomy and it became clear that the karyotypes of taxa that had been previously classified on purely morphological grounds now suggested a completely different status in many cases (for a summary see Savić and Nevo 1990; Nevo *et al*. 2001). On a European scale, blind mole-rats of the Balkan Peninsula were under intense scrutiny through cytogenetic research. Karyotyping specimens from the territory of the former Yugoslavia provided evidence that *S. hungaricus* and *S. syrmiensis* had different number and structure of chromosomes (Savić and Soldatović 1984). During these investigations, the authors also discovered a so far unknown species with a unique karyotype which they named *S. montanosyrmiensis* (Savić and Soldatović 1974; Soldatović and Savić 1983). Additional research into their reproductive biology provided convincing evidence for the species-level separation of these taxa (Savić and Soldatović 1984). In Romania, the cytogenetic investigations of Raicu *et al*. (1968; 1969; 1973) determined the karyotype of *S. transsylvanicus* and *S. graecus*.

In their comprehensive work, Musser and Carleton (2005) listed 13 species of blind mole-rats, accepting all the different karyotypes in Israel as distinct species. However, the authors did not take a stand as to the taxonomic status of the different karyotypes occurring in Europe. Therefore, the current status of the Lesser blind mole-rat which is an aggregation of distinct biological species several of which could be threatened could not be ranked in the latest IUCN publication (IUCN 2014).

Recent investigations. As blind mole-rats in Hungary were not sampled during the extensive cytogenetic mapping of the 70's, no karyological information was available on the central populations of the Carpathian Basin. Due to increasing pressure to conserve these populations, our genetic sampling started in 2005. We first studied chromosomes and later carried out mitochondrial DNA analyses. Instead of the direct bone marrow preparation method routinely used with rodents (which requires culling the sampled individuals), we drafted a novel and less drastic approach. For tissue cultures, we used blood and connective tissue samples taken by experienced veterinarians, applying local and systemic anesthesia (Sós *et al*. 2009). Lymphocyte and fibroblast cultures were used for chromosomal investigations. Even though small sample sizes and bacterial or mycotic infections imposed several difficulties on this approach, we managed to assess the karyotype of four out of the six sampled populations. Our results supported the presence of two chromosomal species in Hungary. The karyotype of populations around Debrecen-Józsa, Hajdúbagos and Hajdúhadház (2*n* = 50, *NF* = 84, Németh *et al*. 2006, 2009) was found to be the same as that of the *S. transsylvanicus* populations in the vicinity of Jucu (Raicu *et al*. 1968). The karyotype of the blind mole-rats in the Kelebia region (2*n* = 54, *NF* = 86 (Németh *et al*. 2013a) agrees with the one that previously had only been found in Serbian populations near Stražilovo and Čortanovci, and described as *S. montanosyrmiensis* (Savić and Soldatović 1974; Soldatović and Savić 1983).

By means of molecular biological methods targeting the sequences of five mitochondrial genes (12S rRNA, tRNA-Val, 16S rRNA, tRNA-Leu (UUR), NADH1, tRNAIle, 3742 bp in total) we could conclude that large and small blind mole-rats belong to distinct genera, *Spalax* and *Nannospalax*, respectively (Hadid *et al*. 2012). The results based on the widest taxonomic and geographic coverage so far also support the hypothesis that Transylvanian representatives of the genus *Spalax* do in fact belong to a species endemic to the Carpathian Basin (Figure 2). Méhely's blind mole-rat (*S. antiquus*) was separated from its closest relatives *S. graecus sensu stricto* and *S. istricus* approximately 1.4 mya (Hadid *et al*. 2012; Németh *et al*. 2013b). The robustness of the mentioned conclusion is supported by the combined evidence of morphology, multilocus phylogeny, species distribution, and taxon history

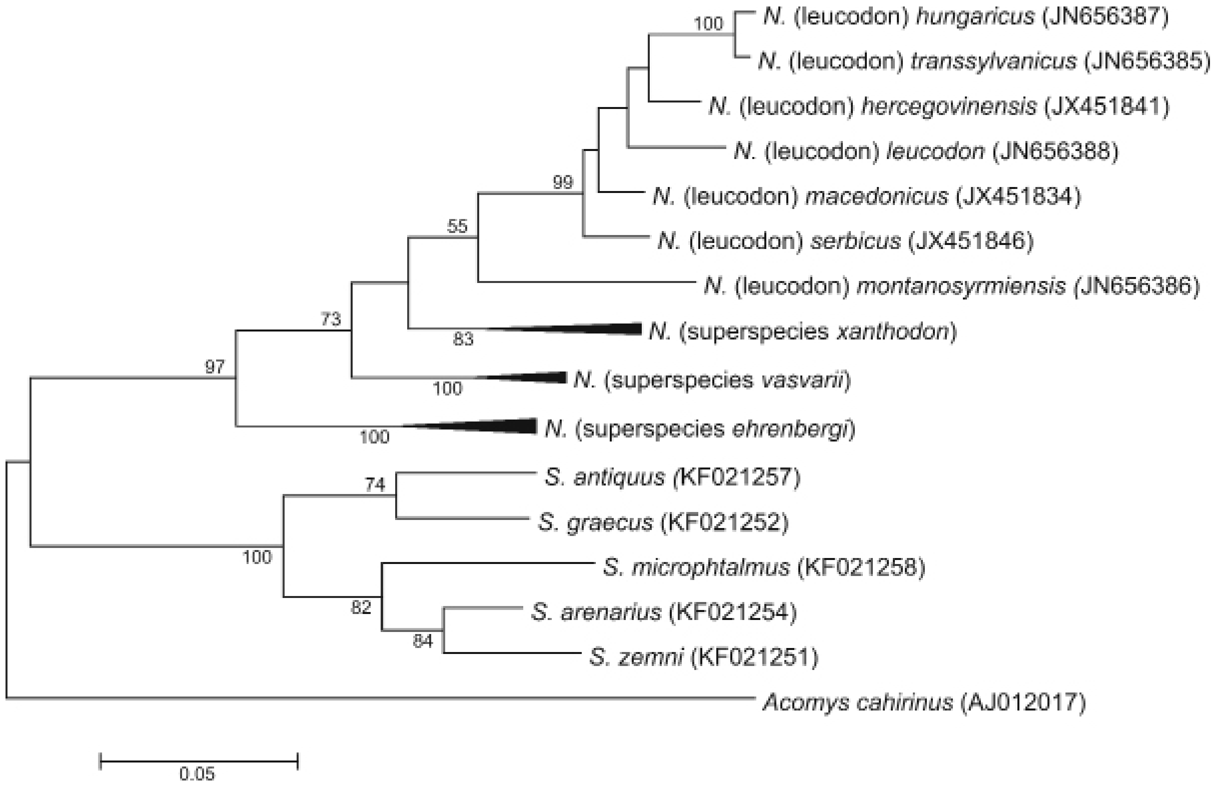

Figure 2. Phylogenetic tree showing evolutionary history of *Spalax* (S.) and *Nannospalax* (N.) species based on 870 bp long partial sequence of cytochome b gene using the Maximum Likelihood method and the Tamura-Nei model. The percentage of trees in which the associated taxa clustered together (after 10 000 replications) is shown next to the branches. Bar represents the number of substitutions per site; GeneBank accession numbers are written in parentheses. Analysis was performed using MEGA6 software (Tamura *et al.* 2013). *Acomys cahirinus* was used as outgroup.

(species congruence with past tectonic and climate events).

Based on an 870-bp-long section of the cytochrom-b gene, the Srem blind mole-rat (*N.* (*leucodon*) *syrmiensis*), the Vojvodina blind mole-rat (*N.* (*leucodon*) *montanosyrmiensis*), the Hungarian blind mole-rat (*N.* (*leucodon*) *hungaricus*) and the Transsylvanian blind mole-rat (*N.* (*leucodon*) *transsylvanicus*) all represent distinct lineages within the genus *Nannospalax* (Németh *et al*. 2013a; Németh unpublished data; Figure 2). These Carpathian Basin taxa were previously distinguished from each other by craniodental attributes as well as by their karyotypes (Savić and Soldatović 1984). Among all studied *Nannospalax* taxa, the Vojvodina blind mole-rat occupies a basal position on the phylogenetic reconstructions, representing an ancient group that parted from other European taxa about 2 million years ago (Hadid *et al*. 2012; Németh *et al*. 2013a). According to our present knowledge, five species of blind mole-rats, representatives of two genera, occurring in the Carpathian Basin are the only terrestrial vertebrate species endemic to the region (Table 1).

Table 1. Extant populations of blind mole-rats, estimated numbers of individuals, extent and protection status of habitats for species inhabiting the Carpathian Basin.

Species	Locations	Number of individuals	Area of occupancy (ha)	Protection status	Reference
Nannospalax (leucodon) hungaricus	Kunmadaras	5	1	not protected	Németh *et al*. 2013c
	Mezőtúr	30	6,6	not protected	Németh *et al.* 2013c
	Tompapuszta	20-30	21	Natura2000-HUKM20009	Horváth and Vadnay 2006
	Battonya	20	37	Natura2000-HUKM 20009	Németh *et al*. 2013c
	Deliblatska peščara	5500-5800	29350	Deliblatska peščara Special Nature Reserve	Németh *et a*l. 2009
Nannospalax (leucodon) montanosyrmiensis	Baja	150-200	120	not protected	Sendula 2014
	Kelebia – Subotićka peščara	150-200	416	partly protected (Kőrös-ér Landscape Protection Area, Natura2000-HUKN20008, Subotićka peščara Protected Area)	Krivek 2014
	Stražilovo - Čortanovci	100	50	not protected	Németh *et al.* 2013a
Nannospalax (leucodon) syrmiensis	not known	0	0	probably extinct	Németh unpublished data
Nannospalax (leucodon) transsylvanicus	Cluj-Napoca - Dăbâca	8800-8900	40000	partly protected (Apahida Spalax Reserve, Fânaţele Clujului Nature Reserves, Natura2000-ROSCI0295, ROSCI0099)	Sugár 2012
	Hajdúhadház	800	1675	Natura2000-HUHN21164	Bihari *et al*. 2009
	Debrecen-Józsa	50	60	Natura2000-HUHN20122	Németh *et al*. 2013c
	Hajdúbagos 1	130-150	265	Natura2000-HUHN20217	Bihari *et al*. 2009
	Hajdúbagos 2	15-20	15	not protected	Németh *et al*. 2013c
Spalax antiquus	Budeşti – Cătina – Mociu	500-600	min. 1800	partly protected (Natura2000-ROSCI0333)	Sugár 2012 and Sugár unpublished data
	Aiton – Cojocna – Iuriu de Câmpie – Ploscoș	2500-2600	19500	partly protected (Natura2000-ROSCI0238, ROSPA0113)	Sugár 2012
	Turda	450-500	1720	partly protected (Natura2000-ROSCI0034, ROSCI0035, ROSPA0087)	Sugár 2009, Sugár and Hegyeli 2010
	Rădeşti – Beța	100-120	min. 350	partly protected (Natura2000-ROSCI0187)	Sugár 2012 and Sugár unpublished data

Mapping of distributions

Early records. As recently as one hundred years ago blind mole-rats were widespread and common all over the Carpathian Basin. They were known to occur in all nonmountainous and unforested regions including steppes of the central Transylvanian Plateau, Romania and were recorded in almost the whole lowland areas of Vojvodina, northern Serbia (Petényi and Glos 1845; Orosz 1902; 1903; 1904; 1905; 1906; Lendl 1899; 1900; Méhely 1909; Horváth 1918a, 1918b; Vásárhelyi 1929; 1931; 1932; 1960; Szalay 1932; Szunyoghy 1937; Sterbetz 1965; 2002; Tóth 1991; Figure 3). Although their occurrence west of the river Danube was last recorded in 1925 (Éhik 1925), blind mole-rats were still common in suitable habitats of the Great Hungarian Plain in the inter-World Wars period (Vásárhelyi 1926; 1932); up to the 1950s Sterbetz (1960) recorded high numbers of blind mole-rats in the southeastern area of the Plain. Blind mole-rats in Vojvodina were abundant even in the 1970s (Savić and Soldatović 1984).

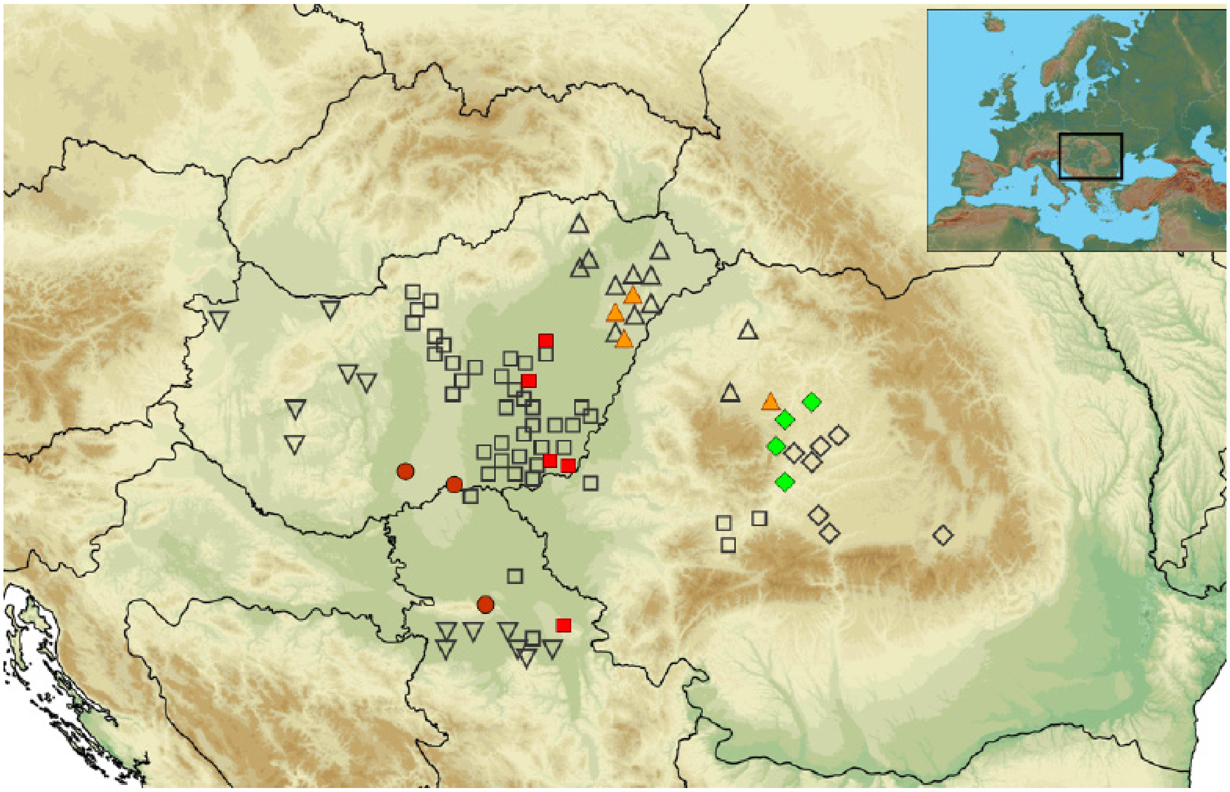

Figure 3. Former and recent distribution of blind mole-rat species in the Carpathian Basin. Full symbols represent existing populations, whereas empty symbols denote historical records.

▽ = *Nannospalax* (*leucodon*) *syrmiensis*
□ = *Nannospalax* (*leucodon*) *hungaricus*
○ = *Nannospalax* (*leucodon*) *montanosyrmiensis*
△ = *Nannospalax* (*leucodon*) *transsylvanicus*
◇ = *Spalax antiquus*

Degradation, transformation of habitats, and shrinking of distribution area can all be blamed for the decrease in the number of mole-rats in the formerly vast grasslands (Csorba 1998; Figure 4). The main cause of population decline is agricultural development which brought about significant changes in cultivation and land use. Extensive livestock farming and pasture-farming were replaced by intensive monocultures. These changes led to the dramatic decline, fragmentation and in many cases to the final disappearance of grasslands (Csorba 1998; Németh *et al* 2013c). Changes in habitat structure had negative impacts on animal species inhabiting steppes of Central Europe. As a result, blind mole-rats, which were formerly defined as a pest, became endangered and therefore gained legal protection in Hungary (Németh *et al*. 2013c).

The very first and most rapid changes in habitat structure took place in Hungary between the second half of the 1950s and the 1970s. A similar progression started in Transylvania at the same time, however on less extensive areas, owing to the scarcity of vast plain areas adequate for large-scale agriculture. Grassland habitats of Vojvodina were affected in the 1990s. As a consequence of habitat deterioration blind mole-rat populations retreated to remnant grassland fragments and became completely isolated from each other. Recent regional development and urbanisation had particularly adverse impacts on the remaining blind mole-rat populations of Hungary and Vojvodina (Németh *et al* 2013c; Krivek 2014; Sendula 2014). In the early 2000s only five populations in Hungary and two in Vojvodina were recorded (Horváth and Vadnai 2006; Delić 2007), and there was no information on either the localities or the size of mole-rat populations in Transylvania.

Figure 4. Vast, dry grasslands are the typical habitats of blind mole-rats (Aiton, Romania)

Recent studies. As a first step in mapping blind mole-rat populations, all the regions in Hungary, the Transylvanian Basin and Vojvodina where previous genuine records were known, supported by scientific publications or voucher specimens, were checked systematically. Maps and aerial photography provided information on the exact location of habitat patches that are supposed to be suitable for blind mole-rats even today, that is, areas not affected by afforestation, housing/industrial developement or large-scale cultivation. In recent years (from 2008 onwards) the survey area was extended to all locations where residents reported on the occurrence of mole-rats.

The investigations were carried out during the peak activity period of blind mole-rats in spring and in autumn months. When large, widely-spaced mounds and tunnels with hard-packed walls (characteristic of blind mole-rats) were found, capture of individuals was attempted. In each of such cases the occurrence of blind mole-rats was succesfully proven by catching live specimens. The animals were caught by opening the tunnel system and capturing the animal trying to mend the damage (Németh *et al*. 2007), a method allowed by research permits issued by the National Inspectorate for Environment, Nature Conservation and Water no. 14/05173-3/2006 and 14/1840-3/2008.

Animals were handled in the field in accordance with guidelines approved by the American Society of Mammalogists (Gannon *et al*. 2007). After genetic sampling and recording body weight and external reproductive features the individuals were released back to their own tunnel system. Locations that were confirmed to have extant populations are listed in Table 1.

Threatening factors

Cultivation. In the 20th century, the expansion of agriculture was the most prominent cause for the loss of the best habitats for wildlife. The most fertile loess soils were the first to undergo changes in land use which has pushed blind mole-rat populations to less favourable areas. The widespread use of deep tillage was the single most important direct effect that so drastically reduced blind mole-rat population sizes and distribution in Hungary as to push the species to the brink of extinction (Csorba 1998). On the one hand, repeated ploughing does not allow the formation of the vegetation type necessary for the survival of blind mole-rats; on the other hand, deep ploughing destroys their underground burrow systems as well as the animals themselves. Nowadays, the most common reason causing tillage is not so much the cultivation itself as the fulfilment of the requirements to apply for funding from the European Community (Németh *et al*. 2010, 2013c). Provided that before its admission to the EU, Romanian agricultural practice sustained adequately large areas to include habitats for blind mole-rats, the present changes in this new member state give rise to grave concerns. Small plot farming with mosaics of fallow land has often given way to intensive crop production in large monocultures. As the same process presumably led to the drastic decrease of the Hungarian populations (Csorba 1998), the same tendencies within the Romanian habitats are more than alarming. Severe reduction in the numbers of Romanian blind mole-rats is imminent (Temple and Terry 2007, 2009; Németh 2011).

Tree plantations. This leads to the complete eradication of the former habitat, and restoration of once afforested areas is a time and resource consuming procedure. Many grasslands have been turned to black locust (*Robinia pseudoacacia*), hybrid poplar (*Populus* x *euramericana*) and pine (*Pinus sylvestris* and *P. nigra*) plantations, which not only exclude blind mole-rats from the transformed areas themselves, but also isolate the population fragments from each other (Németh *et al*. 2010, 2013c).

Natural reafforestation. Arboreal vegetation may spontaneously invade in small meadows surrounded by forest as well as fallow land. This mainly presents a problem when the canopy of trees closes and herbaceous food plants of the blind mole-rats disappear from the undergrowth. Problematic tree species are the black locust (*Robinia pseudoacacia*), grey poplar (*Populus canescens*), box elder (*Acer negundo*), hawthorn (*Crategus* spp) and blackthorn (*Prunus spinosa*) (Németh *et al*. 2010; 2013c). Their appearance is usually the consequence of the lack or reduction of grazing due to the termination of extensive animal husbandry of traditional breeds of cattle and sheep.

Invasive plants. Certain exotics, such as the common milkweed (*Asclepias syriaca*) can grow in such density that other species, including the ones providing forage for the blind mole-rats, disappear from the area. This mainly causes problems on sandy soil; fortunately, the presently known blind mole-rat habitats are not strongly infested yet (Németh *et al*. 2013c; Krivek 2014).

Overgrazing. This is a threat found in some habitats of both *N. (leucodon) transsylvanicus* and *S. antiquus* in Transylvania (Sugár 2009), where overexploitation of the sheep-grazed habitat greatly reduces species diversity, probably causing a significant decrease in the food resources of blind mole-rats.

Urbanization, site development and road constructions. One of the most pressing issues of our times is property development, the construction of new suburbs, industrial parks, solar panel parks, shopping malls, parking lots, and other types of built-up areas. In Hungary, some blind mole-rat populations can be found within settlements (Figure 5). Most of the land in these cases is the property of the municipality and impending industrial investments can mean complete eradication (Krivek 2014; Sendula 2014). A Serbian population inhabits a popular vacation resort, where actual and planned development projects may result in losing the entire population (Németh *et al*. 2013c; Krivek 2014). Road construction can also annihilate populations. This is an omnipresent risk factor in all countries of the region that mainly concerns non-protected areas. In Hungary, one subpopulation disappeared due to the contruction of a new highway exit (Németh *et al*. 2013c).

Figure 5. In many cases, property development poses imminent threat to the remaining population fragments (Mezőtúr, Hungary).

Even though new roads mean the loss of natural habitat, extant roads also pose a threat for wildlife. Heavy traffic kills many animals that set foot on the pavement as it was proven at a location in Hungary where several individuals got hit by vehicles. There is evidence that even lesser roads have a detrimental effect on such isolated and small population fragments (Németh *et al*. 2013c; Krivek 2014). Typically, blind mole-rat habitats are criss-crossed by dirt roads, the effect of which is currently unknown. As a rare type of site development, some localities are the target of specific interventions for military purposes. The Hajdúhadház Military Training Area in Hungary awaits impending development with a large investment and a substantial increase in the frequency of field-days as well as the number of participants. These changes will likely have a dramatic impact on the local Transylvanian blind mole-rat population that was previously counted upon as the only stable population in Hungary, but after the implementation of military plans, their long-term survival is rather doubtful (Németh *et al*. 2013c).

Genetic bottlenecks. Because many populations have become fragmented the resulting limited habitat sizes and low population sizes threaten the long-term viability of populations with inbreeding and other genetic problems (Krivek 2014). Asymmetrical albino spots on each captured individual from the smallest known Transylvanian blind mole-rat population support our assumptions on inbreeding (Németh *et al* 2013c).

Direct and indirect killing. Even though blind mole-rats are protected in all countries within the region, there are still cases of intentional destruction. It is extremely hard to measure this kind of activity, but in small population fragments even the loss of a few individuals may have disastrous effects. Conflicts arise from some individuals living and foraging within human settlements, damaging ornamental plants and vegetables. In the Deliblát region (Serbia), blind mole-rat control incurs an hourly wage rate paid by the human population, even though the species is strictly protected in Serbia (Krivek 2014). It further aggravates the situation that in all countries concerned, rodent traps capable of catching and killing blind mole-rats are routinely available at local vendors. The utility of the traps is sometimes enhanced by using the blind mole-rat in the advertisements. Another anthropogenic threat is the disturbance and destruction caused by pets (dogs as well as cats). Stray dogs and herding dogs are known to have killed several individuals (Németh *et al*. 2010, 2013c).

Natural enemies, predators. The almost exclusively subterranean lifestyle protects blind mole-rats from most predators. As of today, the impact on population dynamics by owls, raptors and mammalian predators is largely unknown.

Extreme weather conditions. Chronically high levels of ground water displaces the mole-rats from lower reliefs, making population fragmentation even more pronounced. Periods of extremely high precipitation or the spring thaw cause inundation at several locations, killing individuals in a number of known populations (Horváth-Vadnay 2006; Németh *et al*. 2010, 2013c).

Global climate change. Hadid *et al*. (2012) analysed the phylogeny of the subfamily Spalacinae calibrated by fossil records. Revealed evolutionary events show a remarkable synchronization with the cycles of solar orbital fluctuations (eccentricity and precession) driving the ice ages. This makes it plausible that global climate changes following the ice ages played an important role in the formation of the unusually high genetic diversity of blind mole-rats.

We can also be sure that the present changes in global climate will significantly impact blind mole-rats, but the direction and the extent of this impact cannot be predicted. In the past, such processes resulted in new taxa of blind mole-rats, but current changes are heavily distorted by human influence. There is a whole host of evidence (Nevo *et al* 1994a, b, 1995; 2000a, b; Reyes *et al*. 2003; Karanth *et al*. 2004) that genetically and geographically distinct taxa adapted to the specific climate of their own range during their speciation. However, blind mole-rat habitats have shrunk to small, isolated fragments that are few and far between, within a matrix impenetrable for blind mole-rats. Isolation is further abetted by their severely limited dispersal capacities. Thus, there is a high likelihood that ongoing climatic changes would rather wipe out blind mole-rat species than give rise to new ones.

Inadequate legal protection. The Natura 2000 system itself is not suitable for blind mole-rat conservation, as it does not target those species that have been completely ignored by Annexes 2 and 4 of the EU Habitats Directory. Another handicap of the Natura 2000 network is that it does not limit infrastructure development, expansion of large-scale agriculture, or renewable energy investments, as long as they do not threaten the survival of species or habitats of community interest in a direct way. As a result, they often ignore conservation needs of taxa outside of EU legislation. The interpretation of Natura 2000 sites as protected areas may therefore be misleading when assessing the conservation status of species that are not of community interest such as blind mole-rats.

Risk Assessment

The Red List categories of the Carpathian Basin blind mole-rats were assessed according to the 2001 criteria (IUCN 2001). Habitats and threats were classified (and terms used) according to the IUCN Habitats Classification Scheme 3.0 and Threats Classification Scheme 2.1, respectively (www.iucnredlist.org).

Nannospalax (*leucodon*) *transsylvanicus* is proposed to be ranked as Vulnerable B1ab (iii); B2ab (iii). Rationale: extent of occurence and area of occupancy are estimated to be no more than 120 square kilometres, known to exist at no more than 10 locations and estimates indicate a continuing decline in area, extent and quality of habitat. Accession of Romania to the EU has already resulted in agricultural intensification (Németh *et al*. 2009).

Nannospalax (*leucodon*) *hungaricus* is proposed to be ranked as Endangered B1ab (iii); B2ab (iii). Rationale: the extent of occurrence and area of occupancy are estimated to be approximately 300 square kilometres; estimates indicate severely fragmented populations in no more than five locations; continuing decline in observed area, extent and quality of habitats. More than 95 % of the population can be found in a single locality.

Nannospalax (*leucodon*) *montanosyrmiensis* is proposed to be ranked as Critically Endangered B1ab (iii); B2ab (iii). This assessment is based on the extent of occurrence which is estimated to be less than 100 square kilometres; area of occupancy is estimated to be less than 10 square kilometres. The populations are severely fragmented, persist in no more than three locations, are continuing to decline in numbers, and are experiencing a loss in the size and quality of habitats.

Nannospalax (*leucodon*) *syrmiensis* is proposed to be ranked as Data Deficient. No definite record is known from the last thirty years. The latest information on the occurrence of this species (determinations were based on karyological data) was published by Soldatović and Savić (1983). No new data pertaining to the distribution and abundance have ever been published (Németh *et al*. 2009). It is very likely that this taxon is extinct (Németh *et al*., in press).

Spalax antiquus is proposed to be ranked as Endangered A3 (c) and B2ab (ii), (iii), (iv)). The categorization is based on the suspected decline in extent of occurrence and quality of habitat within the next 10 years; area of occupancy estimated to be less than 500 km^2, and the species is known to exist at no more than five locations. Accession of Romania to the EU has already resulted in agricultural intensification (Németh *et al*. 2009) that will presumably impact this species negatively.

Conclusions and Future Directions

A decade of investigating the blind mole-rats of the Carpathian Basin fundamentally changed what we had previously assumed about these rodents in this region. The genetic investigations have shown that five, genetically well-differentiated species occur within and exclusively within the Carpathian Basin (Németh 2011; Hadid *et al*. 2012; Németh *et al*. 2013a; 2013b). That is, the blind mole-rats of this region are not locally endangered, peripheral populations of a wide-ranging species, but very localized endemics some of them with extremely low population sizes. One species is probably already extinct, and others are, facing extinction.

Our investigations have also influenced the approach of decision makers towards conservation of blind mole-rats. Already the very first results gave rise to a species action plan laying down the strategy required to protect the blind mole-rat populations of Hungary (Németh *et al*. 2010). The plan has been updated to suit more recent discoveries (Németh *et al*. 2013c). In 2009, a Mole-rat Protection Consulting Committee was established by the relevant ministry in Hungary. It involves experts at national parks, zoological gardens, the nature protection authority, museums, and universities. Its charges are to define priorities, work out conservation actions and offer their opinions on related issues. Members of the Committee were consulted during the protocol of updating Hungary's list of protected species resulting in the acceptance of the latest systematic opinion and in elevating species of the Lesser blind mole-rat complex (*Nannospalax*; superspecies *leucodon*) to the highest conservation rank. Acknowledging the presence of the Vojvodina blind mole-rat near Kelebia was one of the main arguments to establish the Kőrös-ér Landscape Protection Area which provides a safe shelter for approximately 20 % of the remaining individuals of this Critically Endangered species.

A good working relationship has been established between the Mole-rat Protection Consulting Committee and the staff of the Novi Sad Department, Institute for Nature Conservation of Serbia resulting in joint field research and publications. In 2011, the intergovernmental Hungarian–Romanian Joint Committee on the Environment set the investigations of all blind mole-rat species occurring in the two countries as one of its main priorities, so that their habitats and populations can be protected.

The scientific evidence and empirical know-how gathered during the years made it possible to carry out a so far unparalelled conservation intervention on subterranean rodents. As a pilot project, we successfully relocated individuals from the largest Hungarian population of the Transylvanian blind mole-rat to establish new populations and the practical information yielded will make the immediate conservation actions in urgent cases feasible (Németh *et al*. 2013d).

Our research on blind mole-rats of the Carpathian Basin has not only emphasized the importance of scientific investigations for conservation purposes, but also highlighted a phenomenon in which less known and cryptic species can be pushed to the brink of extinction as a result of the lack of information, unclear taxonomic status and unrecognised tasks in conservation. Counterproductively though, conservation initiatives will continue to be biased towards the most studied mammal groups and species (Amori and Gippoliti 2000), while a whole host of less "attractive species" disappears, drastically reducing global biodiversity. Surviving blind mole-rats can serve as umbrella species to protect the wildlife of Central European steppes. We believe it is extremely important that the experts of the IUCN Species Survival Commission re-evaluate the status of the endemic blind mole-rat species of the Carpathian Basin, and possibly also bring their conservation status to the attention of decision makers at the EU level. Moreover, blind mole-rats are unassuming animals; their needs can be satisfied by being appropriately managed and by providing adequately sized grasslands that would allow for population growth (Krivek 2014). With our present knowledge, this is only a question of good intentions and funding. If the latest scientific results serve to raise the awareness of decision-makers to these questions, not only can these endemic mammals evade extinction, but also many other species connected to our remaining Central European steppes can survive as well.

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Resumen

Introducción: De vez en cuando, podría ser útil para revisar y volver ha evaluar los resultados de los programas de conservación y la investigación a largo plazo. Este artículo revisa un programa de investigación en curso que se inició hace 10 años en Europa central sobre las ratas topo ciegas, un grupo de roedores, que no se ha investigado y en consecuencia es enigmático.

Resultados: *Sistemática y Taxonomía*. Por medio de métodos moleculares de secuenciación de genes mitocondriales concluimos que existen cinco especies de ratas topo ciegas, representantes de géneros *Spalax* y *Nannospalax*, en la Cuenca de los Cárpatos. Sobre la base de nuestros conocimientos actuales son las únicas especies de vertebrados terrestres endémicas de la región.

Mapeo de las distribuciones. Las ratas topo ciegas estaban apliamente extendida y eran comunes en toda la Cuenca de los Cárpatos hace cien años. En la última década, todas las regiones de Hungría, la Cuenca de Transilvania y Voivodina, de donde se conocen registros se revisaron sistemáticamente. Mapas y fotografías aéreas proporcionan información sobre la ubicación exacta de los parches de hábitat que se supone deben ser adecuados para las ratas topo ciegas incluso hoy en día. En los últimos años (a partir de 2008) el área de estudio se extendió a todos los lugares donde los residentes informaron sobre la aparición de ratas topo.

Factores que amenazan. La principal causa de la disminución de la población es el desarrollo agrícola que provocó cambios significativos en el cultivo y uso de la tierra. Se definieron los siguientes factores amenazantes específicos: cultivo, plantaciones de árboles, reforestación natural, plantas invasoras, pastoreo excesivo, desarrollo de los sitios, los cuellos de botella genéticos, condiciones tiempo externo, y protección legal inadecuada.

La evaluación de riesgos. Todas las especies de la Cuenca de los Cárpatos ratas topo ciegas fueron evaluados de acuerdo a los criterios de 2001 de las categorías de la Lista Roja. En consecuencia, se propone que una especie a ser clasificado como Vulnerable, dos como en peligro de extinción, una como En Peligro Crítico, y una como Datos Insuficientes (probablemente extinta).

Conclusiones: Los resultados de los estudios biológicos y de sistemática molecular, mapeo de la distribución y la determinación de los factores amenazantes, han tenido efectos profundos en la conservación práctica. Estos incluyen planes de acción, amplias cooperaciones internacionales, el establecimiento de una nueva área protegida, la lista de especies protegidas actualizados, la evaluación de riesgos a nivel de especie, y el primer programa de reubicación de un mamífero subterráneo.

Palabras Clave: distribución reciente, especies protegidas, evaluación de riesgos, factores amenazantes, *Nannospalax*, Spalacinae, *Spalax*

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Confictos de conservación involucrando a mamíferos en Europa

Conservation conflicts involving mammals in Europe

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Introduction: In recent times, conflicts involving wildlife have increased in importance and magnitude. Conservation conflicts occur when two or more parties with strongly held opinions clash over conservation objectives, and when one party is perceived to assert its interest at the expense of another. Conservation conflicts usually emerge from "wildlife impacts", defined as circumstances where people, consciously or unconsciously, negatively impact wildlife, or alternatively where wildlife negatively impacts the well-being or livelihoods of people or biodiversity. In Europe, the most frequent and intense conservation conflict associated with the management of mammals is likely that involving predators. For example, large carnivores depredate on livestock and game species, but at the same time these are flagship-species for European nature conservation. Therefore, conflicts about how these species should be managed emerge frequently. The management of overabundant ungulates that negatively impact natural vegetation as well as that of small mammals that damage crops also lead to frequent clashes between stakeholders in Europe. The global conservation status of most conflictive European mammals is rather good. However, some of their populations are threatened, at least partially by illegal killing and poaching. From this perspective, efforts are needed to mitigate conservation conflicts in these areas. In addition, promoting the investigation of conservation conflicts that incorporates multidisciplinary approaches is essential to increase the understanding of such conflicts and ultimately to mitigate them.

Key words: Crop damage, hunting, large carnivores, livestock loss, overabundant ungulates, poaching, predator control, small mammals, wildlife management

Introduction

Conflicts involving wildlife have existed since time immemorial. For example, several centuries ago European rabbits (*Oryctolagus cuniculus*) were transported from their native range in southern Europe to many places, because they are furry and edible animals. However, these small mammals devastated cereal crops, hence impacting negatively the interests of farmers (Thompson and King 1994), and causing tensions between stakeholders. Over recent times, however, with increasing pressure on ecosystem goods and services and increasing urgency for biodiversity conservation, these conflicts have likely become more important (Young *et al.* 2010). This seems to have captured the attention of the international scientific community, as the number of studies dealing with conflicts involving wildlife has exponentially increased during the last years (Figure 1).

My main goal in this article is to explore conservation conflicts involving mammals in Europe. To do so, I will: 1) define conservation conflicts, since there is currently an important misunderstanding in the literature regarding this issue (Peterson *et al.* 2010); defining conservation conflicts is essential to better understand their significance in order to develop ways to manage them efficiently (Young *et al.* 2010); 2) describe the main types of conservation conflicts involving mammals in Europe; 3) review the impacts caused by wildlife on human well-being or biodiversity, which are ultimately responsible for most of the conflicts; 4) show the main stakeholders involved in conservation conflicts within Europe; 5) provide key examples of the main European mammal species involved in such conflicts; and 6) briefly discuss how conservation conflicts affect the conservation of mammals in the European context.

Conservation conflicts: definition and types

Conflict definitions generally converge around "expressed disagreements among people who see incompatible goals and potential interference in achieving these goals" (Pearce and Littlejohn 1997; Peterson *et al.* 2002; Pruitt and Kim 2004). In this sense, the term "human-wildlife conflict", which is commonly used to refer to conflicts involving wildlife species, is problematic because it suggests that animals are direct human antagonists (Graham *et al.* 2005; Peterson *et al.* 2010). In reality, conflicts tend to occur among humans ascribing different values to wildlife and thus how best to address its potential threats to human property, health, safety, etc. (Conover 2002).

In this context, conservation conflicts are defined as situations that occur when two or more parties with strongly held opinions clash over conservation objectives, and when one party is perceived to assert its interest at the expense of another (Redpath *et al.* 2013). Conservation conflicts emerge when either the positions of parties representing conservation interests are threatened by the positions of those holding other views and interests (*e. g.* farmers, hunters, etc) or when the objectives of conservation are imposed on others, such as when humans are excluded from protected areas or when species of conservation interest have an impact on

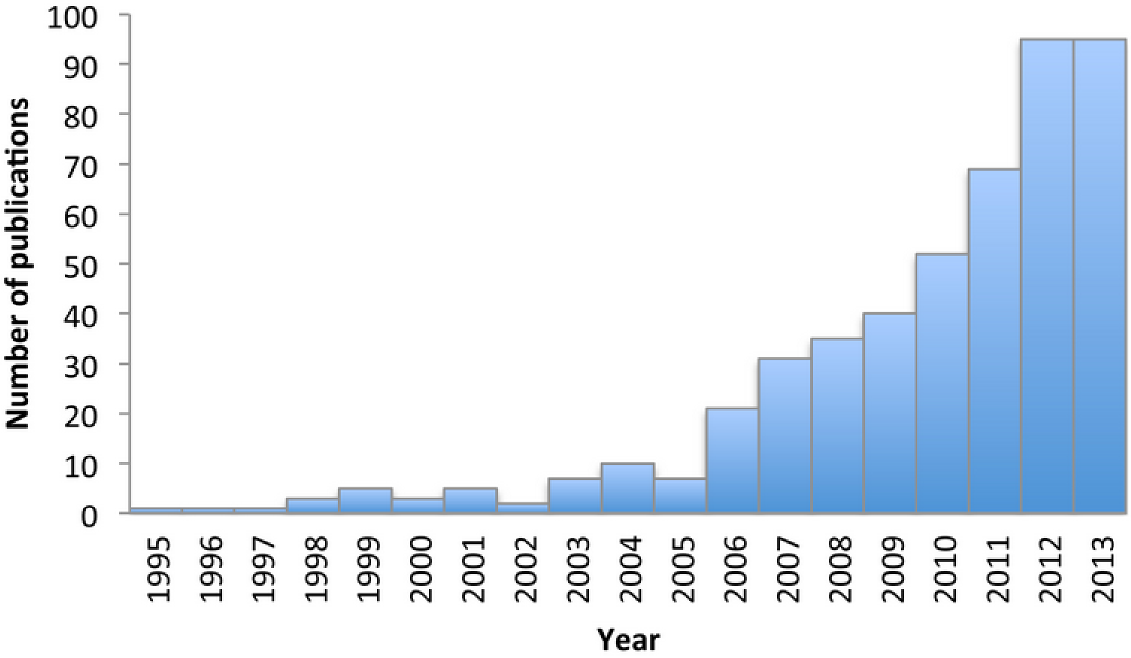

Figure 1. Trend in the number of publications containing the terms human-wildlife and conflict in the abstract, title or keywords, according to the Scopus search engine (www.scopus.com).

humans (Redpath *et al.* 2013). This means that conservation conflicts always involve people with interests in biodiversity conservation (*i. e.* conservationists), excluding therefore conflicts only involving other stakeholders.

The example of reindeer (*Rangifer tarandus*) management in northern Europe illustrates well the differences between conservation conflicts and conflicts involving other stakeholders. On the one hand, reindeer husbandry is tightly connected to the indigenous Sámi people and depends on accessibility to natural pastures, which are menaced by the intensive management of the forestry industry; *i. e.* a conflict between Sámi people and forest owners exists (Pape and Löffler 2012; Saarikoski and Raitio 2013), but this is not a conservation conflict. On the other hand, reindeer overgrazing has been considered on some occasions as synonymous with habitat degradation or even an ecological disaster, causing tensions between conservationists and Sámi people (Pape and Löffler 2012); *i. e.* a conservation conflict.

Typically, conservationists come into conflict with other stakeholders regarding the management of wildlife. On the one hand, conservationists may aim to boost the numbers of a particular species because it is endangered, emblematic and/or plays major ecological roles, but this species negatively impacts the interests of other stakeholders (*e. g.* hunters, farmers, etc), who demand that the species' abundance be reduced (Figure 2a). This would be, for example, the case of the conflicts generated by the management of large carnivores in Europe. On the other hand, conservationists may aim to reduce the abundance of a particular species, because it detrimentally affects other species/habitats, but this reduction clashes with the interests of other stakeholders (*e.g.* hunters), who promote an increase in the species' numbers (Figure 2b). In Europe, a good example of this comes from the management of some overabundant ungulates.

Wildlife impacts leading to conservation conflicts

Conservation conflicts involving wildlife emerge from "wildlife impacts", defined as circumstances where people, consciously or unconsciously, negatively impact wildlife, or alternatively where wildlife negatively impacts the well-being or livelihoods of people (Young *et al.* 2005, 2007), or biodiversity. The impacts of human activities on wildlife are well known and include poaching, poisoning, hunting, habitat degradation, fragmentation and destruction. For example, in Europe, as in other places, some populations of large carnivores have been restricted and reduced because of habitat loss, poaching and poisoning (Liberg *et al.* 2012; Silva *et al.* 2013).

The impact of wildlife on the well-being or livelihoods of people or on biodiversity is usually known as wildlife damage, and it can refer to anything wildlife do that humans dislike (Conover 2002). The most frequent types of wildlife damage are shown in Table 1. Perhaps one of the most extensive types of wildlife damage across the world is the consumption of crops by wild species (*e. g.* Delibes-Mateos *et al.* 2011; Kroos *et al.* 2012; Haney and Conover 2013). Crop damage caused by mammals is frequent across Europe, including the central and southern regions (*e. g.* Barrio *et al.* 2010; Bleier *et al.* 2012; Ficetola *et al.* 2014). On most of these occasions, ungulates and small mammals are responsible for crop damage (see examples below). Interestingly, the intensification of agriculture that has occurred in some European regions has reduced the availability of natural food sources for wildlife, forcing them to feed on crops (Barrio *et al.* 2013), and increasing the possibility that conflicts between stakeholders emerge.

On some occasions, wildlife cause damage in gardens and other human properties that are not used for subsistence purposes (Table 1). For example, in Australia northern brown bandicoots (*Isoodon macrourus*), medium-sized terrestrial marsupials, dig holes in lawns and gardens in search of food (FitzGibbon and Jones 2006). In Europe, damage caused by wildlife in gardens and other human properties is not very common, and rarely leads to conservation conflicts. Examples include

European moles (*Talpa europaea*) that form molehills in gardens and sports fields, and these are viewed as aesthetically unattractive, act as sites for weed invasions and cause soil degradation (Edwards *et al.* 1999), and herbivores that may also cause occasional damage in gardens through grazing, browsing or rooting.

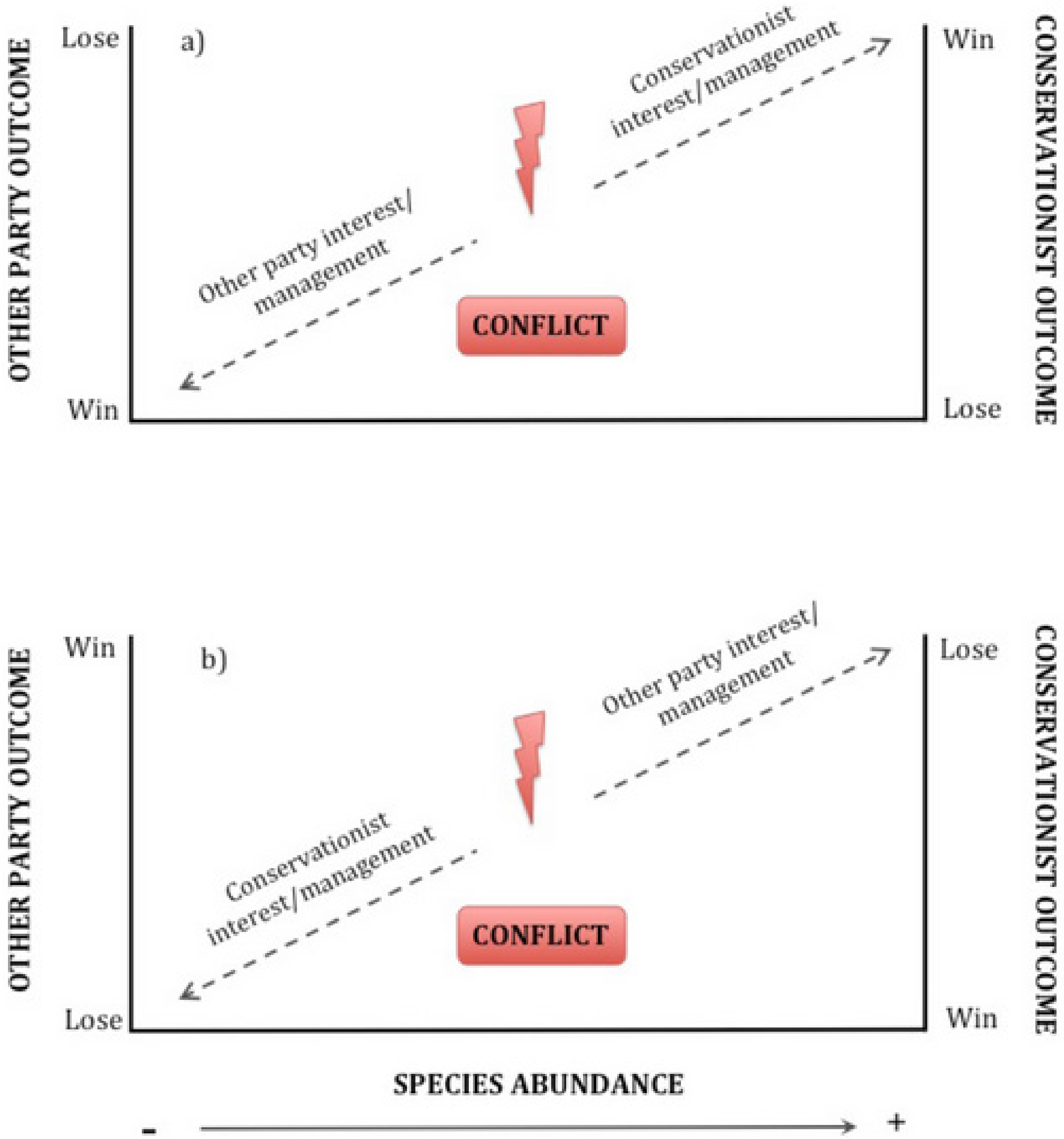

Figure 2. Two typical types of conservation conflicts involving mammals in Europe (inspired by Redpath *et al.* 2013). a) Conservationists aim to increase the numbers of a species of conservation concern (*e. g.* large predators), but this clashes with the interests of other stakeholders, who prefer reducing the species' abundance. b) The interest of conservationists is reducing the abundance of a species that negatively impacts biodiversity (*e. g.* overabundant ungulates), contrasting with the efforts made by other parties to increase the species' numbers. In both cases, conflicts emerge, because either conservationists or the other party are striving to win with little compromise shown towards other interests (see text for more details).

Wildlife can also negatively impact natural ecosystems (Coté *et al.* 2004). In this regard, damage caused by overabundant ungulates to plant diversity and vegetation structure, dynamics and composition constitutes a very good example that has been frequently recorded in diverse European regions (*e. g.* Fuller and Gill 2001; Perea *et al.* 2014). Given that the populations of ungulates have increased notably all over Europe (*e. g.* Acevedo *et al.* 2011), their damage to crops and natural ecosystems have become very common, leading to relatively frequent conservation conflicts.

Other typical examples of wildlife damage is predators' consumption of livestock, poultry, game species or fishes (Table 1), which occur almost all over the world (*e. g.* Amador-Alcalá *et al.* 2013; Li *et al.* 2013). Large carnivore depredation on livestock and big game species occurs in most European regions, particularly in eastern and northern areas (*e. g*. Odden *et al.* 2002, 2006; Kovarik *et al.* 2014). Over the last decades, populations of large carnivores have recovered in many European areas, either because of natural expansion or reintroduction programs (*e. g*. Linnell *et al.* 2009). This has brought a new source of ungulate mortality (*i. e.* depredation) in some places (*e. g.* Nowak *et al.* 2011), potentially creating new conflicts (see examples below). Also, small and medium-sized carnivores often depredate on small game species in different European areas (*e. g.* Díaz-Ruiz *et al.* 2013), and the frequent reaction of game managers is usually reducing the predators' numbers (*e. g.* Delibes-Mateos *et al.* 2013). Predator control either for hunting or conservation purposes is a common source of conflicts between stakeholders, and tensions can be common between conservationists about how these predators have to be managed. For example, some conservationists have requested reducing the numbers of pine martens (*Martes martes*) in the Cantabrian Mountains (northern Spain) as a measure to recover the populations of the endangered carpercaille (*Tetrao urogallus*), but others strongly oppose to this management as martens are legally protected. A particular case of wildlife damage caused by mammalian predators is that concerning the consumption of fishes by otters (*e. g.* Barbieri *et al.* 2012). In Europe, fish predation by Eurasian otters (*Lutra lutra*) has been recorded both in southern and central regions, where this constitutes a source of conservation conflicts (Freitas *et al.* 2007; Vacklavikova *et al.* 2011).

Table 1. Wildlife damage that may lead to conflicts between stakeholders (inspired by Peterson *et al.* 2010). In each particular case, the main damaging mammal species as well as the main stakeholders with opposite interests are shown. Types of wildlife damage are listed as a function of the frequency with which they lead to conservation conflicts in Europe (from the most common to the least).

Wildlife damage	Main damaging mammal species	Main stakeholders promoting species reduction	Main stakeholders promoting species increase/conservation
Depredation on livestock and poultry	Carnivores	Livestock producers	Conservationists
Depredation on game species	Carnivores	Hunters	Conservationists
Crop damage	Small mammals	Farmers	Conservationists
Damage to natural vegetation	Ungulates	Conservationists	Hunters
Depredation on fish species	Eurasian otter (Lutra lutra)	Fishermen	Conservationists
Kill people and disease transmission to humans	Large carnivores and ungulates	Local people	Conservationists
Damage to gardens/properties	Ungulates and small mammals	Local property owners	Conservationists
Damage to transportation infrastructures and car accidents	Ungulates and large carnivores	Governments, Local people	Conservationists
Transmission of diseases to livestock	Ungulates	Livestock producers	Hunters
Crop damage	Ungulates	Farmers	Hunters
Damage to forests	Ungulates	Forestry industry	Hunters

Many wildlife species can play a major role in the transmission of diseases to domestic animals (Table 1). For example, the existence of wildlife reservoirs complicates the control of bovine tuberculosis (bTB), an important re-emerging zoonotic disease that causes major economic losses and constrains international trade of animals and their products (Wedlock *et al.* 2002). In Europe, major problems with TB occur in areas with a high density of susceptible wild species hosts, such as the Eurasian badger (*Meles meles*) in Great Britain and Ireland, or ungulates in the Iberian Peninsula (Gortázar *et al.* 2012).

This usually causes tensions between livestock producers and other stakeholders (*e. g.* hunters who aim to increase ungulate densities), although these conflicts rarely involve conservationists (Table 1).

During the last decades, the increase in transportation infrastructures, traffic volume and traffic speed together with the increase in the numbers of some wildlife species have caused a substantial increase in wildlife-vehicle-accidents (Steiner *et al.* 2014). These not only result in high economic costs due to damage to vehicles and infrastructures, but also result in many injured and dead people every year (Table 1). In general, the most costly accidents caused by wildlife involve large-bodied animals, such as ungulates and large predators. In Europe, collisions between vehicles and wildlife species are distributed from northern to southern regions (*e. g.* Mysterud 2004; Colino-Rabanal *et al.* 2011, respectively). However, conservation conflicts rarely emerge from wildlife-vehicle-accidents, except when the species responsible for such collisions are endangered or protected.

Wildlife can also frighten, or injure, kill humans and transmit infectious agents to them (*i. e.* damage to human safety; Table 1). Wildlife attacks to human are frequent in some regions across the world (Thirgood *et al.* 2005), but at present these only occur very occasionally in Europe (*e. g.* Swenson *et al.* 1999; Linnell *et al.* 2002). The transmission of infectious agents to Europeans is more frequent, but it is not usually associated with conservation conflicts (Table 1), as host wild species are usually abundant and unprotected.

Stakeholders involved in conservation conflicts

In Europe, the main stakeholders that come into conflict with conservationists as a consequence of wildlife impacts are livestock breeders, hunters and farmers (Table 1). Other sectors are only occasionally involved in conservation conflicts or at a local scale; for example, the aforementioned conflict involving otters that depredate fisheries (Table 1).

Livestock breeding is an important economic activity throughout Europe. Thus, in 2007 the total European livestock population amounted to 136 million livestock units, of which cattle represented 47.7 %, followed by pigs (27.6 %), poultry (13.8 %) and sheep (7.8 %; http://epp.eurostat.ec.europa.eu). In many European regions, livestock populations share habitats with wildlife, which facilitates the potential for conflicts between livestock producers and conservationists. In fact, tensions between these stakeholders, for example, as consequence of livestock depredation by wildlife, are very common (Table 1).

Farming has a big influence on Europe's landscapes and ecosystems. Although farmers represent only 4.7 % of the European Union's (EU's) working populations, they manage nearly half of the EU's land area (> 170 million hectares; http://epp.eurostat.ec.europa.eu). The loss of traditional farming practices to intensive agriculture in some European regions has led to biodiversity impoverishment (e. g. Donald *et al.* 2001). However, a large number of highly valuated wildlife species and semi-natural habitats types in Europe are still dependant on continuing low-intensity agricultural practices (Bignal and McCracken 2000). In this context, conflicts can arise between conservationists and farmers about how wildlife species should be managed. For example, farmers may demand reducing the numbers of wildlife species that damage crops, whereas conservationists may promote boosting their populations (Table 1).

In Europe, hunting involves millions of people as participants and beneficiaries. It is undertaken on millions of hectares of land, and it generates millions of euros in income. Hunting is practiced across most of the European territory, and it is mostly focused on wild ungulates (*e. g.* moose *Alces alces*, wild reindeer, roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, fallow deer *Dama dama*, wild boar *Sus scrofa*), carnivores (*e. g.* brown bear *Ursus arctros*, wolf *Canis lupus*, Eurasian lynx

Lynx lynx, red fox *Vulpes vulpes*), lagomorphs (European rabbit *Oryctolagus cuniculus*; European brown hare *Lepus europaeus*, Iberian hare *L. granatensis*, mountain hare *L. timidus*), and game birds (*e. g.* capercaillie *Tetrao urogallus*, black grouse *T. tetrix*, willow grouse *Lagopus lagopus*, Rock ptarmigan *L. muta*, red-legged partridge *Alectoris rufa*, grey partridge *Perdix perdix*, pheasant *Phaisanus colchicus*, woodcock *Scolopax rusticola*, various waders, pigeons, ducks and geese). Hunting involves the killing of animals and this usually leads to tensions between different sectors of society. In particular, hunters frequently come into conflict with conservationists when, for example, species of conservation concern, such as large carnivores, are harvested or killed illegally (Table 1). These tensions also emerge when the hunt of some species is locally banned, owing to the claims of conservationists (Delibes-Mateos *et al.* 2014).

Wildlife species involved in conservation conflicts

In this section, I will provide some key examples of conservation conflicts involving mammals in Europe. Nevertheless, this does not pretend to be an exhaustive review that encompasses all the conflicts nor of all the specific issues within each particular example. The most noticeable conservation conflicts involving European mammals are perhaps those that have to do with large carnivores. The management of Europe's large carnivores is controversial and is increasingly a cause of debate. On the one hand, these species are flagship-species for European nature conservation. On the other hand, they can negatively impact livestock or other human interests (Table 1). In this regard, the conflict between livestock breeders and conservationists about the management of wolf populations is likely one of the best examples. It is estimated that there are a total of some 10,000 wolves spread across Europe, with the largest populations in the eastern regions (Carpathian and Dinaric-Balkan populations) and in northwestern Iberia (Silva *et al.* 2013). One of the biggest threats faced by Europe's wolves is illegal killing as a result of human antipathy of wolf presence. In Sweden, for example, illegal killing accounted for approximately half of the total mortality of wolves, and more than two-thirds of the total illegal killing remained undetected by conventional methods (Liberg *et al.* 2012). Both illegal killing and support for illegal killing and hunting violators are based on anger and fear for children and domestic animals, as well as frustration toward the authorities and the lack of proper management actions (Pohja-Mykrä and Kurki 2014). Illegal killing undermines the strong conservation efforts directed at European wolves (Silva *et al.* 2013), and therefore causes frequent tensions between stakeholders (Gangaas *et al.* 2013).

In addition, wolves are a game species in several European countries, and conflicts between hunters and conservationists regarding the management of wolves are common. For example, the Spanish government has recently requested the EU to approve wolf hunting south of the Douro River, something that is currently prohibited. The Spanish conservation community has immediately reacted and in only a few days collected through social networks the support of > 100,000 people who oppose this petition. Finally, wolf populations have expanded widely across Europe, and wolves have reappeared in areas where they became extinct long ago (Silva *et al.* 2013), increasing the possibility of conflicts not only because people are no longer accustomed to living alongside wolves, but also because the wolves' attacks on livestock may have increased in some areas. In Slovenia, for example, the number of small livestock (sheep and goats) killed by wolves increased from 218 in 2005 to 1931 in 2011 (van Liere *et al.* 2013).

The brown bear is one of the most emblematic large carnivores in Europe, where its number is estimated to have risen to 17,000 individuals, distributed across 10 populations (Silva *et al.* 2013). The Carpathian population in Eastern Europe is the largest, with more than 7,000 individuals, and the Alpine, Pyrenean and central Apennine populations are the smallest, with a few dozen individuals each. The bear is omnivorous and its diet consists of mostly nuts, fruits and many types of vegetables, as well as meat. Bears can damage crops (*e. g.* fruit trees) and depredate livestock (*e. g.* Meryens and Promberger 2000; Knarrum *et al.* 2006), causing certain animosity towards them in some areas (Rigg *et al.* 2011). This low acceptance of bear presence can lead to illegal killing, which is one of the main threats for European bear populations (*e. g.* Kaczensky *et al.* 2011), in addition to habitat loss and fragmentation. Nevertheless, sometimes bears are non-target victims of illegal trapping or poisoning that are directed to the killing of other species like wolves. In addition, disturbances caused by hunting and other recreational activities (hiking, wildlife watching, etc.) may also pose a risk for bear conservation in some European populations (Ordiz *et al.* 2012), hence causing conflicts between conservationists and other stakeholders.

The Eurasian lynx is distributed in northern, eastern and central Europe. It has been reintroduced to several of these areas (Linnell *et al.* 2009), particularly in central Europe, where it became extinct in the past. The latest estimate for the total number of lynx in Europe is 9,000 (Silva *et al.* 2013). It mainly occurs in forested areas and usually at low densities. This means that on many occasions people rarely see or interact with lynx. For example, in the Republic of Macedonia the level of interaction with this species is very low, and the lynx does not appear to be a species associated with conflicts (Lescureux *et al.* 2011). However, lynx frequently prey on game ungulates, such as roe deer, and livestock (*e. g.* Odden *et al.* 2002; Gervasi *et al.* 2014), causing a low acceptance of their presence in some areas, which results in persecution and illegal killing (Andrén *et al.* 2006). This causes conflicts between conservationists and hunters and livestock breeders, particularly in areas where lynx populations are recovering and expanding (*e. g.* Liukkonen *et al.* 2009; Breitenmoser *et al.* 2010). In addition, the legal killing of Eurasian lynx as a game species is often controversial, as conservationists feel that too many are being killed, and hunters and sheep farmers have the opposite feeling (Linnell *et al.* 2010).

The Iberian lynx (*Lynx pardinus*) is likely the most endangered felid in the world. Currently, less than 350 lynx persist in the Iberian Peninsula. During the last decades, huge conservation efforts have been conducted to recover Iberian lynx populations, and large sums of money have been invested to achieve this goal (Simón *et al.* 2012). The Iberian lynx diet is almost exclusively based on European rabbits (Ferreira and Delibes-Mateos 2010), a very important game species in the lynx distribution area. Most Iberian lynx occur in private areas managed for hunting (Simón *et al.* 2012), and poaching is the main cause of lynx mortality in Sierra Morena (López *et al.* 2014), the largest lynx population. This causes important tensions between hunters and conservationists. In addition, conflicts with livestock breeders may also emerge as a consequence of occasional lynx depredation on lambs (Garrote *et al.* 2013). Furthermore, some sectors of society demand the development of new infrastructures (*e. g.* motorways in lynx distribution areas), coming into conflict with conservationists, as road-killing is one of the main causes of mortality of Iberian lynx (López *et al.* 2014).

Another conflict that takes place in southern Europe is that concerning the management of European rabbits. Over the past decades, European rabbit populations have declined sharply on the Iberian Peninsula (Delibes-Mateos *et al.* 2009), their native range. The recovery of rabbit populations is one of the biggest challenges for Iberian conservationists, as rabbits play major ecological roles in Iberian Mediterranean ecosystems (reviewed in Delibes-Mateos *et al.* 2008), including as mentioned serving as prey for endangered predators like the Iberian lynx. On the other hand, the rabbit is also a very important game species in the Iberian Peninsula. In Spain, for example, more than 4 million rabbits are killed annually by hunters. Although hunters employ a diverse array of game management measures to allow rabbit numbers to increase, poorly managed and excessive hunting pressure has reduced their numbers in some areas, leading to clashes with conservationists (Delibes-Mateos *et al.* 2011, 2014). In addition, farmers promote rabbit control and sometimes eradicate them in areas where valuable crops are damaged (Ríos-

Saldaña *et al.* 2013). Farmers' interests are therefore strongly opposed to those of conservationists and hunters, causing frequent conflicts (Delibes-Mateos *et al.* 2011, 2014).

Other European small mammals are also often involved in conservation conflicts. In some European countries, for example, anticoagulant rodenticides (*i. e.* bromadiolone) are sometimes applied intensively to control rodents that cause crop damage, such as common voles (*Microtus arvalis*) and water voles (*Arvicola terrestris*) in Spain and France, respectively (Olea *et al.* 2009; Coeurdassier *et al.* 2014). Anticoagulant rodenticides invariably cause secondary poisoning of non-target species, and bromadiolone particularly is known to affect predators and scavengers (Berny 2007). In France, for example, some raptors of conservation concern like red kites (*Milvus milvus*) and common buzzards (*Buteo buteo*) were poisoned by bromadiolone after a recent vole control campaign (Coeurdassier *et al.* 2014). Similarly, in Spain other protected bird species like the great bustard (*Otis tarda*) were affected by rodenticide treatments (Olea *et al.* 2009). The high level of poisoning of wildlife that follows such treatments over large areas is something that concerns conservationists and leads to frequent tensions between these and farmers (Ferreira and Delibes-Mateos 2012).

Land-use change and game management have favoured an increasing population of wild ungulates in many regions of Europe (Acevedo *et al.* 2011). Temperate European communities may have been currently supporting the highest densities of ungulates ever recorded. Overabundant ungulates usually cause detrimental effects to natural ecosystems. For example, high red deer densities (> 30 individuals/km^2) are causing biotic homogenization of plant communities in Mediterranean scrublands within the Iberian Peninsula and are forcing vegetation to return to earlier successional stages (Perea *et al.* 2014). Similar impacts have been reported for several ungulate species in northern Europe (*e. g.* Austin *et al.* 2013), and increasingly lead to conflicts between conservationists and hunters (Smart *et al.* 2008; MacMillan and Phillip 2010). Thus, while conservation groups frequently request shooting more ungulates (Putman *et al.* 2005), hunters are usually less supportive (MacMillan 2004). Nevertheless, conflicts regarding the management of overabundant ungulates seem to be still more acute when these negatively impact the interests of farmers or the forestry industry (*e. g.* Ezebilo *et al.* 2012).

Conclusion

1) Nearly all mammal species involved in conservation conflicts in Europe are not threatened globally according to the International Union for Conservation of Nature (IUCN 2014). The main exception is the critically endangered Iberian lynx. From this perspective, mitigating conflicts associated with the Iberian lynx management is a big challenge for conservation in Europe. Other mammal species frequently associated with conservation conflicts are mostly classified as "Least Concern", excepting European rabbit and Eurasian otter, which are listed as "Near Threatened". Recovering the declining populations of the European rabbit in the Iberian Peninsula should be still a major concern for European conservationists (Delibes-Mateos *et al.* 2014).

2) Although the global conservation status of most conflictive European mammals is rather good, some of their populations are threatened. For example, the European hamster (*Cricetus cricetus*), which is labelled as Least Concern in the IUCN red list (IUCN 2014), is currently highly threatened in Alsace (France). The main causes of hamster's decline are its persecution by farmers as agricultural pest several decades ago, and changes in agriculture and fragmentation caused by the construction of new infrastructures in the second half of the 20th century. Conservation conflicts in these places are usually intense (*e. g.* Amores 2011), as conflicts tend to be greatest where the conservation of biodiversity and/or the livelihood of the other stakeholders are perceived to be most threatened (Marshall *et al.* 2007). Therefore, important efforts are needed to mitigate conservation conflicts in these areas.

3) Conflicts involving European mammals may also affect other non-target species and ecosystem processes, thus impacting biodiversity. On the one hand, the intensive management aimed at reducing the numbers of some mammal species can kill non-target species, including some of conservation concern (Coeurdassier *et al.* 2014). On the other hand, the reduction in numbers of some mammal species of conservation concern as a consequence of other stakeholders' management may cause important cascading effects on other species and ecosystem processes (Delibes-Mateos *et al.* 2011).

4) Conflicts between people regarding how wildlife should be managed are not frequently addressed in scientific publications (Peterson *et al.* 2010). In addition, although understanding conservation conflicts requires integrating knowledge generated by many disciplines, including natural sciences, social sciences, and humanities (Redpath *et al.* 2013), this rarely occurs (Dickman 2010). From this perspective, promoting the investigation of conservation conflicts that incorporates multidisciplinary approaches is essential for the conservation of mammal species in Europe.

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Resumen

Los conflictos asociados a la gestión de la fauna se han incrementado en tiempos recientes. Los conflictos de conservación ocurren cuando dos o más partes con opiniones fuertemente enfrentadas chocan sobre objetivos de conservación, y cuando una parte mantiene firme sus intereses en detrimento de los de otra. Normalmente los conflictos de conservación surgen de los impactos sobre o de la fauna, definidos como circunstancias donde la gente, consciente o inconscientemente, impacta negativamente en la fauna, o cuando ésta causa efectos negativos en el bienestar o sustento de las personas o en la biodiversidad. En Europa los conflictos de conservación más frecuentes son probablemente aquellos relacionados con la gestión de los depredadores. Por ejemplo, los grandes carnívoros depredan sobre el ganado o las especies de caza, pero al mismo tiempo son especies bandera para la conservación. Por lo tanto, los conflictos sobre cómo se deberían de gestionar estas especies son habituales. La gestión de los ungulados que impactan negativamente en la vegetación natural así como la de los pequeños mamíferos que causan daños a los cultivos también provoca frecuentes enfrentamientos en Europa. El estado global de conservación de los mamíferos europeos conflictivos es bastante bueno. Sin embargo, algunas de sus poblaciones están amenazadas, al menos en parte por la caza ilegal y el furtivismo. Por lo tanto, es necesario realizar esfuerzos importantes para mitigar estos conflictos en estas áreas. Además, se debería de promover la investigación multidisciplinar de los conflictos de conservación para conocerlos mejor y en última instancia para mitigarlos.

Palabras clave: Caza, control de depredadores, daños a cultivos, daños al ganado, furtivismo, gestión de fauna, grandes carnívoros, pequeños mamíferos, sobreabundancia de ungulados

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Manejo y conservación de los mamíferos terrestres de Japón: prácticas y sistema organizacional

Conservation and management of terrestrial mammals in Japan: its organizational system and practices

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Introduction: One hundred and one native terrestrial mammalian species, excluding Sirenia, Cetacea, Phocidae, and Otariidae, inhabit or inhabited Japan, and 51.5 % of them are endemic, most being forest dwellers. Four species, the wolf, the Okinawa flying fox, the Bonin Pipistrelle, and the Japanese river otter went extinct during the modern age. The relatively small extinction rate in Japan is probably because forest destruction has been limited. About two thirds of Japanese lands are still covered by forests (25.10/37.79 million ha; 66.4 % as of 2011 by Forestry Agency of Japanese Government). However, the number of species that are ranked high in conservation status is not small; 5, 15, and 8 species are ranked "Vulnerable" (VU), "Endangered" (EN), and "Critically endangered" (CR), respectively. The total number of species ranked in these three categories is 28, and the percentage (28.9 % = 28/97) is higher than the world standard. This situation may be caused by extensive construction of artificial forests from 1950's to 1970's, during which many natural forests were cut and transformed to man-made forests.

Discussion and Conclusions: The proportion of natural forests was reduced to about 40 % of the total area of forests by 2013. The most influential laws for wildlife conservation and management in Japan are the "Act on the Conservation of Endangered Species of Wild Fauna and Flora" and "Wildlife Protection and Proper Hunting Act". The Amami rabbit (*Pentalagus furnessi*), the Bonin flying fox (*Pteropus pselaphon*), a subspecies of Ryukyu flying fox (*Pteropus dasymallus daitoensis*), and two subspecies of the leopard cat (*Prionailurus bengalensis iriomotensis* and *P. b. euptilurus*) are conserved under the "Act on Conservation of Endangered Species of Wild Fauna and Flora", whereas the conservation of many endemic terrestrial species that are ranked high in conservation status are not implemented in Japanese laws. Recently many management practices have been developed for overabundant populations of the sika deer (*Cervus nippon*) and the wild boar (*Sus scrofa*) under "Wildlife Protection and Proper Hunting Act".

Key words: Amami rabbit, extinction rate, flying fox, forests, Leopard cat, management, Sika deer, wild boar, wildlife legislation

Introduction

Japan is a forest rich country. Therefore, most terrestrial mammals in Japan are forest dwellers (Ohdachi *et al.* 2009). One hundred and one native mammalian species, excluding Sirenia, Cetacea, Phocidae, and Otariidae, inhabit or inhabited Japan, and 51.5 % of them are endemic on the bases of description by Ohdachi *et al.* (2009; Figure 1a). Of the 101 terrestrial species, the wolf (*Canis lupus*), the Okinawa flying fox (*Pteropus loochoensis*), the Sturdee's pipistrelle (*Pipistrellus sturdeei*), and the Japanese river otter (*Lutra lutra*) went extinct during the modern age. The extinction rate in Japan is small (4.0 %) in comparison with the rate in UK (40.5 % = 17/42 species), although both are similar sized island countries and have been highly industrialized. This relatively low rate is probably because forest destruction has been limited in Japan. About two thirds of Japanese lands are still covered by forests (25.10/37.79 million ha; 66.4 % as of 2011 according to the Forestry Agency of Japanese Government 2013), while 90 % of forests had been lost over the past 5,000 years in UK (UK Clearing House Mechanism for Biodiversity). The better situation of forests in Japan may be caused by the relatively strict forest management in the Edo era (1603-1868), the later start of industrialization (from the middle of 19th century), steep terrain preventing logging, and favorable climate for forest regeneration (see Diamond 2005 for details).

Recent status of the conservation system. Although the extinction rate is relatively small, the recent population status of Japanese mammals suggests that the sustainability of many species is not assured. The number of species that are ranked high in conservation status is not small; 5, 15, and 8 species are ranked "Vulnerable" (VU), "Endangered" (EN), and "Critically endangered" (CR), respectively, on the basis of the list made by the Mammal Society of Japan (Figure 1b). The total number of species ranked into these three categories is 28, which is 28.9 % of all extant terrestrial species (97 species). This is higher than the average for mammals in the world as a whole (24.0 % = 1103/4600; IUCN). Japan, the proportion of highly ranked species is high among the Chiroptera (42.9 %) and Carnivora (25.0 %). This situation may be caused by extensive construction of artificial forests from 1950s to 1970s, during which many natural forests were cut and transformed into man-made monocultural forests. By 2013, the proportion of natural forests had been reduced to about 40 % of the total area of forests (the Forestry Agency of Japanese Government 2013). In addition to the changes in forest quality, human disturbance to caves and other roost sites may be having some impacts on Chiroptera populations.

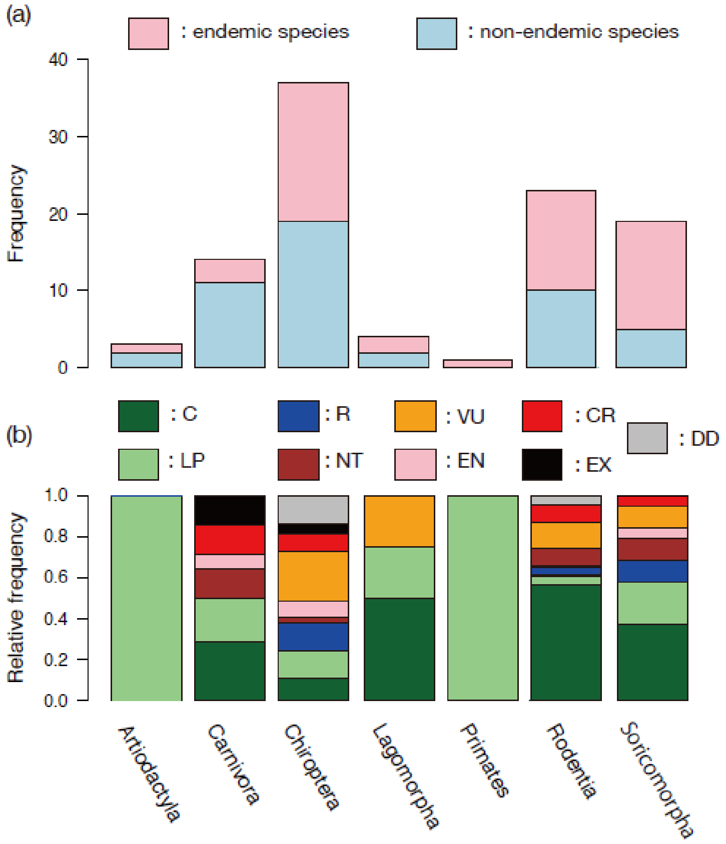

Figure 1. (a) The number of native terrestrial mammalian species in Japan arranged in seven taxonomic orders. (b) The relative frequency of species in each conservation status; C: common; LP: threatened local population; R: rare; NT: nearly threatened; VU: vulnerable; EN: endangered; CR: critically endangered; EX: extinct; DD: data deficient.

The Japanese government has developed legal systems in order to stem the further reduction of biodiversity (Figure 2). Although the system consists of 9 laws, the most influential laws for wildlife conservation and management are "Act on the Conservation of Endangered Species of Wild Fauna and Flora" and "Wildlife Protection and Proper Hunting Act."

"Act on the Conservation of Endangered Species of Wild Fauna and Flora"

Both Japanese and English versions can be accessed through the following website:

http://www.japaneselawtranslation.go.jp. This act is aimed at ensuring the conservation of endangered species of wild fauna and flora, and requests the national government to monitor the status of wild fauna and flora species as well as to formulate and implement comprehensive measures for the conservation of endangered species. Local governments have also responsibility to formulate and implement measures for their conservation. This endangered species legislation is designated by Cabinet Order, and prohibits in principle the taking, transferring, or displaying of species so designated. The Minister of the Ministry of Environment (MOE) may designate, as "natural habitat protection area", the habitat of particular species and the area that needs to be protected. It also establishes a program for the rehabilitation of natural habitats and maintenance of viable populations. However, when applying this Act, ownership and any other property rights must be respected.

Figure 2. The structure of Japanese laws on biodiversity. Basic Act defines the fundamental policy of the Japanese government for conserving biodiversity. Practical policies and strategies are described in the 9 specific acts. Asterisks show the Acts that are highlighted in this study.

This act has been criticized by specialists at least for the following two points (The Nature Conservation Society of Japan 2010):

1. Since Endangered Species are designated by Cabinet Order without hearing the opinions of specialists, scientific priorities may not be sufficiently considered. For instance, although the Amami rabbit (*Pentalagus furnessi*), the Bonin flying fox (*Pteropus pselaphon*), a subspecies of Ryukyu flying fox (*Pteropus dasymallus daitoensis*), and two subspecies of the leopard cat (*Prionailurus bengalensis iriomotensis* and *P. b. euptilurus*) are designated as Endangered Species

under this act, 24 other mammalian species ranked VU, EN or CR are still not being adequately considered for endangered status. It is worse still that 20 of the 24 species are endemic to Japan (Table 1), and arguably these endemics should be given the highest conservation priority in order to support conserving biodiversity on a global level.

Table 1. List of endemic terrestrial species in Japan for which conservation status is ranked [VU: vulnerable], [EN: endangered], [CR: critically endangered], or [DD: data deficient].

Order	Family	Species	English name	Status
Carnivora				
	Mustelidae			
		Martes melampus (Wagner, 1840)	Japanese marten	VU
Chiroptera				
	Rhinolophidae			
		Rhinolophus pumilus Andersen, 1905	Okinawa Little Horseshoe Bat	CR
		Rhinolophus perditus Andersen, 1918	Yaeyama Little Horseshoe Bat	EN
	Vespertilionidae			
		Myotis yanbarensis Maeda and Matsumura, 1998	Yanbaru Whiskered Bat	CR
		Myotis pruinosus Yoshiyuki, 1971	Blackish Whiskered Bat	EN
		Pipistrellus endoi Imaizumi, 1959	Endo's Pipistrelle	EN
		Eptesicus japonensis Imaizumi, 1953	Japanese Northern Bat	EN
		Miniopterus fuscus Bonhote, 1902	East-Asian Little Bent-winged bat	EN
		Murina ryukyuana Maeda and Matsumura, 1998	Ryukyu Tube-nosed Bat	EN
		Nyctalus furvus Imaizumi and Yoshiyuki, 1968	Japanese Little Noctule	VU
		Murina tenebrosa Yoshiyuki, 1970	Tsushima Tube-nosed Bat	DD
	Pteropodidae			
		Pteropus pselaphon Layard, 1829*	Bonin Flying Fox	CR
Molossidae				
		Tadarida latouchei Thomas, 1920	Oriental Little Free-tailed Bat	DD
	Hipposideridae			
		Hipposideros turpis Bangs, 1901	Bang's Leaf-nosed Bat	EN
Lagomorpha				
	Leporidae			
		Pentalagus furnessi (Stone, 1900)*	Amami Rabbit	EN
Rodentia				
	Muridae			
		Diplothrix legata (Thomas, 1906)	Ryukyu Long-furred Rat	EN
		Tokudaia muenninki (Johnson, 1946)	Okinawa Spiny Rat	CR
		Tokudaia osimensis (Abe, 1933)	Amami Spiny Rat	EN
		Tokduaia tokunoshimensis Endo and Tsuchiya, 2006	Tokunoshima Spiny Rat	EN
Soricomorpha				
	Talpidae			
		Mogera uchidai (Abe, Shiraishi and Arai, 1991)	Senkaku Mole	CR
		Mogera etigo Yoshiyuki and Imaizumi, 1991	Echigo Mole	EN
	Soricidae			
		Crocidura orii Kuroda, 1924	Orii's Shrew	EN

2. Since ownership and other property rights must be respected, the Minister may hesitate to establish natural habitat protection areas. Even the above four Endangered Species have no natural habitat protection areas. Furthermore data on two endemic species are still too deficient to consider their conservation status, although the national government has a responsibility to monitor them.

"Wildlife Protection and Proper Hunting Act". The Japanese version is published in on the following website: http://law.e-gov.go.jp/htmldata/H14/H14HO088.html. This act is aimed at ensuring wildlife protection and proper hunting in order to contribute to maintaining biodiversity, conserving living environments, and developing agriculture, forestry, and fisheries. This act targets wild mammals and birds. In addition to various regulations for hunting and taking of wildlife, this act requests the national and local governments to formulate and implement wildlife protection project plans. Under this act a local government may establish a "Specified Wildlife Conservation and Management Plan" to manage a local population which is either overabundant or vulnerable. The local government can be allowed to relax the regulation of hunting and other taking of animals. Many local governments are keen to control local populations of sika deer or wild boars which damage agricultural products and/or forests (see a later section for details).

In addition, Japanese animals and plants can be conserved as "Natural monuments" under the "Act on Protection of Cultural Properties". Nine species and 5 subspecies of Japanese mammals are designated as "Natural monuments" (Table 2). However, the effects of this act are limited, because its purpose is to maintain the situation of the "Natural monument". The act does not request national or local governments to take conservation actions so as to improve the situation for wildlife.

Tabla 2. List of Japanese native terrestrial mammalian species or subspecies that are designated as "Natural monument". Local populations designated as "Natural monument" are not listed, because their conservation status is unclear. Abbreviations of conservation status are as follows: C: common; LP: threatened local population; R: rare; NT: nearly threatened; VU: vulnerable; EN: endangered; CR: critically endangered; EX: extinct; DD: data deficient.

	Latin name	*English name*	Conservation status	Endemism level
Natural monument (special)	*Capricornis crispus* (Temminck, 1845)	Japanese serow	LP	species
	Lutra lutra (Linnaemus, 1758)	River otter	EX	not endemic
	Prionailurus bengalensis iriomotensis (Imaizumi, 1967)	Iriomote cat	CR	subspecies
	Pentalagus furnessi (Stone, 1900)	Amami rabbit	EN	genus
Natural monument	*Glirulus japonicus* (Schinz, 1845)	Japanese dormouse	NT	species
	Diplothrix legata (Thomas, 1906)	Ryukyu long-furred rat	EN	genus
	Tokudaia muenninki (Johnson, 1946)	Okinawa spiny rat	CR	genus
	Tokudaia osimensis (Abe, 1933)	Amami spiny rat	EN	genus
	Tokduaia tokunoshimensis Endo and Tsuchiya, 2006	Tokunoshima spiny rat	EN	genus
	Prionailurus bengalensis euptilurus (Elliot, 1871)	Tsushima leopard cat	CR	subspecies
	Martes melampus tsuensis (Thomas, 1897)	Tsushima marten	VU	subspecies
	Pteropus dasymallus dasymallus Temminck, 1825	Erabu flying fox	CR	subspecies
	Pteropus dasymallus daitoensis Kuroda, 1921	Daito flying fox	CR	subspecies

Conservation of endangered mammals

The Amami rabbit Pentalagus furnessi (Stone, 1900)

The Amami rabbit is a primitive, short-eared rabbit which is endemic to Japan and that has evolved in an insular environment without native mammalian predators (Figure 3; Yamada and Cervantes 2005; Yamada 2008, 2009). It is distributed only on two small islands (Amami-ohshima Isl. and Toku-no-Shima Island) in Kagoshima Prefecture located in southern Japan. Using fecal pellet counts and resident surveys, the number of rabbits is estimated at 2000 to 4800 on Amami-ohshima Isl. in 2003 and 100 to 200 on Toku-no-Shima Island in 2004 (Sugimura and Yamada 2004). The size of its distributional range, as estimated by fecal pellet counts during 1992 to 1994, is 370.28 km^2 (52 % of the Island) on Amami-ohshima Isl. and 32.97 km^2 (13 %) on Tokuno-shima Island. This represents a 20 to 40 % decline in the area inhabited on Amami-ohshima Island in 1992 to 1994 compared to that estimated in 1974 and 1977 (Yamada 2009). In 1921, the Japanese government assigned the Amami rabbit to "natural monument" status which prevented it from being hunted. Then in 1963, it was changed to a "special natural monument" which prevented it from being hunted and trapped, as well. MOE designated the Amami rabbit as a National Endangered Species in 2004.

Figure 3. The Amami rabbit *Pentalagus furnessi* (Stone, 1900) on Amami-ohshima Island. (Photo by H. Katsu).

The Amami rabbit prefers a habitat of both mature and young forests, which provide food, nest sites and shelters. Habitat destruction, such as forest clearing for commercial logging, agricultural development, and residential areas, is the most detrimental activity for rabbits. Hunting and trapping were also causes of decline in their numbers. Furthermore, invasive alien predators, the small Indian mongoose (*Herpestes auropunctatus*), together with feral dogs and cats, have seriously damaged the rabbit population on Amami-ohshima Island. The mongoose was released onto this island in 1979. They were expected to control the population of a local venomous snake (*Protobothrops flavoviridis*), but the control program was in vain. They did not show any predation effect on the snake, while they have made several negative impacts on native species, especially on Amami rabbits (Yamada *et al.* 2009).

Suggested conservation work includes habitat restoration and predator population control.

A new program of mongoose eradication was restarted in 2005 on Amami-ohshima Island under the "Invasive Alien Species Law." The subsequent decrease of the mongoose population and the recovery of the Amami rabbit population are recently recognized (Fukasawa *et al.* 2013; Watari *et al.* 2013). Predation by feral cats and road kills are the next most important issues, and habitat restoration and the connection of isolated habitats should also be considered. Restricting logging would help to keep more forest available for the rabbits. However, we cannot legally stop the logging in the rabbit habitats for their conservation, because MOE does not yet designate any area on Amami-ohshima Island and Toku-no-Shima Island as "natural habitat protection area" under the "Act on Conservation of Endangered Species of Wild Fauna and Flora." Since both islands are a candidate for designation of an Amami and Ryukyu World Natural Heritage Site, a wise use of forest and conservation plan for the rabbits' habitats is under discussion as a most urgent issue.

*The leopard cat (*Prionailurus bengalensis iriomotensis *and* P. b. euptilurus*)*

The leopard cat (*Prionailurus bengalensis*) has the largest distribution among the small cats in Asia, ranging from Siberia, China, Korea, Japan, southeast Asia to Indonesia and is divided into ten or more subspecies. Two subspecies of this cat occur on two southern islands of Japan; the Iriomote cat *Prionailurus bengalensis iriomotensis* (Imaizumi, 1967) on Iriomotejima Island (*ca.* 284 km^2) and the Tsushima leopard cat *P. b. euptilurus* (Elliot 1871) on Tsushima Islands (*ca.* 710 km^2 in total). Both are small-sized felids with body weights of 4-4.5 kg for males and 3-3.5 kg for females.

The Iriomote cat is strictly endemic to Iriomotejima Island in the southern part of the Ryukyu Archipelago (Figure 4). Within the Japanese territory, the Tsushima leopard cat occurs only on Tsushima Islands. Both cats are listed as Critically Endangered in the Red List of the MOE (2012), and the Iriomote cat is listed as a Critically Endangered Subspecies in the Red List of IUCN (2008). The Iriomote cat was designated as a Special Natural Monument (1977) and as a National Endangered Species (1994). The Tsushima leopard cat was also designated as a Natural Monument (1971) and a National Endangered Species (1994).

Iriomote cat numbers have been estimated as 83-109 in 1984 and 99-110 in 1994. Although no clear tendency of decrease or increase was recognized (Ministry of the Environment of Japan 1985; Japan Wildlife Research Center 1994), the survey in 2005-2008 suggested that the population in the coastal lowland showed a decrease of 8-9 % (University of the Ryukyus 2008). The Tsushima leopard cat was reported to inhabit all of the Ryukyu Islands with a population of 200 to 300 until the 1970's (Yamaguchi and Urata 1976), although details were not clear. Recently the population size was estimated at 98-142 in 1988, 92-129 in 1997 and 83-115 in 2005 (Japan Wildlife Research Center 1988; Ministry of the Environment and Nagasaki Prefecture 1997, Japan Wildlife Research Center 2005). The population is declining at the rate of about 10 % every 10 years (Japan Wild life Research Center, 2005).

Habitat loss (deforestation) and road kills are major threats for these two subspecies (Izawa *et al.* 2009). A large part of both islands are covered with forests. The large area of inner mountainous forests on Iriomotejima Island is protected and managed as National Forest and National Park by the national government of Japan. However, in the northern coastal lowlands of the island deforestation through land conversion for agriculture, construction of roads and tourist facilities, and the loss of the forests through road widening have all occurred. Forest protection and management are relatively weak on Tsushima; one-third of the forests are artificial plantations and most forests are private property without any regulation against deforestation.

Frequent road kills directly affect the cat populations on each island. Traffic accidents killed 34 cats from 2000 to 2013 (2.4 cats/year) on Iriomotejima Island and 59 cats from 2000 to 2013 (4.2 cats/year) on Tsushima Island. The recent increase of tourists in Iriomotejima Island has resulted in an increase of traffic volume. Moreover, road widening may cause higher driving speeds on both islands. Considering the small population sizes (*ca.* 100 each), the mortality caused by road kills should not be ignored.

Other threats are derived from invasive animals: predation by dogs, competition with feral cats (Watanabe *et al.* 2003), and the spread of diseases such as Feline immunodeficiency virus from domestic cats (Nishimura *et al.* 1999).

Figure 4. An Iriomote cat *Prionailurus bengalensis iriomotensis* (Imaizumi, 1967) walking in the subtropical forest of Iriomotejima Island. This photo was taken by the Laboratory of Mammal Ecology, University of the Ryukyus.

A recent and future possible threat for the Iriomote cat is the increase in tourists and changes of tourism style. The style of tourism has changed from large groups using a coach to "eco-tour." Now more tourists want to enter the island interior by using a canoe and enjoy bush-walking. These impacts on interior mountainous forests and the ensuing disturbance to wild animals are severe enough to cause concern (Japan Wild life Research Center 2005; University of the Ryukyus 2008).

Conservation activities are conducted by the national and local governments and NGO's, etc. (Izawa *et al.* 2009). Since hunting is prohibited for the felids and poaching is rare in Japan, conservation issues focus on habitat improvement including elimination of invasive species and traffic peril. Although the government has designated some part of the cat's habitat as nature reserves or a national park, the size of these areas is insufficient. The Wildlife Conservation Center of MOE (WCC) on the Iriomotejima Isl. and the Tsushima Islands plays an important role in conservation of the cats. The Forestry Agency of the Japanese government also has conducted a photo-trapping program to monitor the cat population in the national forest since 1993.

Measures to prevent road kills started on Iriomotejima Isl. by a local government and the Iriomote WCC. About 100 underpasses for cats were constructed along a road of about 50 km. Iriomote cats and other animals (including prey animals of Iriomote cats) were confirmed to use them by employing camera traps (Okamura *et al.* 2003; University of the Ryukyus, 2008). Road signs and speed bumps were provided in order to catch driver's attention and reduce driving speed. Some educational programs have also been done for drivers.

Measures to reduce the number of feral cats have been done by NGO's on the Iriomotejima Island. The program by a NGO consists of veterinarians trapping feral cats, removing them from the island, keeping them in a shelter, and seeking a new owner. This program is effective in reducing the number of feral cats. The NGO carries out an educational program for cat owners and promotes breeding control and vaccination. Although a similar program is conducted on the Tsushima Islands, it is more difficult to reduce the number of feral cats because of larger area and more abundant feral and house cats.

The population of Iriomote cats is thought to be almost stable. However, habitat conditions along the coastal area have been degraded by the growth of tourism and road development in the last ten years, and further degradation is anticipated. Measures to reduce road kills, a guideline for ecotourism, and lowland habitat management are required. Similar conservation activities have been conducted for the populations of Tsushima leopard cats. However, more effort is required for them in comparison with the Iriomote population.

Flying foxes. Two species of Pteropodidae occur in Japan. These are both medium-sized *Pteropus* species that occur at the northern limit of Pteropodidae distribution. One is the Bonin flying fox (*Pteropus pselaphon* Layard 1829) which is endemic to the Ogasawara Islands (5 islands) in southern Japan (Yoshiyuki 1989; Inaba *et al.* 2002; Suzuki and Inaba 2010). The other is the Ryukyu flying fox (*Pteropus dasymallus*) ranging from the Ryukyu Archipelago to two small islands in Taiwan, and possibly to a few northern Philippine islands. The Ryukyu flying fox is divided into four subspecies (Yoshiyuki 1989; Kinjo and Nakamoto 2009). Two of them are common, but the other two are endangered. Of most concern is the Daito flying fox, a subspecies (*Pteropus dasymallus daitoensis* Kuroda 1921; Figure 5) that is endemic on the Daito Islands (2 small islands).

The Bonin flying fox is listed as Endangered and the Daito flying fox as Critically Endangered in the Red List of MOE (2012). In addition, the Bonin flying fox is listed as Critically Endangered and the Ryukyu flying fox as Near Threatened in the Red List of IUCN (2008). The Bonin flying fox was designated as a Natural Monument (1969) and as a National Endangered Species (2009). The Daito flying fox was designated as a Natural Monument (1973) and a National Endangered Species (2004).

Little information is available on the population dynamics of these flying foxes, partly because these nocturnal and volant species are very hard to survey. The Bonin flying fox on Chichijima Island (the largest island within its distribution) was considered to be extinct in the 1970's, but they recolonized in the 1980's (Inaba *et al.* 2002). Population size has slowly increased since then and is estimated at 100 to150 individuals by recent surveys (Kinjo and Izawa 2009; Suzuki and Inaba 2010). On the other hand, the population on Hahajima Island (the second largest island) greatly decreased from more than 100 in 1960's to a few individuals in 2000's. As it is hard to access other islands in their distribution, information is very limited. The population on Minami-Iwo-to Island was estimated at more than 100 in 1982 and 2007 (Suzuki 2008; Kinjo and Izawa 2009; Suzuki and Inaba 2010).

For the Daito flying fox, information on their status is even less. The Daito Isls. have a unique history of human activity. These islands have been inhabited since 1900, and almost all natural forests were cut and turned into farmland. Then many native animals including endemic species went extinct. The population of the Daito flying fox may have drastically decreased, although the original population size is unknown. Recent estimation showed that population size was about 300, and it has looked stable in the last 10 years (Izawa *et al.* unpublished).

These two species are frugivores, but also feed on nectar and leaves. Important habitat components are the feeding tree and the roosting (resting) trees. Unlike the small Chiroptera, flying foxes roost in tree canopies in daytime. As the habitats of both species are oceanic islands, there are no natural enemies for them. The only natural harm to their populations is the effect of typhoons (Nakamoto *et al.* 2007; 2011). Typhoons cause direct mortality and also cause food shortages by damaging food plants. For the conservation of flying foxes, various plants should be ensured for their food supply and roosting sites.

Threats for the flying foxes are habitat destruction such as deforestation, disturbance of roosting sites by tourism, and predation by alien predators such as domestic cats. Especially for the Bonin flying fox, which forms permanent colonies and tends to use fixed roosting sites (Sugita *et al.* 2009), human disturbance to these roosting sites is a serious threat. Additionally, these bats conflict with farmers for commercial fruits. Although farmers do not kill flying foxes directly, they are accidentally killed by orchard nets which farmers set to prevent birds and flying foxes from accessing fruit crops.

Figure 5. A male Daito flying fox (*Pteropus dasymallus daitoensis* Kuroda, 1921) feeding on the nectar of the red silk-cotton tree; photographed by Masako Izawa.

The Ogasawara Islands were registered as a world natural heritage site in 2011. Conservation of relatively intact communities is conducted by MOE, the Forestry Agency, the local government and NGO's. In the process of preparation for designation of such reserves, many projects were conducted for eliminating alien species. A project to control the population of feral cats was also done and still continues. It gives steady favorable results so far. On the other hand, the designation of world natural heritage status has brought in more active tourism. This has caused the disturbance of roosting sites and habitat reduction of the Bonin flying fox. For the Daito flying fox, human caused damage to its population is not so serious now. A most serious concern is strong typhoons which reach these islands several times a year. Provision of food after typhoon attacks is a most important conservation measure. Other actions needed to maintain natural habitats are stopping the enlargement of farmlands and eliminating the invasive pest insects on agricultural plants.

Management of overabundant ungulate populations. Two ungulates, Sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*), markedly increased in numbers and extended their geographic distribution in Japan during the last few decades. The range of sika deer and wild boar expanded by 1.7 times and 1.3 times, respectively from 1978 to 2003 (Biodiversity Centre of Japan, MOE). The number of sika deer harvested has increased markedly from the beginning of the 1990s to the present: from 41,949 in 1990 to 363,100 in 2010, corresponding to a 9-fold increase with a mean annual increase rate of 9.8 % during the last 20 years. The number of wild boar harvested has also increased markedly from 70,102 in 1990 to 477,000 in 2010, corresponding to a 7-fold increase with a mean annual increase rate of 10 % during the last 20 years (MOE). These data clearly show a dramatic increase in numbers of these two species in Japan. The rapid increase in the large ungulates may have had multiple causes associated with changes in socio-economic and natural environments. These include elimination of wolves, clear-cutting of forests, increased pasture acreage, increased abandonment of cultivated areas, decrease in the hunter population, and strengthening enforcement to prevent poaching, all of which have most likely contributed to the expansion of distribution and the increase in population size of these two species. In addition, there were no severe winters during the last 25 years, which may have contributed to an increase in the rate of population growth. The decrease of human presence in mountain and rural areas has also favored ungulate populations.

The current wildlife management system in Japan is based on "the Specified Wildlife Conservation and Management Plan" (prefecture-determined management plan system) under "Wildlife Protection and Proper Hunting Act", which was revised in 1999. This revision of the law in 1999 was the beginning of scientific management of wildlife in Japan. Most prefectural governments now have sika deer and wild boar populations incorporated into their management plans. Prefectural governors may designate a certain population of wildlife showing either marked increases or decreases as "Specified Wildlife," and establish a management plan. Under the planning system a local government can extend hunting periods and relax regulation of harvest numbers per day for an overabundant wildlife population, or regulate hunting, incorporate measures to preserve natural habitat, and prevent wildlife conflict for a threatened population, by taking long-term stability and viability of the regional population into consideration.

For damage control, the "Act on Special Measures for Prevention of Damage Related to Agriculture, Forestry and Fisheries Caused by Wildlife (Act on municipality-determined damage control plan system)" was established by the Ministry of Agriculture, Forestry and Fisheries (MOA) in 2007. This act intends to reinforce efforts of municipalities and hunters through subsidies from MOA. Damage control programs are set for about 90 % (1331/1500) of municipalities which suffer damages from wildlife, and half of those municipalities (674) have organized culling programs in 2013 (MOA).

A working group of the Mammal Society of Japan reviewed the management plans for sika deer populations by prefectural governments, and pointed out the following problems (Uno *et al.* 2007):

- High possibility of underestimation of population size
- Difficulty of population reduction due to expanding ranges
- Drastic decrease in the population of hunters
- Lack of programs for sustainable resource management
- Lack of adaptive management systems that incorporate science in wildlife management policies
- Lack of large scale management systems in cooperation with neighboring prefectural governments.

The 1999 version of "Wildlife Protection and Proper Hunting Act" includes both elements of wildlife conservation (≈ protection) and management. However, relatively speaking, it is biased toward the role of conservation. Thus further revision of the Act was requested adding the viewpoint of pest control. To review the "Wildlife Protection and Hunting Law", MOE organized a panel consisting of wildlife professionals to discuss how wildlife management should be organized in Japan. Main points of the review were as follows:

- The "Wildlife Protection and Proper Hunting Act" should be changed so as to explicitly include the practice of wildlife management and professional approaches to pest control.
- There is a need to clarify the role of national, prefectural, and municipal governments, and to construct a cooperative structure among them as well as with NGOs.
- A system to promote effective culling of over-abundant species must be constructed.
- Legal measures for wildlife management need to be authorized.
- For animals that are widely distributed, increasing in numbers, and thereby causing damages, the role of the national government might be important for evaluating the situation and providing leadership for nationwide management solutions.
- The promotion of hunting as a method of population control where appropriate should be discussed.
- The scientific basis for management must be promoted, as well as the public awareness of wildlife management.

The "Wildlife Protection and Proper Hunting Act" was revised again as the "Wildlife Protection and Management, and Proper Hunting Act" on March 11, 2014, in order to further emphasize the importance of management of wildlife. Under the revised law the Minister of MOE can designate a wildlife population as "Specified Wildlife" that should be managed intensively and extensively, and the national or prefectural governments can relax existing regulations for hunting and capture of wildlife under a plan authorized by the law. In particular, organizations that are empowered under the authorized plan can skip the official procedures required to capture designated wildlife, and night shooting can be allowed under specified conditions. In addition, a certificated business operator system is introduced in the revised law. Persons who apply to implement a population control project can be certificated for their skills and knowledge in capturing wildlife by the governor of prefectures based on a specified standard. The revised law is expected to enhance the number of sika deer and wild boars harvested, and thereby reduce their population sizes to a half of the present size for the next 10 years.

Conclusions

The Japanese mammalian fauna is rich and includes many endemic species. Therefore, the Japanese government has a high degree of responsibility to conserve its mammalian fauna, because the extinction of the endemic species in Japan directly results in significant reduction of biodiversity in the world. The Japanese legal system concerned with biodiversity appears to be well organized (Figure 2). However, its implementation is not sufficient. For instance, although four species (or subspecies) are designated as Endangered Species and some conservation measures have been carried out, 20 endemic species ranked VU, EN or CR are still not being adequately considered for endangered status. Furthermore, although habitat loss poses a major threat in most cases, MOE frequently hesitates to establish natural habitat protection areas. Like other developed countries, Japan is distressed by damages caused by overabundant populations of some wildlife. Although the national and prefectural governments have been encouraging pest control by paying a reward to reduce the size of overabundant populations, it is not always easy to keep high culling pressure on those populations because of budget limitation and the decrease in the number of hunters. The reduction in the numbers of hunters is caused by aging of the population and excessive concentration of people into urban centers. In addition, Japan has a cultural problem. Japanese are traditionally a fish-eating people, and we rarely find game meat for sale in Japanese markets. Reformation of Japanese society may be required to solve the long term and complex problems with its wildlife.

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Resumen

Introducción. Ciento un especies de mamíferos terrestres nativos, con exclusión de Sirenia, Cetaceae, Phocidae y Otariidae, habitan o habitaron Japón, el 51.5 % de ellas son endémicas, la mayoría de ellas pertencen a especies nativas de los bosques. Cuatro especies, el lobo, el zorro volador de Okinawa, el murciélago de Bonin, y la nutria de río japonesa se extinguieron durante la edad moderna. Esta relativa baja tasa de extinción de especies en Japón es probablemente debida a que la destrucción del bosque ha sido limitada en este pais. Alrededor de dos tercios del territorio japones todavía está cubierto por bosques (25.10/37.79 millones de hectáreas, el 66.4 % a partir de 2011 de acuerdo con Agencia Forestal del Gobierno japonés). Sin embargo, el número de especies que estan clasificadas bajo un estado de conservación no es pequeña; cinco especies se clasifican "vulnerable" (VU), 15 "en peligro" (EN) y ocho "En peligro crítico" (CR). El número total de especies clasificadas en estas tres categorías es de 28, y lo que representa un porcentaje del 28.9 % (= 28/97), el cual es el porcentaje de especies en categoria de conservacion más alto de en comparación con el estándar mundial. Esta situación puede ser causada por una amplia construcción de bosques artificiales de 1950 a 1970, época durante la cual muchos bosques naturales de Japón se talaron y fueron transformados a bosques artificiales.

Discusión y conclusiones. La proporción de los bosques naturales se redujo a alrededor del 40 % de la superficie total de bosques en 2013. Las leyes más influyentes para la conservación de la vida silvestre y la gestión en Japón son la "Ley sobre la Conservación de Especies Amenazadas de Fauna y Flora Silvestres "y" Ley de Protección Caza Adecuada y Vida Silvestre ". El conejo de Amami (*Pentalagus furnessi*), el zorro volador de Bonin (*Pteropus pselaphon*), una subespecie zorro volador de Ryukyu (*Pteropus dasymallus daitoensis*), y dos subespecies de leopardo (*Prionailurus bengalensis iriomotensis* y *P. b. Euptilurus*) se conservan bajo "Ley sobre Conservación de Especies Amenazadas de Fauna y Flora Silvestres", mientras que la conservación de muchas especies terrestres endémicas que se clasifican en altas categorias de riesgo no son consideradas en las leyes japonesas. Recientemente se han desarrollado prácticas de gestión y manejo para las poblaciones sobreabundantes, como lo son el ciervo sika (*Cervus nipón*) y el jabalí (*Sus scrofa*) bajo la "Ley de Caza Adecuada y Protección de la Fauna".

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Una revisión del estado de conservación de los mamíferos australianos

A review of the conservation status of Australian mammals

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Introduction: This paper provides a summary of results from a recent comprehensive review of the conservation status of all Australian land and marine mammal species and subspecies. Since the landmark date of European settlement of Australia (1788), at least 28 of the *ca*. 272 Australian endemic land mammal species have been rendered extinct.

Results and Discussion: Extinctions have occurred at a more or less consistent rate of one to two species per decade since the 1840s, with that rate continuing unabated. A further 55 species from that original fauna are now threatened, and an additional 42 are Near Threatened. Although many factors have contributed to these declines and extinctions, and the array of threats varies amongst individual species, the threat that has had (and is continuing to have) most detrimental impact upon terrestrial mammal species is predation by the introduced cat *Felis catus* and European red fox *Vulpes vulpes*. There has been some successful broad-scale management of the fox, but the threat posed by feral cats remains largely unabated. For the 55 species occurring in Australian marine waters, the information base is mostly too meagre to assess conservation status other than as Data Deficient. For the Australian mammal fauna generally, the current conservation management effort is insufficient, with ongoing trends for decline in many species – for example, of 49 species whose conservation status changed over the period 1992-2012, 38 had deteriorating conservation status whereas only 11 had improving status.

Key words: extinct, feral cat, fire, marine mammals, marsupial, predation, red fox, threatened, translocation.

Introduction

Australia's mammal fauna is rich and extremely distinctive (Holt *et al.* 2013). It is also diminishing very rapidly (Burbidge and McKenzie 1989; Burbidge *et al.* 2008; McKenzie *et al.* 2007; Woinarski *et al.* 2011). Recognising conservation concern about that trend, we recently undertook the first comprehensive review of the conservation status of the Australian mammal fauna (all terrestrial and marine species and subspecies in Australia, its external territories and territorial waters) (Woinarski *et al.* 2014). In this paper, we summarise some of the main findings of that review.

As Australia is a nation occupying an entire continent, such a national conservation overview is appropriate and can be related readily to national conservation management activity and legislation. We recognise that the conservation status of Australian mammal species has been assessed recently by the IUCN as part of a broader global review (Hoffmann *et al.* 2011; Schipper *et al.* 2008), however that broad assessment has had little consequence for the conservation of Australian mammal species – for example, the global review resulted in no changes in the listing of threatened species under Australian national legislation, and provided no substantial management advice for the conservation of Australia's threatened mammals. Our objectives were: to provide an explicit focus on the conservation of Australian mammals; to provide information in a manner that would be most appropriately formatted for overhaul of the now somewhat sub-optimal listing of threatened species under Australian legislation; to assess the extent to which current conservation management actions were delivering benefits to Australia's threatened mammals; to identify major factors affecting the status of Australian mammals; and to identify research and management priorities.

The approach we adopted was modelled on comparable overviews of Australian birds, that sought to provide not only an assessment of the conservation status of all taxa but also to frame and guide a coherent conservation management response (Garnett and Crowley 2000; Garnett *et al.* 2011). Our review was also substantially informed by now somewhat dated conservation assessments for particular groups of Australian mammals, including marsupials (Maxwell *et al.* 1996), rodents (Lee 1995), bats (Duncan *et al.* 1999), cetaceans (Bannister *et al.* 1996) and seals (Shaughnessy 1999).

More so than most other areas, the status of Australian mammals can be benchmarked to a pivotal historical event, the first settlement of Australia by Europeans in 1788. Although a rich component of the Australian mammal fauna was lost before this date – most notably the extirpation of the extraordinary Australian megafauna over the period from about 60,000 to 20,000 years ago (Johnson 2006) – European settlement saw a marked environmental transformation across many areas of Australia (Bradshaw 2012) and the introduction of very many plant and animal species whose environmental impacts have been profound. Accordingly, we use 1788 as a baseline from which to chart the conservation fate of the Australian mammal fauna.

Material and methods

Our objective was to assess the conservation status of all Australian mammal taxa, using IUCN criteria (IUCN 2001). These criteria mostly relate to distributional extent, and population size and trends. Accordingly, we required an inventory of all Australian mammal taxa, and information on the distribution and population of those taxa.

The taxonomy of Australian mammals is unsettled, with at least 50 endemic species described since 1970. We established a checklist of species and subspecies recorded in Australia and its external territories, based on consensus among a group of taxonomists working actively with Australian mammals, and in part informed by a far more comprehensive taxonomic treatment of the Australian mammal fauna in preparation (Jackson and Groves in press). As evidence of the fluid nature of this taxonomy, six species of Australian endemic mammals (three bats (*Mormopterus* spp.) and three dasyurids (*Antechinus* spp.)) and a nearly-endemic coastal dolphin, *Sousa sahulensis,* have been described since 2012 (Baker *et al.* 2013; Baker *et al.* 2014; Baker *et al.* 2012; Jefferson and Rosenbaum 2014; Reardon *et al.* 2014). The new *Mormopterus* species and the *Sousa* species were included in our review, but the new *Antechinus* were not considered, because their description post-dated our assessments.

There is no comprehensive distributional or monitoring data base for Australian mammals, although *The Atlas of Living Australia* (http://www.ala.org.au/) now provides a reasonable and increasingly comprehensive collation of distributional records. For our review, we collated distributional records for all terrestrial Australian mammal taxa from a wide range of state conservation agency and museum sources. This database used as a foundation a previous collation of mainland non-volant mammal records developed by Fisher *et al*. (2014), and added to it records of bats and Tasmanian mammals, from relevant data bases maintained by state agencies and museums. All resulting maps were inspected for outlying and potentially erroneous records, with any such records then referred back to the original source for confirmation or rejection. Subsequently, we used recent (post 1992) records to calculate area of occupancy and extent of occurrence, following IUCN Standards and Petitions Subcommittee (2013). Distributional data for marine species were too meagre to allow for such analysis.

Reliable estimates of population size are available for only a few Australian mammal species (mostly large and commercially exploited kangaroo species, a few whale species, and a small set of highly localised threatened species). However, there is some information on trends in various measures of relative abundance for more species.

Based on this compilation of relevant conservation parameters, we assessed all taxa using IUCN criteria, as either Extinct, Critically Endangered (Possibly Extinct), Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern or Data Deficient. We allocated some taxa to Near Threatened (Conservation Dependent), a category no longer used by IUCN, but which is available under Australian legislation. These assessments related only to the Australian range of (the minority of) species that were not Australian endemics. This draft assessment and a detailed account were then widely distributed to additional relevant experts, and the assessments and accounts were reviewed in response to feedback. More than 200 experts provided such reviews. We used a cut-off date of December 2012 for all assessments, and also provided retrospective assessments (based on currently available information) of the conservation status of all taxa 10 and 20 years earlier. For extinct species, we documented the most recent record, and estimated the decade of extinction.

In addition to compiling information on these conservation parameters, we documented information on threatening factors for all taxa assessed as threatened or Near Threatened, rating threats according to the extent over which they operated (in relation to the distribution of the considered species), the intensity of their impact, and whether the threats were historical, current or projected.

Results

There is a marked distinction between the conservation status of Australian terrestrial and marine mammals (Table 1). Of 272 terrestrial Australian-endemic mammal species extant in 1788, we considered 28 are now extinct (Tables 1, 2). A recent unsuccessful search for the highly localised (known only from a 5 ha cay) Bramble Cay melomys *Melomys rubicola* suggests that the number of extinctions is now 29, with that loss sometime since its last record, in 2009. In addition, the Christmas Island shrew *Crocidura trichura* was considered Critically Endangered (Possibly Extinct): with no records since 1985, it is likely now also to be extinct. Hence, in the 236 years since initial European settlement of Australia, more than 10 % of the endemic land mammal fauna has been rendered extinct. Our assessment concluded that the first post-1788 extinction was around the 1840s, and that the rate of extinction (of 1-2 species per decade) has continued unabated since then, with two species lost in the last 10 years (the Bramble Cay melomys and Christmas Island pipistrelle *Pipistrellus murrayi*).

Our review assessed a further 55 Australian endemic land mammals as threatened (i.e. Critically Endangered, Endangered or Vulnerable), and a further 42 species as Near Threatened – *i.e.* 46 % of the Australian endemic terrestrial mammal species present in 1788 is now extinct, threatened or Near Threatened (Tables 1, 2). The dominant trend for the threatened and Near Threatened species (for which such information was available) was for ongoing decline (with 38 terrestrial mammal species considered to have worsened conservation status over the period 1992 to 2012 and 11 species showing an improved conservation status over this period). Many species are now reduced to very small population sizes (*e.g.* nine species now have populations of fewer than 1000 individuals), or ranges that are now a minute proportion of their former distributions.

As recognised previously (Burbidge 1999), islands have made a notable contribution to the conservation of Australia's mammals: seven species that have been lost from all of their former extensive mainland ranges have survived solely because subpopulations have persisted on continental islands. However, the fate of Australian mammals restricted to oceanic islands has been far less good: for these six species (five species endemic to Christmas Island and one to Lord Howe Island), four are now extinct, one is Critically Endangered (Possibly Extinct) and the remaining species (the Christmas Island Flying-fox *Pteropus natalis*) is Critically Endangered.

Table 1. Tallies for the Australian conservation status of mammal taxa occurring in Australia. Conservation status codes: EX extinct; CR(PE) Critically Endangered (Possibly Extinct); CR Critically Endangered; EN Endangered; VU Vulnerable, NT(CD) Near Threatened (Conservation Dependent), NT Near Threatened; LC Least Concern; DD Data Deficient.

Taxa considered	No. of taxa	Status assigned									% extinct and threatened	% extinct and threatened*
		EX	CR (PE)	CR	EN	VU	NT (CD)	NT	LC	DD		
All species												
terrestrial species	315	29	2	9	10	36	5	47	175	2	27.3	27.5
marine species	58	0	0	0	4	2	0	5	12	35	10.3	26.1
total all species	373	29	2	9	14	38	5	52	189	37	24.7	24.8
Endemic species												
terrestrial species	272	28	2	9	10	34	4	38	145	2	30.5	30.7
marine species	1	0	0	0	0	1	0	0	0	0	100	100
total all species	273	28	2	9	10	35	4	38	145	2	30.8	31.0
All species and subspecies												
terrestrial	440	36	3	9	21	57	8	63	239	4	28.6	28.9
marine	62	0	0	1	4	2	0	5	12	38	11.3	29.2
total all species	502	36	3	10	25	59	8	68	251	42	26.5	28.9

* excludes DD taxa

Also, as recognised previously, the fate of Australian mammals has varied between different taxonomic groups, sizes, ecologies and distributions (Burbidge and McKenzie 1989; Burbidge *et al.* 2009; Cardillo and Bromham 2001; Chisholm and Taylor 2007; Fisher *et al.* 2014; Johnson and Isaac 2009; Murphy and Davies 2014). Medium-sized (*ca*. 35 g to 5.5 kg) mammals (such as larger dasyurids, larger rodents, smaller macropods, potoroids and bandicoots) have been most affected, arboreal species less affected, and declines and extinctions have occurred mostly in semi-arid, arid and temperate areas, with notable chronological variation. Previously considered relatively stable, the mammal fauna of much of northern Australia is now undergoing rapid and severe decline (Woinarski *et al.* 2011).

Although individual species have differed in the pattern and cause of their decline (or extinction), and many factors may have contributed, the factor that has contributed (and continues to contribute) most to declines for terrestrial species has been predation by two introduced species, the European red fox *Vulpes vulpes* and feral cat *Felis catus* (Woinarski *et al.* 2014). Other major factors implicated

Table 2. List of Australian mammal species assessed as extinct, threatened or Near Threatened in current review (MAP = Mammal Action Plan), ordered by conservation status. The conservation status (as at 2012) according to Australian legislation (EPBCA) and IUCN Red List is also given. Note that the Australian listing does not include a Near Threatened category. For MAP and EPBCA, the conservation status assigned relates (for non-endemic species) to only that part of their population in Australia or Australian waters. Conservation status: EX Extinct, CR(PE) Critically Endangered (Possibly Extinct), CR Critically Endangered, EN Endangered, VU Vulnerable, NT (CD) Near Threatened (Conservation Dependent), NT Near Threatened.

Scientific name	Common name	Australian endemic	MAP status	EPBCA	IUCN	Extinction decade
Zaglossus bruijnii	Long-beaked Echidna	NO	EX		CR	>1901
Thylacinus cynocephalus	Thylacine	YES	EX	EX	EX	1930
Chaeropus ecaudatus	Pig-footed Bandicoot	YES	EX	EX	EX	1950
Perameles eremiana	Desert Bandicoot	YES	EX	EX	EX	1960
Macrotis leucura	Lesser Bilby	YES	EX	EX	EX	1960
Bettongia anhydra	Desert Bettong	YES	EX			1950
Bettongia pusilla	Nullarbor Dwarf Bettong	YES	EX		EX	1880
Caloprymnus campestris	Desert Rat-kangaroo	YES	EX	EX	EX	1930
Potorous platyops	Broad-faced Potoroo	YES	EX	EX	EX	>1875
Lagorchestes asomatus	Central Hare-wallaby	YES	EX	EX	EX	1950
Lagorchestes leporides	Eastern Hare-wallaby	YES	EX	EX	EX	1900?
Macropus greyi	Toolache Wallaby	YES	EX	EX	EX	1970
Onychogalea lunata	Crescent Nailtail Wallaby	YES	EX	EX	EX	1950
Pteropus brunneus	Dusky Flying-fox	YES	EX		EX	1890
Nyctophilus howensis	Lord Howe Long-eared Bat	YES	EX	EX	EX	1920
Pipistrellus murrayi	Christmas Island Pipistrelle	YES	EX	CR	CR	2000
Conilurus albipes	White-footed Rabbit-rat	YES	EX	EX	EX	1860
Conilurus capricornensis	Capricornian Rabbit-rat	YES	EX			?
Leporillus apicalis	Lesser Stick-nest Rat	YES	EX	EX	CR(PE)	>1930
Notomys amplus	Short-tailed Hopping-mouse	YES	EX	EX	EX	1900
Notomys longicaudatus	Long-tailed Hopping-mouse	YES	EX	EX	EX	1900
Notomys macrotis	Large-eared Hopping-mouse	YES	EX	EX	EX	1860
Notomys mordax	Darling Downs Hopping-mouse	YES	EX	EX	EX	>1840
Notomys robustus	Broad-cheeked Hopping-mouse	YES	EX			1870
Pseudomys auritus	Long-eared Mouse	YES	EX			1850
Pseudomys glaucus	Blue-grey Mouse	YES	EX		EX	?
Pseudomys gouldii	Gould's Mouse	YES	EX	EX	EX	>1850
Rattus macleari	Maclear's Rat	YES	EX	EX	EX	1900
Rattus nativitatis	Bulldog Rat	YES	EX	EX	EX	1900
Melomys rubicola	Bramble Cay Melomys	YES	CR (PE)	EN	CR	2010
Crocidura trichura	Christmas Island Shrew	YES	CR (PE)	EN		
Lasiorhinus krefftii	Northern Hairy-nosed Wombat	YES	CR	EN	CR	
Burramys parvus	Mountain Pygmy-possum	YES	CR	EN	CR	
Gymnobelideus leadbeateri	Leadbeater's Possum	YES	CR	EN	EN	
Pseudocheirus occidentalis	Western Ringtail Possum	YES	CR	VU	VU	
Bettongia penicillata	Woylie	YES	CR		CR	
Potorous gilbertii	Gilbert's Potoroo	YES	CR	CR	CR	
Pteropus natalis	Christmas Island Flying-fox	YES	CR			
Zyzomys palatalis	Carpentarian Rock-rat	YES	CR	EN	CR	
Zyzomys pedunculatus	Central Rock-rat	YES	CR	EN	CR	

Dasyurus hallucatus	Northern Quoll	YES	EN	EN	EN
Dasyurus viverrinus	Eastern Quoll	YES	EN		NT
Parantechinus apicalis	Dibbler	YES	EN	EN	EN
Sarcophilus harrisii	Tasmanian Devil	YES	EN	EN	EN
Myrmecobius fasciatus	Numbat	YES	EN	VU	EN
Petaurus gracilis	Mahogany Glider	YES	EN	EN	EN
Bettongia tropica	Northern Bettong	YES	EN	EN	EN
Petrogale coenensis	Cape York Rock-wallaby	YES	EN		NT
Petrogale persephone	Proserpine Rock-wallaby	YES	EN	EN	EN
Hipposideros inornatus	Arnhem Leaf-nosed Bat	YES	EN		VU
Arctophoca tropicalis	Subantarctic Fur Seal	NO	EN	VU	LC
Balaenoptera borealis	Sei Whale	NO	EN	VU	EN
Balaenoptera musculus	Blue Whale	NO	EN	EN	EN
Balaenoptera physalus	Fin Whale	NO	EN	VU	EN
Dasyuroides byrnei	Kowari	YES	VU	VU	VU
Antechinus bellus	Fawn Antechinus	YES	VU		LC
Phascogale pirata	Northern Brush-tailed Phascogale	YES	VU	VU	VU
Sminthopsis butleri	Butler's Dunnart	YES	VU	VU	VU
Sminthopsis psammophila	Sandhill Dunnart	YES	VU	EN	EN
Isoodon auratus	Golden Bandicoot	YES	VU	VU*	VU
Perameles bougainville	Western Barred Bandicoot	YES	VU		EN
Perameles gunnii	Eastern Barred Bandicoot	YES	VU		NT
Macrotis lagotis	Bilby	YES	VU	VU	VU
Phascolarctos cinereus	Koala	YES	VU	(VU)	LC
Petauroides volans	Greater Glider	YES	VU		LC
Bettongia gaimardi	Southern Bettong	YES	VU		NT
Potorous longipes	Long-footed Potoroo	YES	VU	EN	EN
Lagorchestes hirsutus	Mala	YES	VU		VU
Onychogalea fraenata	Bridled Nailtail Wallaby	YES	VU	EN	EN
Petrogale lateralis	Black-footed Rock-wallaby	YES	VU		NT
Petrogale penicillata	Brush-tailed Rock-wallaby	YES	VU	VU	NT
Petrogale sharmani	Mount Claro Rock-wallaby	YES	VU		NT
Setonix brachyurus	Quokka	YES	VU	VU	VU
Lagostrophus fasciatus	Banded Hare-wallaby	YES	VU		VU
Pteropus poliocephalus	Grey-headed Flying-fox	YES	VU	VU	VU
Macroderma gigas	Ghost Bat	YES	VU		VU
Rhinolophus 'intermediate'	Lesser Large-eared Horseshoe-bat	YES	VU		
Nyctophilus corbeni	South-eastern Long-eared Bat	YES	VU	VU	
Chalinolobus dwyeri	Large-eared Pied Bat	YES	VU	VU	NT
Conilurus penicillatus	Brush-tailed Rabbit-rat	NO	VU	VU	NT
Mesembriomys gouldii	Black-footed Tree-rat	YES	VU		NT
Notomys aquilo	Northern Hopping-mouse	YES	VU	VU	EN
Notomys fuscus	Dusky Hopping-mouse	YES	VU	VU	VU
Pseudomys australis	Plains Mouse	YES	VU	VU	VU
Pseudomys fieldi	Shark Bay Mouse	YES	VU	VU	VU
Pseudomys fumeus	Smoky Mouse	YES	VU	EN	EN
Pseudomys novaehollandiae	New Holland Mouse	YES	VU	VU	VU
Pseudomys oralis	Hastings River Mouse	YES	VU	EN	VU

Zyzomys maini	Arnhem Rock-rat	YES	VU	VU	NT
Xeromys myoides	Water Mouse	NO	VU	VU	VU
Neophoca cinerea	Australian Sea-lion	YES	VU	VU	EN
Physeter macrocephalus	Sperm Whale	NO	VU		VU
Dasyurus geoffroii	Chuditch	YES	NT (CD)	VU	NT
Bettongia lesueur	Boodie	YES	NT (CD)		NT
Petrogale xanthopus	Yellow-footed Rock-wallaby	YES	NT (CD)		NT
Pteropus conspicillatus	Spectacled Flying-fox	NO	NT (CD)	VU	LC
Leporillus conditor	Greater Stick-nest Rat	YES	NT (CD)	VU	VU
Ornithorhynchus anatinus	Platypus	YES	NT		LC
Dasycercus cristicauda	Crest-tailed Mulgara	YES	NT	VU	LC
Dasyurus maculatus	Spot-tailed Quoll	YES	NT		NT
Pseudantechinus mimulus	Carpentarian Antechinus	YES	NT	VU	EN
Antechinus godmani	Atherton Antechinus	YES	NT		NT
Phascogale calura	Red-tailed Phascogale	YES	NT	EN	NT
Phascogale tapoatafa	Brush-tailed Phascogale	YES	NT		NT
Sminthopsis archeri	Chestnut Dunnart	NO	NT		DD
Sminthopsis bindi	Kakadu Dunnart	YES	NT		LC
Sminthopsis douglasi	Julia Creek Dunnart	YES	NT	EN	NT
Lasiorhinus latifrons	Southern Hairy-nosed Wombat	YES	NT		LC
Petaurus australis	Yellow-bellied Glider	YES	NT		LC
Hemibelideus lemuroides	Lemuroid Ringtail Possum	YES	NT		NT
Pseudochirops archeri	Green Ringtail Possum	YES	NT		LC
Pseudochirulus cinereus	Daintree River Ringtail Possum	YES	NT		LC
Wyulda squamicaudata	Scaly-tailed Possum	YES	NT		DD
Potorous tridactylus	Long-nosed Potoroo	YES	NT		LC
Dendrolagus bennettianus	Bennett's Tree-kangaroo	YES	NT		NT
Dendrolagus lumholtzi	Lumholtz's Tree-kangaroo	YES	NT		LC
Lagorchestes conspicillatus	Spectacled Hare-wallaby	NO	NT		LC
Macropus bernardus	Black Wallaroo	YES	NT		LC
Macropus parma	Parma Wallaby	YES	NT		NT
Petrogale burbidgei	Monjon	YES	NT		NT
Petrogale concinna	Nabarlek	YES	NT		DD
Petrogale godmani	Godman's Rock-wallaby	YES	NT		LC
Petrogale mareeba	Mareeba Rock-wallaby	YES	NT		LC
Petrogale purpureicollis	Purple-necked Rock-wallaby	YES	NT		LC
Rhinolophus robertsi	Greater Large-eared Horseshoe-bat	YES	NT	VU**	
Hipposideros cervinus	Fawn Leaf-nosed Bat	NO	NT		LC
Hipposideros diadema	Diadem Leaf-nosed Bat	NO	NT		LC
Hipposideros semoni	Semon's Leaf-nosed Bat	NO	NT	EN	DD
Hipposideros stenotis	Northern Leaf-nosed Bat	YES	NT		LC
Saccolaimus mixtus	Cape York Sheath-tailed Bat	NO	NT		DD
Saccolaimus saccolaimus	Bare-rumped Sheath-tailed Bat	NO	NT		LC
Taphozous australis	Coastal Sheath-tailed Bat	NO	NT		NT
Mormopterus eleryi	Bristle-faced Free-tailed Bat	YES	NT		
Mormopterus norfolkensis	East-coast Free-tailed Bat	YES	NT		LC
Murina florium	Flute-nosed Bat	NO	NT		LC

Nyctophilus sherrini	Tasmanian Long-eared Bat	YES	NT		DD
Falsistrellus mackenziei	Western False Pipistrelle	YES	NT		NT
Mastacomys fuscus	Broad-toothed Rat	YES	NT		NT
Mesembriomys macrurus	Golden-backed Tree-rat	YES	NT	VU	LC
Notomys cervinus	Fawn Hopping-mouse	YES	NT		VU
Pseudomys calabyi	Kakadu Pebble-mouse	YES	NT		VU
Pseudomys occidentalis	Western Mouse	YES	NT		LC
Pseudomys shortridgei	Heath Mouse	YES	NT	VU	NT
Uromys hadrourus	Pygmy White-tailed Rat	YES	NT		VU
Dugong dugon	Dugong	NO	NT		VU
*Canis lupus dingo****	Dingo	(NO)	NT		NT
Mirounga leonina	Southern Elephant Seal	NO	NT	VU	LC
Eubalaena australis	Southern Right Whale	NO	NT	EN	LC
Orcaella heinsohni	Australian Snubfin Dolphin	NO	NT		NT
*Sousa chinensis*****	Indo-Pacific Hump-backed Dolphin	NO	NT		NT

* For both subspecies *I. a. auratus* and *I. a barrowensis*; ** as *R. p.* 'large form'; *** contested taxonomy, with some recent treatment as an endemic Australian species, *C. dingo* (Crowther *et al.* 2014); **** now recognised as *S. sahulensis* Australian Hump-backed Dolphin, but with unchanged conservation status in Australian range.

in decline include changed fire regimes, habitat loss and fragmentation, and habitat degradation due to introduced livestock and feral herbivores. The role of introduced disease is generally largely unknown, but there is some strong circumstantial evidence for some species (Abbott 2006), and a particularly unusual (and currently untreatable) disease is entirely responsible for the current rapid decline of Tasmanian devil *Sarcophilus harrisii*, the largest remaining marsupial carnivore (McCallum *et al.* 2009). Climate change has not yet had a major impact, but is projected to cause substantial declines for some species in some areas (particularly in tropical mountain rainforests and alpine areas; Williams *et al.* 2003).

In many cases, individual mammal species are, or have been, affected by multiple threatening factors operating synergistically at any one location, or differently across different parts of the species' range, or at different times. For example, in northern Australia, recent research has indicated that predation by feral cats has greater impact in areas exposed to more frequent and/or extensive fires (McGregor *et al.* 2014). In south-western Australia, concerted management action has led to some benefit through reduction in the abundance of the European red fox, but that change in abundance has now led to increased impacts of predation by feral cats (Marlow *et al.* 2015). Many species now face multiple threats: for example, the koala *Phascolarctos cinereus* is affected by disease (including Chlamydia and a retrovirus), predation by feral (and stray) dogs, timber harvesting, changed fire regimes, road traffic, habitat loss and fragmentation, drought and days of extreme heat.

Largely because of the identification and effective management of factors responsible for decline, some threatened terrestrial mammal species have shown some recovery over the last few decades. The most notable of these successes have involved translocation of individuals from remnant populations to islands or to intensively managed mainland areas (notably predator-proof exclosures) and broad-scale control of foxes (Woinarski *et al.* 2014). Notwithstanding these efforts, the conservation status of only six terrestrial mammal species was considered to have been improved over the last 20 years.

For Australian marine mammals, the conservation status and outlook is far less clear. Only one species, the Australian sea lion *Neophoca cinerea*, is endemic to Australian waters. Of 58 species recorded from Australian waters, the information base for conservation parameters in these waters is so meagre for 35 species that no categorisation other than Data Deficient is justifiable. Many of these species may be imperilled or otherwise declining, but the evidence base is inadequate to demonstrate this. Several previously highly threatened species, most notably the Humpback Whale *Megaptera novaeangliae*, are recovering (and their conservation status was assessed as improving) in Australian waters following cessation of hunting (whaling or sealing). However, a wide range of threats – notably mortality from fisheries interactions, pollution, acoustic disturbance and habitat degradation – continues to affect most marine mammals in Australian waters, and it is likely that climate change and ocean acidification will lead to further declines.

Discussion

This review highlighted the disintegration of a diverse and highly distinctive mammal fauna over a period of little more than two centuries, and – alarmingly – concluded that the rate of loss is unabated. The number of extinct species is appreciably higher than previously recognised under Australian national legislation (where 20 Australian mammal species are currently listed as extinct) or from the most recent global assessment (22 Australian mammal species are currently categorised as extinct in the IUCN Red List). No other country has suffered such a high number of mammal extinctions over recent centuries. Many of the now-extinct mammal species were widespread, abundant and had broad habitat ranges at the time of European settlement (Hanna and Cardillo 2013): they were unlikely candidates for extinction.

The Australian mammal fauna has shown a susceptibility to the impacts of introduced species, particularly two predators, that is characteristic of the frailty of island biodiversity generally (Alcover *et al.* 1998). To some extent, conservation managers have now developed and implemented approaches that provide some control for one of these introduced predators, the European red fox, and sustained and large-scale conservation effort directed at this threat is achieving some impressive reversals of previous declining trends for some threatened species (Morris *et al.* 2003). But to date there has been no successful landscape-scale control of the almost pervasive feral cat. The only remedial actions that have had some success against this threat have been localised and expensive predator-proof exclosures or translocations to cat-free islands.

Other intensive remedial conservation management has helped stave off extinctions for some high profile Australian mammal species faced with a range of sometimes idiosyncratic threats (McCallum *et al.* 2009). However, much of the current decline in the Australian mammal fauna involves poorly-known low profile terrestrial species occurring in remote and ostensibly little modified areas, or is occurring largely unreported but incrementally for marine species, and there is little management attention to, or public awareness of the plight of, these species. Currently, there is insufficient knowledge of the status of many of these species, of the extent to which different threats are driving decline, or of management options to counter these threats. There are insufficient resources to manage the range of threats, and there is no coherent or consolidated response to address this crisis. Without major change in resourcing, management, policy and accountability, it is highly likely that this mammal fauna will continue to substantially erode.

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Resumen

Introducción: En este trabajo se presenta un resumen de los resultados de una reciente revisión exhaustiva del estado de conservación de todas las especies y subespecies de la tierra y de mamíferos marinos Australianos. Desde la fecha histórica de la colonización Europea de Australia (1788), al menos 28 de las 272 especies de mamíferos terrestres endémicos australianos han quedado extintos.

Resultados y Discusión: Las extinciones se han producido a un ritmo más o menos constante de una a dos especies por década desde la década de 1840, con una tasa continua sin cesar. Otras 55 especies de la fauna original ahora se encuentran amenazadas, y otras 42 están en la categoría de "Casi Amenazadas". Aunque muchos factores han contribuido a esta disminución y extinción, y la gama de amenazas varía entre las distintas especies, la amenaza que más ha tenido (y sigue teniendo) un impacto perjudicial es la depredación por el gato introducido *Felis catus* y la zorra roja Europeo *Vulpes vulpes*. Ha habido un cierto éxito a gran escala en el manejo de la zorra, pero la amenaza planteada por los gatos salvajes sigue creciendo y en gran parte sin limites. Para las 55 especies presentes en las aguas marinas de Australia, la base de la información es en su mayoría demasiado escasa para evaluar el estado de conservación de otra forma que como "Datos Insuficientes". Para la fauna de mamíferos australianos en general, el esfuerzo actual de manejo de conservación es insuficiente, con una tendencia para el continuo declive de muchas especies– por ejemplo, de 49 especies cuyo estado de conservación cambió durante el período 1992-2012, 38 mostraban un estado de conservación en deterioro dmientras que sólo 11 tenían mejora de la situación.

Palabras Clave: amenazada, conservación, gato silvestre, extinto , mamífero marino, marsupial , depredación, translocación, zorra roja

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Frenando la ola: el progreso hacia la resolución de las causas de la decadencia y la aplicación de respuestas de manejo ante la desaparición de mamíferos del norte de Australia

Stemming the tide: progress towards resolving the causes of decline and implementing management responses for the disappearing mammal fauna of northern Australia

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Introduction: Recent studies at sites in northern Australia have reported severe and rapid decline of several native mammal species, notwithstanding an environmental context (small human population size, limited habitat loss, substantial reservation extent) that should provide relative conservation security. All of the more speciose taxonomic groups of mammals in northern Australia have some species for which their conservation status has been assessed as threatened, with 53 % of dasyurid, 47 % of macropod and potoroid, 33 % of bandicoot and bilby, 33 % of possum, 30 % of rodent, and 24 % of bat species being assessed as extinct, threatened or near threatened. However, the geographical extent and timing of declines, and their causes, remain poorly resolved, limiting the application of remedial management actions.

Material and methods: Focusing on the tropical savannas of northern Australia, this paper reviews disparate recent and ongoing studies that provide information on population trends across a broader geographic scope than the previously reported sites, and examines the conservation status and trends for mammal groups (bats, macropods) not well sampled in previous monitoring studies. It describes some diverse approaches of studies seeking to document conservation status and trends, and of the factors that may be contributing to observed patterns of decline.

Results and Discussion: *Current trends and potential causal factors for declines.* The studies reported demonstrate that the extent and timing of impacts and threats have been variable across the region, although there is a general gradational pattern of earlier and more severe decline from inland lower rainfall areas to higher rainfall coastal regions. Some small isolated areas appear to have retained their mammal species, as have many islands which remain critical refuges. There is now some compelling evidence that predation by feral cats is implicated in the observed decline, with those impacts likely to be exacerbated by prevailing fire regimes (frequent, extensive and intense fire), by reduction in ground vegetation cover due to livestock and, in some areas, by 'control' of dingoes. However the impacts of dingoes may be complex, and are not yet well resolved in this area. The relative impacts of these individual factors vary spatially (with most severe impacts in higher rainfall and more rugged areas) and between different mammal species, with some species responding idiosyncratically: the most notable example is the rapid decline of the northern quoll (*Dasyurus hallucatus*) due to poisoning by the introduced cane toad (*Rhinella marina*), which continues to spread extensively across northern Australia. The impact of disease, if any, remains unresolved.

Conservation Management Responses. Recovery of the native mammal fauna may be impossible in some areas. However, there are now examples of rapid recovery following threat management. Priority conservation actions include: enhanced biosecurity for important islands, establishment of a network of feral predator exclosures, intensive fire management (aimed at increasing the extent of longer-unburnt habitat and in delivering fine scale patch burning), reduction in feral stock in conservation reserves, and acquisition for conservation purposes of some pastoral lands in areas that are significant for mammal conservation.

Key words: *cane toads, conservation, disease, feral cats, fire, pastoralism, savanna, threats*

Introduction

Recent papers (Fisher *et al.* 2014; Woinarski *et al.* 2010; Woinarski *et al.* 2011a) have identified a substantial recent and ongoing decline in many native land mammal species of the tropical savannas of northern Australia (Figure 1). This decline is occurring notwithstanding that, in a global context, the environments in this region are relatively intact, human population density is very low and the extent of conservation reserves is substantial. Indeed, much of the evidence for declines arises from monitoring studies in large and relatively well-resourced conservation reserves (Woinarski *et al.* 2010; Woinarski *et al.* 2011a).

In global comparisons, this decline is unusual, because severe biodiversity decline is usually associated with marked environmental modification and high human population density (Cardillo *et al.* 2004; Cincotta *et al.* 2000). These contemporary declines are notable in that the mammal fauna of northern Australia was previously considered resilient and largely spared the pattern of decline and extinction that has severely diminished the distinctive Australian mammal fauna, particularly those in the weight range of 35 g to 5.5 kg (the 'Critical Weight Range') in central and southern Australia (Burbidge and McKenzie 1989) (Fig. 2). Furthermore, recent global-scale predictions of future mammal decline based on estimates of latent extinction risk suggest that northern Australia should be experiencing a significant loss (Cardillo *et al.* 2006).

Woinarski *et al.* (2011a) proposed a range of possible causes for the decline of northern Australian mammals, with most relating ultimately to broad-scale but subtle environmental transformation accompanying European settlement of Australia, with particular emphasis given to predation by feral cats, changed fire regimes and vegetation change associated with livestock and feral herbivores. More recently, modelling of life history, morphological and other attributes of individual species suggested that predation by feral cats was likely to be a principal causative factor (Fisher *et al.* 2014; Murphy and Davies 2014; Woinarski 2015). Nonetheless, the evidence is limited, and accordingly it has been difficult to prescribe optimal responsive management, and to understand why feral cats may only now be causing such decline despite being present in the region for at least a century (Abbott 2002). However, a diverse series of recent research initiatives is attempting to better resolve the pattern and extent of decline and its causes, and to propose and demonstrate remedial management priorities. In this paper, we describe some of that current research and review progress since the initial description and review of the problem (Woinarski *et al.* 2011a).

Specifically, we consider:

(1) *Spatial patterning of mammal decline in northern Australia*. Although some earlier papers (Kitchener 1978; McKenzie 1981) documented historical (i.e. over a period of c. 100 years) declines in the mammal fauna of the lower rainfall southeastern and southwestern Kimberley (in northwestern Australia), much of the information on current decline arises from a substantial monitoring program at a single site, Kakadu National Park (hereafter Kakadu). The extent to which this site, and its pattern of decline, is representative of northern Australia remains poorly resolved. Here, we document recent research from a range of other sites in northeastern Australia (Cape York Peninsula in Queensland), more broadly across the 'Top End' of the Northern Territory, and in northwestern Australia, noting in particular whether these areas are also experiencing the extent and rate of declines reported currently from Kakadu.

(2) *The taxonomic and ecological characterisation of declining mammals*. As described above, much of the evidence for decline arises from monitoring studies in Kakadu (Woinarski *et al.* 2010; Woinarski *et al.* 2001). However, these studies were biased, because their methodology collected substantial information on small and medium-sized non-volant mammal species, but provided very little information on larger mammals (notably macropods) and no useful information on bats. Here, we complement the existing evidence concerning small and medium-sized mammals with brief reviews of the status of bats and macropods in northern Australia.

(3) *A brief review of methodologies*. The overall objectives of research to date have been to determine which species are declining, why, and what should be done to remedy the declines? A range of methodologies have been applied to provide complementary insights into the problem and its resolution. These approaches (which include monitoring, modelling, survey using remote cameras, experimentation, and assessment of historical decline through subfossils and ethno-zoological studies), and their utility, are reviewed briefly.

Based on this information, we refine the conceptual framework of the mechanisms of decline presented by Woinarski *et al.* (2011a), and describe the evidence for a set of candidate causal factors, and their inter-relationships. From this basis, we consider whether there are further critical studies required to more definitively resolve the causes of mammal declines, and provide a series of management recommendations.

Material and methods

STUDY AREA

The geographic focus of this paper are the tropical savanna landscapes of northern Australia (Fig. 1), about a 1.8 million km^2 area that is moderately well defined by the marked influence of a monsoonal (wet-dry) climate (Garnett *et al.* 2010; Woinarski *et al.* 2007). As defined here, this area excludes the Wet Tropics bioregion in a small section of northeastern Australia, characterised by diverse rainforest, relatively marked altitudinal variation and a very distinctive biota.

A series of loosely-linked environmental and land-use factors characterise northern Australia. By far the most extensive vegetation type is savanna woodland (featuring relatively open eucalypt forests and woodlands over a tall grassy understorey), varying in structure with annual rainfall, soils and fire regimes. Within this dominant matrix, there are smaller areas of mangroves, rainforests, tussock grasslands, hummock grasslands, wetlands, heathlands and *Acacia* woodlands, with the distribution patterns of vegetation types determined mostly by variation in soils, rainfall, geomorphology and fire regimes (Hutley *et al.* 2011; Russell-Smith *et al.* 2012; Williams *et al.* 1996a). Rainfall shows pronounced spatial variation, typically with highest annual rainfall in coastal areas (to c. 2000 mm in parts of Cape York Peninsula in northeastern Australia and parts of the Tiwi islands, and c. 1400 mm in the north Kimberley) and diminishing gradationally towards central Australia (to about 500 mm at the southern limit of the area considered here as northern Australia). Across this area, rainfall is highly seasonal, with c. 80-90 % falling in a relatively short wet season (ca. November to April). Temperatures are typically high year-round, but peak in the wet season. The monsoonal influence has been long-standing (Bowman *et al.* 2010).

There are no tall mountains in northern Australia, but some regions (notably much of the Kimberley, the Arnhem Plateau and the McIlwraith and Iron Ranges on Cape York Peninsula) are spectacularly dissected and rugged, and these regions have probably been important refugiaas they harbour many narrowly-restricted endemic mammal and other species (Crisp *et al.* 2001; Hitchcock *et al.* 2013; Pepper and Keogh 2014; Potter *et al.* 2012a; Potter *et al.* 2014b; Start *et al.* 2007; Woinarski *et al.* 2006a; Woinarski *et al.* 2009b). There are also many continental islands in northern Australia, ranging from ephemeral islets to some of Australia's largest islands, including Melville Island (5786 km^2), Groote Eylandt (2285 km^2) and Bathurst Island (1693 km^2). Although almost all of these islands, with the exception of some remote cays, have had a long history of intermittent connection to the Australian mainland (and the broader Sahul – New Guinea land mass), mostly last broken 8000 to 6000 years ago, some of these islands support endemic mammal subspecies, and many others are now the sole refuge for species that have disappeared recently from their broader mainland ranges because of pervasive threats (Firth and Panton 2006; Gibson and McKenzie 2012; Woinarski *et al.* 2011b).

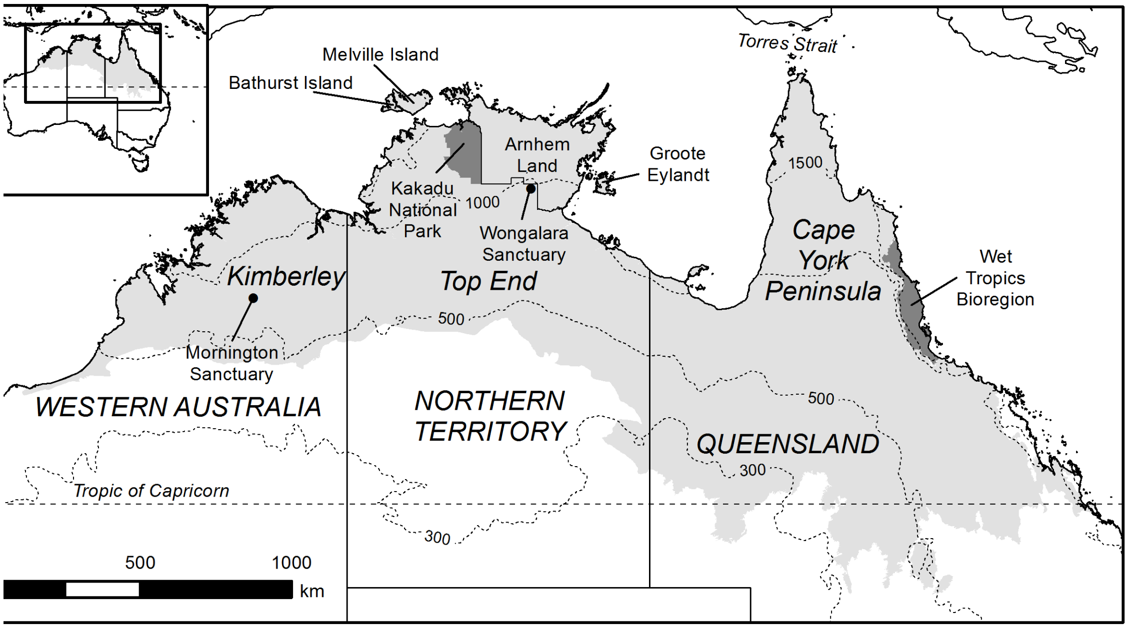

Figure 1. Map of northern Australia (pale grey shading) showing places referred to in text, state/territory boundaries and isohyets (dotted lines). Note that the inland and southern border of the region defined here as northern Australia is diffuse, but follows Fox *et al.* (2001).

Northern Australia comprises three readily distinguished geographic subdivisions, coinciding with state-territory boundaries: the northwestern (Kimberley, in Western Australia), the northern ('Top End' in the Northern Territory) and the northeastern (Cape York Peninsula and the Gulf hinterland in Queensland; Figure 1). Although biota and environments are broadly similar across these regions, there is a complex series of major and minor biogeographic divides, most notably with an arid intrusion (the Carpentarian Barrier) between the northeastern and northern regions, and a less well defined intrusion between northern and northwestern regions (Eldridge *et al.* 2011; Ford and Johnson 2007). Many species occur across all three regions; others are represented by pairs of vicariant species. The northeastern component, particularly Cape York Peninsula, has some notable distinctions in its biota, with greater diversity of rainforest-associated species and bats, related to the region's closer proximity to New Guinea, higher rainfall and larger extent of rainforest vegetation (Hitchcock *et al.* 2013).

Across northern Australia, human population density is low (typically <0.1 person km^{-2}) and Indigenous people comprise much (20-30 %) of the population and own 30-50 % of the land. By far the most extensive land-use is pastoralism, typically based on native vegetation. Except in the south-east, there has been little intensive environmental modification, but there are pervasive and more subtle changes due to introduced animals, plants and changed fire regimes. Largely driven by the climate, fire is very frequent in this landscape, especially in higher rainfall areas, where 30 to 50% of the area is burnt annually (Russell-Smith and Edwards 2006). It is likely that this regime has changed significantly since European settlement 150 to 110 years ago (Ash *et al.* 1997b), in part due to changes in the demography and priorities of Indigenous land owners (Russell-Smith *et al.* 2003). More recently, the spread in some areas of introduced African pasture grasses, particularly gamba grass (*Andropogon gayanus*), has led to more destructive fires and fire regimes in weed-invaded areas, and to predictions that these will drive major environmental transformation (Grice *et al.* 2013; Setterfield *et al.* 2013; Setterfield *et al.* 2010).

The extant native land mammal fauna of northern Australia (Table 1) is broadly typical of Australia as a whole, with a high diversity of marsupials (about 68 spp.; note that tallies vary with different treatments of distributional limits around the diffuse border of the region here considered as northern Australia), rodents (33 spp.) and bats (55 spp.), plus two monotremes and the dingo (*Canis dingo*), a eutherian carnivore introduced by humans to Australia c. 4000 years ago (Ardalan *et al.* 2012; Savolainen *et al.* 2004). Fifty-five of these species (about one third of the northern Australian tally) are restricted to this region; 62 species are Australian endemics that also occur elsewhere in Australia; 30 species occur elsewhere in Australia and extralimitally; and 12 species also occur extralimitally (but not elsewhere in Australia). Three now highly restricted and threatened mammal species – bridled nailtail wallaby (*Onychogalea fraenata*), northern hairy-nosed wombat (*Lasiorhinus krefftii*) and mahogany glider (*Petaurus gracilis*) – occur only at a few sites in the extreme southeastern fringe of the region considered here, and are not a primary focus of this review (at least in part because a major threat for these species has been extensive vegetation loss, atypical of the broader region).

Some species (e.g. ghost bat (*Macroderma gigas*), spectacled hare-wallaby (*Lagorchestes conspicillatus*)) or species-groups (e.g. *Conilurus*, the rabbit-rats) persist in northern Australia but have declined or disappeared from their former range in other Australian regions. Although some megafauna species disappeared from northern Australia in the last tens of thousands of years, until recently it was considered that no mammal species had disappeared from northern Australia since European settlement, a markedly different and better fate than that for Australian mammals more generally (Woinarski *et al.* 2014; Figure 2).

All native mammals in northern Australia are protected under state/territory legislation, other than, a) some instances where dingoes are subject to broad-scale 'control' (poison-baiting and trapping) due to perceived detrimental impacts on pastoralism, b) some more localised 'control' of flying-foxes due to perceived detrimental impacts on horticulture and nuisance value of colonies in urban areas, c) some culling of macropods (principally agile wallaby (*Macropus agilis*)) where populations are perceived to be over-abundant and detrimentally affecting pastoral profitability (Gooding and Harrison 1954), d) some commercial hunting of macropods for meat (mostly in parts of Queensland at the southeastern fringe of the region considered here), and e) ongoing and relatively small-scale hunting of a range of mammal species (but mostly macropods) in some Indigenous communities (Altman 1987; Vardon *et al.* 1999).

Many introduced mammals now have a far greater biomass and ecological influence in this region than do native mammals (Woinarski 2014). Large populations of feral pig (*Sus scrofa*), cattle (*Bos* spp.), water buffalo (*Bubalus bubalis*), horse (*Equus caballus*) and donkey (*E. asinus*) occur across much to most of mainland northern Australia. Feral camels (*Camelus dromedarius*) are widespread in the more arid fringes, and there are localised populations of goats (*Capra hircus*), sambar deer (*Cervus unicolor*) and banteng (*Bos javanicus*). Feral cats (*Felis catus*) are ubiquitous on the mainland and occur on some islands. However, most of northern Australia is beyond the normal range of the other main introduced predator, the European red fox (*Vulpes vulpes*), and another introduced mammal pest, the European rabbit (*Oryctolagus cuniculus*) (Smith and Quin 1996). The introduced black rat (*Rattus rattus*) currently has a highly localised distribution and is often associated with human settlements, but may be expanding its range.

METHODS

In this section, we review briefly the range of approaches that have been used to help refine the current status of, and the causes of decline in, the native mammal fauna of northern Australia.

Inventory and taxonomic sorting

Native mammals of northern Australia have not been thoroughly studied, and it is likely that further species remain to be discovered and that existing species concepts will need further resolution. Twenty-six species (~18 % of the north Australian mammal fauna) have been described since 1975. Most taxonomic uncertainty relates to cryptic species, the extent of taxonomic divergence across the biogeographic regions of northern Australia, and the relationship oftaxa occurring on Cape York Peninsula and in New Guinea (or, for a few bat taxa, more broadly across southeastern Asia and Indo-Papua). Detailed genetic and morphological studies for several groups have resolved many previously challenging species-groups, and highlight a previously unrecognised level of endemism and speciation in some parts of northern Australia (Moritz *et al.* 2013; Potter *et al.* 2014a; Potter *et al.* 2012a; Potter *et al.* 2012b; Reardon *et al.* 2014; Westerman *et al.* 2012). Groups requiring further taxonomic resolution include the bat genera *Miniopterus*, *Myotis*, *Nyctophilus*, *Phoniscus*, *Scotorepens, Vespadelus*, *Rhinolophus, Rhinonicteris*, *Hipposideros*, *Taphozous*, *Nyctimene* and *Mormopterus*, the marsupial genera *Sminthopsis*, *Planigale, Phascogale, Isoodon* and *Petrogale* and the rodent genera *Pseudomys, Xeromys* and *Melomys*.

Subfossils

Knowledge of the native mammal fauna present in northern Australia at the ‘baseline’ time of European settlement is limited and fragmentary, because few substantial inventories were conducted in the first few decades following that settlement. However, information from some of these very few early surveys, most notably those by Knut Dahl in northern and northwestern Australia (Dahl 1897; Dahl 1926), points to substantial changes (mostly losses) of native mammals compared to contemporary inventories (Kitchener 1978; McKenzie 1981).

Recently, some assessments of subfossils (from owl pellets and cave deposits), albeit at few sites in northern Australia, similarly indicate that the contemporary native mammal fauna of northern Australia is notably diminished from that present at about the time of European settlement (Cramb and Hocknull 2010; Foley 1985; Start *et al.* 2012; White and Mason 2011). This is in contrast to the assertion of an intact fauna presented in previous accounts (e.g. Figure 2). At least four species (two *Notomys* species, a *Pseudomys* species, and the Capricorn rabbit-rat (*Conilurus capricornensis*)) now known from subfossils most likely post-dated European settlement, and have never been recorded as living animals. They had not been previously recognised as part of the northern Australian mammal fauna although they disappeared recently, but before we were aware of their existence (Cramb and Hocknull 2010; Start *et al.* 2012). Subfossils have revealed much about historical changes in this fauna, but it remains tantalising because of the very small number of locations at which they have been reported, as well as relatively few sites where subfossils may persist, and the constraints on interpretation of dating for some of this material.

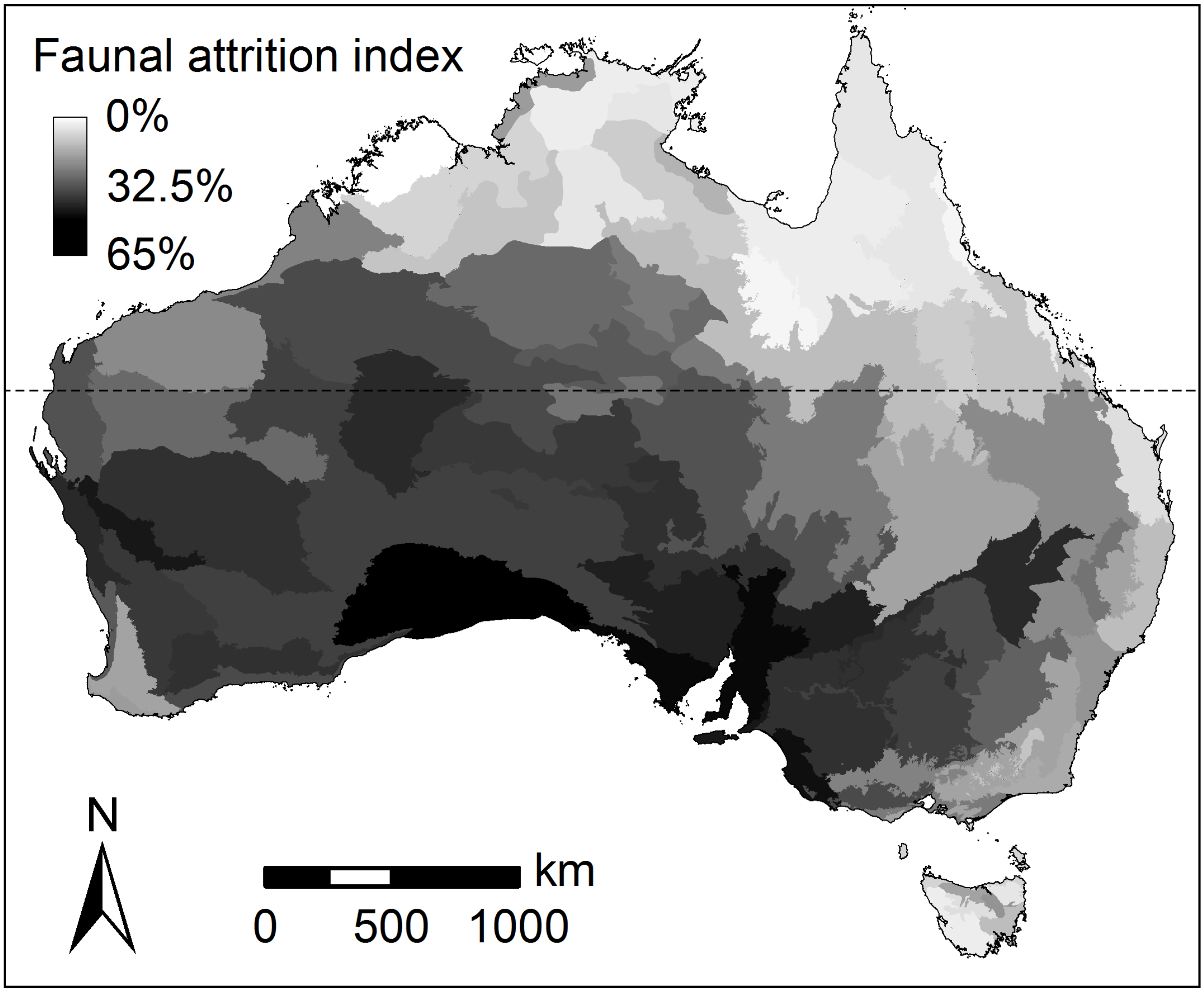

Figure 2. The extent of historical changes in the mammal fauna of continental Australia, using a Faunal Attrition Index (FAI) defined by McKenzie *et al.* (2007). FAI is calculated as (N+E-P)/2N, where N is the number of species originally in the region's fauna, P is the number of species still present and E is the number of species extirpated from the regional fauna: the Index varies from 0 (if all species have persisted) to 1 (if all species have been extirpated). Map from Murphy and Davies (2014).

Integrated distributional databases

Interpretation of the spatial and temporal patterns of decline in mammals of northern Australia has been hampered until recently by the relative lack of integrated distributional data sets. For continental-scale analyses, Burbidge *et al.* (2008) and McKenzie and Burbidge (2002) compiled a broad bioregional-scale distributional matrix for Australian mammals with interpretation of historically changing distributions, but this database is too coarse for detailed examination of changes in the mammal fauna within northern Australia. More recently, a national distributional database for non-volant mammals has been collated from the separate holdings of conservation agencies and museums of Australia's states and territories (Fisher *et al.* 2014), with bats added and the database updated by Woinarski *et al.* (2014). These data sets have been used to analyse changes in conservation status of native mammals. However, compared to similar analyses for other taxa such analyses may be constrained by a lack of detailed data for mammals. For example, whereas assessments of patterns of decline of bird species in northern Australia incorporate detailed mapping of putative causal factors (Franklin *et al.* 2005; Reside *et al.* 2012), the number of distributional records in the region for birds far exceeds that for mammals, so a comparable analysis for mammals may not be so revealing. Nevertheless, improving data sets and the development of new analytical methods may offer further approaches for addressing the declining mammals issue.

Monitoring

Much of the evidence for the current decline of mammals in northern Australia arises from a small set of monitoring programs. These programs were specifically established to measure trends in abundance of mammals (and other components of biodiversity) and their responses to management actions (Russell-Smith *et al.* 2014; Russell-Smith *et al.* 2009a). To date, the most informative and substantial of these programs has been in Kakadu, with establishment in 1996 and continuation to date, mostly at five yearly intervals (Woinarski *et al.* 2010). Complementary, but smaller, monitoring programs (using similar sampling protocols) have been established in other nearby conservation reserves in the Northern Territory (Russell-Smith *et al.* 2014; Russell-Smith *et al.* 2009a) and in the north Kimberley, Western Australia (Corey *et al.* 2013). More recently, monitoring programs have also commenced in some non-government conservation reserves (Kutt *et al.* 2012; Legge *et al.* 2011a; Legge *et al.* 2011b), with less comprehensive monitoring also established recently in some Indigenous Protected Areas (Fitzsimons *et al.* 2012).

These monitoring programs have been instrumental in detecting the extent of change in the status of mammal species, and in providing some information on its causation. However, collectively they sample only a very small proportion of northern Australia, and do not represent other land tenures and management practices; they provide little information on some groups of mammals (particularly bats, larger macropods and feral mammals); they typically use relatively crude measures of abundance; mostly they rely on short-term and insecure funding; and most are not specifically designed to measure responses to particular threats or management actions.

In contrast to the recent integration of previously separate mammal distributional databases, there has been no integration of information across the limited number of monitoring programs for mammals in northern Australia. This constrains analyses of the spatio-temporal variability in population trends, and limits identification of causality and management efficacy. Existing monitoring programs should be secured, consolidated, and integrated.

Ethnozoology

Indigenous ecological knowledge has been increasingly recognized as a valuable complement, or even alternative, for documenting and monitoring the status, distribution and life history of a range of taxa (Anadon *et al.* 2009; Burbidge *et al.* 1988; Ferguson and Messier 1997; Grech *et al.* 2014; Telfer and Garde 2006), and for its contribution to land and sea management and conservation efforts (Ens *et al.* 2012; Karadada *et al.* 2011; Yibarbuk *et al.* 2001). While there are acknowledged limitations to data based on local knowledge, information derived from such sources may be particularly valuable for species and regions that are otherwise poorly known and for which data may be otherwise unavailable. Recognising the limited documented knowledge of native mammals across much of northern Australia, a recent study in the Top End of the Northern Territory recorded Aboriginal knowledge of the changing status of terrestrial mammal species in the region (Ziembicki *et al.* 2013). The study's conclusions mirrored and extended findings from other sources. It found notable declines across the region, particularly in recent decades and especially for medium-sized (critical weight range 35 g to 5,500 g) species. The study also provided valuable new information regarding the past and present range and status and aspects of the ecology of several poorly known species.

Other recent ethno-ecological studies in northern Australia that have improved our understanding of mammals, their habitats, and the threats they face, include studies of traditional fire management (Russell-Smith *et al.* 2009b) and the use of Indigenous knowledge (including tracking skills) in feral cat research and management in western Arnhem Land (A. Stevens, unpublished data). Such projects demonstrate the value of Indigenous knowledge in contemporary conservation practice and natural resource management, particularly on Indigenous-owned lands, which comprise over a third of northern Australia (see 'Indigenous Protected Areas' section below).

Remote survey and sampling: camera trapping and other techniques

Advances in automated remote camera technology have seen a rapid expansion of their use in wildlife research and conservation worldwide. Camera traps provide a cost effective means of studying rare and/or elusive species that may otherwise be difficult to detect. In studies of mammals in northern Australia, camera traps have been incorporated into systematic biodiversity inventory surveys and monitoring programs (e.g. G.Gillespie; B.Murphy, unpublished data), used in targeted surveys of rare or threatened species (e.g. Hohnen *et al.* 2013), and employed in the study of the ecology and movements of feral cats (McGregor 2014; Frank *et al.* 2014). Camera based methods have also been developed to estimate the density of species (e.g. northern quolls and feral cats) based on capture mark-recapture analyses where individuals can be reliably identified (Hohnen *et al.* 2013; McGregor 2014).

The increasing affordability, sophistication and application of other forms of technology have similarly expanded our capacity to survey and monitor cryptic and poorly known mammal species in northern Australia. Bat survey methods based on echolocation call detectors, for example, has greatly expanded the effectiveness and coverage of sampling for insectivorous bats. The continued development of call libraries in tandem with advances in software and hardware technology has significantly improved the number and accuracy of species detected, while automation, along with improved data storage capacity and battery life, has enabled long-term use of detectors at multiple sites in remote areas. Consequently, there is a rapidly improving knowledge base of the distribution and status of the region's rich bat fauna (Reardon *et al.* 2010). It is now possible to plan ambitious survey and monitoring projects employing many hundreds of passive bat detectors across large geographic areas recording for months at a time.

Scat surveys and faecal DNA analyses have been a useful adjunct to some mammal surveys in the region, particularly to detect rare, cryptic, and trap-shy species. Recent advances in genetic analysis now allow for reliable, rapid and cost-effective identification of prey items in predator faeces, predators from prey remains (Banks *et al.* 2003a), herbivore species from their faeces, including north Australian macropods (Telfer *et al.* 2006; Wadley *et al.* 2013), and individuals from faeces or hair samples, which may enable the monitoring of highly threatened species (Banks *et al.* 2003b). Extraction and analyses of DNA extracted from leeches, carrion flies and mosquitoes, may also provide novel methods for improving monitoring of a range of mammal species (Calvignac-Spencer *et al.* 2013; Schnell *et al.* 2012).

Given the resource and logistical constraints of sampling mammals over large and sparsely settled regions of northern Australia, such advances may also allow for greater involvement of landholders and 'citizen scientists', thereby improving our capacity for inventory and monitoring studies across many more sites.

Experimental manipulation

Much of the evidence base about mammal decline and causation has come from inferential or correlative studies. However, is increasing use of experimental manipulation to determine factors contributing to the decline of native mammal fauna. Notable examples include studies of mammal responses to imposed contrasts in fire regimes (Begg *et al.* 1981; Corbett *et al.* 2003; Griffiths 2013; Leahy 2013), predator access (Frank *et al.* 2014), pastoralism (Kutt *et al.* 2012; Legge *et al.* 2011a; Woinarski and Ash 2002), and exposure to cane toads (*Rhinella marina*) (Cabrera-Guzmán *et al.* in press; O'Donnell *et al.* 2010; Webb *et al.* 2008; Webb *et al.* 2011). The results of such studies are described in more detail in sections below on threats.

Modelling

There have been many modelling and other analytical studies that aim to identify the characteristics of Australian mammal species that are most associated with propensity for decline and extinction. Some of these studies specifically or by implication also attempt to evaluate the relative impacts of putative drivers of this decline (Burbidge and McKenzie 1989; Cardillo and Bromham 2001; Chisholm and Taylor 2007; Fisher *et al.* 2014; Johnson and Isaac 2009; McKenzie *et al.* 2007). To date, only one of these studies has focused specifically on decline in the mammal fauna of northern Australia (Fisher *et al.* 2014). That study reported that smaller mammal species, and those in more open habitats, were most likely to have exhibited decline in northern Australia. Fisher *et al.* (2014) concluded from this apparent contrast that predation by feral cats acted in synergy with disturbances that reduced ground cover and simplified vegetation, exposing smaller mammals to greater risk of predation.

Narrowly focussed modelling of demographic parameters of individual species has extrapolated data from short-term studies to indicate marked impacts on population viability in response to different fire regimes (Firth *et al.* 2010; Griffiths 2013; Pardon *et al.* 2003). A constraint of this approach is the relatively limited amount of detailed life history information available for most mammal species in this region, and particularly the extent to which threatening factors and the management of them may affect those parameters.

CURRENT TRENDS ACROSS NORTHERN AUSTRALIA

Much of the evidence for decline in northern Australian mammals derives from intensive monitoring studies on small- to medium-sized (< 5.5 kg) non-volant mammals in Kakadu (Woinarski *et al.* 2010; Woinarski *et al.* 2001). In this section, we assess whether such trends also apply more generally across northern Australia, and across the two mammal groups least well considered in the Kakadu studies, bats and larger macropods.

Status of small and medium-sized non-volant mammals in northern Queensland

Land degradation in northern Australia has been unequal in extent and severity (Figure 3), limited by European settlement patterns, access to markets, human population size and legislative frameworks that have either encouraged or discouraged landscape modification and Indigenous dislocation (Bradshaw 2012). In contrast to the Northern Territory and northern Western Australia, much of Queensland has a long history of agricultural intensification and broad-scale tree clearing which generally pre-dates systematic vertebrate surveys (Fensham 2008; Kutt and Fisher 2011), and there are very few established long-term monitoring programs for mammals in northeastern Australia. Much of the survey effort and reported declines for Queensland mammals have occurred in the fragmented rainforests of the Wet Tropics (Laurance 2004; Williams *et al.* 1996b), not considered as a focus here, where threatening processes are less subtle and similar to processes occurring in transformed landscapes of southern Australia (Lindenmayer *et al.* 1990).

The most threatened assemblage of the extant fauna of northern Queensland comprises species associated with tall eucalypt forests (typically at higher elevations), and mostly adjacent to or intermingled with rainforests in the Wet Tropics region. These relictual forests support a mammal fauna with close links to southeastern Australia (Winter 1997). Prevailing threats are habitat loss and fragmentation, habitat degradation from changed fire regimes (mostly fire suppression), and predation by feral cats. Consequently, the mammals most closely associated with this habitat, such as the northern bettong (*Bettongia tropica*) and an undescribed subspecies of yellow-bellied glider (*Petaurus australis*), are declining (Woinarski *et al.* 2014).

Information on the pre-disturbance state of small mammal populations outside of the unusual elevated east coast is limited, but where available (Kirkpatrick and Lavery 1979; Woinarski *et al.* 2006b) replicates the trends of decline recorded elsewhere in northern Australia (Woinarski *et al.* 2011a). Furthermore, recent analyses of subfossil and other historic records suggest a previously largely undocumented broad-scale decline of many mammal species in the Queensland savannas in the decades following initial European settlement (Cramb and Hocknull 2010; Dickman *et al.* 2000).

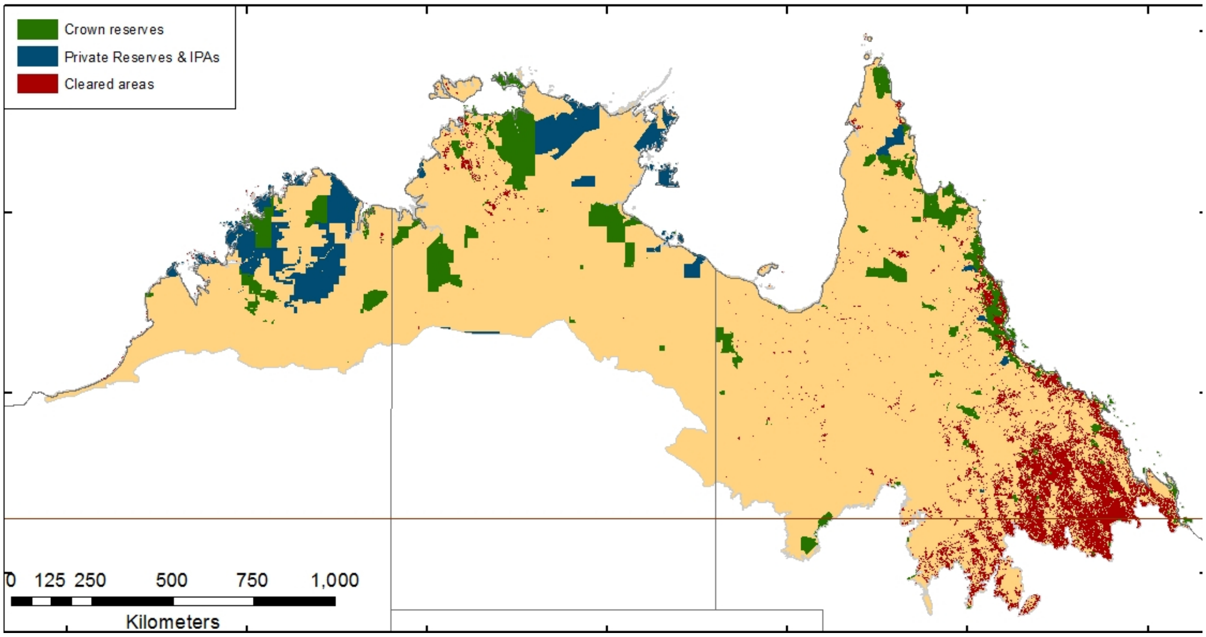

Figure 3. Extent of conservation reserves and habitat loss for savanna woodland environments in northern Australia, illustrating that most native vegetation is relatively intact, other than in the southeast part of the region. Crown reserves (National Parks and similar reserves, with protection under State, Territory or Federal legislation), private reserves (under private tenure, but not conservation protection), and Indigenous Protected Areas (secure tenure, but not necessarily for conservation). Native vegetation clearing data current to 2007 (NT), 2010 (Qld), 2004/5 (WA) from SLATS data (Qld), NT data and NVIS data (WA). Source: Franklin and Preece (2014).

One anomaly may be parts of the Einasleigh Uplands region in central Queensland – an apparent refuge area for mammal populations. A recent survey in Blackbraes National Park in this region uncovered a surprising richness and abundance of mammals (Vanderduys *et al.* 2012). This area, embedded within the broader savanna environment, is among the highest elevation sites in the wet/dry tropics (>1000 m asl), has had comparatively limited disturbance and is characterized by a unique climate (being notably less seasonal than surrounding regions) (Vanderduys *et al.* 2012). However, the Blackbraes site may be a local exception: surveys of six other properties (36 sites) in the Einasleigh Uplands from 2009 to 2012 consistently revealed a low number of mammals, with the trap rate being at the lowest end of what was considered to be 'extremely low' (Russell-Smith *et al.* 2009a) in the Northern Territory (N. Preece, unpublished data).

One unusual example of recent mammal decline in northeastern Australia is the possible extinction since 2009 of the Bramble Cay melomys (*Melomys rubicola*), a species previously endemic to a 5 ha islet in Torres Strait (Figure 1). Its likely extinction seems to have been caused by erosion of the cay and stripping of its vegetation due to storms and rising sea levels (Woinarski *et al.* 2014).

Status of small and medium-sized non-volant mammals in the Top End

The timing, rate and severity of declines in the mammal fauna has varied across the Top End, with earlier and more severe declines generally in lower rainfall inland areas (Finlayson 1961; Ziembicki *et al.* 2013). Rapid recent declines, such as observed in Kakadu since about the 1980s (Woinarski *et al.* 2010; Woinarski *et al.* 2001), occurred later in the 1990s in nearby Litchfield National Park (Russell-Smith *et al.* 2014), and comparably low richness and abundance of small mammals have been recorded for sites in Nitmiluk National Park since 2005 (DLRM, unpublished data). Wildlife surveys at Fish River Station (170 km south of Darwin) in 2011/12 using conventional trapping techniques envountered low site richness and abundance of small mammals, although the subsequent deployment of remote cameras has been very valuable in revealing the persistence, albeit at low densities, of most of the expected regional complement of small mammal species (DLRM, unpublished data).

Previous studies had indicated a probable retention of relatively intact mammal faunas in part of northwestern Arnhem Land subject to ongoing traditional fire management (Yibarbuk *et al.* 2001). However, recent resampling of small mammals at the same sites recorded only the exotic black rat, and further sampling of a number of sites in western Arnhem Land since 2011 has indicated a much diminished small mammal fauna (DLRM, unpublished data). Curiously, some sites in peri-urban areas around Darwin have maintained high densities of several mammal species shown to be declining in more intact Top End environments (Price *et al.* 2005), although recent resampling of these sites indicates a decline of 75 % in overall capture rates between 2001 and 2011 (DLRM, unpublished data).

Mammal faunas appear to have remained relatively intact on some islands –notably Groote Eylandt and the Tiwi islands, although more extensive sampling is required to confirm whether this pattern is consistent across all mammal taxa. Recent surveys on Bathurst Island have shown very high densities of common brushtail possum (*Trichosurus vulpecula*) and confirmed the persistence of brush-tailed rabbit-rat *(Conilurus penicillatus*) but had low reporting rates for smaller ground-active mammals (DLRM, unpublished data). Groote Eylandt is notable for continuing to support high densities of northern quoll (Woinarksi *et al.* 2007, J. Heiniger, pers. comm.) although a current study has had low detection rates for northern hopping mouse (*Notomys aquilo*) in sites where it was previously abundant (R. Diete, pers. comm.), and previously-recorded populations of brush-tailed rabbit-rat have been very rare or absent in more recent sampling.

The localised persistence of mammal species that are declining elsewhere is likely to provide insights into causal factors and requires more systematic attention. For example, high reporting rates on camera traps have recently been reported for black-footed tree-rats (*Mesembriomys gouldii*) within the Gove bauxite mining lease (B. Prowse, pers. comm.), which may be linked to the relatively low frequency and low intensity fire regime maintained within the lease boundaries. Current data suggest that the most recently "intact" small mammal fauna on the Northern Territory mainland is on the Cobourg Peninsula, although systematic monitoring since 2004 shows a substantial decline for brush-tailed rabbit-rat and pale field-rat (*Rattus tunneyi*), and more idiosyncratic changes over time for other mammals, (including fawn antechinus (*Antechinus bellus*), northern brown bandicoot (*Isoodon macrourus*), black-footed tree-rat and common brushtail possum (DLRM, unpublished data; Firth *et al.* 2010; Ziembicki *et al.* 2013).

In contrast to some instances in the Kimberley (Legge *et al.* 2011a), there has been no evidence of recovery of mammal populations in the Top End of the Northern Territory following the imposition of presumed improved management of threats. Recent resampling of the long-term monitoring sites within Kakadu indicates that, while site richness and abundance of small mammals remain very low, there has at least been no further change between the 2012 to 2014 period compared to 2007 to 2009 (DLRM, unpublished data).

Status of small and medium-sized non-volant mammals in the Kimberley

Intact mammal assemblages in recent decades (1994 to 2013) have been restricted to the relatively high rainfall (mean annual rainfall > 900 mm) northwestern Kimberley region adjacent to the coast (Corey *et al.* 2013; McKenzie *et al.* 2007; Radford *et al.* 2014; Start *et al.* 2012). Mammal groups commonly recorded during surveys in this region include all major functional groups found historically: these include marsupial predators (northern quoll, brush-tailed phascogale (*Phascogale tapoatafa*)), omnivores (golden bandicoot (*Isoodon auratus*), northern brown bandicoot, common brushtail possum) and herbivores (e.g. monjon (*Petrogale burbidgei*), scaly-tailed possum (*Wyulda squamicaudata*)); larger rodents (>150 g) (brush-tailed rabbit-rat, golden-backed tree-rat (*Mesembriomys macrurus*) and Kimberley rock-rat (*Zyzomys woodwardi*)); medium (35-150 g) and small rodents (<35 g) (e.g. northern short-tailed mouse (*Leggadina lakedownensis*), grassland melomys (*Melomys burtoni*), delicate mouse (*Pseudomys delicatulus*), western chestnut mouse (*P. nanus*), pale field-rat, common rock-rat (*Zyzomys argurus*)) and small insectivorous dasyurids (*Pseudantechinus ningbing, Sminthopsis* spp.) (Radford *et al.* 2014). However, some medium-sized species have uncertain status in the region. For example, the black-footed tree-rat has not been recorded in the Kimberley since last captured by Bradley *et al.* (1987) in 1981/82 (Corey *et al.* 2013; Radford *et al.* 2014; Start *et al.* 2007). The once common nabarlek (*Petrogale concinna*), a very small rock-wallaby has not been recorded on the Kimberley mainland since 1974, and is now confirmed in the Kimberley on four islands only (Potter *et al.* 2012a; Woinarski *et al.* 2014). The brush-tailed phascogale is another species for which few data are available since surveys in the 1980s, however recent sightings near Mitchell Falls (Woinarski *et al.* 2014) and at Yampi Sound in 2008 (N. Preece, unpublished data) confirm its continued presence in the region albeit at low frequency. Nevertheless, most species found historically are still present.

In contrast to the high rainfall zone, mammal assemblages of the eastern, central and southern Kimberley, with annual rainfall <900 mm, are in disarray and are now predominantly devoid of marsupials and rodents between 150 g and 2 kg (Legge *et al.* 2011a; Legge *et al.* 2008; McKenzie 1981; McKenzie *et al.* 2007; Radford *et al.* 2014; Start *et al.* 2012; Start *et al.* 2007). Scattered localised populations of medium-sized marsupials (e.g. northern quoll, northern brown bandicoot, scaly-tailed possum and golden-backed tree-rat) are occasionally trapped or observed in refuge habitats in the region such as in gorges, on islands or adjacent to townships where some fire protection is apparent

(Gibson and McKenzie 2012; Legge *et al.* 2011a; Potter *et al.* 2014; I. Radford, unpublished data). In recent years (1994-2010), smaller mammals (< 150 g) were at relatively low abundance throughout the medium and low rainfall Kimberley (mammals captured in 2 to 9 % of traps) (Radford *et al.* 2014), but this is still substantially higher than recent documented trap success in much of the Northern Territory and Queensland savannas (Kutt and Gordon 2012; Kutt *et al.* 2012; Woinarski *et al.* 2010). Higher mammal abundance in the medium to low rainfall Kimberley has been recorded at a few sites where careful management of fire and introduced herbivores has led to recovery (Legge *et al.* 2011a; Legge *et al.* 2011b), or where periodic irruptions have occurred in association with major rainfall events (Radford *et al.* 2014). The greater bilby *Macrotis lagotis*, a specialist arid and semi-arid zone medium-sized marsupial, is still present in the arid and semi-arid southern and western Kimberley, however data on its abundance in the region are sparse (Start *et al.* 2012).

Mammal assemblages in the Kimberley are now partitioned along productivity or annual rainfall gradients (McKenzie *et al.* 2007; Radford *et al.* 2014), though this was not the case historically (Johnson 2006; McKenzie 1981; Woinarski *et al.* 2014) with species such as golden bandicoot, northern quoll, pale field-rat and golden-backed tree-rat previously having much wider distributions into more arid areas, even into central Australia. Explanations for this change include a collapse of ecosystem productivity in more fragile arid ecosystems due to intensification of fire and cattle grazing regimes (McKenzie *et al.* 2007), and increased loss of vegetation cover. These changes have resulted in increased predation by introduced cats and foxes (Johnson 2006), more marked predation pressure associated with less extensive shelter (ground vegetation cover) in lower rainfall areas, and changed trophic interactions between top and introduced meso-predators (dingoes versus cats/foxes) (Johnson 2006; Letnic *et al.* 2012; Radford *et al.* 2014).

There is little evidence of declines among the very small (<35 g) mammals in the Kimberley region, with most small species including the small dasyurids (e.g. most *Planigale* spp.) still common. However, data are limited for these species due to their low capture rates using conventional trapping methods (e.g. Elliott traps and wire cage traps). Accurate assessment of the conservation status of this group is therefore problematic and will require significantly more targeted sampling effort (notably pitfall-trapping). Nevertheless, the status of at least one species, Butler's dunnart (*Sminthopsis butleri*), in the Kimberley is of concern. Despite numerous surveys it has not been recorded in the region since its initial discovery in the mid 1960s (Woinarski *et al.* 2014).

Bats

Fifty-five bat species have been recorded from mainland northern Australia (of a total of 80 extant species for the Australian mainland and Tasmania); 33 are Australian endemics. Twenty-nine species have their primary or entire distribution in north Australia. Overall, the group is well represented taxonomically with all eight families and 23 of the 25 genera of Australian bats present. They encompass the full trophic range for Australian bats with frugivores, nectarivores, insectivores, one specialist arachnivore, one partial piscivore and one partial carnivore (Van Dyck and Strahan 2008). Roosting preferences include tree-hollows, caves and rock crevices, open and closed foliage, abandoned bird nests and a range of human-made structures (Churchill 2008).

Only one systematic study has assessed long-term, large-scale distributional changes in bats for mainland Australia (Burbidge *et al.* 2008). The study found that all but one bat species had persisted in more than 50 % of its pre-European settlement range in each of the 18 bioregions that comprise northern Australia. However the geographic distribution of most species is less precisely known than generally appreciated. Surprisingly few records inform the distribution maps. In reviewing the threatened status of microbats on Cape York Peninsula, Reardon *et al.* (2010) found only 1600 records on the best available distributional database (Queensland's 'Wildnet'). Nearly half of the

31 species were known from fewer than 10 localities. The number of records for each species was also low with 75 % of the species known from fewer than 50 records each. The sparseness of information is similar in the Northern Territory, where Milne and Pavey (2011) reported that bats comprised only 11% of all terrestrial mammal records. This percentage translates to about 3000 records from that area, a mean of about 100 records per species. These studies also highlight two important issues with the historic records: the first is that the large area encompassing southwestern Cape York Peninsula, the Gulf region and eastern Arnhem Land has been substantially under-surveyed, and secondly, that wet season records are poorly represented.

The bat fauna of the Torres Strait Islands is particularly poorly documented. Over 250 islands span the 150 km gap between the tip of Cape York Peninsula and New Guinea. Most of these are too small to support bat populations but at least 20 are large enough to have resident or transient bat populations. About 22 bat species are common to northern Australia and New Guinea, and a further 20 endemic species (5 from Australia and 15 from southern New Guinea) could potentially contribute to the complement for all the islands (Bonaccorso 1998; Van Dyck *et al.* 2013). Australia has a vital interest in biosecurity threats arriving from this northern route. For many bat species, bridging the gap between New Guinea and Australia via stepping stone islands is very plausible. Thus far the only confirmation of individual bats crossing the gap is for the large flying–fox *Pteropus alecto* (Breed *et al.* 2010). Possible threats to the bat fauna of the islands include habitat loss to agriculture, hunting (flying-foxes for food), and rising sea level. There is a substantial need for bat survey work across the straits.

Although bats make up a significant component of native mammal fauna of northern Australia, in contrast to the comparatively better defined conservation trends for non-volant mammals, relevant information is largely unavailable for most bats and they have received much less research attention than other mammal groups. Recent assessments of the conservation status of bats for the Action Plan for Australian Mammals (Woinarski *et al.* 2014) and Queensland's Back on Track Threatened Species Priority program, have highlighted the lack of robust information about populations for most bat species. Because occurrence records have been so patchily accumulated over time and space, they do not form an adequate basis for population size and trend analyses. Of concern is the possibility that many bat species could be suffering significant local or even widespread declines without our knowledge. At this time, there is evidence that four bat species are undergoing population declines in the north. Population monitoring of spectacled flying-fox (*Pteropus conspicillatus*) in parts of its range suggest a potential decline of up to 50% in the last decade (Buettner *et al.* 2013; Fox 2011). Three cave-dwelling bat species have disappeared from several formerly occupied sites including the Arnhem leaf-nosed bat (*Hipposideros inornatus*) from Litchfield National Park, northern leaf-nosed bat (*H. stenotis*) from many caves across its range (Milne and Pavey 2011), and the ghost bat from sites in Boodjamulla National Park (in northwestern Queensland) and some roost sites in Kakadu (A. White, pers. comm.). There is a need for a concerted effort to establish a baseline, and improvements in technology now make this feasible.

In the absence of information on trends for bat species in northern Australia, it is difficult to identify threats, and the risk posed by putative threats, and to recommend conservation management responses. Indeed, even where declines (including extinctions) have been reported for Australian bats, it has sometimes been very difficult to identify the principal causal factors, and a decline may be due to a complex interaction of multiple threats (Lunney *et al.* 2011). However, some factors are recognised, or are likely, to be causing population-level declines in some bat species in northern Australia. This complement of threats is likely to differ among bat groups, and to differ between bats and other native mammals. Flying-foxes face a medley of threats, with persecution in some areas (particularly in orchards and around towns), tick paralysis, disease, and vegetation loss and change (Fox 2011). Bats that roost colonially in caves and abandoned mines are affected by disturbance and mining activity. Bats that roost in tree hollows may be affected by competition with introduced species (such as honey bees) and increased abundance of some other native hollow-nesting species, particularly in areas where hollow availability may be reduced because of vegetation loss or changed fire regimes. Like non-volant mammals, insectivorous bats in northern Australia may respond to pastoralism and changes in fire regimes, where these affect the abundance of their invertebrate prey. Frugivorous and nectarivorous bats may in turn respond to changed fire regimes where these affect the timing and abundance of fruit and nectar. The decline in non-volant small mammals may directly affect the abundance of the ghost bat, whose diet includes small mammals. Broad-scale decline of non-volant small mammals may also affect bats indirectly, if predators (such as owls and raptors) are forced to prey more substantially on bats in compensation for reduced availability of non-volant mammals. Substantially more research is required to resolve the impacts of such probable threats on the population and conservation security of the bat fauna of northern Australia.

Macropodids and potoroids

Elsewhere in Australia, potoroids (bettongs, potoroos and rat-kangaroos) have suffered a very high rate of extinction and decline, and many macropods (wallabies, tree-kangaroos, rock-wallabies, pademelons and kangaroos) have also exhibited substantial declines. In contrast, in northern Australia there have been no extinctions among the diverse assemblage of macropodids, or of the two bettong species.

With a focus here on tropical savannas, we exclude from consideration a small suite of macropods restricted to, or largely associated with rainforests of the Wet Tropics: these comprise two tree kangaroos (*Dendrolagus* spp.), the musky rat-kangaroo (*Hypsiprymnodon moschatus*) and red-legged pademelon (*Thylogale stigmatica*).

The bridled nailtail wallaby is arguably a component of the north Australian fauna, with a former range encompassing much of inland eastern Australia. This species has disappeared from almost all of its range except for a single remnant population, of about 100 individuals, at Taunton Scientific Reserve near the northern extremity of its former range (this population is at the southeastern edge of the north Australian region considered here). It has recently been reintroduced to three additional sites, with marked population increase at the one site at which introduced predators have been excluded by fencing. This site, Scotia Wildlife Sanctuary, now supports > 90% of individuals of the species (Woinarski *et al.* 2014).

With 14 species, the rock-wallabies (*Petrogale* spp.), are the most speciose group of macropods in northern Australia. Reflecting the highly fragmented nature of the rocky environments of northern Australia, and the rock-wallabies' limited dispersal ability, many of these species have very small and fragmented distributions (Potter *et al.* 2014a; Potter *et al.* 2012a). Although there have been no substantial and long-lasting monitoring programs, the limited available evidence suggests that many rock-wallabies in northern Australia are undergoing rapid decline, most likely associated with predation by feral cats, inappropriate fire regimes and, in some localities, habitat degradation due to livestock and feral animals (Woinarski *et al.* 2014). Of the 14 rock-wallaby species occurring in northern Australia, four are now considered threatened and five Near Threatened (Woinarski *et al.* 2014).

The remaining macropodids in northern Australia include 14 species from seven genera (*Aepyprymnus, Bettongia, Lagorchestes, Macropus, Onychogalea, Thylogale,* and *Wallabia*). Of these species, only the northern bettong is considered threatened: this species occupies a narrow band of forest on the south-east margin of the study area, subject to a suite of specific threats (see above). None of the other macropodids are threatened, but two of these species (spectacled hare-wallaby and black wallaroo (*M. bernardus*)) are Near Threatened (Woinarski *et al.* 2014). As a group, macropodids are very poorly studied within the region (Ritchie 2010), and rufous bettong

(*A. rufescens*), spectacled hare-wallaby and northern nailtail wallaby (*O. unguifera*) in particular, all appear to be good candidates for species at risk. The causes of their poor status are likely the same set of threats as for other species, given that congeners or species of similar size and ecology have shown marked declines or extinctions elsewhere in Australia. Macropodids typically occur at very low abundance across the region (Ritchie *et al.* 2008), especially as compared to the high abundance of some species of *Macropus* in southern Australia. Due to a lack of systematic historical baselines it is hard to know whether this pattern represents a natural state, perhaps in part based on low fertility soils (Ritchie *et al.* 2009), or if it reflects changes to savanna habitats through intensified cattle grazing, altered fire regimes and introduced pasture plants, as well as the impacts of cats and foxes on the smaller-bodied macropodids.

The most recent and extensive research work on macropodids within northern Australia examined the distribution and abundance of antilopine wallaroo (*M. antilopinus*), eastern grey kangaroo (*M. giganteus*) and euro (*M. robustus*) at 50 sites spanning Cape York Peninsula, the Top End of the Northern Territory, and Kimberley region of Western Australia (Ritchie *et al.* 2009; Ritchie *et al.* 2008). Fire regime, the availability of water, geology and soil type, and climate were the most important factors influencing macropodids at a broad scale. Antilopine wallaroos appear to be favoured by frequent fires whereas euros are not, and indeed frequent fires within savanna habitats that remove understorey vegetation and dry out rainforest, may reduce habitat for species such as black-striped wallaby (*M. dorsalis*) and red-legged pademelon (in northeastern Australia). Decreasing available cover also exposes other species to increased risk of predation by feral cats and (in the southern edge of the region considered here) the introduced red fox. Climate change is expected to increase the frequency and severity of fire, as well as affecting water availability, with some species (antilopine wallaroo) predicted to suffer extensive range contractions as a result (Ritchie and Bolitho 2008).

To enhance their conservation management and security, considerably more research and monitoring is required for macropodids within the region, with the most pressing needs being for black wallaroo (Telfer and Garde 2006; Telfer et al. 2008), spectacled hare-wallaby, northern nailtail wallaby and most rock-wallaby species.

Numbers and trends for threatened species

The conservation status of all native mammal species in northern Australia, as recognised globally, under Australian legislation, and as assessed in the most recent comprehensive review is given in Table 1. For a variety of reasons, these status assessments vary markedly. Of 160 mammal species, 18 are listed by the IUCN as threatened, 23 are listed under national legislation as threatened, and 26 were assessed as threatened (with a further two species considered extinct, and another 29 species considered Near Threatened) in the most recent review (Woinarski *et al.* 2014).

All of the more speciose taxonomic groups of mammals in northern Australia have some species whose conservation status has been assessed as threatened by Woinarski *et al.* (2014), but the proportions vary among groups, with 53 % of dasyurids, 47 % of macropods and potoroids, 33% of bandicoots and bilby, 33 % of possums, 30 % of rodents, and 24 % of bats assessed as extinct, threatened or Near Threatened.

The overall conservation status of mammals endemic to northern Australia is still substantially better than for the mammal fauna elsewhere in Australia (Figsures 2, 4), which suffered very severe rates of decline and extinction, mostly in the period from the 1840s to the 1960s (Woinarski *et al.* 2014). However, the current rate of decline for mammals in northern Australia probably now surpasses that elsewhere in Australia (Figure 4; Woinarski *et al.* 2014).

Table 1. List of mammal species occurring in northern Australia at the time of European settlement. Note that this excludes the Wet Tropics area of northeastern Australia. Distribution (at the time of European settlement) is *in addition to* northern Australia: R=other parts of Australia; X=extralimital. Conservation status is given as for Australian national legislation (EPBCA), the IUCN Red List, and as assessed in the 2012 Action Plan for Australian Mammals (MAP) (Woinarski *et al.* 2014). Conservation status categories: EX extinct, CR(PE) Critically Endangered (Possibly Extinct), CR Critically Endangered, EN Endangered, VU Vulnerable, NT (CD) Near Threatened (Conservation Dependent), NT Near Threatened, LC Least Concern, DD Data Deficient. Note that MAP and EPBCA status refer to Australian range only.

Scientific name	**Common name**	**Distribution**	**Conservation status**		
			EPBCA	**IUCN**	**MAP**
TACHYGLOSSIDAE					
Tachyglossus aculeatus	Short-beaked echidna	RX		LC	LC
Zaglossus bruijnii	Western long-beaked echidna	X		CR	EX
ORNITHORHYNCHIDAE					
Ornithorhynchus anatinus	Platypus	R		LC	NT
DASYURIDAE					
Antechinomys laniger	Kultarr	R		LC	LC
Antechinus bellus	Fawn antechinus			LC	VU
Antechinus leo	Cinnamon antechinus			LC	LC
Pseudantechinus bilarni	Sandstone antechinus			NT	LC
Pseudantechinus mimulus	Carpentarian antechinus		VU	EN	NT
Pseudantechinus ningbing	Ningbing antechinus			LC	LC
Dasyurus hallucatus	Northern quoll	R	EN	EN	EN
Phascogale pirata	Northern brush-tailed phascogale		VU	VU	VU
Phascogale tapoatafa	Brush-tailed phascogale	R		NT	NT
Planigale ingrami	Long-tailed planigale	R		LC	LC
Planigale maculata	Common planigale	R		LC	LC
Sminthopsis archeri	Chestnut dunnart	X		DD	NT
Sminthopsis bindi	Kakadu dunnart			LC	NT
Sminthopsis butleri	Butler's dunnart		VU	VU	VU
Sminthopsis douglasi	Julia Creek dunnart		EN	NT	NT
Sminthopsis macroura	Stripe-faced dunnart	R		LC	LC
Sminthopsis virginiae	Red-cheeked dunnart	X		LC	LC
PERAMELIDAE					
Echymipera rufescens	Long-nosed echymipera	X		LC	LC
Isoodon auratus	Golden bandicoot	R	VU*	VU	VU
Isoodon macrourus	Northern brown bandicoot	RX		LC	LC
Isoodon peninsulae	Cape York brown bandicoot				LC
Perameles pallescens	Northern long-nosed bandicoot				LC
THYLACOMYIDAE					
Macrotis lagotis	Bilby	R	VU	VU	VU
PHASCOLARCTIDAE					
Phascolarctos cinereus	Koala	R	(VU)	LC	VU

Scientific name	Common name	Distribution	Conservation status		
			EPBCA	IUCN	MAP
VOMBATIDAE					
Lasiorhinus krefftii	Northern hairy-nosed wombat	R	EN	CR	CR
PETAURIDAE					
Dactylopsila trivirgata	Striped possum	RX		LC	LC
Petaurus australis	Yellow-bellied glider	R		LC	NT
Petaurus breviceps	Sugar glider	RX		LC	LC
Petaurus gracilis	Mahogany glider		EN	EN	EN
Petaurus norfolcensis	Squirrel glider	R		LC	LC
PSEUDOCHEIRIDAE					
Petauroides volans	Greater glider	R		LC	VU
Petropseudes dahli	Rock ringtail possum			LC	LC
ACROBATIDAE					
Acrobates pygmaeus	Feathertail glider	R		LC	LC
PHALANGERIDAE					
Spilocuscus maculatus	Common spotted cuscus	RX		LC	LC
Phalanger mimicus	Southern common cuscus	RX		LC	LC
Trichosurus vulpecula	Common brushtail possum	R		LC	LC
Wyulda squamicaudata	Scaly-tailed possum			DD	NT
POTOROIDAE					
Aepyprymnus rufescens	Rufous bettong	R		LC	LC
Bettongia lesueur	Boodie	R		NT	NT (CD)
Bettongia tropica	Northern bettong		EN	EN	EN
MACROPODIDAE					
Lagorchestes conspicillatus	Spectacled hare-wallaby	RX		LC	NT
Macropus agilis	Agile wallaby	RX		LC	LC
Macropus antilopinus	Antilopine wallaroo			LC	LC
Macropus bernardus	Black wallaroo			LC	NT
Macropus dorsalis	Black-striped wallaby	R		LC	LC
Macropus giganteus	Eastern grey kangaroo	R		LC	LC
Macropus parryi	Whiptail wallaby	R		LC	LC
Macropus robustus	Euro	R		LC	LC
Macropus rufus	Red kangaroo	R		LC	LC
Onychogalea fraenata	Bridled nailtail wallaby	R	EN	EN	VU
Onychogalea unguifera	Northern nailtail wallaby			LC	LC
Petrogale assimilis	Allied rock-wallaby			LC	LC
Petrogale brachyotis	Western short-eared rock-wallaby			LC	LC
Petrogale burbidgei	Monjon			NT	NT
Petrogale coenensis	Cape York rock-wallaby			NT	EN
Petrogale concinna	Nabarlek			DD	NT

Scientific name	Common name	Distribution	Conservation status		
			EPBCA	IUCN	MAP
Petrogale godmani	Godman's rock-wallaby			LC	NT
Petrogale herberti	Herbert's rock-wallaby			LC	LC
Petrogale inornata	Unadorned rock-wallaby			LC	LC
Petrogale lateralis	Black-footed rock-wallaby	R		NT	VU
Petrogale mareeba	Mareeba rock-wallaby			LC	NT
Petrogale persephone	Proserpine rock-wallaby		EN	EN	EN
Petrogale purpureicollis	Purple-necked rock-wallaby			LC	NT
Petrogale sharmani	Mount Claro rock-wallaby			NT	VU
Petrogale wilkinsi	Eastern short-eared rock-wallaby			LC	LC
Thylogale stigmatica	Red-legged pademelon	RX		LC	LC
Wallabia bicolor	Swamp wallaby	R		LC	LC
NOTORYCTIDAE					
Notoryctes caurinus	Kakarratul	R	EN	DD	LC
PTEROPODIDAE					
Dobsonia magna	Bare-backed fruit bat	X		LC	LC
Macroglossus minimus	Northern blossom bat	RX		LC	LC
Nyctimene robinsoni	Eastern tube-nosed bat	R		LC	LC
Pteropus alecto	Black flying-fox	RX		LC	LC
Pteropus conspicillatus	Spectacled flying-fox	RX	VU	LC	NT (CD)
Pteropus macrotis	Large-eared flying-fox	X		LC	LC
Pteropus scapulatus	Little red flying-fox	R		LC	LC
Syconycteris australis	Eastern blossom bat	RX		LC	LC
MEGADERMATIDAE					
Macroderma gigas	Ghost bat	R		VU	VU
RHINOLOPHIDAE					
Rhinolophus megaphyllus	Eastern horseshoe-bat	RX		LC	LC
Rhinolophus 'intermediate'	Lesser large-eared Horseshoe-bat				VU
Rhinolophus robertsi	Greater large-eared Horseshoe-bat		VU**		NT
HIPPOSIDERIDAE					
Hipposideros ater	Dusky leaf-nosed bat	X		LC	LC
Hipposideros cervinus	Fawn leaf-nosed bat	X		LC	NT
Hipposideros diadema	Diadem leaf-nosed bat	X		LC	NT
Hipposideros inornatus	Arnhem leaf-nosed bat			VU	EN
Hipposideros semoni	Semon's leaf-nosed bat	RX	EN	DD	NT
Hipposideros stenotis	Northern leaf-nosed bat			LC	NT
Rhinonicteris aurantia	Orange leaf-nosed bat	R		LC	LC
EMBALLONURIDAE					
Saccolaimus flaviventris	Yellow-bellied sheath-tailed bat	R		LC	LC
Saccolaimus mixtus	Cape York sheath-tailed bat	X		DD	NT
Saccolaimus saccolaimus	Bare-rumped sheath-tailed bat	X		LC	NT

Scientific name	Common name	Distribution	Conservation status		
			EPBCA	IUCN	MAP
Taphozous australis	Coastal sheath-tailed bat	RX		NT	NT
Taphozous georgianus	Common sheath-tailed bat	R		LC	LC
Taphozous kapalgensis	Arnhem sheath-tailed bat			LC	LC
Taphazous troughtoni	Troughton's sheath-tailed bat			DD	LC
MOLOSSIDAE					
Austronomus australis	White-striped free-tailed bat	R		LC	LC
Chaerephon jobensis	Greater northern free-tailed bat	RX		LC	LC
Mormopterus eleryi	Bristle-faced free-tailed bat	R		LC	LC
Mormopterus lumsdenae	Northern free-tailed bat	R			LC
Mormopterus ridei	Eastern free-tailed bat	R			LC
Mormopterus halli	Cape York free-tailed bat				DD
Mormopterus cobourgianus	North-western free-tailed bat	R			LC
MINIOPTERIDAE					
Miniopterus australis	Little bent-winged bat	RX		LC	LC
Miniopterus orianae	Common bent-wing bat	RX		NT	LC
VESPERTILIONIDAE					
Chalinolobus gouldii	Gould's wattled bat	R		LC	LC
Chalinolobus nigrogriseus	Hoary wattled bat	RX		LC	LC
Murina florium	Flute-nosed bat	RX		LC	NT
Myotis macropus	Large-footed myotis	RX		LC	LC
Nyctophilus arnhemensis	Northern long-eared bat	R		LC	LC
Nyctophilus bifax	Eastern long-eared bat	RX		LC	LC
Nyctophilus daedalus	Pallid long-eared bat				LC
Nyctophilus geoffroyi	Lesser long-eared bat	R		LC	LC
Nyctophilus gouldi	Gould's long-eared bat	R		LC	LC
Nyctophilus walkeri	Pygmy long-eared bat			LC	LC
Phoniscus papuensis	Golden-tipped bat	RX		LC	LC
Pipistrellus adamsi	Cape York pipistrelle			LC	LC
Pipistrellus westralis	Northern pipistrelle			LC	LC
Scotorepens balstoni	Inland broad-nosed bat	R		LC	LC
Scotorepens greyii	Little broad-nosed bat	R		LC	LC
Scotorepens sanborni	Northern broad-nosed bat	RX		LC	LC
Vespadelus caurinus	Western cave-bat			LC	LC
Vespadelus douglasorum	Yellow-lipped cave bat			LC	LC
Vespadelus finlaysoni	Inland cave bat	R		LC	LC
Vespadelus troughtoni	Eastern cave bat	R		LC	LC
MURIDAE					
Conilurus capricornensis	Capricornian rabbit-rat	R			EX
Conilurus penicillatus	Brush-tailed rabbit-rat	X	VU	NT	VU
Hydromys chrysogaster	Water-rat	RX		LC	LC
Leggadina lakedownensis	Northern short-tailed mouse	R		LC	LC
Melomys burtoni	Grassland melomys	R		LC	LC

Scientific name	Common name	Distribution	Conservation status		
			EPBCA	IUCN	MAP
Melomys capensis	Cape York melomys			LC	LC
Melomys cervinipes	Fawn-footed melomys	R		LC	LC
Melomys rubicola	Bramble Cay melomys		EN	CR	CR (PE)
Mesembriomys gouldii	Black-footed tree-rat			NT	VU
Mesembriomys macrurus	Golden-backed tree-rat		VU	LC	NT
Notomys alexis	Spinifex hopping-mouse	R		LC	LC
Notomys aquilo	Northern hopping-mouse		VU	EN	VU
Pogonomys sp.	Tree mouse	R		LC	LC
Pseudomys calabyi	Kakadu pebble-mouse			VU	NT
Pseudomys delicatulus	Delicate mouse	RX		LC	LC
Pseudomys desertor	Desert mouse	R		LC	LC
Pseudomys gracilicaudatus	Eastern chestnut mouse	R		LC	LC
Pseudomys johnsoni	Central pebble-mouse	R		LC	LC
Pseudomys nanus	Western chestnut mouse			LC	LC
Pseudomys patrius	Eastern pebble-mouse	R		LC	LC
Rattus colletti	Dusky rat			LC	LC
Rattus fuscipes	Bush rat	R		LC	LC
Rattus leucopus	Cape York rat	RX		LC	LC
Rattus lutreolus	Swamp rat	R		LC	LC
Rattus sordidus	Canefield rat	R		LC	LC
Rattus tunneyi	Pale field-rat	R		LC	LC
Rattus villosissimus	Long-haired rat	R		LC	LC
Uromys caudimaculatus	Giant white-tailed rat	RX		LC	LC
Xeromys myoides	Water mouse	RX	VU	VU	VU
Zyzomys argurus	Common rock-rat	R		LC	LC
Zyzomys maini	Arnhem rock-rat		VU	NT	VU
Zyzomys palatalis	Carpentarian rock-rat		EN	CR	CR
Zyzomys woodwardi	Kimberley rock-rat			LC	LC
CANIDAE					
Canis dingo	Dingo	R		LC	NT

* for subspp *Isoodon auratus auratus* and *I. a. barrowensis*; ** as *Rhinolophus philippensis* 'large form'

The number and timing of mammal extinctions following European settlement in northern Australia is not well resolved. In addition to the four recent extinctions based on subfossil records, the western long-beaked echidna (*Zaglossus bruijni*), formerly considered endemic to New Guinea, has been recognised recently to have occurred in Australia on the basis of a single quixotic, but apparently reliable, specimen record from the Kimberley in 1901 (Helgen *et al.* 2012).

IDENTIFICATION OF POTENTIAL CAUSES OF DECLINES

The important drivers of declines in north Australian mammal assemblages act in synergy and present a complex set of interactions, with varying levels of impact on mammals, that has hampered co-ordinated and focussed management and conservation actions. Here we examined the suite of drivers of change in mammal status in north Australia.

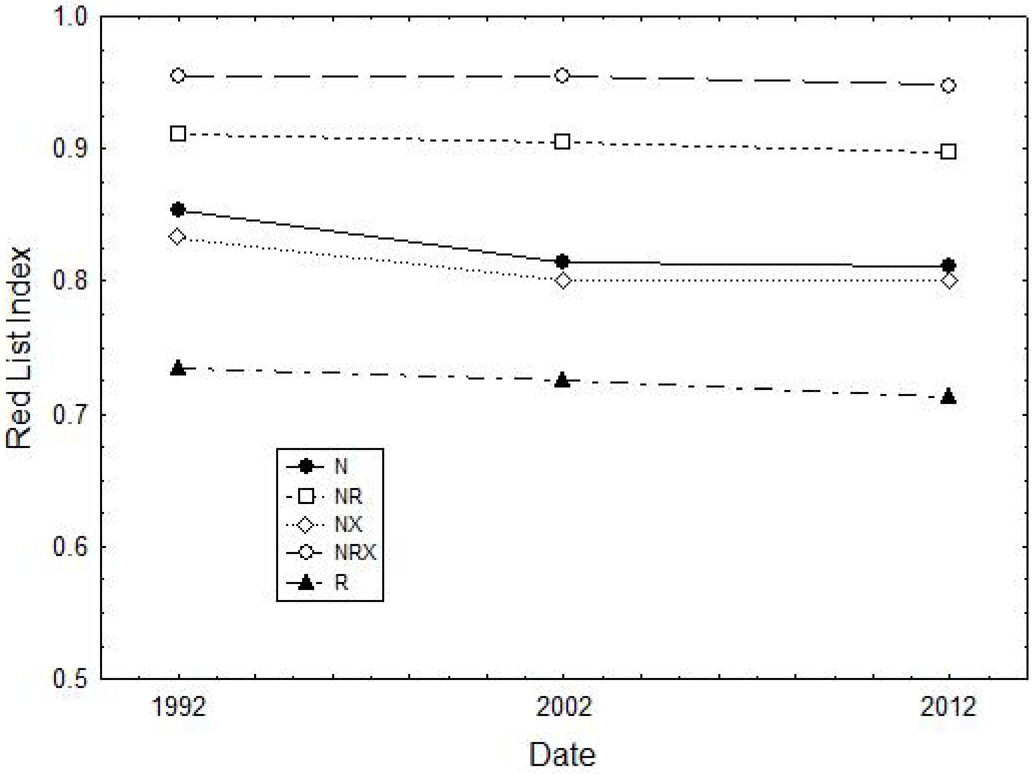

Figure 4. Change over the last 20 years in overall conservation status of geographic groupings of mammals. Note that this uses the Red List Index (Butchart *et al.* 2010; Hoffmann *et al.* 2010; Szabo *et al.* 2012), which varies from 0 (if all species formerly present are now recognised to be extinct) to 1 (if all species are recognised as Least Concern). Values are calculated from information in (Woinarski *et al.* 2014), and use a benchmark date of 1788 (the time of initial European settlement of Australia).

Groups of species: N=mammal species occurring only in northern Australia (n=53), NR= mammal species occurring in northern Australia and elsewhere in Australia (n=61); NX=mammal species occurring in northern Australia (but not the rest of Australia) and extralimitally (n=12); NRX=mammal species occurring in northern Australia, elsewhere in Australia, and extralimitally (n=31); R=mammal species endemic to Australia but not occurring in northern Australia (n=150).

A conceptual model

A conceptual framework, summarised below, was recently put forward in an attempt to unify current theory on mammal declines in northern Australia (Radford *et al.* 2014). This schematic model is based on evidence from the Kimberley region and has not yet been tested, hence its accuracy and broader applicability remains to be determined. The framework tackles competing hypotheses and inconsistent observations within a context of limited understanding of the functional relationships between mammal assemblages and their savanna environments and processes. A simplified conceptual framework that summarises the primary factors and their interactions responsible for declines in north Australian mammal assemblages is presented in Figure 5.

This framework is a state and transition model similar to that developed for arid zone plant populations (Westoby et al. 1989) and more recently for Australian arid zone mammals (Letnic and Dickman 2010). In this framework, successive assemblage states are defined by functional composition and profile. In application of this model to the Kimberley savannas of northwestern Australia, "State 3" assemblages included all the critical weight range mammal functional groups (including slow reproducing arboreal rodents, omnivorous peramelids, predatory dasyurids, fast reproducing omnivorous rodents and low resource requiring small dasyurids); "State 2" assemblages had fewer functional groups and were dominated by omnivorous rodents, but also with small dasyurids as a minor component; and "State 0" assemblages had very low numbers of omnivorous rodents and small dasyurids (Radford *et al.* 2014). "State 1", an assemblage dominated by small dasyurids, was seldom observed in savannas (Radford *et al.* 2014) and may be restricted to arid grasslands (Letnic and Dickman 2010). Transition processes causing change between states included previously identified threatening processes (e.g. fire, cat predation and cattle grazing: Woinarski *et al.* 2011a), or processes leading to population irruption (high rainfall: Letnic and Dickman 2010). Transitions may occur periodically in savannas, for instance, with boom-bust cycles caused by major rainfall events followed by drought (Letnic and Dickman 2010; Radford *et al.* 2014). However, longer term trends within this framework, particularly declines in assemblage functional diversity, could lead to irreversible transitions at local or national scales.

The distribution of mammal assemblage states in the Kimberley provides insights into the tenability of hypotheses raised to explain mammal declines. The importance of productivity in assemblage distributions lends support to the ecosystem productivity collapse hypothesis proposed by McKenzie *et al.* (2007). Under this hypothesis, loss of functional diversity is directly linked to natural productivity gradients and collapse is due to degradation through grazing and fire. Preferential loss of functional diversity in lower rainfall, lower production savannas may indicate productivity collapse in these more marginal areas for mammals. Conversely, regional assemblage patterns do not support a dominant effect of fire regime (Andersen *et al.* 2005; Legge *et al.* 2008; Woinarski *et al.* 2010) or cattle grazing in isolation (Legge *et al.* 2011a). This is because diverse mammal assemblages (State 3) in the high rainfall region of north Kimberley do not coincide with the lowest fire and cattle activity. The distribution of "State 3" assemblages in high productivity areas is also not consistent with predictions relating to the cat predation hypothesis (Johnson 2006).

Cat predation impacts should be highest under high ecosystem resource levels in the high rainfall north Kimberley because of greater and more predictable food resource availability and increased abundance of mammal 'prey', leading to larger cat populations and greater predation rates. Increases in cat populations that result in increased predation pressure have been observed in arid zone systems after major rainfall events (Letnic and Dickman 2010). Cat predation effects may however be ameliorated by interacting processes in high rainfall savannas. Predation rates by cats may be limited by increased vegetation complexity/cover for mammals in high rainfall savannas (Johnson 2006; Radford 2012). Similarly cat predation rates may be reduced by interactions with increasing numbers of the meso-predator, the dingo, in high rainfall regions (Johnson 2006; Letnic *et al.* 2012; Radford *et al.* 2014). It is difficult to predict outcomes of interactions between vegetation complexity and predators because cats also gain greater protection from dingoes in high productivity ecosystems due to their more complex vegetation. Nevertheless, cats should be more vulnerable to predation by dingoes, and small mammals should experience greater release from predation, in low production, arid and semi-arid ecosystems where there is less habitat cover to protect cats. More research is needed to evaluate the relative importance of productivity-mediated predator interactions (McKenzie *et al.* 2007; Radford *et al.* 2014) versus habitat structure-mediated interactions (Johnson 2006), in determining mammal assemblage structure in northern savannas. Research of the effects of grazing and fire regimes on site productivity and predation rates will also be useful in establishing a functional link between predators and land management. Experiments are necessary to isolate the potential effects of site productivity, productivity degrading processes (e.g. cattle and fire), predator interactions and habitat simplification to disentangle the key mechanisms that are responsible for mammal declines across northern Australian savannas (Radford 2010; Williams *et al.* 2003a; Woinarski *et al.* 2011a).

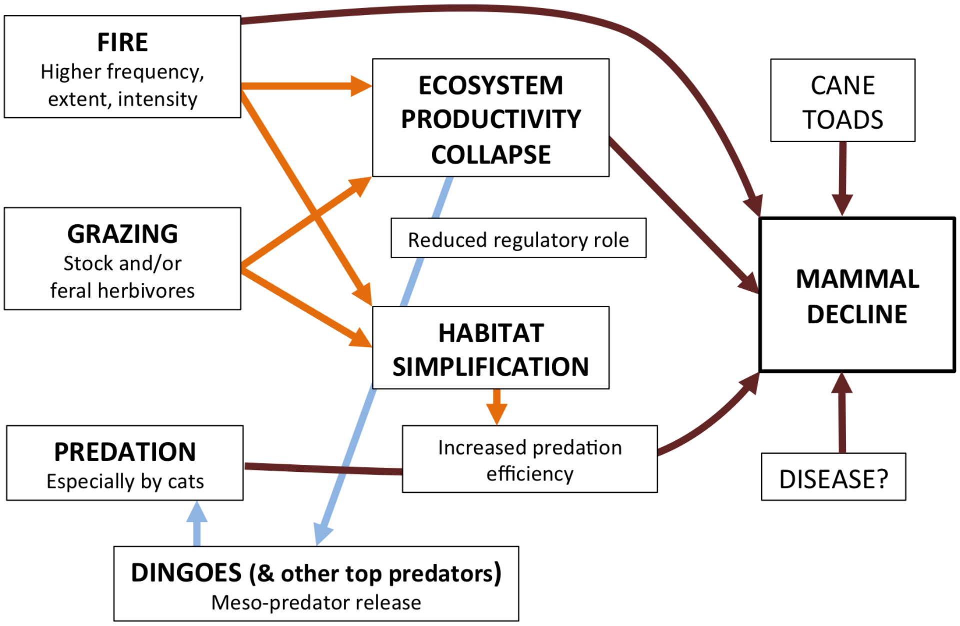

Figure 5. A conceptual framework outlining the main factors contributing to the decline of native mammals in northern Australia

Predation by feral cats

In other parts of Australia several studies have demonstrated remarkable recovery of many native mammal species to the control of feral predators, particularly through the establishment of predator-proof fencing (Moseby *et al.* 2009). In northern Australia, recent studies have either used relatively small-scale exclosure fencing to quantify cat predation behaviour and rates, or larger-scale manipulations of fire and stock management to explore their effects on feral cat (and native mammal) behaviour and survival. Exclosure fencing has been used to explore cat impacts in two complementary studies. A recent manipulative experimental study at Wongalara about 200 km southeast of Kakadu (Figure 1) compared the survival of translocated long-haired rats *Rattus villosissimus* in two sets of matched pairs of 12.5 ha enclosures. Each pair was comprised of one enclosure that was accessible and another that was inaccessible to feral cats (Frank *et al.* 2014). In a first translocation of 77 individuals, rats in the cat-accessible plots were rapidly extirpated due to predation by cats, while rats in the cat-proof plots persisted (Frank *et al.* 2014). Rats used in this translocation were sourced from cat-free Quoin Island in the Northern Territory and captive bred to increase numbers prior to release; two factors that may have compromised the ability of these translocated rats to evade predation. A second translocation using pale field-rats was initiated in a wild-to-wild translocation, with rats sourced from an area where native mammals coexist with feral cats. A program of cat removal and deterrence was conducted around the experimental plots before and during the translocation. Similar results ensued: the pale field-rat populations in the cat-accessible plots were rapidly extirpated (Tuft *et al.* 2014). These experiments suggest that it may be difficult to re-establish small mammal populations in areas where the original mammal fauna has collapsed when feral cats are present.

At Kakadu, two exclosure fences (of 64 ha each) were constructed and cleared of feral cats in late 2013 to examine whether native mammals can 'naturally' rebound in cat-free areas without translocating individuals. Intensive baseline sampling of mammals and reptiles was undertaken within the exclosures and in four unfenced control sites nearby demonstrated extremely low mammal species richness and capture rates (<1 %) across all sites (DLRM, unpublished data). Two surveys of the exclosures within the first eight months of the study failed to detect signs of mammal recovery. These are preliminary findings, however, and it may take several years for species with low baseline population sizes to exhibit an increase. This experimental approach has several limitations: the size of the enclosures potentially limits the population base size from which a treatment response can be elicited. Although the exclosures are permeable to small rodents and dasyurids, medium sized species such as adult quolls and bandicoots are excluded. Furthermore, in addition to excluding feral cats, the fences exclude dingoes/dogs, pigs, macropods and buffalo, thus limiting inference of the cause of treatment effects.

In a different approach, recent work in the Kimberley has demonstrated how changes to vegetation structure wrought by fire and introduced herbivores can substantially amplify the effect of feral cats on native mammals. The research provides a mechanistic explanation underpinning mammal declines. Cat movement and hunting behaviour were compared across large areas (tens of thousands of hectares) with varying cattle stock densities and fire treatments in the central Kimberley. This study examined the movements of thirty-two GPS-collared cats, and the novel deployment of miniature cameras on collars attached to cats to visualise very fine-scale habitat selection and hunting preferences. Grazing by introduced herbivores, and high fire intensities, both modified vegetation structure in ways that advantaged cats. The cameras showed that the likelihood of a cat making a successful kill increased nearly three fold in open habitats, compared with dense grass or complex rock habitats (McGregor 2014). GPS collar data showed that cats preferred to spend time hunting in areas of open grass cover, especially heavily grazed areas and areas burnt in high intensity fires, particularly if those habitats had a high abundance of small mammals (McGregor *et al.* 2014). In fact, areas burnt by intense fires were so attractive to cats that almost all cats within a 15 km radius of the fire edge made extra-territorial forays to visit these burnt areas. The influxes of cats to these burnt areas created localized increases in cat density that amplified up to 16-fold the predation rates by cats on resident small mammals (McGregor 2014).

In a complementary study, the movement, fecundity and survival of native rodents in contrasting experimental fire treatments were contemporaneously examined in Mornington Sanctuary. High intensity (all understorey vegetation removed) and low intensity (understorey vegetation partially removed) fire treatments were applied to adjacent areas, and resident populations of native rodents (pale field rats and western chestnut mice) were monitored by trapping and radio-tracking. Compared with the unburnt control area, post-fire mortality in the high intensity fire treatment increased 21-fold and increased 5-fold in the low intensity fire treatment. Even in the high intensity fire treatment, the direct effects of fire, post-fire starvation, emigration, and lowered breeding activity caused little or no mortality; mortality was thus directly attributable to post-fire predation by cats and dingoes. An influx of feral cats and dingoes occurred after the fire, coinciding with rodent declines, and there was direct evidence of predation by cats on the native rodents (Leahy 2013; Leahy *et al.* in review).

Taken together, these studies provide new insights into the mechanisms by which sparse populations of cats can have large effects on populations of small mammals at landscape scales. The collapse of the experimental populations of small mammals in the Wongalara study was due to a few individual cats who concentrated their hunting on small areas with locally high densities of small mammals, until all had been killed. The studies of the intensity of cat predation in recently burnt areas and the movement behaviour of cats, revealed the behavioural mechanisms responsible for their highly concentrated effect on prey populations. Cats are versatile predators that will switch their diet as their preferred prey is depleted. However, they will often continue hunting their preferred prey to much lower levels than more generalist predators (Molsher *et al.* 1999). This makes cats particularly dangerous to small mammal populations because not only will they continue hunting a species to local extinction, their ability to persist once small mammals have declined in an area prevents populations from recovering.

Dingoes

Dingoes (including 'stray dogs' and hybrids) may have a complex effect on native mammal assemblages in northern Australia, which may vary for different species, in different areas, and under different land management regimes. Dingoes may benefit native mammal populations where they reduce the abundance or impacts of feral cats, but may also predate and reduce mammal populations. In Kakadu, a study of a declining population of northern quolls found that predation by dingoes was a significant cause of mortality, especially in open savanna habitats that provided few structural refuges from predation (Oakwood 2000). Camp dogs or stray dogs in the vicinity of communities and Aboriginal outstations may also have an under-estimated impact on local mammal populations. These dogs supplement their diet with food from human sources, thus maintaining their numbers and their effect on mammals may be considerable (Newsome *et al.* 2014b; Ritchie *et al.* 2014). There is also evidence that similarly 'subsidised' dingoes may preferentially hunt small mammals (Newsome *et al.* 2014a).

However, the effect of predation by dingoes on the demography and population size of small mammals is expected be less than the effect of feral cats, for three reasons. First, dingoes tend to occur at low population densities, typically one or two individuals per 10 km^2 (Fleming *et al.* 2001; Johnson and Ritchie 2013), while feral cats densities are often much higher than this (Denny and Dickman 2010). Second, while cats appear to prefer small mammals as prey, dingoes generally hunt larger prey and small mammals are usually only a small part of their diet (Allen and Leung 2012; Brook and Kutt 2011; Kutt 2012; Letnic *et al.* 2012). However, one study in Kakadu demonstrated substantial take by dingoes of small and medium-sized mammals (Corbett 1989) and a recent study in the Tanami Desert, just beyond the southern edge of the study area, also found similar results (Newsome *et al.* 2014a). Third, being smaller predators, cats are better able to enter small spaces that small mammals could use to evade dingoes, and they can also hunt in trees.

Consistent with the mesopredator release hypothesis (Crooks and Soulé 1999), there is evidence that dingoes suppress the abundance of feral cats and enforce changes in their behaviour that reduce their impact on small mammals. Because dingoes do not prey as intensively on small mammals as cats do, by suppressing cat numbers dingoes may provide a net benefit to small mammal populations (Ritchie and Johnson 2009). Across northern Australia, cat activity tends to be higher where dingo activity is low (Brook *et al.* 2012; Kennedy *et al.* 2011). Although cats are not significant prey for dingoes, an experimental study by Moseby *et al.* (2012) found that dingoes killed free-ranging feral cats, leaving their bodies uneaten. Brook *et al.* (2012) found that in central and northern Australia, cats adjusted their daily activity patterns to avoid encounters with dingoes, being less active around dusk and in the early evening in places where dingo activity at those times was high. This might have led to reduced mortality rates of small mammals, because small mammals showed a peak in activity at dusk and in the early evening, and hunting during that period probably gives cats their best opportunity to kill small mammals. Also, simultaneous GPS tracking of coexisting dingoes and feral cats showed that cats avoid dingoes in space as well as time, adjusting their movements to avoid coming within a few hundred metres of a dingo (Brook 2013).

Fire regimes

In the fire-prone savanna landscapes of monsoonal northern Australia, one of the ecological processes that has been most obviously disrupted at regional scales is fire. There is much evidence, though largely anecdotal, that the breakdown of traditional fire management by Aboriginal people across northern Australia by the mid-20th century significantly altered fire regimes (Yibarbuk *et al.* 2001). In the absence of purposeful Indigenous fire management, fires (ignited by people and also lightning) now tend to occur later in the dry season (*c.* August–November), burn with higher intensity, reach larger sizes, and recur more regularly across any one area (Russell-Smith and Edwards 2006; Russell-Smith *et al.* 2003). Conversely, in some pastoral areas consumption of grass by cattle has significantly reduced vegetation biomass and hence fire intensities and/or frequencies (Russell-Smith *et al.* 2003). Convincing evidence of a widespread increase in fire intensities in the high rainfall savannas of the Northern Territory over the last century is the well-documented decline of the fire-sensitive northern cypress-pine (*Callitris intratropica*) across much of the savannas of northern Australia (Bowman and Panton 1993). High-intensity fires also tend to be larger (Yates *et al.* 2008), and are more likely to cross natural barriers, such as creek lines (Price *et al.* 2007).

The breakdown of Aboriginal fire management leading to a fire regime characterised by frequent and spatially extensive late dry season fires has been well-documented on the Arnhem Plateau in northern Australia, and has led to significant impacts on a range of plant taxa and communities, including cypress-pine, sandstone heathland and rainforest (Russell-Smith *et al.* 2002; Russell-Smith *et al.* 1998). A critical aspect of Aboriginal fire management is that it reportedly maintains a fine-scale mosaic of vegetation of varying time since fire (Bliege Bird *et al.* 2008; Bowman *et al.* 2004), and spatiotemporal heterogeneity of fire regimes – sometimes called 'pyrodiversity' (Martin and Sapsis 1992). The breakdown of Aboriginal fire management may have led to a widespread decrease in pyrodiversity, both in the high-rainfall savannas (Bowman *et al.* 2004) and the arid hummock grasslands at the southern fringe of the region considered here (Bliege Bird *et al.* 2008; Burrows *et al.* 2006).

Assessing the effects of changing fire regimes on northern Australia's mammals has been the focus of an increasing body of research. Unravelling the relative effects of these changes, however, is inherently complex because of the difficulty of accounting for variations in specific attributes of a fire regime (i.e. frequency, intensity, extent and timing of fires) in different landscapes, on different species and in combination with other threats and ecological and climatic processes.

The effects of fire on small mammals can be classed as either short- or long-term. Short-term effects include killing or injuring individuals, decreasing (or sometimes increasing) food availability, and reducing understorey cover (e.g. grasses, shrubs, litter) that would otherwise provide shelter. The short-term negative impact of large hot fires on survival of small mammals has been demonstrated in a number of studies in the northern savannas (Corbett *et al.* 2003; Firth *et al.* 2010; Legge *et al.* 2008; Pardon *et al.* 2003). Recent work in the Kimberley region suggests that the reduction in understorey cover caused by spatially homogeneous hot fires significantly increases predation pressure by cats (Leahy *et al.* in review; McGregor *et al.* 2014). A similar model has been proposed by numerous other authors to explain declines of a range of mammal species (Firth *et al.* 2010; Fisher *et al.* 2014; Pardon *et al.* 2003; Radford 2012; Woinarski *et al.* 2011a), but the work by McGregor *et al.* (2014) and Leahy *et al.* (in review) provides the first direct evidence for this mechanism of decline.

A number of studies have shown clear negative relationships between recent fire frequency and the abundance or diversity of small mammal populations within a single landscape (Corbett *et al.* 2003; Corey *et al.* 2013; Firth *et al.* 2006; Woinarski *et al.* 2010). Longer-term effects of repeated fires are likely to include indirect impacts, via reductions in habitat suitability, with frequent hot fires reportedly reducing key habitat qualities, such as a diverse layer of shrubs (Friend and Taylor 1985) and grasses (Firth *et al.* 2010) and abundant hollow logs. A recent systematic review of the effects of fire on small mammals globally supports this, concluding that species dependent on fire-sensitive habitats (e.g. requiring dense ground vegetation) have higher abundances in unburnt sites (Griffiths and Brook 2014). In addition, a recent evaluation of the relative importance of attributes of fire regimes to mammal declines in Kakadu demonstrates that large, homogeneous fires have been most closely associated with small mammal declines since the early-2000s (Lawes *et al.* in press). Those authors hypothesized that small mammals, with small home ranges (<10 ha) and limited capacity for dispersal, are particularly vulnerable to large fires that simplify habitats.

Notwithstanding the pervasiveness of fire, and the complexity associated with understanding the impacts of different types of fire, there have been relatively few experimental studies in northern Australia that have manipulated fire regimes and examined biodiversity responses (Williams et al. 2003a). The most notable is the landscape-scale (c. 670 km^2) experimental manipulation of four different fire regimes (fire exclusion, annual fire lit in the early dry season, annual fire lit in the late dry season, and 'progressive' burning across the dry season) each replicated three times at Kapalga in Kakadu (Corbett *et al.* 2003). However, the experiment was sustained for only four years (1990-1994) and, probably as a consequence, relatively few differences in abundance of mammal species between treatments were reported (Corbett *et al.* 2003). Furthermore, the imposed fires – even those applied in the early dry season – were atypical, being applied at unusually high intensity and low patchiness, (G.D. Cook and J. Russell-Smith, pers. comm.). Hence it is very difficult to generalise the Kapalga results to ambient fire regimes.

Nonetheless, more recent analysis of the Kapalga data has demonstrated that high fire frequency regimes result in significantly lower rates of survival and recruitment of several species. In addition,, spatially explicit population viability analyses show that increasingly frequent fires presented a substantial risk to population persistence for the four mammal species modelled, namely the northern brown bandicoot, common brushtail possum, northern quoll and grassland melomys (Griffiths 2013). Data for the northern brown bandicoot from this experimental study were also modelled by Pardon *et al.* (2003), who concluded that this species declined under all experimental fire treatments, suggesting that this species requires a fine-scale mix of fire regimes.

There have been few other experimental manipulations of fire to assess mammal responses. In a sandstone massif (with mixed woodlands and rainforest patches) in Kakadu, Begg *et al.* (1981) lit a relatively high intensity fire and compared the post-fire abundance, reproductive success, and timing of breeding of several mammal species to their pre-fire states. At Mornington Sanctuary in the Kimberley, Leahy (2013) monitored the survival of individually marked small mammals in an experimentally burnt and nearby control area.

In a more serendipitous and retrospective study near Darwin, Woinarski *et al.* (2004) compared the abundance of mammals (and other vertebrates, and plants) in a 120 ha savanna woodland patch from which fire had been excluded for 23 years with a comparable adjacent patch subjected to ambient (annual) fire regimes, and reported almost complete turnover in mammal species composition between the two areas. On a far briefer time scale, Legge *et al.* (2008) compared the abundance of mammal species in a range of areas burnt by a single high intensity late dry season fire (five weeks before sampling) with matched nearby unburnt areas, in a savanna woodland in the Kimberley, and found higher richness and a 4-fold higher abundance of mammals in the unburnt sites.

Evidence of the effects of increased fire frequency has been fairly well established in the more intact parts of northern Australia. Yet in pyrophytic systems, such as Australia's tropical savanna, a reduction in fire frequency may also affect some components of the biota (Crowley and Garnett 1998). In the intensely grazed (pastoral) rangelands and savanna of northern Queensland there is evidence of a reduction in fire frequency over recent decades (Russell-Smith *et al.* 2003). Such changes may be detrimental to some native mammal species, for example by changing the phenology and diversity of plant species, and hence the availability of seed resources.

Overall, there is mounting evidence that historical increases in the frequency of extensive, hot fires have negatively impacted small mammals by both increasing mortality rates, especially via predation by cats; and reducing habitat quality (Lawes *et al.* in press). However, whether changes to fire regimes are a major driver of the current mammal decline in northern Australia remains uncertain. There is relatively little evidence in this region, or indeed from the few studies elsewhere in Australia (Pastro *et al.* 2011), relating the responses of small mammals to pyrodiversity (the mosaic grain of patches of varying fire history), and the issue remains contested (Parr and Andersen 2006). Furthermore, there is little direct evidence of a spatio-temporal association between mammal declines and the transition from Aboriginal fire management. The apparent ubiquity of the mammal decline is difficult to reconcile with spatially variable modes of fire management. For example, Yibarbuk *et al.* (2001) described a healthy mammal assemblage on an Aboriginal estate in central Arnhem Land, and attributed this to the maintenance of traditional management of the local fire regime (see also Whitehead *et al.* 2003). However, the mammal assemblage at this location has since collapsed, despite the lack of any apparent changes in fire management or the local fire regime (A. Fisher, unpublished data).

Pastoralism and feral herbivores

Studies of the role of introduced herbivores in mammal declines in northern Australia have produced variable results. A recent de-stocking study in northeastern Australia reported no benefit for native mammals, possibly because a long history of intensive grazing in that area had led to long-term declines in the population size of many native mammal species to such an extent that there was no realistic likelihood of short-term recovery after de-stocking (Kutt *et al.* 2012). Several opportunistic studies that have examined mammal responses at sites subjected to a longer history of contrasting livestock regimes. These have demonstrated some pastoral impacts, with significant variation in the composition of native mammal assemblages between comparable sites of varying livestock-grazing intensities (Kutt and Woinarski 2007; Woinarski and Ash 2002).

An initial landscape-scale experiment involving the removal of stock (mostly cattle) from 40,000 ha at Mornington Sanctuary in the Kimberley resulted in an immediate improvement in mammal species richness and abundance (Legge *et al.* 2011a). Following these early results, stocking treatment was then contrasted against fire treatments, focussing on differences between frequent, large, high intensity fires with less frequent, smaller, lower intensity fires to explore the interaction of these potential threats. Mammal recovery after stock removal was only pronounced when fires were simultaneously managed to be lower in frequency, size and intensity. When fire is not simultaneously managed (and fires were of higher frequency, larger size, and higher intensity), mammal recovery post-destocking was limited. In addition, the study suggested that fire frequencies need to be *substantially* reduced (or vegetation age increased) before the benefits of fire management are observed. In this relatively low rainfall area of the Kimberley (750 mm pa), fire frequencies as low as 1 in 4 years were required (from a starting frequency of 1 fire in 2 years – mostly intense late dry season fires) before mammal recovery was evident (S. Legge, unpublished data). This is a lower frequency than most land managers maintain. The interacting influence of fire pattern on introduced herbivore impacts (and vice versa) may partly explain the confusing variation reported by some earlier studies that focussed on either fire or introduced herbivores without adequately considering their interactions. Based on the results of the Mornington research, landscape-scale manipulations of stock (involving removals from areas as large as 100,000 ha) and fire (across entire properties of 200,000-300,000 ha) have been initiated at five other Australian Wildlife Conservancy properties across northern Australia. At three sites these manipulations are being implemented experimentally, with before-after, control-impact designs.

Cane toads

The highly toxic cane toad was deliberately introduced to Queensland in 1935, and has since spread across northern Australia. In the Northern Territory, the cane toad invasion has caused massive declines in populations of freshwater crocodiles (*Crocodylus johnstoni*; Letnic *et al.* 2008), varanid lizards (*Varanus* spp. ; Doody *et al.* 2009), blue-tongue lizards (*Tiliqua* spp.; Brown *et al.* 2011) and northern quolls (Woinarski *et al.* 2010). Cane toads are currently invading the Kimberley region of Western Australia, and have already caused the extirpation of northern quolls at El Questro Station (S. Doody, pers. comm.). In parts of north Queensland, however, quoll populations appear to be recovering, despite the presence of cane toads (Ujvari *et al.* 2013).

Cane toads clearly present a serious threat to northern quoll populations, but we know less about their effects on other native mammals. Small dasyurids such as planigales, antechinus and dunnarts do not appear to be at risk from toad poisoning. Unlike quolls that encounter and attack large, lethal toads, these smaller dasyurids encounter smaller, less toxic toads that provide learning opportunities via conditioned taste aversion (Webb *et al.* 2008). In laboratory trials, most planigales and dunnarts that attacked and ingested small toads became ill, and subsequently refused to attack toads for several weeks (Webb *et al.* 2008; Webb *et al.* 2011). Rodent populations are also unlikely to be affected by cane toad poisoning. Although cane toads were implicated in declines of pale field-rats in Kakadu (Woinarski *et al.* 2010), laboratory studies revealed that individuals of pale field-rat, grassland melomys and dusky rat (*Rattus colletti*) can consume cane toads without ill effects, suggesting that these species possess physiological resistance to bufotoxins (Cabrera-Guzmán *et al.* in press). In the wild, native rodents such as the water rat (*Hydromys chrysogaster*), and introduced black rats, have also been observed preying on cane toads (Fitzgerald 1990; St Cloud 1966). Nevertheless, there is still cause for concern for some native mammal species. For example, there is recent anecdotal and correlative evidence suggesting a link between cane toads and a substantial decline in the carnivorous ghost bat in parts of northern Australia (White and Madani 2014), but this link has not yet been conclusively demonstrated.

The biggest impact of cane toads on small mammal assemblages may occur via indirect pathways (Shine 2010). Cane toad invasion results in the rapid collapse of varanid lizard ('goannas') populations, which can lead to increases in the abundance of species previously preyed on by goannas. For example, in the Daly River region, green tree snakes (*Dendrelaphis punctulata*) increased in abundance after cane toads severely reduced populations of three species of varanid lizards (Doody *et al.* 2013). Likewise, increases in the abundance of some snakes at Fogg Dam probably resulted from the disappearance of yellow-spotted monitors (*Varanus panoptes*), which are major predators of snakes and their eggs (Brown *et al.* 2011). Indirect effects of cane toads on small mammals are therefore likely; for example, the removal of large varanid lizards might cause increases in the abundance of feral cats or some snakes, thereby increasing rates of predation on small mammals. Increases in raptor populations might also occur after toads invade, due to the presence of a plentiful food source (Beckmann and Shine 2011). Food-supplemented raptor populations could reduce small mammal populations, particularly in frequently burnt areas. A potential recovery of predators in the Northern

Territory following initial collapse may provide an opportunity to study the relationships among these trophic levels in the future. At present, we know virtually nothing about the interplay of cane toads with other threatening processes (predation, fire, and grazing), making it difficult to evaluate exactly how cane toads have affected small mammal populations in northern Australia.

Diseases and pathogens

Most previous studies of disease in native mammals in northern Australia have focused on mammals as vectors for diseases that affect humans, rather than on the potential impacts of disease on the conservation of native mammals (Bell and Whelan 1993; Cook *et al.* 1967; Doherty *et al.* 1968; Plowright *et al.* 2008; Slack *et al.* 2006; Smythe *et al.* 2002). Many (>54 %) emerging infectious diseases are zoonoses and are caused by bacteria or rickettsia (Jones *et al.* 2008), making a study of the vectors of these diseases imperative. Low reporting rates of disease in the tropics makes detecting these zoonoses difficult (Jones *et al.* 2008).

Disease is potentially implicated in the demise of native mammals under current changing climate and emerging infectious diseases (Cox-Witton *et al.* 2014; Thompson and Conlan 2011; Thompson *et al.* 2010a). Much of our current understanding of disease and epidemics in Australian mammals derives from anecdotal evidence (Abbott 2006). Previous research elsewhere in Australia on the effects of diseases on native mammals has identified that diseases may be implicated in the declines of some mammal species (Abbott 2006; Appelbee *et al.* 2005; Bettiol *et al.* 1997; Buettner *et al.* 2013; Skerratt 2005; Thompson and Conlan 2011; Thompson *et al.* 2010b; Warren *et al.* 2003; Wayne *et al.* 2013a; Wayne *et al.* 2013b; Wyatt *et al.* 2008). For example, in southwestern Australia, the woylie (*Bettongia penicillata*) experienced a sudden catastrophic decline in population abundance and distribution, and there is some suggestion that disease was a contributing factor (Smith *et al.* 2008; Wayne *et al.* 2013b), along with increased predation by feral cats.

Disease in wildlife is notoriously hard to detect, and efforts to date in northern Australia have been meagre. Sick and dying animals are rarely trapped, and it is difficult to find dead animals. Most previous studies of disease in mammals in northern Australian savannas have involved necropsies of roadside carcasses or of euthanized trapped individuals. The few previous studies in northern Australia aimed at assessment of conservation risk associated with disease have investigated just one or two potential disease causes, such as toxoplasmosis, and parasite loads, and these studies have not produced evidence that these diseases are implicated in declines (Oakwood and Pritchard 1999; Oakwood and Spratt 1999).

Introduced mammal species are likely to spread ‘novel’ diseases to native mammals, and the extinctions of two Christmas Island endemics, Maclear’s rat (*Rattus macleari*) and bulldog rat (*R. nativitatis*), has been linked to trypanosomiasis brought to the island by introduced black rats (Green 2014; Wyatt *et al.* 2008). One study of wild populations of the introduced black rat in the Top End of the Northern Territory investigated the presence of six ‘novel’ diseases but found none of them (Jackson *et al.* 2010).

Research is currently underway in the Northern Territory to evaluate the potential role of disease as a contributing factor to mammal declines in northern Australia. Four target species have been selected (common brushtail possum, northern brown bandicoot, northern quoll and brush-tailed rabbit rat). These species represent a cross-section of ecological guilds and still have populations in various ‘states’ of persistence across different landforms, including on islands and the mainland. To date, over 200 individuals have been sampled across several sites in the Top End and screened for a variety of infectious diseases. In addition, indicators of health have been recorded, including body condition, reproductive status, observed health status, haematological and biochemical profiles, and ectoparasites collected (G. Gillespie, unpublished data).

Climate change

The extent of climate change, and its likely impacts, for northern Australia are not well resolved. The most likely change is for fire regimes, with increasing severity of fires because of longer dry seasons and perhaps higher wet season rainfall (Williams *et al.* 2009). Such change will exacerbate the existing detrimental effects of fire regimes upon biodiversity. Whereas there are well developed predictions for catastrophic impacts of climate change (including food-plant responses to elevated atmospheric concentrations of CO_2) upon many mammal species with sharply defined climatic thresholds and dietary specialisations in the distinctive montane environments of the Wet Tropics of northeastern Australia (Kanowski 2001; Kanowski 2004; Williams *et al.* 2003b), the predictions for change in the mammal fauna of the tropical savannas of northern Australia are far less settled. Nonetheless, very severe declines due to climate change have been predicted within 20 years for the small number of species modelled, including brush-tailed rabbit-rat, black wallaroo, northern brush-tailed phascogale (*Phascogale pirata*) and Arnhem rock-rat (*Zyzomys maini*). All of these are expected to decline 90% in distributions, while the northern short-tailed mouse and black-footed tree-rat are expected to decline by 60% (Kutt *et al.* 2009). Coastal changes due to rising sea level have also been modelled to very significantly increase the extinction risk to the water mouse (*Xeromys myoides*) (Traill *et al.* 2011).

Habitat loss and fragmentation

Habitat loss, one of the major drivers of biodiversity decline globally, is not yet a major threat across northern Australia's tropical savannas. However, there are some currently isolated cases of broad-scale clearing (of the order of 100 to 500 km^2) associated mostly with strip-mining (for example in northeastern Arnhem Land, Groote Eylandt and western Cape York Peninsula), plantation forestry (the Tiwi Islands), and intensification of agriculture (the eastern Kimberley, Darwin-Katherine area, and parts of northeastern Australia) (Woinarski 2004a), and particularly in the southeastern agricultural region of the tropical savannas (Franklin and Preece 2014) (Fig. 3). Unsurprisingly, such habitat loss has severe consequences for local native mammal assemblages (Firth *et al.* 2006; Woinarski 2004a; Woinarski *et al.* 2009a), although an exception may be where post-mining rehabilitation is intensively managed using fire exclusion (Woinarski *et al.* 2008).

CONSERVATION MANAGEMENT

Policy responses

There has been no coherent integrated policy or management response to the current spate of declines in the north Australian mammal fauna. In part, this reflects the fragmentation of responsibilities across different jurisdictions, and because national and Queensland, Western Australia and Northern Territory conservation agencies also have well-established conservation needs and priorities in the larger part of their jurisdictions outside monsoonal northern Australia. In addition, the declines have been identified relatively recently, and because the evidence for causation has been weak, the main priorities for responsive management are not well defined.

The typical and sometimes successful policy response for threatened species in Australia has been the development and implementation of Recovery Plans mostly for individual threatened species across their entire range, but sometimes also for regional sets of such species. Such plans set out management priorities and responsibilities, and help coordinate research and management responses across agencies. They have some, albeit weak, foundations in national legislation. Recovery Plans have been developed for most threatened mammal species in northern Australia, including northern quoll (Hill and Ward 2010), bare-rumped sheath-tailed bat (*Saccolaimus*

saccolaimus nudicluniatus; Schulz and Thomson 2007), lesser large-eared horseshoe-bat (*Rhinolophus* sp. 'intermediate'; Thomson *et al.* 2001), greater large-eared horseshoe-bat (*Rhinolophus robertsi* (Thomson *et al.* 2001), Semon's leaf-nosed bat (*Hipposideros semoni*; Thomson *et al.* 2001), Troughton's sheath-tailed bat (*Taphozous troughtoni*; Thomson *et al.* 2001), Carpentarian antechinus (*Pseudantechinus mimulus*; Woinarski 2004b), Butler's dunnart (Woinarski 2004b), northern hopping-mouse (Woinarski 2004b), golden bandicoot (Palmer *et al.* 2003), golden-backed tree-rat (Palmer *et al.* 2003), Bramble Cay melomys (Latch 2008), bilby (Pavey 2006), northern bettong (Dennis 2002), and water mouse (Department of the Environment and Resource Management 2010). The effectiveness of most of these plans, however, has not been assessed, and it is likely that they have provided relatively little benefit, largely because their implementation has been supported by little or no funding (Bottrill *et al.* 2011; Woinarski *et al.* 2014).

The other main policy response has been directed at the management of landscape-scale threats, rather than on threatened species. National legislation allows for the recognition of Key Threatening Processes and the establishment of Threat Abatement Plans to coordinate responses to those threats. The most relevant of these to the conservation effort for mammals in northern Australia are plans for the management of feral cats (Department of Environment Water Heritage and the Arts 2008) and cane toads (Department of Sustainability Environment Water Population and Communities 2011). However, as with the Recovery Plans, these Threat Abatement Plans have been largely ineffective due to very limited resourcing.

Notwithstanding the relative ineffectiveness of these responses, the issue of decline of native mammals in northern Australia has recently received greater attention, with some increase in funding for targeted research and management. For example, the issue was identified as a priority for funding in the recent establishment of the National Environmental Research Program and the Threatened Species Recovery Hub within the programme, and is increasingly recognised as a concern in many regional natural resource management plans (www.environment.gov.au/science/nesp). However, state and federal government policy initiatives for intensification of agriculture and mining have increased the pressure on north Australian environments (Department of Prime Minister and Cabinet 2014; Ritchie *et al.* 2013).

Indigenous Protected Areas

A program commencing in 1998 has seen the establishment and rapid proliferation of Indigenous Protected Areas (IPAs). These are Indigenous-owned areas of land or sea that have been identified and declared by traditional landowners and formally recognised by the Australian government as part of the country's National Reserve System. There are currently more than 50 IPAs in Australia covering more than 500,000 km^2, representing more than a third of all area under formal protection. Many of these (15 IPAs, with a total area of c. 85,000 km^2) are wholly or in part located in northern Australia, including many areas that hold substantial populations of threatened or declining mammal species. IPAs are actively managed by their Indigenous owners, often in collaboration with government and non-government organisations. Accordingly, the recent establishment and expansion of the IPA network has substantially increased the number of Indigenous rangers actively managing reserves for biodiversity outcomes. IPAs present opportunities for bringing together traditional Indigenous knowledge systems with modern science to aid management and conservation. By doing so they also help build capacity among Indigenous communities, strengthen or in some cases help re-establish cultural ties to traditional lands, and help non-Indigenous people understand what is important to traditional landowners as well as what may be learnt and applied from their knowledge and practices.

Non-government conservation reserves

Non-government conservation organisations have a substantial presence in northern Australia. The Australian Wildlife Conservancy (AWC) owns and manages nine large reserves across the north, with a particularly strong presence in the Kimberley. AWC focuses on utilising threat management and integrated research. In particular, they manage introduced herbivores and fire at large spatial scales, embedded in an experimental paradigm, and work within and across properties that have varying histories of pressures and landscape contexts. This comparative approach may yield valuable information on when certain management actions will succeed or fail to elicit recovery. Management interventions have been ambitious, with multiple de-stocked areas of up to 100,000 ha each, and fire management programs that are regional in scope (e.g. 4 million hectares in the Kimberley) (Legge *et al.* 2011b). In addition, focussed research on feral cats and threatened mammals is helping to fine-tune management requirements appropriately. Another large non-government conservation organisation, Bush Heritage Australia, supports improved land management on some areas of Indigenous-owned land, with a focus on capacity-building and management planning.

Islands

Across Australia, more than 140 species of native mammals are known to occur on islands (Abbott and Burbidge 1995). Of particular importance are island populations of threatened mammal species (Burbidge 1999; Dickman 1992). Without islands, Australia's appalling record of 28 to 30 modern mammal species extinctions would be even worse, as seven species that became extinct on continental Australia have persisted on islands.

Northern Australia has many continental islands with the Kimberley having more than 2600, the Northern Territory has 973, and there are 1955 in Queensland (including some islands beyond the northern Australia area considered here). Many island groups in northern Australia have been relatively well surveyed for mammals (Firth and Panton 2006; Gibson and McKenzie 2012; Woinarski *et al.* 1999; Woinarski *et al.* 2011b), although this sampling is far from comprehensive and has concentrated on the larger islands. This sampling has demonstrated that many islands have significant populations of threatened mammal species, including species that have declined severely on the mainland because of pervasive threats (that may not yet occur on islands). Examples include northern quoll, Butler's dunnart, golden bandicoot, nabarlek, black-footed tree-rat, and golden-backed tree-rat.

Probably because of their relatively recent isolation, and notwithstanding the large size of some northern Australian islands, only one endemic mammal species is restricted to a single island, or set of islands. This exceptional case (the Bramble Cay melomys) is unusual in that the species is (or, was) restricted to a very small sand cay. However, some of the larger islands (notably Bathurst and Melville Islands) have endemic subspecies of mammals (Kemper and Schmitt 1992), although subspecies differentiation on these islands is generally not well resolved.

Many to most islands of northern Australia are under Indigenous ownership or claim and the conservation management of these islands will be dependent upon the interests and capability of these owners. An increasing number of islands are now managed as Indigenous Protected Areas, or otherwise managed by Indigenous ranger groups. As elsewhere in Australia, the maintenance of the conservation values of islands in northern Australia is highly dependent upon the establishment and implementation of adequate biosecurity measures (Nias *et al.* 2010). Currently, only a few of the high-value islands have active biosecurity plans.

Such biosecurity measures are required because island mammal populations are extremely vulnerable to local extirpation by invasive species, especially of introduced predators (Burbidge and Manly 2002; Woinarski *et al.* 2014). In northern Australia the introduction or immigration of cane toads is also an issue. Rafting of toads to islands has probably been responsible for at least one case of island extirpation of northern quolls in the Northern Territory, and toads have colonised another quoll-inhabited island (Augustus) in the Kimberley since 2013.

Islands have also been a focus of several translocation programs which have proven to be an effective technique for the conservation of many threatened Australian mammals (Woinarski *et al.* 2014). To date, however, there have been few such island translocations in northern Australia, partly because many islands in this region already hold important populations of threatened mammal species, and partly because declines in mainland areas have been relatively recent, so there has been little need to attempt translocation. A notable exception is the translocation of northern quolls to two islands off northeastern Arnhem Land. This was in response to the rapid decline of this species on the mainland due to the rapid range expansion of the introduced cane toad (Rankmore *et al.* 2008). The translocated populations on these (toad-free) islands increased rapidly, whereas their source populations continued to suffer severe declines (Rankmore *et al.* 2008; Woinarski *et al.* 2010). A similar effort has involved the recent translocation of small numbers of golden bandicoot from one island (its only known occurrence in the Northern Territory) to two other nearby islands (Woinarski *et al.* 2014).

The persistence or increased abundance of translocated populations to islands provides compelling insights into the detrimental impacts of some factors, typically introduced predators, operating elsewhere in the species' range. A contrasting 'natural' experiment on the Sir Edward Pellew island group involving the introduction of cats by landholders to some islands, and the natural colonisation of toads to many islands resulted in dramatic declines of the native mammal fauna of these islands (Woinarski *et al.* 2011b).

Captive breeding, *ex situ* conservation, and translocations

Ex situ conservation is an important part of the conservation response for many highly imperilled species across the globe, particularly for those species confronted with extreme habitat loss or severe hunting pressure. Major and sustained captive breeding programs have been established for some threatened Australian mammal species, extending over several decades (Ford and Hogg 2012; Serena 1994). Most have used captive breeding as a stage towards attempted reintroduction or other translocation programs, with particular emphasis on release into intensively-managed sites within their former range or to predator-free islands. Some of these programs have been extraordinarily successful, and have been responsible for preventing extinctions (Langford and Burbidge 2001; Moseby *et al.* 2011).

However, there have been few cases of *ex situ* conservation and no examples of the establishment of large-scale predator-proof exclosures for the mammal fauna of northern Australia. This may be because of the very recent recognition of the conservation problem in this area, and because declines in other parts of Australia have been recognised for appreciably longer periods. Captive breeding may have prevented the extinction of the Bramble Cay melomys sometime in the last decade (Latch 2008).

There is scope and probably a need for a substantial increase in the use of captive breeding and translocation in conservation management of the current decline of north Australian mammals. This should include strategic consideration of the establishment of insurance populations for some of the most imperilled species, the establishment and use of large-scale predator-proof exclosures, and the careful use of predator-free (and toad-free) islands as translocation sites.

Priority actions for species, threats, and management

To date, much investment in conservation management in northern Australia has been *ad hoc*, localised and short-term, often driven by conventional wisdom and current practice, by the preferences and outlook of individuals, or by the shifting fashion of available government funding streams.

The most strategic attempt to prioritise management responses for the conservation of mammals, and other vertebrate species, in northern Australia is a recent approach in the Kimberley (Carwardine *et al.* 2011; Carwardine *et al.* 2012). This used expert testimony to evaluate the relative benefits (in terms of increase in the predicted persistence of individual species over a 20 year time period) of a prescribed set of alternative management actions, with each action carefully costed and its feasibility of implementation estimated. From these estimates, the overall benefit per unit cost of each action was calculated, along with the expenditure required to ensure all species persisted in the region, and the optimal combination of management responses under a range of available management funds. The study concluded that the wildlife of the Kimberley could be secured over a 20-year period with an initial investment of $A95 million, followed by annual investment of $A40 million. This figure compares with the current annual investment of $A20 million for biodiversity conservation in the area, an amount that is larger than that provided to other northern Australian regions. The single most cost-effective management action related to the control of feral cats, even though the study concluded that the likelihood of eradication of feral cats was low. The next most cost-effective response was a combination of enhanced fire management and control of introduced herbivores, and this combined response was considered to have a high likelihood of success. To date, this program has not yet been fully implemented.

Recently a similar approach was adopted for optimising management actions in Kakadu (Woinarski and Winderlich 2014), and comparative analyses are currently underway for several other regions in northern Australia, including the Fitzroy River in the Kimberley, the Daly River in the Northern Territory and the Northern Gulf region in Queensland (J. Alvarez-Romero, pers. comm.).

A different approach, namely that of prioritising species rather than of management efficiency has been applied in Queensland (the 'Back on Track' process: Marsh *et al.* (2007)) and the Northern Territory (S. Ward, unpublished data). This approach aims to identify and prioritise not only which species are most threatened but also which have the greatest potential for recovery, thereby informing the strategic allocation of limited conservation resources. However, these approaches have not yet been substantially implemented or resourced.

Management responses to specific threats

Feral cats

There are currently no viable options for the direct control of feral cats over large landscapes. Cats are extremely cautious, live-prey specialists, making them unlikely to enter traps, or take standard poison-baits. Small-scale intensive control efforts appear ineffective due to rapid reinvasion by other cats (McGregor, unpublished data). In addition, any control method with a collateral negative impact on dingoes (including poison-baiting) is likely to be counter-productive given that dingoes suppress cat populations (Brook *et al.* 2012; Kennedy *et al.* 2011) and may not recieve landowner approval on Indigenous-owned land. The results of AWC's Kimberley research suggests that by reducing the frequency of high intensity fires and by removing introduced herbivores from mammal-rich areas (including riparian zones and wetlands), cat impacts can be reduced sufficiently to allow some recovery for at least some mammal species (e.g. small-medium sized rodents). Whether such interventions are enough to enable the recovery of more sensitive species such as the larger rodents and some marsupials, and whether such results can be repeated across other parts of northern Australia with a longer and deeper history of small mammal decline remains to be determined.

One management response that may be practically implemented for part of northern Australia is the regulation of, or greater education about, the risks associated with the deliberate movement of 'pet' cats to north Australian islands, which are currently cat-free and contain important populations of native mammals. Most of these islands are Indigenous-owned, and some Indigenous agencies (such as Anindilyakwa Land Council on Groote Eylandt) have been proactive in implementing such controls.

Dingoes

With some exceptions, the available research suggests that the best conservation management approach for dingoes in northern Australia is to leave them alone, because management that reduces their numbers is likely to lead to increased predation pressure on native mammals from feral cats. This approach conflicts with the concerns of pastoralists in some northern Australia regions, who control dogs and dingoes because they are held responsible for significant levels of stock losses (WoolProducers Australia 2014), although it has also been argued that their impacts have been overstated (Forsyth *et al.* 2014). Three mechanisms are needed to resolve this possible conflict: (i) the development and implementation of broad-scale integrated pest management, that considers the interactions among different pest species and the consequences of such interactions for biodiversity (Ritchie *et al.* 2012; Ritchie and Johnson 2009); (ii) a clearer understanding and quantification of the costs (to pastoral production and potentially also to biodiversity) and benefits of a range of dingo management options (Prowse *et al.* 2014); and (iii) the development of alternative dingo control mechanisms that minimise impacts upon trophic interactions and biodiversity. There is increasing evidence that stock guardian animals may be a practical alternative to broad-scale persecution of dingoes, and this method of dingo control is being applied in some pastoral areas (Van Bommel and Johnson 2012).

Fire

Given the strong evidence that frequent and extensive hot fires have a negative impact on small mammals (Lawes *et al.* in press)– most likely by increasing predation pressure and decreasing habitat quality – fire management represents an important tool for maintaining mammal populations. Ideally, the frequency of large, hot fires should be minimised. This can be achieved using strategic prescribed burning early in the dry season, under mild fire weather conditions (Corey *et al.* 2013; Legge *et al.* 2011a; Russell-Smith *et al.* 2013).

However, there is also a conservation case to increase the proportion of savanna landscapes that remain unburnt for at least 5 years in the mesic savannas of northern Australia (Andersen *et al.* 2005; Andersen *et al.* 2012). Anderson *et al.* (2005)> have proposed that this can be best achieved by reducing the 'randomness' of burning, where prescribed burning strongly targets recently burnt areas, and avoids long unburnt areas. Indeed, a recent evaluation of fire management on the Arnhem Plateau within Kakadu suggests that this approach is highly effective at increasing the proportion of the landscape that is long unburnt (Murphy *et al.* in review). Similar results have been obtained in the Kimberley region (S. Legge, unpublished data). It is clear that highly strategic prescribed burning is an effective means of imposing fire regimes that are more favourable to the persistence of small mammals, but care must be taken to avoid indiscriminate application of fire throughout the landscape. Attempts at fire management interventions should take place within an 'adaptive management' framework, with adequate monitoring of the response of small mammals to management actions (Corey *et al.* 2013; Legge *et al.* 2011a).

For such adaptive management to be effective, it is crucial that knowledge gained from ongoing monitoring is incorporated into fire planning, and that land managers are accountable for, and responsive to, biodiversity outcomes. Until recent improvements, an example of an ineffective fire management program is from Kakadu, where monitoring and research results have not been incorporatedsuccessfully into ongoing fire management (Parr and Andersen 2006; Parr *et al.* 2009). This failure has been in spite of the local collapse of mammal populations (Woinarski *et al.* 2010), and recognition extending back decades that many mammal species in the area required longer-unburnt habitat which was disappearing under prevailing fire management practices (Friend 1987; Friend and Taylor 1985; Kerle 1985).

Pastoralism and feral stock

Pastoralism is the most extensive land use across northern Australia. There is increasing evidence that this land use can have significant detrimental impacts upon biodiversity, including native mammals. In general, these impacts are greater as stocking rates increase and the environment is modified for pastoral purposes (including through the introduction and spread of invasive pasture grasses and the control of dingoes) (Legge *et al.* 2011a; Woinarski and Ash 2002; Woinarski and Fisher 2003; Woinarski *et al.* 2013). High densities of feral stock (including cattle, water buffalo, horses and donkeys) are likely to have comparable effects on non-pastoral lands, including within conservation reserves (Bradshaw *et al.* 2007). Removal of feral animals has been shown to result in increases in some native mammal fauna in the north Kimberley (Corey *et al.* 2013).

Management responses to these findings may be difficult and expensive, but there are some options, including: (i) the ongoing gradual reduction in the high proportion of northern Australia devoted to beef cattle production, some of which is caused by the acquisition and de-stocking of current pastoral properties for conservation purposes. We note, however, that such purposeful change may be inconsistent with the current regulatory obligations for pastoral leases; (ii) encouragement of, or regulation to enforce, pastoral practices that benefit biodiversity and discouragement of practices that are antithetical to biodiversity (such as use of introduced pasture plants, vegetation clearing, dingo persecution, increase in the spread of artificial water points, and over-stocking) (Woinarski and Fisher 2003); and (iii) the establishment and maintenance of broad-scale and long-term programs to eradicate feral ungulates, particularly from conservation reserves.

Toad invasion

Cane toads are currently invading the Kimberley region of northwestern Australia and are expected to eventually colonise the Pilbara (Kearney *et al.* 2008), one of the last strongholds for northern quolls. In hot, semi-arid regions, the Achilles heel for the cane toads is their dependence on water; during the late dry season, cane toads require access to standing water every 72 h to avoid desiccation (Florance *et al.* 2011). The installation of farm dams at approximately 10 km intervals throughout semi-arid grazing regions has allowed cane toads to penetrate into arid regions where they could not persist without the addition of artificial water sources (Letnic *et al.* 2014). It may be possible to slow the spread of cane toads into semi-arid landscapes by excluding their access to artificial water sources (Florance *et al.* 2011). Recent modelling suggests that to reach the Pilbara, cane toads will have to travel via a narrow coastal corridor where the only permanent water sources are bore fed dams. The strategic replacement of 100 earthen dams with plastic water tanks in this corridor, at relatively low cost, could prevent cane toads from reaching the Pilbara (Tingley *et al.* 2013). However, the potential for toads to 'hitch-hike' or be otherwise introduced to the Pilbara may make their arrival there inevitable.

Even if the spread of cane toads cannot be stopped, the extinction of northern quoll populations is preventable. One approach is to bring quolls from toad-free populations into captivity before cane toads invade. Zoos could breed the quolls, and juveniles could be trained not to eat cane toads prior to their release back into the wild (O'Donnell *et al.* 2010). This approach is promising as following return to the wild, 'toad smart' quolls had higher short-term survival than toad-naïve quolls (O'Donnell *et al.* 2010). Importantly, some 'toad smart' females survived long-term and reproduced, and some of their offspring survived and reproduced (J. Webb, unpublished data). These results suggest that each generation of quolls learns to avoid toads as food, either via social learning, or from ingesting small, non-lethal sized toads that induce a long-term aversion to toads. A second strategy worth considering is to deploy 'toad aversion baits' to train wild quolls not to eat cane toads before the toads invade. If wild quolls that consumed baits subsequently avoided live toads, then these populations might persist after toads invaded (Webb *et al.* 2008). A third approach worth investigating is to introduce 'toad smart' quolls, if they exist, to quoll populations ahead of the toad invasion front. For example, Ujvari et al. (2013) suggested that northern quolls have persisted in Queensland because they possess an innate avoidance to cane toads. If quolls possess genes for toad avoidance, then males from toad-infested populations could be translocated to toad-free populations.

Finally, it is worth noting that quolls are affected by other threats and there is evidence that they were declining in several regions prior to the arrival of cane toads (Ziembicki *et al.* 2013), most likely because of predation and inappropriate fire regimes. Radio-tracking studies in one toad-infested area of Kakadu revealed that camp dogs and dingoes were the major cause of mortality of juvenile quolls (Cremona *et al.* in review). These findings are not new since prior to the toad invasion, dingoes were identified as an importantcause of mortality for quolls in savanna woodlands, and quolls were most susceptible to predation in burnt areas (Oakwood 2000).

DISCUSSION AND OUTLOOK

Greater recent resolution and recognition of the plight of the mammal fauna of northern Australia has stimulated a series of research and management initiatives aimed at improving our knowledge of population trends across the region, and to ascertain the causal factors behind population changes and potential solutions to stem the declines. In this paper we bring together these disparate efforts to summarise the current state of knowledge, refine the conceptual framework for declines presented by Woinarski *et al* (2011), assess the efficacy of several recent conservation management interventions, and identify key priorities for further research and management.

Apart from a handful of seminal studies, understanding population trends of mammals in northern Australia and their causation has been constrained by a lack of detailed research and long term monitoring programs. Recent efforts to improve our understanding have drawn on a range of different approaches, including improving taxonomic resolution for poorly known taxa (Potter *et al.* 2014a; Potter *et al.* 2012b; Reardon *et al.* 2014; Westerman *et al.* 2012), assessment of historical and subfossil evidence (Cramb and Hocknull 2010; Start *et al.* 2012), documentation of Indigenous knowledge (Ziembicki *et al.* 2013), modelling and other analytical studies to identify characteristics of declining species (Fisher *et al.* 2014; Murphy and Davies 2014; Woinarski 2015), experimental manipulation to determine relative impacts of specific factors (Frank *et al.* 2014; Griffiths 2013; Legge *et al.* 2011a; Webb *et al.* 2011), application of new technologies to facilitate surveys and research (Hohnen *et al.* 2013; McGregor *et al.* 2014), and improved integration of regional distributional databases (Fisher *et al.* 2014; Woinarski *et al.* 2014). These studies demonstrate that the extent and timing of decline and impacts of threats has been variable across the region. However, a general gradational pattern of earlier and more severe decline from inland lower rainfall areas to the higher rainfall of the coastal north is evident, particularly in the Kimberley and Top End regions (Finlayson 1961; Radford *et al.* 2014; Start *et al.* 2007; Ziembicki *et al.* 2013). A small area of the high rainfall, rugged coastal Kimberley region remains the last mainland stronghold for several species that have disappeared elsewhere (Corey *et al.* 2013; McKenzie *et al.* 2007; Radford *et al.* 2014; Start *et al.* 2007). Islands also remain critical refuges retaining much of their original mammal faunas (Firth and Panton 2006; Gibson and McKenzie 2012; Woinarski *et al.* 1999). However, these populations are highly susceptible to the introduction of novel threats and several islands have rapidly lost their refugial value following the arrival of cats and/or cane toads (Woinarski *et al.* 2011b).

In some regions, such as parts of northeastern Australia, there has been less or no discernible change in the mammal fauna. Here, a relatively longer and more substantial history of environmental modification may have led to mammal declines that were never clearly documented (although some changes are evident from the subfossil record). Other areas, such as some parts of the Einasleigh Uplands, may have retained a relatively intact mammal fauna possibly due to minor landscape change, or unusual environmental characteristics that have facilitated the persistence of mammal populations (Vanderduys *et al.* 2012).

Causes of decline are likely to be a combination of interacting threats acting differently in different regions for different species. Recent research implicates predation by cats as a major cause of severe depletion of several native northern mammals (Frank *et al.* 2014; McGregor 2014; Woinarski *et al.* 2011b). The severity and impact of cat predation is likely to be exacerbated through interactions with other environmental changes, most notably prevailing fire regimes (McGregor *et al.* 2014), the reduction in shelter offered by ground vegetation due to pastoralism (McGregor *et al.* 2014), and in some areas, the degree and nature of interaction between dingoes and cats (Brook *et al.* 2012; Kennedy *et al.* 2011). Such synergistic impacts may explain the perceived lag between the onset of specific threats and the recent rapid decline of native mammals. For example, although feral cats have been present in the region for over a century with limited discernible effects on mammals, the impacts of cat predation may have been magnified only recently by changes in other management factors. However, this general conclusion does not yet explain all observed declines, with the most notable remaining enigma being the recent broad-scale decline of many mammal species across much of Arnhem Land, despite retention there of dingo populations, maintenance in many parts of traditional Aboriginal fire regimes, and lack of pastoralism.

The demonstration of interactive factors affecting mammals gives conservation managers some options for reducing their impacts. Cat predation may be mitigated to some degree through manipulation of fire (aimed at increasing the extent of longer unburnt habitat and area of fine-scale patch burning), reducing the impacts of livestock and feral herbivores, and maintaining dingo populations. Some localised instances of conservation management (involving fire and reduction in livestock) in parts of the central and north Kimberley have produced relatively rapid and substantial increases in some native mammal species (Legge *et al.* 2011a). However, such techniques may not be effective in areas that now have severely depleted mammal assemblages, because even small numbers of feral cats may impose unsustainable predation pressure on native mammal species with very low population size. In such areas, and elsewhere, extensive predator-exclusion fencing may be required to maintain or reintroduce some threatened mammal species. A complement to such an approach may be to increase translocations of threatened species to cat-free islands, eradicate cats from islands on which they currently occur and increase biosecurity measures to reduce the risks of introduction to cat-free islands.

The westward spread of the cane toad across northern Australia has added an idiosyncratic factor to these broad spatial patterns of decline, with documented direct impact on at least one species, the northern quoll (Woinarski *et al.* 2010). Indirect impacts on other mammal species through perturbation of the predator assemblage remain unresolved. Likewise, there is too little information to assess the contribution, if any, of disease in the current pattern of mammal decline in northern Australia, and research to address this information gap is a priority.

The Australian national, state and territory governments are currently actively promoting significant large-scale development in northern Australia. These developments are likely to introduce or intensify threats to which northern Australia has so far only had limited exposure but that are responsible for most biodiversity loss in other parts of the world (notably habitat loss, overexploitation and high human population density). Improved knowledge, adequate planning and effective management strategies, underpinned by integrated long-term adaptive monitoring (Lindenmayer *et al.* 2013), are required to better understand and limit existing threats and the introduction or intensification of new ones. Without such concerted action a significant component of the north Australian mammal fauna is destined to contribute further to Australia's already woeful record for contemporary mammal extinctions.

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Resumen

Introducción: En estudios recientes en sitios al norte de Australia se ha informado una rápida y severa disminución de algunas especies de mamíferos nativos, a pesar de un contexto ambiental favorable (de baja población humana, pérdida de hábitat limitado, de un grado sustancial reservas) que debe proporcionar una seguridad relativa de conservación. Todos los grupos taxonómicos con mayor riqueza de especies de mamíferos en el norte de Australia tienen algunas especies cuyo estado de conservación se ha evaluado como amenazadas, con un 53 % de dasyuridae, el 47 % de macropodae y potoroidae, el 33% de bandicoot y bilby, el 33 % zarigüeyas, el 30 % de los roedores, y el 24 % de las especies de murciélagos están evaluados como extintas, amenazadas o casi amenazadas. Sin embargo, el alcance geográfico y cronológico de las disminuciones, y sus causas, siguen estando mal resueltos, lo que limita la aplicación de medidas de gestión de recuperación.

Material y métodos: Centrándose en las sabanas tropicales del norte de Australia, en este trabajo se revisan los estudios recientes y se proporciona información sobre las tendencias de población a través de un ámbito geográfico más amplio y se proporciona información sobre el estado de conservación y las tendencias de mamífero grupos (murciélagos, macropodos) no así la muestra en los estudios de seguimiento anteriores. Se describen algunos enfoques diversos de los estudios que documentan sobre el estado de conservación, las tendencias, y de los factores que pueden estar contribuyendo a los patrones observados de declive.

Resultados y discusión: Las tendencias actuales y los posibles factores causales de caídas. Los estudios publicados demuestran que la magnitud y oportunidad de los impactos y amenazas han sido variables en toda la región, a pesar de que existe un patrón gradual general de descenso que antes, y más grave de zonas de precipitaciones inferiores a las regiones costeras de mayor precipitación. Algunas pequeñas zonas aisladas parecen haber conservado sus especies de mamíferos, al igual que muchas islas en las que permanecen refugios críticos. En la actualidad existe cierta evidencia convincente de que la depredación por gatos salvajes está implicada en la disminución observada, con estos impactos podrían verse agravados por los regímenes de fuego (fuego frecuente, extensa e intensa), que prevalece por la reducción de la cobertura vegetal del suelo debido a la ganadería y, en algunas áreas, por "control" de los dingos. Sin embargo, los impactos de los dingos pueden ser complejos, y sin embargo, no están bien resueltas en esta área. Los impactos relativos de estos factores individuales varían espacialmente (con la mayoría de los impactos severos en áreas de mayor precipitación y áreas escarpadas) y entre las diferentes especies de mamíferos, no obstante con algunas especies de responder idiosincrásicamente: el ejemplo más notable es la rápida disminución del quoll del norte (Dasyurus hallucatus) debido a la intoxicación por el sapo de caña introducido (Rhinella marina), que continúa propagándose ampliamente en todo el norte de Australia. El impacto de la enfermedad, en su caso, sigue sin resolverse.

Respuestas de la Administración de Conservación. La recuperación de la fauna de mamíferos nativos puede ser imposible en algunas áreas. Sin embargo, ahora hay ejemplos de una rápida recuperación siguiente a la gestión de amenazas. Acciones prioritarias de conservación incluyen: una mayor bioseguridad para las islas importantes, establecimiento de una red de exclusiones de depredadores salvajes, manejo de incendios intensivos (dirigido a aumentar la extensión del hábitat más extenso sin quemar y en el suministro de una escala fina del parche de quema), reducción de acciones salvajes en las reservas de conservación y adquisición con de algunas tierras de pastoreo en áreas que son importantes para la conservación de los mamíferos.

Palabras clave: sapos de caña, conservación, enfermedad, gatos salvajes, fuego, pastoreo, sabana, amenazas

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Distribution, abundance and threats to populations of Baird's tapir (*Tapirus bairdii)* and white-lipped peccary (T*ayassu peccary*) populations in Mexico

Distribución, abundancia y amenazas a las poblaciones de tapir centroamericano (*Tapirus bairdii*) y pecarí de labios blancos (*Tayassu pecari*) en México

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Introduction: Baird's tapir (*Tapirus bairdii*) and the white-lipped peccary (*Tayassu pecari*) play important roles in the dynamics of tropical forests where they live through herbivory, seed dispersal, and seed predation. These mammals have constituted relevant food sources for residents of rural communities of Mesoamerica. Both ungulates are listed as endangered species in Mexico´s Official Norm 059 (NOM-059-SEMARNAT-2010). Their main threats are habitat loss and poaching throughout their distribution range in Mexico. The central purpose of this study was to assess the population status of Baird´s tapir and the white-lipped peccary in Mexico, proposing a strategy for their conservation.

Methods: From November 2010 through November 2012 we did rapid assessments of presence, relative abundance, and threats for Baird´s tapir and white-lipped peccary populations in ten localities across five states of southeastern Mexico. We used three complementary techniques: line transect sampling, camera-trapping, and interviews with inhabitants of rural communities. We analyzed our own data and available information on both focal species in Mexico for generating proposals confirming their status as endangered in the Official Norm 059 by means of the Risk Assessment Method (MER, for its Spanish initials), required by the Ministry of Environment and Natural Resources.

Results and discussion: Current verified distribution areas of the white-lipped peccary are located in the states of Campeche, Chiapas, Oaxaca, Quintana Roo, Veracruz, and Yucatan. Baird's tapir is present in even more localities within the same states excluding Yucatan. Because of their extensive area and good habitat quality, the critical locations for conserving both species in the country are: Calakmul-Balamkú-Balam-Kin (Campeche), Montes Azules-Lacantún (Chiapas), Los Chimalapas (Oaxaca), and Sian Ka'an-forest ejidos of central Quintana Roo. The highest estimates of tapir abundance were recorded in La Fraylescana, Uxpanapa, and Los Chimalapas (sightings and tracks), as well as in Uxpanapa, Selva Lacandona, and Balam-kin (photographs). The highest white-lipped peccary abundances were found in Sian Ka'an and Calakmul (sightings and tracks), as well as in Balam-kin and Calakmul (photographs).

The main threats for conserving both ungulate species in Mexico are deforestation and habitat fragmentation, unregulated hunting, forest fires, and disease transmitted by livestock. Unexpected recent records of the two species in specific localities of Campeche, Veracruz, and Yucatan encourage the continuity and widening of research on the distribution and conservation status of these endangered mammals in southern and southeastern Mexico.

Key words: Abundance, conservation, distribution, Mexico, *Tapirus bairdii*, *Tayassu pecari*, threats.

Introducción

La conservación y el uso sustentable de especies de fauna silvestre requieren necesariamente de información básica sobre la distribución, abundancia y biología de las poblaciones de interés (Caughley y Sinclair 1994; Ojasti y Dallmeier 2000). Esta clase de información es particularmente importante cuando las especies de interés se encuentran amenazadas o en peligro de extinción debido a la pérdida de hábitat y a la cacería sin control, como es el caso de numerosos vertebrados neotropicales, entre los que se encuentran el tapir centroamericano (*Tapirus bairdii*) y el pecarí de labios blancos (*Tayassu pecari*). Además de representar recursos alimentarios importante para los pobladores de comunidades rurales de Mesoamérica, estos dos mamíferos juegan un papel importante en la dinámica de los bosques tropicales donde habitan a través de los procesos de herbivoría, dispersión y depredación de semillas de numerosas especies vegetales (Bodmer 1991; March 1993; Olmos 1997).

En México, el tapir y el pecarí de labios blancos están considerados en peligro de extinción (SEMARNAT 2010), y ambas se encuentran en la lista de especies prioritarias de la Comisión Nacional de Areas Naturales Protegidas (CONANP 2009). La distribución histórica de ambas especies en México incluía gran parte de los bosques tropicales y mesófilos del sur. Sin embargo, en la actualidad estos ungulados se encuentran solamente en algunas áreas silvestres extensas remanentes, principalmente dentro de áreas protegidas (March 2005; March y Naranjo 2005). Aunque el estado de las poblaciones de las dos especies se conoce para algunas áreas de Chiapas, Campeche y Oaxaca, parece evidente que las tendencias apuntan hacia la declinación y el aislamiento ante el avance de la actividad humana en las áreas tropicales del país (Naranjo 2009; Naranjo 2014; Reyna 2007; Reyna et al. 2014). De aquí se desprende la importancia de generar información que ofrezca un panorama más completo y actualizado sobre la situación de ambas especies en apoyo a las estrategias y políticas que requieren aplicarse para evitar su extinción en México. A continuación se presenta una síntesis del conocimiento sobre el estado de las poblaciones de cada especie en el país:

El tapir en México. El tapir centroamericano (Figura 1) se encuentra en peligro de extinción tanto a nivel nacional (SEMARNAT 2010) como internacional (IUCN 2012), y es considerado especie prioritaria por la CONANP (2009). La información disponible para el tapir en el subsistema de especies en riesgo y prioritarias del Sistema Nacional de Información Biológica (SNIB) que administra la Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) es deficiente y no está actualizada (Gómez-Nísino 2006). Sin embargo, dos trabajos publicados en los últimos años (Naranjo 2009; Naranjo 2014) resumen el estado del conocimiento de esta especie en México de una manera más completa. La distribución histórica de este ungulado incluyó gran parte de las áreas tropicales húmedas del sur y sureste del país (March 1994). Sin embargo, en la actualidad esta especie solamente está presente en algunas áreas silvestres extensas en los estados de Campeche, Chiapas, Oaxaca, Quintana Roo, Veracruz, y posiblemente Yucatán y Tabasco (Botello *et al.* 2014; Mendoza *et al.* 2013; Naranjo *et al.* 2013). Las regiones con presencia verificada de tapires son: Reserva de la Biósfera Calakmul y sureste de Campeche; Reserva de la Biósfera Sian Ka'an, centro y sur de Quintana Roo; Reservas de la Biósfera El Ocote, El Triunfo, La Sepultura, Lacantún y Montes Azules, Selva Lacandona y Sierra Madre de Chiapas; Los Chimalapas, Parque Nacional Lagunas de Chacahua y Sierra Mixe, Oaxaca; y Uxpanapa, Veracruz (Botello *et al.* 2014; Mendoza *et al.* 2013; Naranjo *et al.* 2013). Aunque no existen registros verificados recientes, es probable que aún existan pequeñas poblaciones aisladas de tapires en la Reserva de la Biósfera Pantanos de Centla y zona fronteriza de Tabasco, y en el extremo sur del estado de Yucatán (Naranjo 2009; Naranjo *et al.* 2013).

La investigación realizada sobre el tapir en el país se ha limitado a unas pocas poblaciones. La abundancia poblacional, las preferencias de hábitat, el rango de acción individual y los hábitos de alimentación de tapires han sido estudiados en algunas localidades de Chiapas Campeche y Oaxaca mediante conteos de individuos y rastros en transectos lineales (Lira y Naranjo 2005; Muench 2001; Naranjo y Cruz 1998; Naranjo y Bodmer 2002), observación de plantas ramoneadas y análisis de excrementos (Cruz 2001; Naranjo y Cruz 1998; O'Farril *et al.* 2006; Rivadeneyra 2007; Naranjo 2009), radiotelemetría (Lira 2006; Naranjo y Bodmer 2002) y foto-trampeo (Carbajal-Borges *et al.* 2014; Lira *et al.* 2014; Pérez y Matus 2010). Las estimaciones de densidad disponibles para México se ubican entre 0.01 y 0.5 tapires/km^2 (Carbajal-Borges *et al.* 2014; Naranjo 2009). Considerando estas densidades tan bajas, resulta evidente que solo unas pocas reservas en el país parecen ser suficientemente grandes para albergar poblaciones viables de tapires conformadas por varios cientos de individuos (Naranjo 2009). Los factores de amenaza más importantes para el tapir son indudablemente la pérdida de hábitat y la cacería sin control (March y Naranjo 2005; Naranjo 2014).

Figura 1. Tapir centroamericano (*Tapirus bairdii*). Selva Lacandona, Chiapas. Foto: Eduardo Naranjo.

*El pecarí de labios blancos en México. E*l pecarí de labios blancos (Figura 2) ha sido escasamente estudiado en México, y a solicitud (mediante el procedimiento MER) de dos de los autores del presente estudio (EJN y RRH), ha sido incluido recientemente como especie en peligro de extinción en la NOM-059-2010 (SEMARNAT 2010). Este pecarí además figura en la lista de especies prioritarias de la CONANP (2009). La distribución histórica de este mamífero en el país incluyó las planicies costeras cubiertas por bosques tropicales húmedos y subhúmedos del Golfo de México, Mar Caribe y Pacífico sur, incluyendo los estados de Veracruz, Tabasco, Campeche, Yucatán, Quintana Roo, Oaxaca y Chiapas (Reyna *et al.* 2014). En estos últimos dos estados, los bosques mesófilos de montaña por debajo de los 2 mil metros de altitud también albergaron poblaciones de pecaríes de labios blancos hasta hace algunas décadas (March 1993; Naranjo 2002; Reid 1997; Sowls 1997).

El pecarí de labios blancos se distingue considerablemente de otros mamíferos neotropicales por las grandes manadas que llega a formar y que pueden sobrepasar los 100 individuos (Sowls 1997). El tamaño promedio de los grupos registrados en México es de 13 - 28 individuos (Naranjo 2002; Reyna 2002). Su densidad poblacional se ha estimado entre 1 y 15 individuos/km^2, aunque con frecuencia estas cifras se encuentran por debajo de 5 ind/km^2 en sitios con cacería persistente (Bodmer *et al.* 1997; Naranjo *et al.* 2004a; Sowls 1997). Este mamífero requiere para sobrevivir de áreas forestales extensas (>10,000 ha) y sin actividad humana, preferentemente selvas altas y medianas húmedas, así como bosques bajos inundables (March 2005; Mayer y Wetzel 1987; Reyna 2007).

Figura 2. Pecaríes de labios blancos (*Tayassu pecari*). Reserva de la Biosfera Calakmul, Campeche. Foto: Rafael Reyna.

En la actualidad esta especie prácticamente ha desaparecido de Tabasco, y en Veracruz (Uxpanapa) y Yucatán (Dzilam) sobreviven pequeñas poblaciones aisladas (Naranjo *et al.* 2013). Solo los estados de Campeche, Chiapas, Oaxaca y Quintana Roo conservan poblaciones importantes en las Reservas de la Biosfera de Calakmul, Montes Azules, región de Los Chimalapas y Reserva de la Biosfera de Sian Ka'an, respectivamente (Lira y Briones 2011; Naranjo *et al.* 2013; Reyna *et al.* 2009). En Quintana Roo además sobreviven algunas poblaciones pequeñas en ejidos forestales cercanos a la Reserva de Sian Ka'an y al sur del estado y en Campeche en los alrededores de la Reserva de Calakmul (March 1990; Naranjo *et al.* 2013; Quijano 2001; Reyna *et al.* 2009). La superficie total estimada en la que subsiste la especie en México es de alrededor de 2 millones de hectáreas (20,000 km^2), lo que apenas representa un poco más del 1 % del territorio nacional (Naranjo y Reyna 2007). Existe una intensa cacería sin control de esta especie en casi toda su área de distribución, pues su carne es muy apreciada por los pobladores del medio rural en el sureste de México (Escamilla *et al.* 2000; Naranjo *et al.* 2004b; Weber 2000). Este hecho aunado a la severa deforestación ocurrida durante las últimas décadas en el sureste del país han ocasionado que el pecarí de labios blancos probablemente sea el ungulado tropical más raro de México en la actualidad (Naranjo y Bodmer 2007; Reyna *et al.* 2014).

El objetivo central del presente estudio consistió en generar un diagnóstico sobre el estado actual de las poblaciones de tapir y pecarí de labios blancos en México, proponiendo una estrategia para su conservación. En particular, 1) se sistematizó información actualizada sobre la distribución, abundancia y estado de las poblaciones de ambas especies en el país; 2) se identificaron las amenazas más importantes para la supervivencia de las dos especies en México, elaborando una propuesta de acuerdo al Método de Evaluación de Riesgo (MER) para cada una de ellas; y 3) se propusieron líneas de acción útiles para integrar los Programas de Acción para la Conservación (PACE) de ambos mamíferos en México.

Métodos

Área de estudio

Las únicas poblaciones de tapir que han sido parcialmente estudiadas en México son las que se encuentran en la Selva Lacandona (Reserva Montes Azules), Sierra Madre de Chiapas (Reservas El Triunfo y La Sepultura), Los Chimalapas y Calakmul. En el caso del pecarí de labios blancos, el conocimiento de las poblaciones se limita a las Reservas Montes Azules y Calakmul, y a parte de Los Chimalapas. Por lo anterior, las áreas de estudio consideradas en esta investigación fueron aquellas para las cuales existía información publicada escasa o nula, y que además cuentan con gran extensión y buenas cualidades para soportar poblaciones importantes de al menos una de las dos especies objeto del estudio. Dado que algunos de los sitios de estudio propuestos son muy extensos, se seleccionaron localidades puntuales en cada uno de ellos para realizar las evaluaciones de campo (Figura 3, Tabla 1). Estas localidades se escogieron con base en su ubicación dentro de los polígonos propuestos, la existencia de fragmentos forestales extensos en sus territorios, la presencia confirmada o probable de alguna de las dos especies focales, su accesibilidad durante el período de estudio, y la anuencia de sus pobladores para permitir la realización de los muestreos y entrevistas.

Selva Zoque: La Selva Zoque incluye las regiones de Uxpanapa en Veracruz, Los Chimalapas en Oaxaca y la Selva El Ocote (Reserva de la Biosfera, 481 km^2) en el estado de Chiapas, constituyendo una enorme ecoregión de más de 6,000 km^2 caracterizada por su gran heterogeneidad topográfica (40 – 1,400 msnm) que origina variantes climáticas de tipo cálido húmedo y subhúmedo con abundantes lluvias en verano (Am, Aw y A(C)w; Arriaga *et al.* 2000; SEMARNAT 2001). La precipitación anual y la temperatura media anual varían entre 1,450 y 3,500 mm, y 22 a 27°C, respectivamente. Los principales tipos de vegetación son las selvas altas perennifolias, medianas subperennifolias, bajas caducifolias, bosques mesófilos de montaña, acahuales y pastizales inducidos. En la región se han registrado 149 especies de mamíferos incluyendo al tapir y al pecarí de labios blancos (Lira *et al.* 2012; SEMARNAT 2001), aunque en la Selva El Ocote no existen registros recientes de ésta última. Entre los principales problemas ambientales de la región están la deforestación, la expansión de la ganadería y los desmontes para el cultivo de estupefacientes, conflictos territoriales entre comunidades de Chiapas y Oaxaca, la apertura de carreteras, la cacería sin control y en particular los incendios forestales y quemas de acahuales y pastizales (Arriaga *et al.* 2000; Lira y Briones 2011; SEMARNAT 2001). Los muestreos en la Selva Zoque se llevaron a cabo en: 1) el Ejido La Fortaleza, municipio de Santa María Chimalapa, Oaxaca; 2) Ejido Loma de Oro y Predio El Jaguar cercano al poblado El Quince, municipio de Uxpanapa, Veracruz; y 3) cercanías del Ejido Emilio Rabasa en la Reserva de la Biosfera Selva El Ocote, municipio de Ocozocoautla, Chiapas.

La Fraylescana: Esta región enclavada en la Sierra Madre de Chiapas constituye un área protegida (Zona de Protección Forestal; 1,514 km^2) y presenta relieve abrupto, con altitudes entre 250 y 2,550 msnm (Vargas y Escobar 2000). Los climas presentes incluyen el cálido y semicálido húmedo y subhúmedo (Am, Aw, A(C)w y A(C)m), y templado húmedo. La precipitación anual fluctúa entre 1,200 y 3,500 mm, y la temperatura media anual varía entre 18 y 24 °C. Los tipos de vegetación presentes son las selvas bajas caducifolias, selvas medianas subperennifolias, bosques de pino, bosques de encino y bosques mesófilos de montaña. En el área existen registros recientes de tapir, pero no de pecarí de labios blancos. Parte del área protegida está ocupada por pastizales inducidos, cafetales y cultivos de temporal. En el área existen procesos de deforestación por extracción de madera, expansión de la ganadería y la agricultura, cacería furtiva, erosión e incendios forestales (Pérez-Farrera *et al.* 2006). Los muestreos se efectuaron en la Finca Arroyo Negro, municipio de La Concordia, Chiapas.

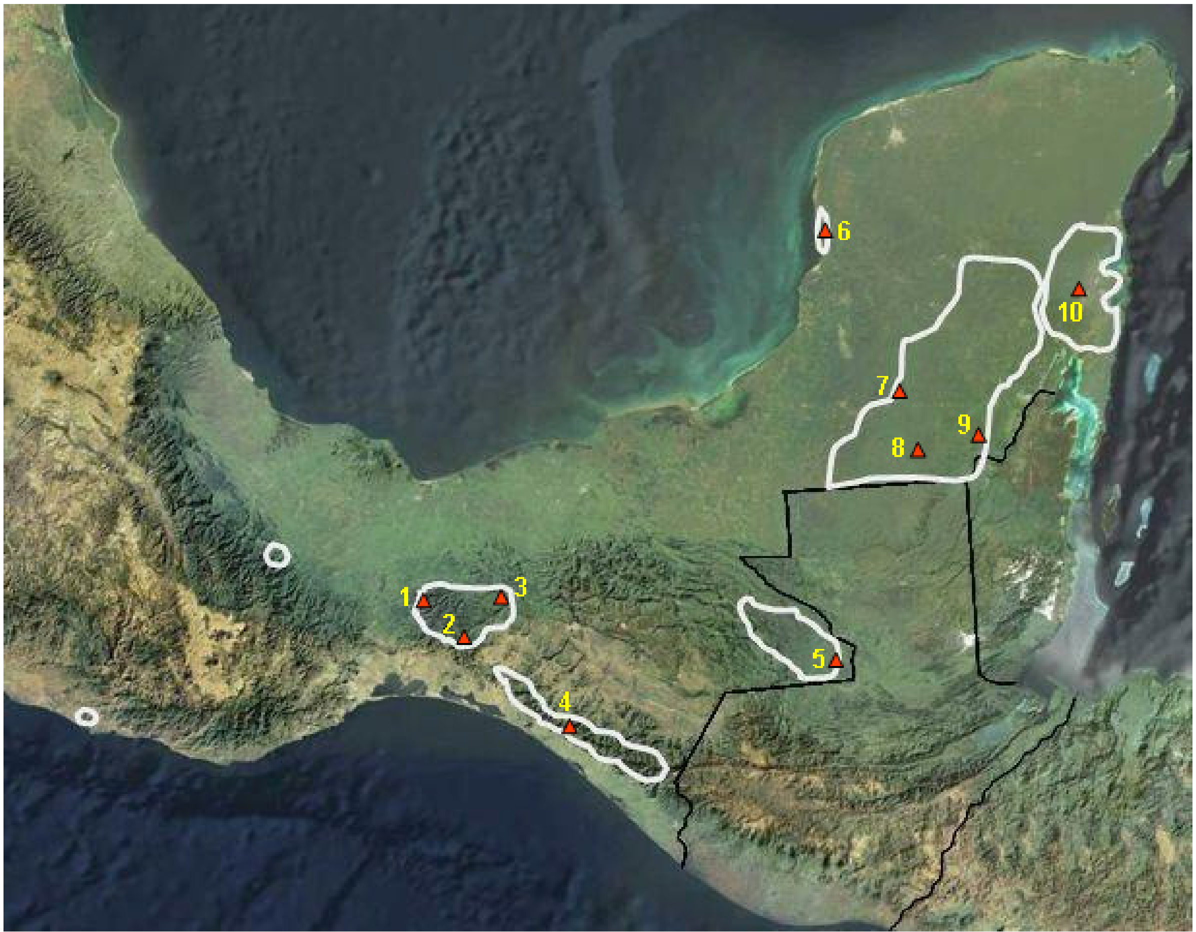

Figura 3. Ubicación de los sitios de estudio donde se evaluaron poblaciones de tapir y pecarí de labios blancos: 1) Uxpanapa, 2) Los Chimalapas, 3) Selva El Ocote, 4) La Fraylescana, 5) Marqués de Comillas, 6) Los Petenes, 7) Balam-kin y Balamkú, 8) Calakmul, 9) Ejidos forestales de Quintana Roo, 10) Sian Ka'an. Las áreas delineadas indican la distribución aproximada del tapir.

Marqués de Comillas: La subregión Marqués de Comillas de la Selva Lacandona está repartida en numerosos ejidos con habitantes provenientes de varias regiones de Chiapas y de otros estados del país. Su relieve es relativamente plano con algunos lomeríos hacia el suroeste y su altitud es de 150 a 200 msnm. El clima predominante es cálido húmedo (Am). La precipitación media anual es de casi 3,000 mm, y la temperatura media anual es de 25 °C. La vegetación predominante es selva alta perennifolia en diversos estadíos sucesionales, pastizales inducidos, cultivos de temporal y plantaciones de cacao. La fauna de la región incluye 118 mamíferos entre los que se encuentran el tapir y el pecarí de labios blancos (Naranjo 2002). Entre los factores de impacto ambiental en la región se encuentran el avance de la ganadería extensiva, la extracción maderera, la cacería sin control, los incendios forestales y las quemas de áreas agropecuarias (INE 2000b). El trabajo de campo se realizó en las cercanías del río Lacantún dentro de la Reserva de la Biosfera Montes Azules, municipio de Ocosingo, y en los Ejidos Adolfo López Mateos, Belisario Domínguez, Chajul, El Pirú, Flor del Marqués, Galacia, José López Portillo, Loma Bonita, Quiringuicharo, Playón de la Gloria, Reforma Agraria y Zamora Pico de Oro, municipio de Marqués de Comillas, Chiapas.

Los Petenes: Esta área protegida abarca 3,824 km^2 de ecosistemas terrestres y acuáticos en la planicie costera del norte de Campeche sujeta a inundaciones semipermanentes y estacionales. La topografía es plana y la altitud promedio es inferior a 10 msnm. En el área existen islas circulares de vegetación arbórea conocidas como petenes. Los tipos de clima predominantes son el cálido subhúmedo con lluvias en verano (Aw), y el semiseco cálido (BS'h'w). La temperatura y precipitación medias varían de 26 a 28 °C, y de 700 a 1,100 mm, respectivamente. La vegetación terrestre consiste en bosques de manglar, tulares, selva baja subperennifolia (inundable) y petenes. Se han observado 47 especies de mamíferos, con al menos un registro verificado de tapir (INE 2006; Naranjo *et al.* 2013). Las actividades con impacto en los ecosistemas de la reserva son la tala de manglares y selvas, la cacería furtiva y la pesca no regulada (INE 2006). El trabajo de campo se llevó a cabo en el interior de la Reserva de la Biosfera Los Petenes y el Ejido Zodzil, municipio de Hecelchakán, Campeche.

Calakmul, Balam-kin y Balamkú: Las Reservas Calakmul, Balam-kin y Balamkú abarcan una extensión conjunta de 7,760 km^2. El relieve es predominantemente plano con algunos lomeríos de hasta 300 msnm. El manto de caliche que cubre la mayor parte de las tierras altas es poroso y absorbe gran

Tabla 1. Localización de los sitios de estudio donde se realizaron las evaluaciones poblacionales de tapir y pecarí de labios blancos.

Estado	Sitio	Vértices aproximados	Tapir	Pecarí
Veracruz	1. Región Uxpanapa	17º12’ N - 93º52’ O 17º13’ N - 94º03’ O 17º18’ N - 93º59’ O	X	X
Oaxaca	2. Región Los Chimalapas	16º54’ N - 94º13’ O 16º54’ N - 94º30’ O 17º00’ N - 94º02’ O 17º06’ N - 94º30’ O	X	X
Chiapas	3. Reserva de la Biosfera Selva El Ocote	16º54’ N - 93º34’ O 16º59’ N - 93º32’ O 17º00’ N - 93º44’ O 17º04’ N - 93º37’ O	X	
Chiapas	4. Zona de Protección Forestal La Fraylescana	15º51’ N - 93º15’ O 15º52’ N - 93º09’ O 15º54’ N - 93º15’ O 15º56’ N - 93º09’ O	X	
Chiapas	5. Selva Lacandona, Subregión Marqués de Comillas	16º06’ N - 90º48’ O 16º06’ N - 90º51’ O 16º15’ N - 90º47’ O 16º17’ N - 90º50’ O	X	X
Campeche	6. Reserva de la Biosfera Los Petenes	20º00 N - 90º22’ O 20º00 N - 90º26’ O 20º13 N - 90º22’ O 20º13 N - 90º26’ O	X	
Campeche	7. Reservas Estatales Balam-kin y Balamkú	18º39’ N - 90º31’ O 18º39’ N - 90º36’ O 18º45’ N - 90º31’ O 18º45’ N - 90º36’ O	X	X
Campeche	8. Reserva de la Biosfera Calakmul	18º06’ N - 89º56’ O 18º06’ N - 90º19’ O 18º26’ N - 89º56’ O 18º26’ N - 90º17’ O	X	X
Quintana Roo	9. Ejidos forestales del centro y sur	18º16’ N - 88º54’ O 18º16’ N - 88º57’ O 18º19’ N - 88º54’ O 18º19’ N - 88º57’ O	X	X
Quintana Roo	10. Reserva de la Biosfera Sian Ka’an	19º08’ N - 87º57’ O 19º08’ N - 88º01’ O 19º11’ N - 87º57’ O 19º11’ N - 88º01’ O	X	X

parte del agua de lluvia, por lo que no existen corrientes de agua permanentes y ésta se encuentra disponible solamente en lagunas dispersas de baja profundidad llamadas "aguadas". El clima es cálido subhúmedo (Aw), la precipitación varía de 600 a 1200 mm y la temperatura media anual es de 24 a 26 ºC. Las selvas altas y medianas perennifolias y subperennifolias dominan el paisaje, aunque también están presentes selvas bajas caducifolias inundables y vegetación acuática. Entre las casi 100 especies de mamíferos presentes se encuentran el tapir y el pecarí de labios blancos (INE 2000a; Reyna 2007). La escasez de agua en la región limita la expansión de la agricultura y la ganadería, pero persisten la extracción forestal, la cacería ilegal, los incendios forestales y la apertura de carreteras (INE 2000a). Los muestreos de abundancia se hicieron en las cercanías de la zona arquelógica de Calakmul y en el interior de la Reserva de Balam-kin, ambos en el municipio de Calakmul, Campeche. Las entrevistas se realizaron en los Ejidos Nuevo Becal, 20 de Noviembre y Conhuas, todos del mismo municipio.

Sian Ka'an y Ejidos Forestales de Quintana Roo: La gran extensión forestal de esta región (> 6,000 km^2) la hacen una de las más importantes del país desde el punto de vista de conservación del tapir y el pecarí de labios blancos. El relieve es predominantemente plano, los suelos son pedregosos y someros, y el clima es cálido subhúmedo con lluvias en verano (Aw). La temperatura y precipitación medias son de 26.5 °C y 1,200 mm, respectivamente. Dominan el paisaje las selvas medianas subperennifolias, selvas bajas subcaducifolias y caducifolias, bosques de manglar, acahuales y dunas costeras. Se han registrado en la región 114 especies de mamíferos, entre ellos el tapir y el pecarí de labios blancos (Escobedo 2011; SEDESOL 1993). Entre los problemas ambientales de esta región se encuentran la extracción forestal sin control, los incendios, la construcción de autopistas y los desarrollos turísticos a gran escala (Lozano y Olivares 2011). El trabajo de campo se llevó a cabo en los ejidos Chanká Veracruz y X-Hazil (municipio de Felipe Carrillo Puerto) y Caobas (municipio de Othón P. Blanco), Quintana Roo.

Trabajo de campo. El trabajo de campo de este estudio se desarrolló de noviembre 2010 a noviembre 2012. Durante los primeros meses se hizo una recopilación y sistematización de la información publicada (artículos y libros) y no publicada (tesis, informes de investigación, bases de datos) sobre las poblaciones mexicanas de las dos especies bajo estudio. Para ello se recurrió a los sistemas de información documental de instituciones como El Colegio de la Frontera Sur (ECOSUR), la Universidad Nacional Autónoma de México (UNAM), la Universidad de Ciencias y Artes de Chiapas (UNICACH), los Grupos de Especialistas en Tapires y Pecaríes de la Unión Internacional para la Conservación de la Naturaleza (UICN), y el Sistema Nacional de Información sobre Biodiversidad (SNIB) de la Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO).

Evaluaciones poblacionales

En cada sitio de trabajo se realizó una evaluación rápida de la presencia y abundancia relativa de tapir y pecarí de labios blancos mediante tres técnicas complementarias con ayuda de pobladores locales, técnicos y tesistas. La primera técnica consistió en la colocación de una retícula de 3 x 3 cámaras-trampa (modelos Moultrie D55 y D55IR) ubicadas a 1 km de distancia entre sí por cada localidad. Las cámaras se ajustaron a una altura de entre 50 y 70 cm del suelo en troncos de árboles, y se programaron para tomar series de 3 fotografías con tiempo de espera de 1 minuto entre eventos. Cada retícula de cámaras permaneció entre 25 y 40 días en un mismo sitio de muestreo. A partir de las imágenes capturadas se calcularon índices de abundancia (tasas fotográficas: número de fotos/ número de cámaras/ número de días de muestreo x 100; Conroy 1996; Cutler y Swann 1999; O'Connell *et al.* 2011) para cada especie en cada sitio de trabajo.

Durante el tiempo que las cámaras-trampa permanecieron funcionando en el campo se aplicó una segunda técnica de muestreo, consistente en recorridos diurnos a lo largo de dos a tres transectos lineales de 2-5 km de longitud por localidad. Durante estos recorridos se hicieron conteos de individuos o rastros (huellas y excretas frescas) de cualquiera de las dos especies. Cada transecto fue recorrido cuando menos dos veces durante el estudio, anotando el número de individuos y rastros observados de cada especie, así como la fecha, posición geográfica (coordenadas) y las características del hábitat (tipo de vegetación, geomorfología, presencia de cuerpos de agua y distancia a asentamientos humanos) correspondientes a cada registro. A partir de las observaciones logradas en los transectos se estimaron índices de abundancia relativa (número de rastros o individuos/ 10 km recorridos; Conroy 1996; Naranjo 2000).

La tercera y última técnica de muestreo fue la aplicación de entrevistas semi-estructuradas a pobladores de las comunidades rurales más cercanas a las áreas visitadas. Se utilizó un cuestionario guía para recopilar información sobre la presencia y abundancia estimada de tapires y pecaríes de labios blancos, en el que se incluyeron preguntas sobre la antigüedad de los avistamientos de ambas especies en la localidad, así como las características del hábitat (arriba citadas) en el que fueron observados los ejemplares, la existencia de cacería y otras amenazas potenciales para las especies objeto del estudio. Para evitar dudas en la identificación de las especies por los entrevistados, se mostraron ilustraciones a color de las mismas tomadas de guías de campo (Emmons y Feer 1997; Reid 1997). Cuando se obtuvieron referencias de animales cazados recientemente en una comunidad, se procuró localizar y examinar los restos de los mismos (cráneos o pieles) para corroborar la especie y estimar la categoría de edad (juvenil o adulto) con base en las dimensiones de las partes disponibles (Naranjo y Bodmer 2002). Los restos localizados fueron depositados en la colección mastozoológica de El Colegio de la Frontera Sur en San Cristóbal de Las Casas, Chiapas.

Análisis de la información

La distribución espacial del tapir y el pecarí de labios blancos se determinó en base a su presencia o ausencia en cada transecto y sitio de estudio. Se registró la presencia actual de las dos especies en cada sitio a través de las cámaras-trampa, los recorridos para observación de animales o sus rastros, y las entrevistas a pobladores locales. Estas últimas aportaron también información sobre la distribución histórica de ambas especies. Una vez confirmada o descartada la presencia real de tapires y pecaríes de labios blancos en cada sitio de estudio, con la ayuda de un sistema de información geográfica (ArcView; ESRI 2008) se elaboraron mapas de distribución actual verificada de cada especie. Los factores de amenaza a las especies bajo estudio (deforestación, fragmentación, incendios, cacería y presencia de animales domésticos) se identificaron en cada sitio de estudio y se clasificaron utilizando una escala semi-cuantitativa (bajo = 0-1 factores presentes; medio = 2-3; alto > 3).

Método de Evaluación de Riesgo (MER). Como resultado de la recopilación de información y las evaluaciones de campo arriba descritas, se generó un diagnóstico del estado de las poblaciones de tapir y pecarí de labios blancos en el país que se plasmó en un protocolo denominado "Método de Evaluación de Riesgo" (MER; SEMARNAT 2010). Para realizar estos protocolos se revisó la literatura disponible sobre ambas especies en todas sus áreas de distribución. La amplitud de la distribución de cada especie en el país (criterio A del MER) se estimó con base en los mapas de distribución real generados en este proyecto. El estado del hábitat (criterio B) se evaluó a partir tanto de la información sobre factores de amenaza y características del hábitat obtenidas en este estudio, como del análisis de la literatura disponible sobre los requerimientos vitales de ambos mamíferos y el estado de los ecosistemas en cada sitio de trabajo. La vulnerabilidad biológica intrínseca (criterio C) de cada especie se derivó de la literatura: 2 crías/hembra/año para el pecarí de collar (vulnerabilidad media; Bodmer *et al.* 1997; March 2005), y 0.5 crías/hembra/año para el tapir (vulnerabilidad alta; March y Naranjo 2005; Naranjo 2009). El impacto de la actividad humana sobre las dos especies (criterio D) se determinó con base en el análisis de factores de amenaza generado en el presente proyecto, así como en la revisión de literatura disponible y en las experiencias de más de dos décadas de investigación realizada por los miembros del equipo de trabajo en el sureste del país.

Resultados y Discusión

Distribución. Puesto que ya existían modelos recientes de la distribución potencial de ambas especies en el país (realizados mediante algoritmos GARP y otros; Ceballos 2008: Mendoza *et al.* 2013; Nolasco 2009), y considerando que dichos modelos son susceptibles a la sobreestimación de la distribución real (Loiselle *et al.* 2003), el análisis de distribución en este estudio se concentró en la verificación selectiva en campo de la presencia actual de los dos ungulados. Durante la investigación se lograron 105 registros de tapir (*n* = 79) y pecarí de labios blancos (*n* = 26; Tabla 2). Los muestreos de distribución realizados durante el proyecto permitieron obtener evidencias de la presencia de tapires en los 10 sitios seleccionados (Figura 4), lo que coincide plenamente con el modelo de distribución del hábitat potencial de esta especie en México desarrollado por Mendoza *et al.* (2013). En contraste, el pecarí de labios blancos solamente se detectó en seis de ellos, estando ausente de las regiones de la Selva El Ocote, La Fraylescana (Sierra Madre de Chiapas) y Los Petenes, Campeche (Figura 5 y Tabla 2). Aunque no se logró obtener evidencia de la presencia del pecarí de labios blancos en Los Chimalapas durante este proyecto, existe información previa de su presencia y abundancia en la región (Lira y Briones 2011; Lira *et al.* 2012). Lo anterior concuerda con propuestas previas sobre la disminución del hábitat para este pecarí (March 2005; Reyna *et al.* 2014), y fortalece la percepción de los pobladores de la mayoría de las localidades de estudio que se describe a continuación.

El total acumulado de entrevistas realizadas con pobladores de 20 comunidades rurales en los sitios de estudio fue de 111. Los análisis de la información relacionada con la distribución de ambas especies recabada en las entrevistas confirmaron que el tapir está presente en todos los sitios de estudio y en 18 de las 20 comunidades visitadas, faltando solamente en Benemérito de la Américas y Quiringuicharo (Selva Lacandona) desde hace 10 - 20 años. Por el contrario, el pecarí

Figura 4. Distribución actual del tapir (*Tapirus bairdii*) en México con base exclusivamente en los registros obtenidos (*n* = 79) en el trabajo de campo del presente proyecto. Mapa: Fredy Falconi Briones.

de labios blancos solamente persiste en siete de los 10 sitios de estudio (ausente de La Fraylescana, Selva El Ocote y Los Petenes) y en 12 de las 20 comunidades visitadas. Prácticamente todos (100 %) los pobladores consultados conocen a las dos especies ya sea por observación directa de animales vivos o cazados, o por referencia directa de sus padres y abuelos. La gran mayoría (81 %; 90/111) de los entrevistados aseguró que el tapir está presente en sus comunidades, mientras que el 15.3 % (17/111) afirmó que esta especie ya no está presente, y el restante 3.7 % (4/111) dijo no estar seguro. En el caso del pecarí de labios blancos, solamente el 34.2 % (38/111) de los entrevistados dijo que la especie aún está presente en su comunidad, mientras que la mayoría de ellos (59.5 %; 66/111) afirmó que ya no está presente, y el restante 6.3 % (7/111) no sabía. La percepción de los habitantes de los sitios de estudio evaluada a través de las entrevistas realizadas sugiere que el pecarí de labios blancos tiene actualmente una distribución notablemente más restringida que la del tapir en el país, lo cual coincide plenamente con los registros fotográficos y avistamientos de ejemplares y sus rastros logrados en este estudio.

Figura 5. Distribución actual del pecarí de labios blancos (*Tayassu pecari*) en México con base exclusivamente en los registros obtenidos (*n* = 26) en el trabajo de campo del presente proyecto. Mapa: Fredy Falconi Briones.

Los registros de presencia del tapir (Figura 6) logrados en el presente trabajo confirman que sus áreas de distribución actuales y verificadas en México se encuentran en los estados de Campeche (Reservas de Calakmul, Balamkú, Balam-kin, Los Petenes y Laguna de Términos); Chiapas (Reservas Selva El Ocote, El Triunfo, La Sepultura, Lacantún y Montes Azules, Comunidad Lacandona y algunos ejidos de Marqués de Comillas y de la Sierra Madre); Oaxaca (Los Chimalapas, Bajo Río Verde, Sierra Veinte Cerros y Sierra de Ixtlán de Juárez); Quintana Roo (Reserva Sian Ka'an y ejidos forestales del centro y sur), y Veracruz (cuenca alta del río Uxpanapa). En el caso del pecarí de labios blancos, las áreas de distribución verificadas coinciden con las del tapir, a excepción de la Reservas Los Petenes y Selva El Ocote, y la Sierra Madre de Chiapas. Entre éstas áreas, por su gran extensión y buena calidad de hábitat para las dos especies destacan las de Calakmul-Balamkú-Balam-kin (Figura 7), Montes Azules-Lacantún, Los Chimalapas, y Sian Ka'an-ejidos forestales del centro de Quintana Roo, las cuales pueden considerarse como críticas para la conservación de ambas especies en el país.

Es muy importante señalar que, gracias a la comunicación con investigadores de otras instituciones, se ha confirmado recientemente la presencia del pecarí de labios blancos mediante registros con cámaras-trampa en las cercanías de la Laguna de Términos en el municipio de Palizada, y en los ejidos Reforma Agraria y Pixtún, municipio de Champotón, ambos en la porción occidental del estado de Campeche (Mircea Hidalgo, Universidad Juárez Autónoma de Tabasco, com. pers. 2012). Otro hallazgo muy relevante de esta especie con la misma técnica es el logrado en septiembre de 2011 en el Rancho El Edén, dentro de la Reserva de Dzilam de Bravo, en la costa central de Yucatán (Luis Pereira y Carlos Alcérreca, BIOCENOSIS, A.C., com. pers. 2012).

Estos nuevos registros hacen evidente la necesidad de realizar exploraciones más detalladas de los sitios señalados, así como de otras áreas (*i. e*. Sierra Madre de Chiapas, Sierra Mixe de Oaxaca, Uxpanapa, Laguna de Términos, Champotón, Los Petenes y áreas costeras de Yucatán), lo que permitirá verificar la presencia o ausencia de tapires y pecaríes de labios blancos y evaluar el estado de conservación de las poblaciones encontradas así como la posible conectividad de éstas con otras más grandes, de manera que se tengan mayores elementos para hacer un diagnóstico realista sobre su persistencia a largo plazo.

Abundancia. Los índices de abundancia estimados a partir de muestreos en transectos lineales variaron entre 0.26 - 4.52 rastros de tapires, y 0.15 - 0.63 rastros de pecaríes de labios blancos por 10 km recorridos (Figuras 7 y 8, Tabla 3). En el caso del tapir, los valores de abundancia obtenidos en este estudio se encuentran dentro del rango de abundancias estimadas en estudios previos realizados en México (0.05 a 8.1 rastros por 10 km; Lira *et al.* 2004; Naranjo 2009; Naranjo y Bodmer 2002; Naranjo y Cruz 1998; Reyna y Tanner 2007; Tejeda *et al.* 2009) y en otros países

Figura 6. Hembra adulta de tapir (*Tapirus bairdii*) fotografiada durante el proyecto con cámara-trampa en la Reserva Balam-kin, Campeche. Foto: Eduardo Naranjo, Fredy Falconi y Saúl Amador.

de Mesoamérica (1.5 a 6.6 rastros por 10 km; Flesher 1999; Naranjo 1995). En el caso del pecarí de labios blancos, las estimaciones realizadas en los sitios de estudio de la Selva Lacandona y Balam-kin se encuentran ligeramente por debajo del rango de abundancia encontrado en estudios previos en el país (0.21 a 2.0 rastros por 10 km; Naranjo *et al.* 2004b; Reyna y Tanner 2007; Tejeda et al 2009), mientras que el resto se ubican dentro de dicho intervalo. Los índices de abundancia estimados mediante foto-trampeo se ubicaron entre 0.38 - 2.00 (tapir) y 0.17 - 1.33 (pecarí) fotografías por 100 días-cámara (Figuras 7 y 8; Tabla 3). Las abundancias de ambos mamíferos estimadas con esta técnica fueron similares comparadas con las registradas en estudios previos en Los Chimalapas (0.8 y 2.5 fotografías por 100 días-cámara para tapir y pecarí, respectivamente; Lira y Briones 2012) y en general más bajas que las estimadas en localidades de Centro y Sudamérica (1 a 20 fotografías por 100 días-cámara; Harmsen *et al.* 2010; Silveira *et al.* 2003). No obstante lo anterior, al considerar las variantes metodológicas y ambientales (*i. e.* distintos hábitat, diseños y esfuerzos de muestreo, diferentes modelos de cámaras) aplicadas en los diversos estudios realizados, resulta difícil formular conjeturas convincentes que expliquen las diferencias encontradas en las abundancias relativas de ambas especies entre dichos estudios y el presente.

Aunque los mayores números de registros totales de ambas especies se obtuvieron en la Selva Lacandona, ésta no presentó en todos los casos los mayores índices de abundancia una vez considerado el gran esfuerzo de muestreo invertido (kilómetros recorridos y cámaras-trampa/día). Las mayores abundancias relativas de tapir estimadas mediante rastros y avistamientos directos se registraron en La Fraylescana, Uxpanapa y Los Chimalapas, mientras que las tasas fotográficas más elevadas para esta especie se obtuvieron en Calakmul, Uxpanapa, la Selva Lacandona y Balam-kin. En el caso del pecarí de labios blancos, las mayores abundancias a partir de rastros y avistamientos directos se estimaron en Sian Ka'an, Calakmul y Uxpanapa, mientras que los mayores valores a partir de foto-trampeo se obtuvieron en Calakmul y Balam-kin. Es interesante señalar que en este estudio no se lograron obtener fotografías con las cámaras-trampa en la Selva El Ocote, Los Petenes y Sian Ka'an para ninguna de las dos especies, y además en La Fraylescana, los ejidos forestales de Quintana Roo, y Los Chimalapas para el pecarí de labios blancos. Se esperaría que los sitios donde se registraron las mayores abundancias coincidieran en poseer grandes extensiones de bosque tropical húmedo con buena disponibilidad de agua y recursos alimentarios, además de no presentar elevada presión de cacería por los pobladores locales. Sin embargo, las abundancias tan diversas estimadas en este trabajo sugieren que las condiciones del hábitat para los tapires y los pecaríes de labios blancos en México son muy heterogéneas debido a una variedad de factores ambientales (clima, geomorfolgía, vegetación y disponibilidad de agua, entre otros) y sociales (usos del suelo, presión de cacería y presencia de asentamientos humanos, entre otros), lo que coincide con las apreciaciones de

Tabla 2. Número de registros de tapir y pecarí de labios blancos (LB) y entrevistas aplicadas en los sitios de estudio visitados en el período mayo - octubre 2012 y cifras totales. La presencia de al menos una de las dos especies ha sido confirmada en todos los sitios.

Sitio	Registros Tapir	Registros Pecarí LB	Registros Totales	Entrevistas
Selva Lacandona	22	10	32	58
Selva El Ocote	1	0	1	5
La Fraylescana	7	0	7	4
Uxpanapa	12	5	17	7
Los Chimalapas	14	0	14	6
Ejidos Forestales de Quintana Roo	7	2	9	6
Sian Ka'an	4	1	5	10
Calakmul	6	7	13	6
Balam-kin	5	1	6	4
Los Petenes	1	0	1	5
Totales	79	26	105	111

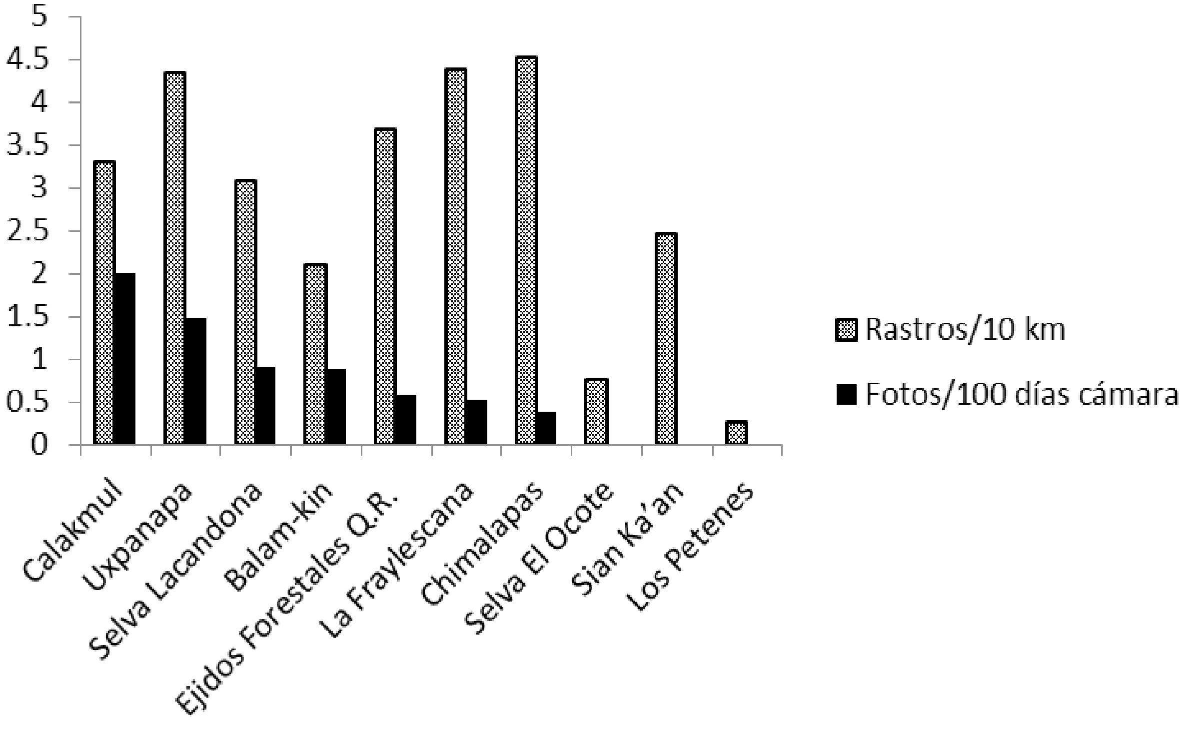

Figura 7. Abundancia del tapir (*Tapirus bairdii*) estimada mediante foto-trampeo y conteos de rastros en las localidades de estudio.

Naranjo (2009, 2014) y Reyna *et al.* (2014). Además, debe considerarse que los métodos de estudio empleados pueden ser afectados por las condiciones meteorológicas durante los períodos de muestreo (Naranjo 2000; O'Connell *et al.* 2011), de manera que los animales pueden modificar sus patrones de actividad, por ejemplo, si se presentan lluvias abundantes o días extremadamente calurosos, como sucedió en algunos de los sitios de estudio.

Amenazas. Las visitas al campo y las entrevistas con pobladores locales realizadas en este estudio permitieron atestiguar que entre las amenazas principales para la conservación del tapir y el pecarí de labios blancos en sus áreas de distribución actuales destacan en primer lugar la deforestación y fragmentación del hábitat (fundamentalmente selvas húmedas y subhúmedas), seguida de la cacería sin control (más notable para el pecarí) y otros factores como los incendios forestales, la sequía, las inundaciones, los huracanes y posiblemente las enfermedades transmitidas por animales domésticos (Naranjo *et al.* 2013; Reyna *et al.* 2014; Romero *et al.* 2008). Al respecto, la mayoría de los residentes entrevistados en los sitios de estudio opinaron que tanto el tapir (94 %) como el pecarí de labios blancos (78 %) se encuentran en situación de riesgo dentro de sus comunidades. Las amenazas más importantes para ambas especies percibidas por los entrevistados fueron la deforestación y fragmentación del hábitat, citadas por aproximadamente el 75 % de los entrevistados, seguida por la cacería sin control (38 %), los incendios forestales (18 %) y otros factores como la sequía, las inundaciones, las carreteras y las enfermedades (6 %). Las proporciones de los primeros dos factores (pérdida de hábitat y cacería) coinciden plenamente con nuestras observaciones en los sitios de trabajo, donde en muchos casos fue evidente el avance de la frontera agropecuaria sobre áreas hasta hace poco cubiertas con selvas maduras, además de la detección de evidencias de cacería (por ejemplo, cartuchos vacíos, plataformas construidas en árboles para esperar a las presas y cráneos perforados, entre otras). Sin embargo, fue sorprendente la elevada proporción de entrevistados que perciben a los incendios como una amenaza importante para las dos especies objeto del estudio, particularmente en la Selva El Ocote, Uxpanapa y Los Chimalapas, donde en las pasadas dos décadas se han presentado varios eventos de gran magnitud (Naranjo 2012; Ortega del Valle *et al.* 2012). En la Tabla 4 se muestran en orden de importancia las principales amenazas observadas tanto por el equipo de trabajo del proyecto como por los pobladores entrevistados en las comunidades visitadas. Por la cantidad observada de factores de amenaza, las áreas de mayor riesgo para las poblaciones evaluadas de tapir son Los Petenes, Uxpanapa y Los Chimalapas, en tanto que para el pecarí de labios blancos son también las dos últimas y además los ejidos forestales de Quintana Roo y ejidos del Marqués de Comillas en la Selva Lacandona (Tabla 4).

A pesar de la variedad e intensidad de las amenazas observadas para el tapir y el pecarí de labios blancos en los sitios de estudio, se recopilaron también algunos signos alentadores de recuperación de poblaciones en sitios puntuales como el Ejido Playón de la Gloria (Selva Lacandona), donde desde el año 2010 se han vuelto a observar rastros de tapir después de casi dos décadas de ausencia de esta especie en el territorio de la comunidad. Otro caso interesante fue el de las selvas de la cuenca alta del río Uxpanapa, donde se encontraron considerables extensiones de hábitat en excelente estado de conservación que albergan poblaciones de tapires, pecaríes de labios blancos, jaguares, pumas, monos y otros mamíferos grandes que han desaparecido desde hace ya décadas en la mayor parte de la cuenca baja de dicho río. Un tercer caso relevante es el del ejido El Pirú (Selva Lacandona), donde persisten poblaciones de ambas especies objeto del estudio. En esta comunidad los ejidatarios han decidido tomar medidas para restringir al mínimo la cacería y evitar deforestar las casi 3,000 hectáreas de selvas altas perennifolias que aún quedan en su territorio. Por último, los recientes registros arriba citados de tapir en Los Petenes y pecarí de labios blancos en el occidente de Campeche y el norte de Yucatán constituyen estímulos importantes para continuar y ampliar las investigaciones sobre la distribución y el estado de conservación de estas especies en el país.

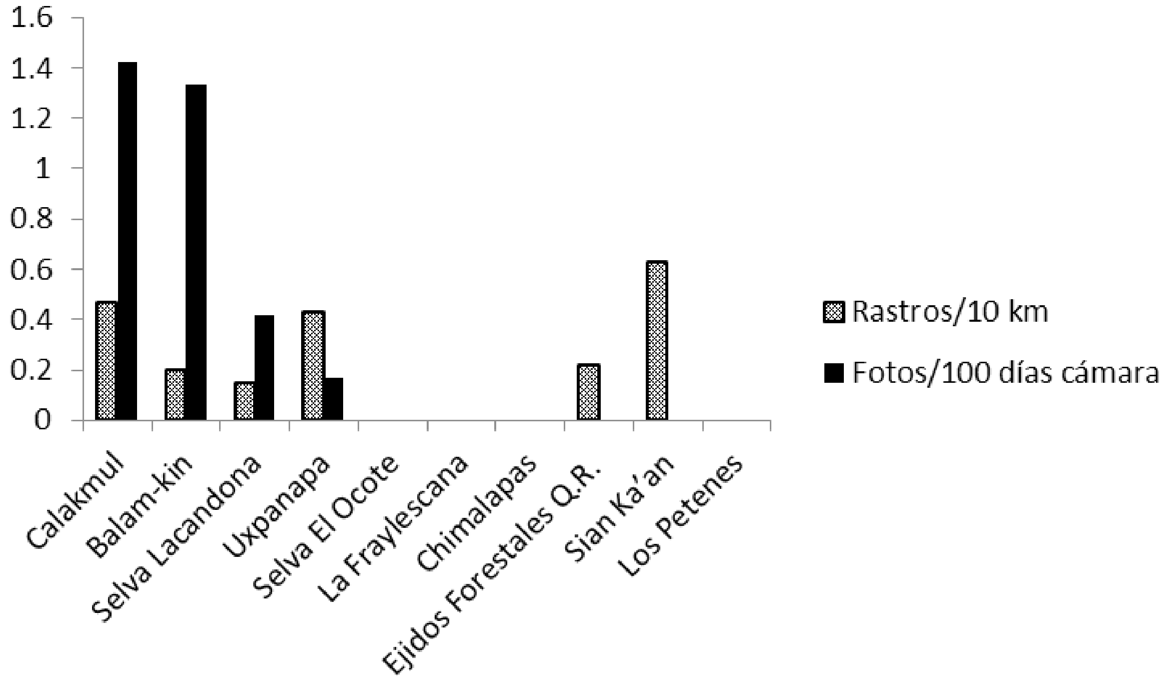

Figura 8. Abundancia del pecarí de labios blancos (*Tayassu pecari*) estimada mediante foto-trampeo y conteos de rastros en las localidades de estudio.

Tabla 3. Índices de abundancia de tapir y pecarí de labios blancos obtenidos en transectos lineales y muestreos con cámaras-trampa en los sitios de estudio visitados entre noviembre 2010 y octubre 2012.

Sitio	*Tapirus bairdii*			*Tayassu pecari*		
	Registros totales	Rastros/ 10 km	Fotografías/ 100 días-cámara	Registros totales	Rastros/ 10 km	Fotografías/ 100 días-cámara
Selva Lacandona	22	3.09	0.90	10	0.15	0.42
Selva El Ocote	1	0.77	0	0	0	0
La Fraylescana	7	4.38	0.53	0	0	0
Uxpanapa	12	4.35	1.49	5	0.43	0.17
Chimalapas	14	4.52	0.38	0	0	0
Ejidos Forestales Q. R.	7	3.68	0.59	2	0.22	0
Sian Ka'an	4	2.47	0	1	0.63	0
Calakmul	6	3.30	2.00*	7	0.47	1.42*
Balam-kin	5	2.11	0.89	1	0.20	1.33
Los Petenes	1	0.26	0	0	0	0

* Las cámaras se colocaron en aguadas.

Conclusiones

La información generada en el presente trabajo permitió mejorar el conocimiento acerca de la distribución actual, abundancia relativa y estado de conservación de las poblaciones de tapir y pecarí de labios blancos en México. Las áreas de distribución actuales y verificadas para el pecarí de labios blancos incluyen las Reservas de Calakmul, Balamkú, Balam-kin y Laguna de Términos (Campeche); las Reservas Lacantún y Montes Azules, la Comunidad Lacandona y algunos ejidos de Marqués de Comillas (Chiapas); Los Chimalapas (Oaxaca); Reserva Sian Ka'an y ejidos forestales del centro y sur (Quintana Roo), la cuenca alta del río Uxpanapa (Veracruz), y la Reserva de Dzilam (Yucatán). El tapir se encuentra en todas las anteriores a excepción de Dzilam, y además está presente en el Bajo Río Verde y partes bajas de las Sierras Mixe y Veinte Cerros (Oaxaca), Los Petenes (Campeche), y las Reservas El Ocote, El Triunfo, La Sepultura y algunos ejidos de la Sierra Madre (Chiapas). Por su gran extensión y buena calidad de hábitat, las áreas críticas para la conservación de ambas especies en el país son: Calakmul-Balamkú-Balam-kin, Montes Azules-Lacantún, Los Chimalapas, y Sian Ka'an-ejidos forestales del centro de Quintana Roo.

En este estudio se estimó con base en rastros y avistamientos directos una abundancia de 0.26 - 4.52 tapires, y 0.15 - 0.63 pecaríes de labios blancos por 10 km recorridos. Además se estimaron abundancias relativas de 0.38 - 1.49 (tapir) y 0.17 - 1.33 (pecarí) fotografías por 100 días-cámara. Estas cifras son las primeras estimadas mediante foto-trampeo para los dos ungulados en algunos de los sitios de estudio (Balam-kín, La Fraylescana y Uxpanapa), lo cual constituye una contribución significativa al estado del conocimiento sobre el estado de sus poblaciones. Las mayores abundancias de tapir se registraron en La Fraylescana, Uxpanapa y Los Chimalapas (rastros y avistamientos), y en Uxpanapa, Selva Lacandona y Balam-kin (fotografías). Las mayores abundancias de pecarí de labios blancos correspondieron a Sian Ka'an y Calakmul (rastros y avistamientos directos), y en Balam-kin y Calakmul (fotografías).

Tabla 4. Principales amenazas detectadas para las poblaciones de tapir y pecarí de labios blancos en las comunidades visitadas en el sureste de México de marzo 2011 a octubre 2012.

Sitio	Amenazas observadas Tapir	Riesgo* Tapir	Amenazas observadas Pecarí LB	Riesgo* Pecarí LB
Selva Lacandona, Subregión Marqués de Comillas (Ejidos Adolfo López Mateos, Belisario Domínguez, Benemérito de las Américas, Chajul, Flor del Marqués, Galacia, José López Portillo, Loma Bonita, Quiringuicharo, Playón de la Gloria, Reforma Agraria y Zamora Pico de Oro).	DEF, CAZ, ENF	Medio	CAZ, DEF, FRA, ENF	Alto
Selva El Ocote (Ejido Emilio Rabasa)	DEF, INC	Medio	Ausente	-
La Fraylescana (Finca Arroyo Negro)	DEF, INC	Medio	Ausente	-
Uxpanapa (Ejido Loma de Oro y Poblado El Quince)	DEF, FRA, INC, CAZ, ENF	Alto	DEF, CAZ, FRA, INC, ENF	Alto
Los Chimalapas (Ejido La Fortaleza)	DEF, INC, CAZ, ENF	Alto	CAZ, INC, DEF, ENF	Alto
Ejidos Forestales de Quintana Roo (Ejido Caobas)	INC, FRA	Medio	CAZ, INC, FRA, DEF	Alto
Sian Ka'an (Ejidos X-Hazil y Chanká Veracruz)	INC, FRA	Medio	CAZ, INC, FRA	Medio
Calakmul (Ejidos Nuevo Bécal y 20 de Noviembre)	INC	Bajo	CAZ, INC, ENF	Medio
Balam-kin (Ejido Conhuas)	INC, CAZ	Medio	CAZ, INC	Medio
Los Petenes (Ejido Zodzil)	DEF, FRA, INC, CAZ	Alto	Ausente	-

DEF: Deforestación; FRA: Fragmentación, CAZ: Caza; INC: Incendios; ENF: Enfermedades
* Escala de riesgo de acuerdo al número de factores de amenaza observados: Bajo (0-1); Medio (2-3); Alto (>3).

Las amenazas principales para la conservación del tapir y el pecarí de labios blancos en sus áreas de distribución actuales son la deforestación y fragmentación del hábitat, la cacería sin control, los incendios forestales, la sequía, las inundaciones y los huracanes. Algunos casos registrados de presencia inesperada de ambas especies en localidades puntuales de Campeche, Veracruz y Yucatán hacen evidente la necesidad de continuar y ampliar las investigaciones sobre la distribución y el estado de conservación de estos mamíferos en el sur y sureste del país.

Los resultados logrados en la presente investigación constituyen un avance significativo en el conocimiento acerca del estado de las poblaciones de tapir y pecarí de labios blancos en México. Se generó información actualizada sobre la distribución, abundancia y estado de conservación de diez poblaciones de tapir y seis de pecarí de labios blancos en los estados de Campeche, Chiapas, Oaxaca, Quintana Roo y Veracruz, aportando 105 registros de calidad al Sistema Nacional de Información sobre Biodiversidad (SNIB). A partir de las observaciones realizadas durante el estudio se identificaron los factores de amenaza más importantes para las poblaciones de las dos especies en el país. Esta información complementada con la revisión de literatura disponible, permitió elaborar propuestas para la ratificación de ambas especies en la NOM-059-SEMARNAT-2010 de acuerdo al Método de Evaluación de Riesgo (MER), así como proponer líneas de acción útiles para enriquecer las nuevas versiones de los Programas de Acción para la Conservación (PACE) de ambos mamíferos en México.

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Resumen

Introducción: El tapir centroamericano (Tapirus bairdii) y el pecarí de labios blancos (Tayassu pecari) juegan papeles importantes en la dinámica de los bosques tropicales en toda su área de distribución donde habitan a través de los procesos de herbivoría, dispersión y depredación de semillas. Estos mamíferos han constituido recursos alimentarios para los pobladores de comunidades rurales de Mesoamérica. Ambas especies aparecen en la NOM-059-SEMARNAT-2010, encontrándose en peligro de extinción debido principalmente a la pérdida de su hábitat y a la cacería sin control. El objetivo central del presente estudio consistió en generar un diagnóstico sobre el estado actual de las poblaciones de tapir y pecarí de labios blancos en México, proponiendo una estrategia para su conservación.

Métodos: De noviembre 2010 a noviembre 2012 se realizaron evaluaciones rápidas de la presencia, abundancia relativa y amenazas del tapir y el pecarí de labios blancos en diez localidades de cinco estados del sureste de México mediante tres técnicas complementarias: recorridos de transectos lineales, foto-trampeo y aplicación de entrevistas con pobladores locales. Con la información recabada y el análisis de la literatura disponible sobre ambas especies en México se generaron propuestas para confirmar su estatus de riesgo en la Norma Oficial Mexicana 059 mediante el Método de Evaluación de Riesgo (MER) requerido por la Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT).

Resultados y discusión: Las áreas de distribución actuales y verificadas para el pecarí de labios blancos se encuentran en los estados Campeche, Chiapas, Oaxaca, Quintana Roo, Veracruz y Yucatán. El tapir se encuentra en un mayor número de localidades dentro de los estados citados a excepción de Yucatán. Por su gran extensión y buena calidad de hábitat, las áreas críticas para la conservación de ambas especies en el país son: Calakmul-Balamkú-Balam-Kin (Campeche), Montes Azules-Lacantún (Chiapas), Los Chimalapas (Oaxaca), y Sian Ka'an-ejidos forestales del centro de Quintana Roo. Las mayores abundancias poblacionales estimadas de tapir se registraron en La Fraylescana, Uxpanapa y Los Chimalapas (rastros y avistamientos), y en Uxpanapa, Selva Lacandona y Balam-kin (fotografías). Las mayores abundancias estimadas de pecarí de labios blancos correspondieron a Sian Ka'an y Calakmul (rastros y avistamientos directos), y en Balam-kin y Calakmul (fotografías). Las amenazas principales para la conservación de ambas especies en México son la deforestación y fragmentación del hábitat, la cacería sin control, los incendios forestales y las enfermedades transmitidas por animales domésticos. Los registros inesperados de la presencia de ambas especies en localidades puntuales de Campeche, Veracruz y Yucatán estimulan la necesidad de continuar y ampliar las investigaciones sobre la distribución y el estado de conservación de estos mamíferos en el sur y sureste del país.

Palabras clave: amenazas, conservación, distribución, México, Tapirus bairdii, Tayassu pecari.

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Human–Andean bear *Tremarctos ornatus* interaction in Peru: consumption of crops and predation on livestock

Interacciones humano–oso andino *Tremarctos ornatus* en el Perú: consumo de cultivos y depredación de ganado

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Introduction: The Andean bear *Tremarctos ornatus* has been hunted since the Inca times primarily because it was considered to be a pest that preyed on vicuñas and guanacos. Later, with the arrival of the Spaniards and the subsequent implementation of cattle ranching bears exploited this new and abundant food source. This resulted in a strong negative attitude of people towards the bear as they were perceived to be preying upon cattle and they did not take into consideration the fact that bears may have just been scavenging on carcasses. In addition, the expansion of cornfields in the area resulted in more incidences of bears raiding crops. Reports of these negative interactions continue to date. This paper utilizes extensive surveys, based on interviews with farmers, in order to learn how, when and where these interactions occur, as well as to understand their perception about bears. Moreover, knowledge of these interactions in the mitigation of other ursid species and experiences in other countries are discussed.

Methods: Fifty communities in 12 regions of Peru, located in neighboring areas or buffer zones of 16 protected areas with records of the Andean bear were visited between 2002 and 2008. Three hundred and ten personal interviews were conducted mainly with hunters, farmers and ranchers. A semi–estructured interview was carried out in which the following basic questions were queried: date, time, place and type of interaction (livestock or crop), record type (observation, traces), crop species eaten or species of preyed animal, event description (solitary or groups of bears entering the fields, ages of bears, etc.) and reason for killing the bear.

Results: Eighty six records of bear kills were obtained in 66 villages of the 16 protected areas that were evaluated. A large proportion of the people interviewed (60.8 %) said that they had killed a bear and 48.5 % of them said that they killed the bear because they considered it to be detrimental to the crops and 42.2 % of them considered them detrimental to the livestock. Twelve types of crops were reported to be consumed by bears and maize was the one most frequently consumed (n = 150, 93.3 %). In addition, five species of livestock were consumed and cattle (bovine) was preyed the most frequently (n = 131, 95.9 %). The frequency and types of attacks were highly variable, mostly conducted by solitary adult males bears. Thirteen people claimed to have seen a total of ten attacks, giving a detailed description, while three people commented that they only observed scavenging behavior.

Discussion and conclusions: Corn crop raiding by Andean bears is an opportunistic event, because it is a food with high levels of energy and protein, and crops are within easy access to premontane and montane forest and adjacent areas. Furthermore, although there are studies that confirm bear predation on cattle in Venezuela, Colombia, Ecuador and Bolivia, to date, studies on this had not been undertaken in Peru. However, 13 people provided very detailed information about their observations, which agreed with other studies in other countries, confirming that bear predation on cattle also occurs in Peru. Since both events are a strong motive to hunt Andean bears, it would be important to conduct research in order to determine the reasons why some bears prey on livestock and raid crops. Further work needs to be conducted in close collaboration with the local communities in order to raise appropriate mitigation measures taking into consideration the conditions of each place, in order to reduce human-bear conflicts and therefore diminish the hunting of this species.

Key words: Andean bear, conservation, consumption of crops, hunting, livestock depredation, mitigation, Peru.

Introducción

La mayoría de las especies de osos son omnívoros oportunistas que pueden ser considerados plagas cuando son atraídos por los cultivos, y perjudiciales cuando atacan a los animales domésticos. El oso solar *Helarctos malayanus*, puede devastar plantaciones de coco, piña, papaya, caña de azúcar y palma aceitera (Normua *et al*. 2004; Fredriksson 2005). Los osos bezudos *Melursus ursinus*, dañan sembríos de caña de azúcar y maní (Iswariah 1984 en Fredriksson 2005). El oso negro asiático *Ursus thibetanus*, ingresa a los cultivos de melocotón, ciruela, ciruela pasa, pera, papaya, maíz, plátano, mijo italiano y camote (Hwang *et al*. 2002) y a granjas de peces (Huygens y Hayashi 1999). El oso pardo *U. arctos* y el oso negro americano *U. americanus*, se alimentan de los apiarios, cultivos de maíz, avena y frutales, así como de ovejas, cabras, caballos, vacunos y cerdos (Jonker *et al*. 1998; Garshelis *et al*. 1999; Vargas y Hernández 2001).

En el caso del oso andino *Tremarctos ornatus*, este fue considerado como un animal dañino durante la época incaica (1,438 – 1,532) junto con el puma *Puma concolor*, por ser depredadores del "ganado silvestre" como vicuñas *Vicugna vicugna*, guanacos *Lama guanicoe*, tarucas *Hippocamelus antisensis* y venados *Odocoileus virginianus*, por lo que fueron capturados en la "cacería real del Inca", conocida como *chaco* (Garcilaso de la Vega 1609). Posteriormente, con la llegada de los españoles, los valles costeños, sierras y montañas se poblaron del ganado traído por ellos (bovino, ovino, caprino, equino, mular y porcino). Esto proporcionó una nueva y abundante fuente de alimento para los osos, principalmente de ganado vacuno, lo que conllevó a una mayor interacción con los humanos (Ponce 1991 [siglo XVI]; Jiménez de la Espada 1965 [1582]; Lequanda 1793b; Acosta 1849; Tschudi 2003 [1838–1842]), quienes no diferenciaron si se trataba de un evento predatorio o carroñero. Asimismo, los españoles extendieron los cultivos de maíz y frutales en algunas regiones (Rostworowski 1981), por lo que los osos también aprovecharon de estos (Lequanda 1793a; Tschudi 2003 [1838–1842]). Estas interacciones se presentan hasta la actualidad tanto en el Perú (Peyton 1980, 1983; Figueroa y Stucchi 2002; Baiker 2011; Figueroa *et al.* 2013) como en Venezuela, Colombia, Ecuador y Bolivia (Goldstein *et al*. 2006).

A diferencia del consumo de los cultivos por parte de los úrsidos de forma extendida, el ataque al ganado solo se realiza por algunos individuos (Jorgensen 1979; Wick 1995; Castellanos *et al*. 2011; Laguna 2013), cuyas causas exactas aún se desconocen. Sin embargo, debido a la percepción de que todos los osos son depredadores, los eventos de interacción oso–ganado provocan la cacería del oso "infractor" y de osos "inocentes" de la zona (Goldstein 2002; Achig 2009; Castellanos *et al*. 2011).

La depredación del ganado y el consumo de los cultivos por parte del oso andino, influyen directamente en la economía de los campesinos y la conservación de la especie, la cual aún no se ha analizado a profundidad. Si bien los resultados que se presentan a continuación se basan en entrevistas, que en algunos casos podrían estar sesgadas por el temor de los campesinos a dar información sobre la cacería ilegal de una especie, estas nos brindan su percepción y un alcance sobre cómo, cuándo y dónde se producen estas interacciones en el Perú. Esta recopilación podrá servir como una herramienta de trabajo inicial para establecer propuestas de mitigación acorde con las condiciones de cada localidad.

Materiales y métodos

Área de estudio. Entre los años 2002 y 2008 se visitaron 50 comunidades de 12 regiones del Perú, ubicadas en las zonas de amortiguamiento o aledañas a 16 áreas protegidas con registros de presencia del oso andino (Figura 1, Tabla 1).

Evaluación. Se realizaron 310 entrevistas personales, principalmente a cazadores, agricultores y ganaderos, de edad adulta y con mucha experiencia en el campo. Se aplicó una entrevista semi–estructurada, en la que se mantuvo una conversación fluida, basada en una lista de preguntas desarrollada previamente. Estas fueron: fecha, hora, lugar y tipo de interacción (ganado o cultivos), tipo de registro (observación, rastros), especie de cultivo consumido o animal depredado, descripción del evento (ingresaron osos solitarios o en grupos, edades de los osos, etc.), motivo de la cacería. Se visitaron algunas áreas donde se reportaron la depredación del ganado y el consumo de cultivos para observar las características del lugar.

Resultados

En todas las zonas de amortiguamiento de las áreas protegidas evaluadas se observó una ganadería extensiva y cultivos en áreas rodeadas por bosques montanos y premontanos, o limitados por estos, muy distantes a una vivienda (Figura 2a, 2b). Se visitaron 32 áreas donde ocurrieron eventos de interacción oso–ganado y oso–cultivo de maíz. De los 19 cultivos observados, 15 (78.9 %) se encontraron colindantes al bosque, mientras que cuatro (21.1 %) estuvieron a menos de 1 km de una carretera o caserío. Las 13 áreas donde se produjeron interacciones con el ganado se encontraron colindantes al bosque; en estas, se observó una escasa supervisión, el ganado era visitado solo una vez cada 20 o 30 días, sin ningún control de las hembras preñadas ni de los individuos jóvenes.

Se obtuvieron 86 registros de la cacería del oso en 66 poblados localizados en las zonas de amortiguamiento de las 16 áreas protegidas evaluadas (Figura 3a, 3b, 3c, Tabla 2). El 60.8 % (n = 310) de los entrevistados señalaron que cazan al oso andino, y que esta se realiza principalmente por ser considerado un animal perjudial ya que se alimenta de los cultivos (48.5 %) y ataca al ganado (42.2 %) (Tabla 3). El 7.0 % señaló que lo cazan para su uso alimenticio, y un 2.3 % para la obtención de oseznos como mascotas. El reporte más antiguo de cacería fue en 1953, continuando hasta el mismo año en que se dio la entrevista en cada una de las áreas visitadas. Los principales meses de caza fueron abril (n = 19, 31.6 %) y mayo (21.0 %).

Consumo de cultivos (Figura 4a, 4b, 4c). Se reportaron 12 cultivos consumidos por el oso andino, donde el maíz fue señalado como el principal producto (n = 150, 93.3 %). Las demás especies reportadas fueron: caña de azúcar (1.6 %), palta/aguacate (1.4 %), tuna (1.3 %), zapallo macre (0.5 %), calabaza (0.4 %), chirimoya (0.4 %), zapallo loche (0.3 %), guayaba (0.2 %), lúcuma (0.2 %), papa (0.2 %) y piña (0.2 %; Tabla 4).

Existen reportes de hasta 10 individuos comiendo en un mismo cultivo de maíz en Yanachaga Chemillén (Cañachacra), de ocho en Machu Picchu y más de cuatro en Bahuaja Sonene (Sandia). De los individuos cazados por el ingreso a los campos de maíz (n = 40), el 35.9 % fueron machos adultos, 17.9 % hembras adultas, 15.4 % hembras con crías, 23.1 % oseznos y 7.7 % jóvenes. Los ingresos se produjeron entre las 05:00 y 07:00 h y las 16:00 y 18:00 h. Estos se dieron entre diciembre y agosto, pero principalmente en marzo y abril (17.0 %, n = 24), época en la que el maíz se encuentra tierno y jugoso (choclo).

En Tingo María y Yanachaga Chemillén se comentó que un oso podía llevarse diariamente entre 20 y 35 tallos de maíz a un lugar seguro para comerlos. Empieza a comer en la parte más alta, desde el borde del bosque con el maizal. Se reportó su preferencia por el maíz blanco, pero también puede alimentarse del maíz "pintado" si aún está en estado de choclo. Tres personas comentaron del consumo del maíz seco y almacenado en áreas adyacentes a Megantoni (cerca al Pongo de Mainique), Machu Picchu (San Miguel) y Huascarán, en donde también se encontraron restos vomitados por el oso.

Depredación de ganado (Figura 5a, 5b, 5c). La depredación al ganado vacuno fue la más frecuente (n = 131, 95.9 %), seguida de lejos por el ataque a las cabras (1.6 %), ovejas (1.1 %),

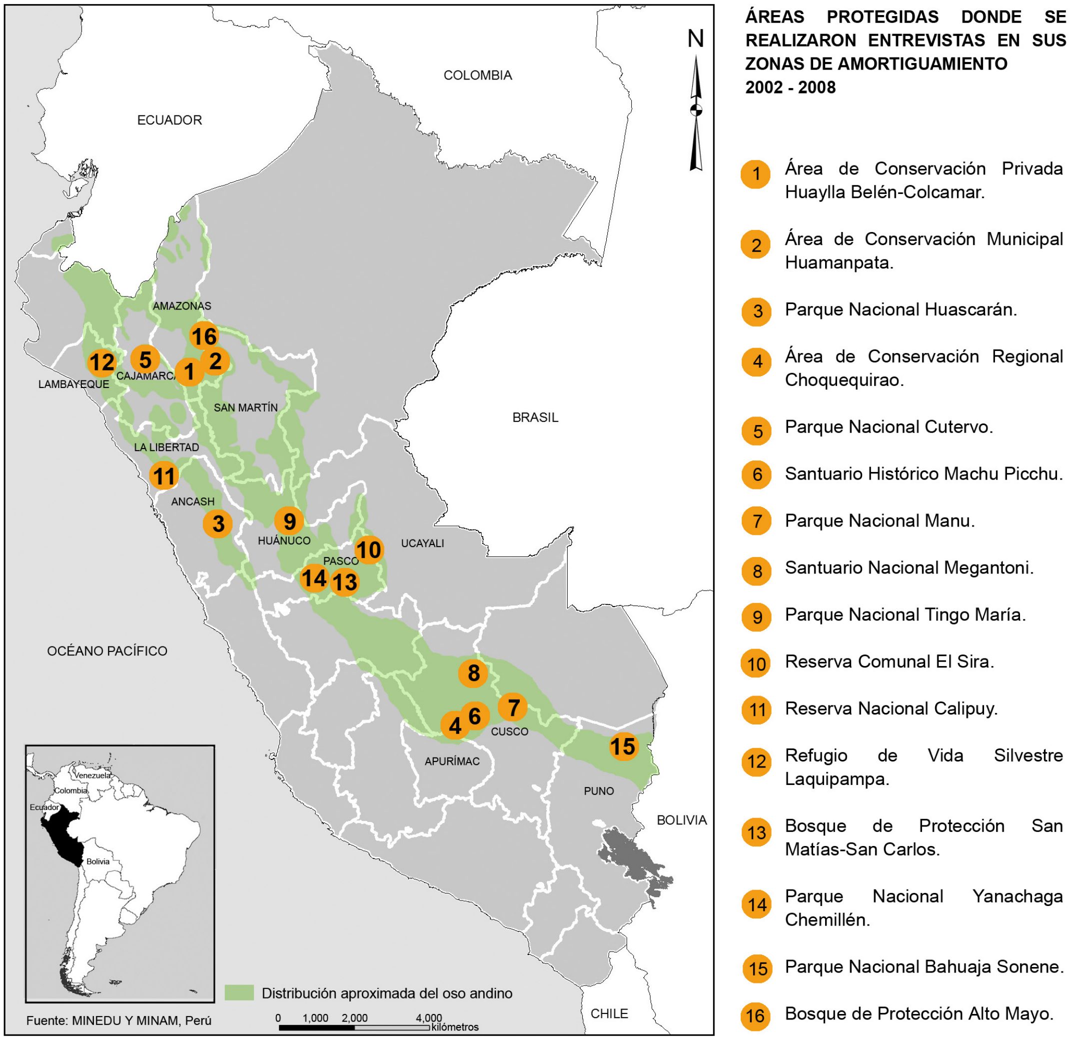

Figura 1. Áreas protegidas donde se realizaron las entrevistas en sus zonas de amortiguamiento o aledañas.

cerdos (0.7 %) y caballos (0.7 %) (Tabla 5). De las 310 personas entrevistadas, 13 aseguraron haber presenciado un total de diez eventos, dando una descripción detallada. Estos eventos depredatorios se produjeron principalmente en abril y mayo (*n* = 11, 36.4 %), entre las 19:00 h y 04:00 h. Se obtuvieron varios reportes de estos ataques en diferentes periodos: en Cutervo, Laquipampa y Tingo María cesaron en 1982, 1990 y 1993, respectivamente. En Megantoni, Huaylla Belén–Colcamar, Huamanpata, Machu Picchu, Manu, Yanachaga Chemillén y Alto Mayo se obtuvieron reportes hasta el mismo año en que se realizaron las entrevistas.

De igual manera, las frecuencias de ataques fueron bastante variables. En Choquequirao (Lucmabamba) un oso macho atacó cinco vacas en un mes. En Yanachaga Chemillén (Huaylas y Santa Bárbara), en la década de 1990 el oso podía atacar entre una y tres vacas al año. En Bahuaja Sonene (Iparo), en el 2005, un oso macho atacó y se alimentó de 20 vacas. Al cazarlo, se observó que sus dientes estaban muy desgastados. Por ello, la persona entrevistada aseguró que los osos que atacan al ganado vacuno, son los viejos que no pueden desplazarse largas distancias en busca

Tabla 1. Comunidades entrevistadas entre el 2002 y 2008.

Zona de amortiguamiento o aledaña - Área protegida	Región	Localidades visitadas	Año	Entrevistados
ACP Huaylla Belén-Colcamar	Amazonas	Luya, Leimebamba y La Jalca	2002	16
ACM Huamanpata	Amazonas	Rodríguez de Mendoza y Huambo	2002	6
PN Huascarán	Ancash	Ecash y Colcas	2002	17
ACR Choquequirao	Apurímac	Huanipaca, Cachora y Abancay	2002	9
	Cusco	Lucmabamba	2002	7
PN Cutervo	Cajamarca	Paraíso, Pucarilla, San Andrés de Cutervo, La Capilla y Santo Tomás	2002, 2003	31
SH Machu Picchu	Cusco	Santa Teresa y Mándor	2002, 2003	26
PN Manu	Cusco	Challabamba y Paucartambo	2003	11
SN Megantoni	Cusco	Timpía, Matoriato y Shivankoreni, Lacco, Yanacocha y Lorohuachana	2004, 2008	15
PN Tingo María	Huánuco	Juan Santos Atahualpa	2002	19
RC El Sira	Huánuco	Puerto Inca, Zúngaro, El Sira y Yuyapichis	2002	28
	Ucayali	Atalaya, Padre Abad y Aguaytía		
RN Calipuy	La Libertad	Calipuy y Paibal	2002	8
RVS Laquipampa	Lambayeque	Mochumí, Higuerón y Laquipampa	2002, 2003, 2004	25
BP San Matías-San Carlos	Pasco	Iscozasín y San Francisco	2003, 2007	8
PN Yanachaga Chemillén	Pasco	Santa Bárbara, Huayruro, Cañachacra, Mal Paso, Pozuzo y Yulitunqui	2003, 2005, 2007	54
PN Bahuaja Sonene	Puno	Sandia	2006	7
BP Alto Mayo	San Martín	Alto Mayo y Nueva Cajamarca	2002	23

ACM – Área de Conservación Municipal, ACP – Área de Conservación Privada, ACR – Área de Conservación Regional, BP – Bosque de Protección, PN – Parque Nacional, RVS – Refugio de Vida Silvestre, RC – Reserva Comunal, RN – Reserva Nacional, SH – Santuario Histórico, SN – Santuario Nacional.

de su alimento natural. Señalaron que el oso tiende a atacar al ganado en un sector por un periodo de tiempo y luego migra hacia otra área.

El 67.7 % (*n* = 31) de los osos que atacaron al ganado fue cazado, ya que los campesinos siguieron los rastros dejados por estos al jalar sus presas para alimentarse en otras zonas. El 83.9 % fueron machos adultos solitarios, solo en cinco ocasiones (16.1 %) se informó que las hembras tuvieron este comportamiento: dos hembras adultas solitarias, una hembra con un macho de pareja y dos hembras con oseznos. En Manu (Sunchubamba), en 1999, una osa mató una vaca, la que comió durante tres días. En Calipuy (Paibal), en el 2001 una osa mató a 15 terneros en menos de un mes. Otra desbarrancó a un toro de 300 kg, del cual se alimentaron ella y sus dos oseznos por cinco días. De la misma manera, se reportó en Cutervo (La Capilla) este comportamiento de una hembra con dos crías en 1982. En Machu Picchu (Chachabamba), en 1999, un campesino presenció a una pareja

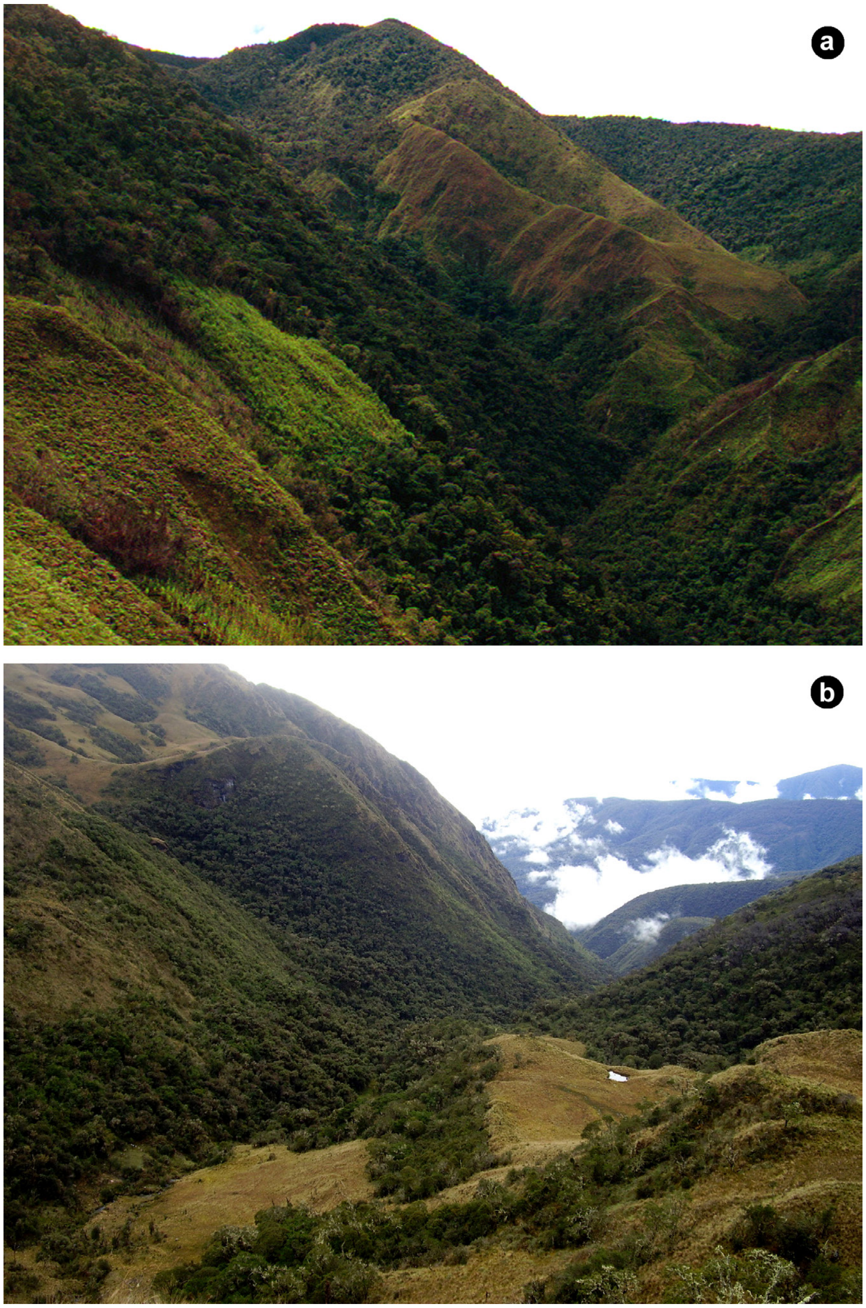

Figura 2. Áreas con reportes de interacción humano–oso andino. a) Cañachacra (Pasco), cultivos de maíz rodeados de bosque. b) Lorohuachana (zona de amortiguamiento de Megantoni), área ganadera limitando con el bosque.

de osos corriendo detrás de un grupo de vacunos, concentrándose luego en un individuo al cual lograron desbarrancar; este fue comido en el mismo lugar donde cayó. Otro caso similar se dio en el 2000 en Choquequirao (Rajche) con un oso solitario. En Calipuy, tres pobladores que observaron el hecho, comentaron que seis osos dirigieron a las vacas cerca al precipicio, luego a una de ellas un oso "le agarró y giró la cola" para que esta caiga con su propio peso. En Laquipampa (El Naranjo), en 1990, observaron que un oso se subió sobre el lomo de la vaca para morderla y quebrarle las escápulas con el fin de inmovilizarla. En la zona de amortiguamiento de Alto Mayo (hacia el lado de Amazonas) en el 2000, un poblador presenció el ataque de tres osos a una vaca; cerca a esta área, un año después un oso mató a un perro cuando este defendió el potrero. Algo similar ocurrió en Carpish (Huánuco), cuando un perro protegió un grupo de

Tabla 2. Localidades donde se reporta el ingreso a los cultivos de maíz y ataque al ganado según las entrevistas.

Zona de amortiguamiento o aledaña – Área protegida	Ingreso a cultivo de maíz	Ataque a ganado
Huaylla Belén-Colcamar	San Carlos, Poblado Cortadera, Bongará	Quijalca, Leimebamba, Lajasbamba
Huamanpata		Huambo, Yamaniau
Huascarán		Musho (Poquia), Waripata, Chacas, Quitaraxa, Wicsonga
Choquequirao		Sacsara, Yanatile y Lucmabamba
Cutervo		Gruta de los Guacharos, San Pedro, sector Capilla, Playa Grande y Pucarilla
Machu Picchu	Mándor	Santa Teresa, Chachabamba
Manu	Televán, Otocani, Pucará, El Rocotal y San Pedro, cerca al río Yavero–Mapacho	Challabamba, Trigomontón, Huaysampilla, El Rocotal, Buenos Aires, Qurqurpampa y Nuevo Oriente
Megantoni	Áreas adyacentes al río Yavero–Mapacho, al Pongo de Mainique y Lacco	Yanacocha, Lorohuachana y Mishkiuno
Tingo María	Panao, Carpish, San Luis, Tambillo Grande y El Mirador	
El Sira	Santa Teresa y Cinchuna	
Calipuy		Paibal, Quibal, Moyupuquio, Pichipata, Huaraday y Tuntus
Laquipampa		El Naranjo, La Calera
San Matías-San Carlos	Áreas bajas de 200 m de altitud adycante a Iscozasín	
Yanachaga Chemillén	Alto Palmapampa, Alto Lagarto Mallapampa, Jushi, Osopampa, La Suiza, Choropampa, La Rinconada, Cantarizú, Palmazú, Seso, Yulitunqui, Delfín, Prusia, Chontabamba, Mal Paso, Río Seco y Cañachacra	Santa Bárbara, Huaylas y Chinchango
Bahuaja Sonene	Sandia, Maucallajta, Acañiputo, Huancaluque, Chichanaco, Mororía, Putina, Huancané y Chaco	Iparo
Alto Mayo	No detallaron la localidad exacta	No detallaron la localidad exacta

ovejas. En Megantoni (Mishkiuno), se observó el cráneo de un oso macho adulto, con las piezas dentarias muy desgastadas (Figura 5d), que fue cazado en el 2007 por atacar a un vacuno. Según nos informó el ganadero, después de cazar tres osos en la zona, la depredación concluyó.

Se observaron las características de los dientes de 14 cráneos de osos machos que fueron cazados, según nos comentaron, por depredar ganado vacuno, en todos los casos estos se encontraron muy desgastados o los caninos rotos. Los bovinos atacados (n = 34) fueron un 58.8 % adultos, que incluyeron individuos de hasta siete años de edad (Manu, Nuevo Oriente) y hembras preñadas (Bahuaja Sonene, Sandia), y un 41.2 % terneros.

Respecto a las partes de las cuales se alimenta el oso, en Manu (Qurqurpampa) un oso macho que mató a dos vacas, se alimentó de las ubres. En Laquipampa se reportó el ataque a vacas de 100 a 150 kg, de las que solo consumió la carne, dejando las vísceras. En Yanachaga Chemillén (Santa Bárbara), se reportó el ataque a vacunos, carneros y cerdos, de los que comió las vísceras y el hocico.

En tres casos el oso andino fue señalado como un animal carroñero. En Huascarán, en la laguna Parón en 1982, se observó a un oso jalando una vaca en estado de putrefacción para alimentarse de ella. En Cutervo, en el 2000, observaron a un oso macho jalando un ave en avanzado estado

Figura 3. Cacería del oso andino por ingreso a los cultivos o depredación de ganado. a) Yanatile (zona de amortiguamiento de Machu Picchu), oso joven cazado en junio 1999 (Foto: Alan Valdeiglesias). b) Chinchalmainiyuj (zona de amortiguamiento de Manu), osa cazada en el 2001 (Foto: Milton Cabrera). c) Mishkiuno (zona de amortiguamiento de Megantoni), oso cazado en el 2007 por evento de depredación (Foto: Roberto Gutiérrez).

de descomposición en el borde de una laguna. En Calipuy, se observaron adultos y oseznos alimentándose de los restos de una vaca muerta en la orilla de un río.

Como consecuencia de la depredación de ganado, se manifestaron dos agresiones físicas de parte del oso a personas. En una oportunidad el oso rasguñó a un pastor que le tiró una piedra para que no ataque a sus ovejas en Huascarán (Ecash). En el año 2000, en Laquipampa (Rumichaca), un oso macho atacó a un campesino que arriaba a su ganado cuando intentó espantarlo.

Tabla 3. Motivos de la cacería del oso andino según las entrevistas.

Zona de amortiguamiento o aledaña - Área protegida	Entrevistas	¿Cazan al oso andino? (%)			De los que respondieron "Sí", a la pregunta anterior: ¿por qué cazaron al oso andino? (%)		
		Sí	No	No sabe	Ingreso a cultivos	Ataque al ganado	Otros*
Huaylla Belén-Colcamar	16	56.3	31.3	12.4	55.6	33.3	11.1
Huamanpata	6	83.3	16.7		60.0	20.0	20.0
Huascarán	17	88.2	11.8		6.7	93.3	
Choquequirao	16	56.3	43.7		88.9	11.1	
Cutervo	31	9.7	87.1	3.2	66.7	28.0	5.3
Machu Picchu	26	76.9	15.4	7.7	70.0	20.0	10.0
Manu	11	90.9	9.1		70.0	30.0	
Megantoni	15	46.7	53.3		14.3	85.7	
Tingo María	19	21.1	73.7	5.2	100.0		
El Sira	28	10.7	89.3		86.7	13.3	
Calipuy	8	100.0				100.0	
Laquipampa	25	52.0	48.0		7.7	92.3	
San Matias-San Carlos	8	25.0	75.0		20.0		80.0
Yanachaga Chemillén	54	70.4	24.1	5.5	71.1	23.7	5.2
Bahuaja Sonene	7	85.7	14.3		50.0	33.3	16.7
Alto Mayo	23	100.0			8.7	91.3	
Total (%)	310	60.8	37.0	2.2	48.5	42.2	9.3

*Alimento, mascota.

Discusión

La mayoría de las personas entrevistadas reconocen que la cacería del oso es un hecho ilícito, sin embargo, no consideran que atentan contra la ley cuando cazan a un oso para la defensa de sus cultivos o ganado, o como un acto para la obtención de una compensación por la pérdida: alimenticio, medicinal, venta de la piel o sus partes. En algunos casos, esta "defensa" es un pretexto para obtener un beneficio económico o como afición, como lo señalado por una persona en Quebrada Seca (Pasco), quien comentó que sembraba maíz cerca del bosque adrede para cazar al oso. Asimismo, en Challabamba (Cusco) un cazador señaló que era contratado por los campesinos perjudicados por el oso para ayudarlos con su problema. Las pieles y otras partes, productos de esta cacería, eran vendidas en los mercados de Cusco. El aseguraba que su trabajo era importante para la comunidad. Se pudo observar que tenía a la venta varias pieles de osos. Un reporte similar se dio en el norte del Perú, con un cazador que compensaba a los agricultores que le avisaban en qué maizal cazar al oso (Peyton 1980).

La cacería del oso, debido a las interacciones con el hombre se viene incrementando debido al crecimiento de la población y su invasión en las áreas boscosas (Figueroa *et al.* 2013). Desafortunadamente las mejores zonas para los cultivos y pastoreo coinciden con el mejor hábitat de producción natural de alimentos para el oso andino (Peyton *et al.* 1998).

En el presente estudio, los entrevistados señalaron que el consumo de los cultivos era el principal motivo de la cacería del oso, seguido del ataque al ganado. Resultados similares fueron encontrados en Colombia ($n = 66$), en el primer caso fue de 54.5 % y el segundo de 39.4 % (Jorgenson y Sandoval 2005).

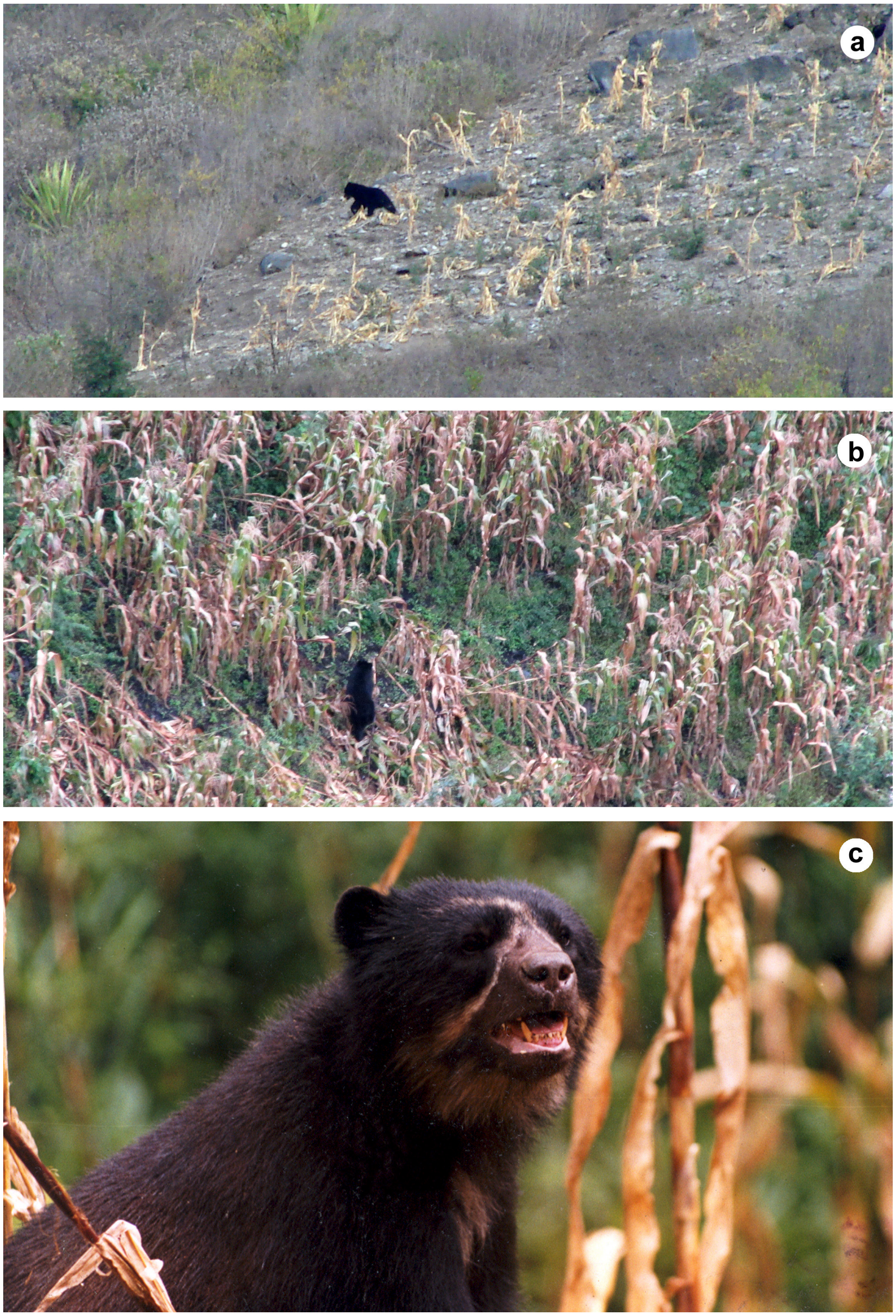

Figura 4. Ingreso del oso andino a los cultivos de maíz. a) Pilcomarca (Apurímac) (Foto: Jan Baiker/Ecobona–Cosude). b) Otocani (zona de amortiguamiento de Manu) (Foto: ProBosque Manu/Sociedad Zoológica de Frankfurt Perú). c) Puente San Pedro (zona de amortiguamiento de Manu; Foto: Oscar Mujica).

Consumo de cultivos

En las entrevistas se identificaron 12 cultivos consumidos por el oso, de los cuales maíz, palta/aguacate, caña de azúcar, lúcuma y tuna ya habían sido registrados anteriormente por otros autores en Cusco y Apurímac, al sureste del Perú (Peyton 1980; Baiker 2011). Estos, junto con los siete nuevos registros en este trabajo (zapallo macre, zapallo loche, calabaza, chirimoya, guayaba, papa y piña), se suman a los de Chucén (Cajamarca) donde se reportó el consumo de plátano/banana y yuca/mandioca (Figueroa *et al.* 2013), y al de Quillabamba (Cusco) con la arracacha (Figueroa y Stucchi 2013), teniendo un total de 15 cultivos registrados en el Perú. Esto complementaría la recopilación de Figueroa (2013), teniendo un total de 18 cultivos reportados como consumidos por el oso andino en su área de distribución (Tabla 6). A excepción del maíz, estos cultivos representan recursos nutritivos de bajos niveles de energía, proteína y fibra en comparación con los frutos silvestres (Figueroa 2013), además, tomando en cuenta la baja frecuencia en estos ingresos, su ingesta sería un evento netamente oportunista. Por el contrario, en el caso particular del maíz, este presenta un alto nivel de energía y proteínas, siendo un alimento muy nutritivo (Dierenfeld 1989), que incluso, ha sido comido seco en algunos depósitos ubicados en la zona de amortiguamiento de Machu Picchu (Peyton 1983), así como en Megantoni y Huascarán. Esto explicaría su frecuente consumo en diversas áreas donde se distribuye. Esta se incrementa debido a que los campesinos siembran el maíz en áreas adyacentes a los bosques premontanos y montanos, donde habita naturalmente esta especie, y donde pueden alimentarse también de los frutos silvestres, bromelias y palmeras (Peyton 1980; Castellanos *et al.* 2005), esto se observó en el presente estudio y en otras áreas adyacentes al río Marañón (Figueroa *et al.* 2013). Sin embargo, también ingresan a campos de cultivo a menos de 1 km de la carretera, aunque de una forma menos frecuente; esto también fue observado por Leite Pitman (2008) en Cusco, a 2 km de la Carretera Interoceánica. Coincidiendo con Peyton (1980), los ingresos a los maizales ocurren principalmente cuando se encuentra como choclo. Los osos empiezan a alimentarse de esta planta entre los 1,500 a 2,000 msnm en febrero–marzo hasta los 2,700 msnm, en mayo–junio (Peyton 1987).

La cantidad de maíz comido por los osos fue muy variable. De igual manera, Peyton (1980) observó en el Perú, que de 25 cultivos de maíz, tres fueron completamente comidos por el oso y cinco solo parcialmente. En Ecuador comentaron que un oso podía acabar 1 ha de maíz en 15 días, otra persona estimó que de una producción de 4 ha que son 15,000 kg de maíz desgranado, el oso comió 1,000 kg; otros agricultores perdieron toda su cosecha (Bejarano 1999).

Las agrupaciones temporales de los osos, en la época de cosecha para fines alimenticios, reportadas en Yanachaga Chemillén, Machu Picchu y Bahuaja Sonene, también fueron registradas anteriormente en maizales en Machu Picchu (hasta 10 osos) y tunales en Apurímac (hasta nueve osos; Peyton 1980). En Chucén (Cajamarca), se reportó un grupo de siete individuos (seis adultos y un osezno) alimentándose de yucas (Figueroa *et al.* 2013).

Hay que tomar en cuenta que, a diferencia de los cultivos de maíz para su venta a los grandes mercados, donde se aplica tecnología para obtener un mayor rendimiento de mazorcas por hectárea, en las áreas donde se realizaron las entrevistas los campesinos siembran el maíz en pequeñas parcelas que no cuentan con ningún soporte tecnológico ni vías de acceso para la salida de sus productos, y cuyos principales objetivos son el autoconsumo, intercambio por otros cultivos de zonas más altas (como por ejemplo papa) y alimento para sus animales de corral. Por ello, en estos casos, el ingreso de los osos a sus cultivos les origina una gran pérdida. Esto conlleva a que señalen al oso como un animal perjudicial, lo que motiva a su cacería cuando los ven cerca a sus propiedades e incluso si estos están en el bosque y no han ocasionado daños, o a usar cebos con plaguicida Paratión para envenenarlo, como ocurrió anteriormente en Machu Picchu (Peyton 1987).

Depredación de ganado

En base a los resultados de las entrevistas y los registros de otros autores, se tendría un total de siete especies de ganado como parte de la dieta del oso andino (Tabla 7). Si bien, existen investigaciones que confirman la depredación del ganado vacuno en Venezuela (Goldstein 1992), Colombia (Poveda 1999; Rodríguez *et al.* 2004), Ecuador (Castellanos 2002; Castellanos *et al.* 2011; Laguna 2013) y Bolivia (Nallar *et al.* 2008), en el Perú aún no se ha hecho un estudio al respecto. Sin embargo, 13 personas

Tabla 4. Cultivos reportados como alimento del oso andino en las entrevistas.

Zona de amortiguamiento o aledaña - Área protegida	Entrevistas	Cacería	Motivo: ingreso a cultivos	Maíz *Zea mays*	Caña de azúcar *Saccharum officinarum*	Palta/Aguacate *Persea americana*	Tuna *Opuntia ficus-indica*	Zapallo macre *Cucurbita maxima*	Calabaza *Cucurbita pepo*	Chirimoya *Annona cherimola*	Zapallo loche *Cucurbita moschata*	Guayaba *Psidium guajava*	Lúcuma *Lucuma obovata*	Papa *Solanum tuberosum*	Piña *Ananas comosus*
Huaylla Belén–Colcamar	16	56.3	55.6	100.0											
Huamanpata	6	83.3	60.0	100.0											
Huascarán	17	88.2	6.7	100.0											
Choquequirao	16	56.3	88.9	67.7		12.4	19.9								
Cutervo	31	9.7	66.7	80.2	19.8										
Machu Picchu	26	76.9	70.0	83.9	4.1	9.2									2.8
Manu	11	90.9	70.0	96.8										3.2	
Megantoni	15	46.7	14.3	100.0											
Tingo María	19	21.1	100.0	100.0											
El Sira	28	10.7	86.7	100.0											
Calipuy	8	100.0													
Laquipampa	25	52.0	7.7	84.6						6.2	3.8	2.9	2.5		
San Matías-San Carlos	8	25.0	20.0	100.0											
Yanachaga Chemillén	54	70.4	71.1	85.6				7.8	6.6						
Bahuaja Sonene	7	85.7	50.0	100.0											
Alto Mayo	23	100.0	8.7	100.0											
Total (%)	310	60.8	48.5	93.3	1.6	1.4	1.3	0.5	0.4	0.4	0.3	0.2	0.2	0.2	0.2

proporcionaron información muy detallada de sus observaciones, las cuales coincidieron con otras sobre el ataque del oso al ganado, hechas en diversas zonas del Perú (Peyton 1980; Figueroa *et al.* 2013) y en otros países (Goldstein *et al.* 2006; Castellanos *et al.* 2011), lo que confirmaría que esta depredación también se da en el Perú.

Lamentablemente, la percepción del oso como depredador de ganado está muy generalizada, a pesar que la mayoría de los entrevistados señalaron que no presenciaron directamente el ataque, sino que refieren los comentarios de terceros o que observaron el consumo de la carroña. En algunos casos, estos comentarios tienden a magnificarse, como se ha visto en otros estudios relacionados a la cacería del oso andino basados en entrevistas (Torres *et al.* 1995; Balarezo 1999), o podrían ser exageraciones de los campesinos locales para justificar la cacería de la especie (Peyton 1980; Goldstein 1991; Poveda 1999).

La pérdida del ganado podría deberse a muchos otros factores, como enfermedades, accidentes e incluso robo por abigeos, sin embargo, la fama de depredador de ganado vacuno se afianza al encontrar heces, rasguños o signos de alimentación de los osos alrededor del cadáver (Peyton 1980; Goldstein 1991, 1992; Poveda 1999; Paisley 2001).

Figura 5. Reportes de ataque del oso andino al ganado vacuno. a) Otocani (zona de amortiguamiento de Manu), se observan rasguños dejados por el oso (Foto: ProBosque Manu/Sociedad Zoológica de Frankfurt Perú). b) Pacopampa (Apurímac; Foto: Jan Baiker/Ecobona–Cosude). c) Otocani (Foto: ProBosque Manu/Sociedad Zoológica de Frankfurt Perú). d) Mishkiuno (zona de amortiguamiento de Megantoni), oso cazado por evento de depredación, se pueden observar los dientes muy desgastados (Foto: Judith Figueroa).

Estos registros no constituyen necesariamente una prueba de depredación, sino más bien de alimentación de huesos y carne (Paisley 2001). Asimismo, el reporte de los dientes desgastados en algunos osos cazados, tampoco comprobaría la depredación del ganado. Si bien las fracturas y roturas en el esmalte estarían relacionadas con la masticación de huesos (Soibelzon 2002), esto podría deberse a un evento carroñero. El desgaste y ruptura de los dientes también podrían estar relacionados con la edad y una dieta rica en carbohidratos (Stucchi y Figueroa 2013).

Por ello, se debe de considerar de manera prioritaria la diferenciación de los reportes de interacción oso–ganado, entre depredación o carroña, para conocer el alcance real del primero en el área evaluada. Peyton (1980) revisó 14 cueros de ganado vacuno cuyas muertes fueron atribuidas al oso andino, las marcas de los rasguños mostraron que nueve correspondían a pumas. En el Parque Nacional de Chingaza (Colombia) los pobladores reportaron 18 vacas supuestamente atacadas por osos en 1996 y 43 muertas por la misma causa en 1997; después del trabajo de verificación de Poveda (1999), los reportes disminuyeron drásticamente pasando a cinco y cuatro durante 1998 y 1999, respectivamente.

Todas las áreas que fueron visitadas, donde los campesinos señalaron la depredación del ganado, estuvieron rodeadas de bosques, donde a partir de la tarde la visibilidad era muy baja debido a la espesa neblina. Todas estas condiciones serían favorables para el ataque sorpresa de un oso. Esta cercanía del bosque a los sitios de ataque también fue observada en Colepato (Parque Nacional

Sangay, sur de Ecuador; Achig 2009). Sin embargo, en otras áreas de Ecuador y Venezuela, se registraron conflictos cerca de zonas ocupadas por humanos, en el segundo caso, en áreas abiertas ubicadas hasta 8 km del bosque (Goldstein *et al.* 2006).

A continuación, en base a las entrevistas y revisión bibliográfica, se comentan tres tipos de eventos que estarían relacionados con el consumo de carne de ganado por el oso andino:

Consumo como carroña del ganado muerto por causas externas a la depredación. Los hábitos carroñeros del oso andino han sido registrados en Ecuador. En la región Intag, un oso andino consumió los restos de un individuo de la misma especie (Castellanos 2006). En el Perú, en Machu Picchu, se alimentó de los restos de un perro y una llama (Figueroa 2013); en Lambayeque, de los restos de un venado de cola blanca *Odocoileus virginianus* (Van Russ *et al*. 2014); y en el presente estudio, de los restos de ganado vacuno (Huascarán y Calipuy) y un ave (Cutervo). En Machu Picchu los osos se desplazan por la puna (3,400–4,000 msnm) durante los meses de lluvias, entre noviembre y abril, en busca de *Puya* spp. y frutos maduros de Ericaceae, y en agosto, cuando no hay frutos en los bosques más bajos. En estos meses también se reporta la depredación al ganado (Peyton 1983). En la época de lluvias, debido a las condiciones climáticas y a la cosecha de papa y maíz, los campesinos suben solo un día cada dos semanas a la puna a darle sal a su ganado, por lo que señalan que el oso aprovecha esta circunstancia para atacar a los vacunos (Peyton 1980). Reportes similares se obtuvieron en el páramo del norte del Perú (Peyton 1987). Paisley (2001) encontró en Apolobamba (Bolivia) un mayor consumo de carne de vacuno por los osos durante la época de lluvias, esto fue relacionado con la posibilidad de que el ganado pueda resbalarse en los terrenos escarpados cuando buscan los brotes del pasto después de la quema al final de la estación seca.

Depredación del ganado por parte del puma y el consumo de los restos por parte del oso como carroña. En Quindio (cordillera central de los Andes, Colombia), durante dos años se obtuvieron 75 registros de ataques a ovejas, cabras, mulas, caballos, vacas y perros, perpetrados en su totalidad por pumas (Payán 2004). Este hecho llamó la atención, ya que se tenía la confirmación de eventos de depredación por parte del oso andino en la cordillera oriental (Rodríguez *et al.* 2004), y en la zona donde se dieron la mayoría de los ataques, entre los 2,800 y 3,000 msnm, habitaban el puma y el oso (Payán 2004). Algunas personas entrevistadas en el Perú (Cutervo, Huascarán y comunidad de Sandia), comentaron que el ganado es depredado por el puma y los restos consumidos como carroña por el oso. Una característica determinante del puma, es que esconde los restos de sus presas para protegerlas de otros depredadores, si la presa es de gran tamaño, la distribuye por diversos sitios (Nallar *et al*. 2008). Se conoce que el puma y el oso utilizan las mismas áreas (Goldstein 2002) e incluso los mismos senderos y árboles para la marcación de su territorio (Payán 2004; Figueroa 2005), por lo que debido al comportamiento alimenticio oportunista del oso, no sería raro este hecho.

En Glacier (EE.UU.), los osos pardo y negro americano ubican el 15 % de las presas cazadas por el puma, apropiándose del 7 % de estas; mientras que en Yellowstone, ubican el 33 % y se apropian del 12 % (Murphy *et al.* 1998). Entre Eslovenia y Croacia, los osos pardos encontraron y se apropiaron del 32 % de las presas cazadas por el lince boreal *Lynx lynx* (Krofel *et al.* 2012). La disminución de las poblaciones de pumas podría también incidir en el comportamiento del oso andino como depredador, debido a la disminución de la carroña.

Ataque del oso al ganado para su consumo. No sorprende que algunos individuos de oso andino depreden ganado vacuno, ya que existen reportes del ataque y consumo a otros mamíferos grandes silvestres, como venado, guanaco, vicuña (Tschudi 1844 en Peyton 1980; Luscombe 1989) y tapir de montaña *Tapirus pinchaque* (Peyton 1980; Castellanos 2011; Rodríguez *et al.* 2014).

A pesar de obtener en las entrevistas diversas descripciones sobre el ataque del oso al ganado, estas se centran en dos técnicas. En la primera, el oso sorpresivamente persigue al rebaño hasta

Tabla 5. Ganado depredado por el oso andino según las entrevistas.

Zona de amortiguamiento o aledaña - Área protegida	Entrevistas	Cacería	Motivo: ataque a ganado	Vacunos *Bos taurus*	Cerdos *Sus domesticus*	Ovejas *Ovis orientalis*	Cabras *Capra aegagrus*	Caballos *Equus caballus*
Huaylla Belén-Colcamar	16	56.3	33.3	100				
Huamanpata	6	83.3	20	100				
Huascarán	17	88.2	93.3	69.4	6.8	7.3	7.3	9.2
Choquequirao	16	56.3	11.1	100				
Cutervo	31	9.7	28.0	100				
Machu Picchu	26	76.9	20	100				
Manu	11	90.9	30	100				
Megantoni	15	46.7	85.7	100				
Tingo María	19	21.1						
El Sira	28	10.7	13.3	100				
Calipuy	8	100	100	100				
Laquipampa	25	52	92.3	85.1			14.9	
San Matias-San Carlos	8	25						
Yanachaga Chemillén	54	70.4	23.7	88.2	3.3	8.5		
Bahuaja Sonene	7	85.7	33.3	100				
Alto Mayo	23	100	91.3	100				
Total (%)	310	60.8	42.2	95.9	0.7	1.1	1.6	0.7

guiar a uno al barranco para hacerlo caer. En este punto, se comentó incluso la participación de más de un oso. En la segunda, el vacuno solitario es sorprendido por el oso quien se trepa sobre su espalda, mordiéndole y rasguñándole el lomo, el área de los omóplatos, la nuca y la cola, hasta derribarlo. En el primer caso, se señaló que el oso come la presa en el mismo lugar, mientras que en el segundo, el oso arrastra los restos hacia un lugar más seguro dentro de la cobertura vegetal o hacia una plataforma construida por el oso para alimentarse. Solo este último coincide con los registros de Goldstein (1992, 2002) y Poveda (1999). Es muy probable que debido a la inaccesibilidad del área donde cayó el ganado desbarrancado este no pueda ser trasladado a un lugar más seguro. La relación de la construcción de la plataforma con eventos de depredación ha sido anteriormente registrada (Peyton 1980; Goldstein 1991, 1992, 2002; Castellanos 2002) y reportada en otras zonas (Figueroa *et al.* 2013).

Adicionalmente, Nallar *et al.* (2008) señalan que los osos matan a su presa con golpes y mordeduras en la cabeza y el cuello, ocasionando fracturas en los huesos del cráneo, cuello y hombros. La presa puede ser consumida aún estando viva, sin importar que esté en decúbito o parada (Castellanos 2002). Los osos además, pueden retirar casi por completo la piel de la presa y dejar sus huesos intactos (Goldstein 1992; Nallar *et al.* 2008). Los restos son movidos de un lugar a otro en varias oportunidades (Goldstein 1991, 2002).

A diferencia de los felinos, que se encuentran perfectamente conformados para la depredación de presas grandes por sus hábitos carnívoros: dientes modificados que cortan la carne, garras retráctiles para aferrarse y amplia apertura de la boca, el oso andino siendo filogenéticamente un carnívoro, ha experimentado cambios morfológicos a nivel del cráneo y mandíbula que le permiten alimentarse de una dieta omnívora, con preferencia en las plantas (Figueirido *et al.* 2009). Estas características conllevan a que el éxito de su ataque se base en su fuerza corporal, por lo que el tamaño del cuerpo del oso podría influir en la selección del tamaño de las presas. En consecuencia, los osos grandes pueden tener más probabilidades de matar al ganado adulto que los osos más pequeños. Esto se observó en la depredación de alces *Alces alces* y ganado por parte del oso pardo, la cual se limitada a osos machos grandes (Haglund 1968 en Zimmermann *et al*. 2003). Los osos machos más pequeños y las hembras podrían preferir el ataque a becerros, como se ha visto anteriormente en Ecuador y Colombia (Castellanos y Laguna 2012) y como se ha reportado en el presente estudio.

Esto podría explicar los reportes de depredación del ganado, principalmente por los osos andinos machos adultos en este estudio y en otras áreas (Castellanos *et al.* 2011). Los machos pueden llegar a medir hasta 2 m y pesar 200 kg, mientras que las hembras llegan a los 2/3 de estas dimensiones (Peyton 1999; Castellanos 2010). Esto también podría explicar la ausencia de depredación de vacunos de la raza Brahman en Cosanga (Ecuador, Castellanos *et al.* 2011), debido a su gran talla con cabeza ancha y joroba en su lomo, llegando a pesar un macho adulto entre 800 a 1,100 kg y una hembra entre 450 y 600 kg; además de su comportamiento gregario por lo que pastan en grupos como medio de defensa, y al instinto maternal muy fuerte de las hembras, que protegen a las crías contra los enemigos naturales (Asocebú 2014).

En el caso que el ganado sea muy grande para el oso atacante, este podría preferir desbarrancarlo que enfrentarse directamente con él, para no salir lastimado. Esto se relacionaría con los comentarios de varios campesinos "el oso observa al vacuno sobre el cual va a saltar, para medirle la gordura y fuerza". Si bien la mayoría de los eventos de depredación de los osos se dan por individuos solitarios, en algunos reportes se describieron ataques grupales de osos, que incluyeron una pareja reproductora (Machu Picchu), y un grupo de tres osos (Alto Mayo) y otro de seis (Calipuy). Estos últimos podrían ser subadultos o hembras con crías de hasta dos años de edad trabajando de forma coordinada para la obtención de una presa. Estos ataques grupales de osos de diferentes edades también se registraron en otros úrsidos como el oso pardo en Yellowstone (parejas reproductoras, subadultos, hembras con oseznos y con crías mayores de un año; Gunther y Renkin 1990).

El mayor registro de depredación a ganado vacuno adulto (58.8 %) sobre terneros (41.2 %), podría responder a la teoría del forrajeo óptimo (Stephens y Krebs 1986), donde los osos deben comer las presas, o partes de la presa que proporcionan la mayor obtención de energía, para la supervivencia y el éxito reproductivo. En Noruega, se observó este comportamiento en el oso pardo hacia las ovejas, en áreas con alto número de presas; consumió principalmente la grasa de la caja torácica y las ubres (Knarrum *et al.* 2006). Para el caso del oso andino, los entrevistados reportaron el consumo de estas partes en algunas áreas y en otras las vísceras, al igual que en Cosanga (Ecuador, Castellanos 2002) y Apolobamba (Bolivia, Nallar *et al.* 2008). Por otro lado, también podría deberse al comportamiento agresivo de algunos vacunos en enfrentar a los depredadores y no huir, o a la tendencia de la vaca a proteger a su ternero contra las amenazas.

Los registros de ataques de hembras al ganado, podrían estar relacionados a las necesidades y exigencias de su organismo en obtener mayor calidad y cantidad de proteínas en la época de celo

Tabla 6. Cultivos reportados como alimento del oso andino en su área de distribución.

	Nombre común	Especie	Familia	Venezuela	Colombia	Ecuador	Perú	Bolivia
1	Chirimoya	*Annona cherimola*	Annonaceae				Ra[f, g]	
2	Arracacha	*Arracacia xanthorrhiza*	Apiaceae				En[e]	
3	Piña	*Ananas comosus*	Bromeliaceae			Ra[b]	En[g]	
4	Tuna	*Opuntia ficus-indica*	Cactaceae				Ra[a, d, g]	
5	Calabaza	*Cucurbita pepo*	Cucurbitaceae				En[g]	
6	Zapallo macre	*Cucurbita maxima*	Cucurbitaceae				Ra[g]	
7	Zapallo loche	*Cucurbita moschata*	Cucurbitaceae				Ra[g]	
8	Yuca/Mandioca	*Manihot esculenta*	Euphorbiaceae				En[f]	
9	Palta/Aguacate	*Persea americana*	Lauraceae				Rf[d, g]	
10	Plátano/Banana	*Musa paradisiaca*	Musaceae	En[a]		Ra[a]	En[f]	En[e]
11	Cambur	*Musa sapientum*	Musaceae	En[c]				
12	Guayaba	*Psidium guajava*	Myrtaceae			Ra[a]	En[g]	En[e]
13	Caña de azúcar	*Saccharum officinarum*	Poaceae	En[a]	En[a]	Ra[a]	Ra[a, f, g]	En[c]
14	Maíz	*Zea mays*	Poaceae	En[a, b]	En[a]	Ra[b, c]	Ra[a, b, c, f, d]	En[b, d]
15	Naranja	*Citrus* sp.	Rutaceae					En[a]
16	Lúcuma	*Lucuma obovata*	Sapotaceae				Ra[a, f, g]	
17	Naranjilla	*Solanum quitoense*	Solanaceae			Ra[b]		
18	Papa	*Solanum tuberosum*	Solanaceae	En[a]	En[a]		En[g]	

En: Entrevista. Ra: Registro alimenticio. Rf: Registro fotográfico. Venezuela: a) Herrera *et al.* 1994 (Parque Nacional Sierra Nevada); b) Torres 2006; c) Lameda y Monsalve com pers. en Castellanos 2010. Colombia: a) Perico y García 2001 en Ojeda y Pesca 2006 (Mamapacha, Boyacá). Ecuador: a) Castellanos *et al.* 2005 (Reserva Biológica Maquipucuna y Parque Nacional Sangay); b) Castellanos 2010 (Intag y Cosanga); c) Bejarano 1999 (entre Baeza y Cosanga). Perú: a) Peyton 1980; b) Butchart *et al.* 1995 (Cordillera de Colán, Amazonas); c) Tschudi 2003 [1838-1842]; d) Baiker 2011 (Bosque de Chinchay y Pilcomarca, Apurímac); e) Figueroa y Stucchi 2013 (Corredor Vilcabamba-Amboró); f) Figueroa *et al.* 2013 (áreas aledañas al río Marañón, Cajamarca-Amazonas); g) Presente estudio. Bolivia: a) Yáñez y Eulert 1996 (Serranía de Los Milagros, Chuquisaca); b) Rumiz *et al.* 1999 (Parque Nacional Amboró y Carrasco); c) Paisley 2001 (Pusupunko); d) Albarracín 2010 (Chuñavi y Lambate); e) Ríos-Uzeda y Zenteno com pers. en Castellanos 2010.

y del cuidado de las crías en áreas con recursos alimenticios limitados. Al respecto, en un estudio en cautiverio, se encontró una variación significativa en la dieta y comportamiento de la hembra en los meses de los picos reproductivos, donde aumentó radicalmente el consumo de proteínas, e incluso se registraron arrebatamientos de carne al macho. Este cambio de conducta llamó la atención, ya que normalmente el macho siempre se mostró dominante en la elección e ingestión de la carne sobre la hembra (Figueroa y Stucchi 2003).

En algunos casos, los reportes de ataques de un mismo individuo de oso andino durante un lapso de tiempo en un área (presente estudio; Goldstein 1992), coinciden con los patrones reportados para especies de otros carnívoros (Treves *et al.* 2004). En el caso del oso pardo, el riesgo de un segundo ataque a ovejas a la siguiente semana, en una misma área, fue de 47 % y en la quinta semana de 63 %. Esto podría deberse a que el depredador regresa al mismo sitio para alimentarse de la carroña o para buscar nuevas presas. Por ello se recomendó implementar medidas disuasivas en las fincas dentro de las cinco semanas del primer evento (Karlsson y Johansson 2010). En otros casos, como en el norte de Ecuador, diferentes osos atacaron al ganado vacuno en un mismo sector y periodo (Castellanos y Laguna 2012; Laguna 2013). Estos ataques estarían relacionados con el éxito del oso en ocultar su presa para evitar interactuar con otros carnívoros como pumas, zorros, perros asilvestrados, u otros osos, en este caso tendría entre 8 y 10 días para consumirla; en el caso de que sea arrebatada por algún competidor, el oso emprenderá una nueva cacería (Laguna 2013).

Tabla 7. Ganado reportado como parte de la dieta del oso andino.

	Nombre común	Especie	VE	CO	EC	PE	BO
1	Caballo	*Equus caballus*			Ra[d, g]	En[d]	Ra[d, e]
2	Mula	*Equus caballus x E. asinus*					En[d]
3	Cerdo	*Sus domesticus*				En[d]	
4	Vacuno	*Bos taurus*	Ra[a,b]	Ra[a, b]	Ra[a, b, c, d, e, f, g]	Ra[a, d]	Ra[b, d, e]
5	Cabra	*Capra aegagrus*	En[b]			Ra[a, d]	
6	Oveja	*Ovis orientalis*	En[a,b]		Ra[d]	En[b, d]	
7	Llama	*Lama glama*				Rf[c]	En[c]

En: Entrevista. Ra: Registro alimenticio. Rf: Registro fotográfico. Venezuela: a) Goldstein 1989; b) Herrera *et al.* 1994 (Parque Nacional Sierra Nevada). Colombia: a) Poveda 1999 (Parque Nacional Natural Chingaza); b) Rodríguez *et al.* 2004 (Mamapacha, Bijagual, San Cayetano, Ubala, páramo de Guasca y Chingaza). Ecuador: a) Suárez 1988 (Volcán Antisana, 3550-4500 msnm); b) Bejarano 1999 (Entre Baeza y Cosanga); c) Castellanos *et al.* 2005 (Reserva Biológica Maquipucuna, 1200-2700 msnm y Parque Nacional Sangay); d) Flores *et al*. 2005 (Oyacachi); e) Castellanos 2010 (regiones de Intag y Cosanga); f) Castellanos *et al.* 2011 (Cosanga); g) Laguna 2013 (norte de Ecuador). Perú: a) Peyton, 1980: varias áreas del Perú; b) Figueroa 2008 (Carpish, Huánuco); c) Figueroa 2013 (Machu Picchu); d) Presente estudio. Bolivia: a) Yáñez y Eulert 1996 (Serranía de Los Milagros, Chuquisaca); b) Rumiz *et al.* 1997; c) Rumiz *et al.* 1999 (Parque Nacional Amboró y Carrasco, 550-3700 msnm); d) Paisley 2001 (Pusupunko, 2700-4300 msnm); e) Rivadeneira 2001 (región Apolobamba, 2800-4000 msnm).

Relación entre la disponibilidad de los frutos silvestres con el ataque al ganado e ingresos a los cultivos

Los daños ocasionados por el oso andino fueron diferentes en cada localidad. Esta variación también se presentó en muchas otras especies de carnívoros grandes (Treves 2009). En algunas zonas el oso andino ingresó a comer diversos tipos de cultivos, mientras que en otras, se limitó solo al maíz, a pesar de que también estaban presentes los cultivos de los cuales se alimentan en otras áreas.

Por otro lado, existen áreas donde no se reportó la depredación del ganado, desde la década de 1990, como en Laquipampa y Cutervo. En las comunidades aledañas al río Marañón, entre Cajamarca y Amazonas, que fueron entrevistadas el 2012, los eventos más recientes fueron en el 2003. En algunas localidades de La Libertad esta depredación se dio entre 1982 y 2002 (Figueroa *et al.* 2013). En Alto Mayo, la depredación se registró solo en las comunidades del lado de Amazonas y no hacia el lado de San Martín (presente estudio; Vela 2008). En San Miguel (Machu Picchu) no se reportó ningún evento de depredación a pesar de ser una zona ganadera (Figueroa y Stucchi 2013). En Colombia, el mayor número de eventos de ataques al ganado y consumo de cultivos se dieron en la cordillera occidental (29), seguida de la oriental (27) y la central (10; Jorgenson y Sandoval 2005).

De la misma manera, las frecuencias también variaron. En algunas áreas de Venezuela se reportaron eventos predatorios en un intervalo de 10 años (Goldstein 1992). En el norte de Ecuador, entre 2009 y 2013, se registraron periodos de tres meses (abril - junio) en los que un oso macho dejó de atacar al ganado (Laguna 2013).

Algunos estudios en otros úrsidos atribuyeron las interacciones ganado–oso y cultivo–oso a una menor disponibilidad de alimento silvestre (Witmer y Whittaker 2001). En el caso del oso solar, los daños causados en los cultivos fueron mayores después del Evento El Niño 1997–1998, en donde hubo una gran sequía y varios incendios forestales, lo que redujo su hábitat y disponibilidad de los frutos (Fredriksson 2005). Por otro lado, se encontró que los daños del oso negro americano a los cultivos cesaron cuando los frutos silvestres que forman parte de su dieta se encontraron más disponibles (Ziegltrum y Nolte 1996). En Yellowstone, Harting (1985 en Gunther y Renkin 1990) observó que los osos pardos depredaron menos mamíferos grandes en las zonas con mayor abundancia de alimentos vegetales.

Figueroa (2013) realizó una revisión de las crónicas de los españoles escritas a partir del siglo XVI sobre los registros del oso andino, no encontrando ninguna relacionada al ingreso a los cultivos de maíz en la época incaica. Incluso, en las descripciones detalladas de Guamán Poma de Ayala (2004 [1615–1616]) sobre la siembra, cuidado y cosecha del maíz en esa época, solo se nombraron como animales perjudiciales de este cultivo a las llamas, zorros, venados, zorrinos, perros, tordos, perdices, loros y papagayos. Al parecer los ingresos de los osos a los maizales fueron muy poco comunes, a pesar de haber sido ampliamente extendido su cultivo en la época incaica (Inocente *et al.* 2006). Con la llegada de los españoles, se produjeron rápidos cambios debido a la extracción de los recursos (Rostworowski 2005), lo que pudo ocasionar una disminución de las fuentes de alimento para el oso en algunas zonas, forzándolo a ingresar a los cultivos de maíz. Posteriormente, el crecimiento poblacional y la expansión de la frontera agrícola, podría haber influido en la frecuencia de estos ingresos en relación a la disminución de su alimento natural o al fácil acceso a los nuevos recursos alimenticios cultivados.

Con respecto al ataque de los osos andinos al ganado, Humboldt (2004 [1801–1802]) señaló que este solo se daba cuando no disponían de las plantas de las que se alimentaban naturalmente. Poveda (s/f) encontró que en las zonas donde el bosque estaba mejor conservado y más continuamente distribuido, a pesar de haber ganado, los ataques no fueron un comportamiento habitual por parte del oso. Sin embargo, en el Perú sí se reportaron ataques en bosques en muy buen estado con abundantes recursos alimenticios, lo que podría estar relacionado a una mayor facilidad y disponibilidad de presas.

Medidas que buscan reducir la cacería del oso andino

Compensación. La compensación monetaria para la protección de los osos como retribución por los daños causados a los cultivos y ganado, a cambio de que no sea cazado, ha sido un éxito en algunos programas, como el del oso pardo en Europa (Klenzendorf 1997). Esta fue tomada en cuenta para el oso andino dentro del "Plan de acción para la conservación de los osos" (Peyton 1999). Sin embargo, en algunos casos podría tornarse conflictivo debido al uso de disposición a pagar/aceptar, que se refiere a la forma cómo se debe abordar una situación que necesite de una política, porque no está resuelto si se debe aplicar desde una perspectiva de compensación o desde una de adquisición (Pearce y Turner 1990 en Bejarano 1999).

En Ecuador, la Corporación de Conservación y Desarrollo (CCD 1994) elaboró un estudio sobre la factibilidad de realizar una compensación financiera por los daños que hicieran los osos en Cuyuja, Sardinas y Bermejo (Napo). El análisis de las encuestas y las cifras de comercialización concluyeron que el maíz no constituía la fuente principal de subsistencia para los agricultores y que los daños producidos sobre los cultivos por los osos eran mínimos. Se encontró que la caza y el comercio del oso andino eran más rentables, en términos económicos, que la producción y comercialización del maíz. Por ello, se determinó que la razón de sembrar maíz era para cazar al oso (CCD 1994). En Colombia tampoco se recomendó la compensación económica por los daños al ganado debido a la dificultad de diferenciar su depredación o carroñeo (Jorgenson y Sandoval 2005). Sin embargo, actualmente para el norte de Ecuador, debido a la fuerte tendencia creciente de los ataques (Laguna 2013), se evalúa la posibilidad de crear fondos de compensación por la pérdida de ganado, lo que podría influir de forma positiva en la tolerancia de estos eventos (Castellanos *et al.* 2011). En Oyacachi, entre los años 2001 y 2004, se registraron 41 eventos de ataques que dieron muerte a 61 vacunos, lo que representó una pérdida de USD$ 31,516 en carne y USD$ 42,534 en leche, para las familias afectadas (Flores *et al.* 2005). En las provincias de Carchi e Inambura, entre noviembre de 2009 y mayo de 2012, se comprobaron 163 ataques a ganado (141 muertos y 22 heridos; Castellanos y Laguna 2012), y hasta marzo de 2013, se registraron 98 eventos adicionales, sumando un total de 261 ataques (Laguna 2013). En el sur de Ecuador (Colapato), entre 1998 y 2008, se reportaron 40 vacunos muertos y uno herido (Achig 2009).

Otro tipo de compensación monetaria, podría estar relacionada con un ecoturismo basado en la observación del oso andino alimentándose en los maizales en la época de producción del choclo. El campesino sería compensado por su pérdida del maizal y por el tiempo que dedicaría al cuidado de los cultivos cuando no hay turistas (Peyton 1994).

Mitigación. El control letal lejos de ser un método efectivo, preventivo o correctivo, para la reducción de las interacciones humano–oso andino, podría conllevar a impactos negativos en sus poblaciones. Se analizaron varios estudios sobre la efectividad de la cacería de grandes carnívoros en la disminución de los daños ocasionados por estos a la ganadería; debido a la gran complejidad de los casos de depredación, se determinó que los datos científicos aún son escasos para tomar en consideración esta política de manera general (Treves 2009).

En Japón, no se encontró asociación entre los costos de los daños ocasionados por el oso negro asiático y su cacería, a pesar de que se cazaron más de 1,000 individuos cada año (Huygens *et al*. 2004). Respecto al oso negro americano, si bien en el Parque Nacional Fundy (Canadá) hubo una reducción de los conflictos después de su cacería, en otras tres áreas, dos en EE.UU. y una en Canadá, no se obtuvo el mismo efecto (Treves 2009; Treves *et al.* 2010).

Estudios en el oso pardo en cuatro áreas de caza entre la frontera de Canadá y EE.UU., sugirieron que la población era más susceptible a su disminución e incluso a una extinción rápida. Esto se debía a que la cacería de los machos adultos ocasionaba un aumento de la inmigración de nuevos machos, que reducía la supervivencia de los oseznos debido al infanticidio. Además, las hembras al evitar a los machos inmigrantes también se alejaban de los hábitats ricos en alimentos, lo que daba lugar a una disminución del tamaño de la camada (Wielgus y Bunnell 2000; Wielgus *et al.* 2001).

Por otro lado, lejos de lo esperado, la caza deportiva de pumas en Washington (EE.UU.) aumentó drásticamente los casos de depredación del ganado de un 36 a 240 %. Se sugirió que estos hechos estuvieron relacionados con el aumento de la inmigración de los machos jóvenes, que eran más propensos a atacar al ganado, en sustitución de los machos residentes cazados (Peebles *et al.* 2013).

Existen varios estudios donde se demostró que los carnívoros aprenden rápidamente a evitar las fincas después de aplicar diversos métodos de disuasión, debido a que los estímulos aversos se activan en respuesta a un comportamiento indeseable (Treves 2009). Para el caso del oso andino, existen documentos muy detallados donde se dan una serie de recomendaciones para la reducción de las interacciones con el maíz (Morales 2003) y el ganado (Nallar *et al.* 2008; Castellanos *et al.* 2011) cuya experiencia e información deben de ser tomados en cuenta.

Como punto inicial para plantear alternativas de mitigación que se ajusten a la realidad de cada área, será importante trabajar participativamente durante todo el proceso con los campesinos, revalorar sus conocimientos, comprender su temor hacia la pérdida económica, la percepción que tienen del animal que causó el daño, conocer el manejo de los agricultores y ganaderos, explicarles los objetivos y alcances del proyecto, y colectar información científica, para juntos buscar una solución a los conflictos y hasta prevenirlos.

Se recomienda la organización de las comunidades para las vigilancias de los campos de cultivos (Morales 2003) y del ganado (Castellanos *et al.* 2011). Este cuidado es básico e incluso es el control de mitigación más económico (Morales 2003). En la época incaica y colonial, se realizó una participación muy activa de hombres y mujeres en el cuidado de los maizales, principalmente en octubre (semillas recién sembradas), febrero (producción del choclo) y marzo–abril (maduración). Los hombres cuidaban durante el día y las mujeres, a partir de febrero, durante la noche, haciendo ruidos con un tambor (Guamán Poma de Ayala 2004 [1615–1616]). Con los años estas prácticas se fueron perdiendo en algunas zonas, y los cultivos ya no son atendidos continuamente, entre varios factores, porque se encuentran en áreas lejanas (Peyton 1999).

Para el caso de los ingresos del oso andino a los maizales hay que tomar en cuenta algunas observaciones realizadas anteriormente por Peyton (1980) en el Perú. Este autor encontró que los osos normalmente se alimentaron del maíz dos semanas antes de que esté maduro. Si un oso no fue asustado de un cultivo era probable que regresase al día siguiente, de lo contrario, se alimentaban de frutas y bromelias en el bosque o iban a otro maizal. Si el oso era asustado, podía regresar entre dos a 10 días después al mismo lugar. Además, observó que algunos mecanismos no detuvieron el ingreso del oso a un cultivo de maíz en Machu Picchu. El oso ingresó a pesar de la presencia de banderas azules de plástico en el perímetro, y regresó al día siguiente de la quema de caucho en el área donde ingresó el primer día.

Una experiencia exitosa de mitigación de daños a cultivos de maíz por el oso, gracias a la organización comunal, se realizó en Bolivia, en las comunidades de Pajan, K'apna y Wayrapata. En el 2001, 39 familias perdieron aproximadamente 6,701.8 kg de maíz (USD$ 1,718.40), siendo consumidas por los osos, loros *Aratinga mitrata*, zorrinos *Conepatus chinga* y roedores *Phylotis oscilae*. Después de realizar un cuidado más intenso de los maizales (día y noche), con ahuyentamiento sonoro con petardos, ahuyentamiento visual con banderines plásticos de colores, y trampeo de ratones, el daño fue notablemente menor. Para el 2002, 39 familias perdieron 1,508.2 kg (USD$ 385.97), y el 2003, 35 familias perdieron 2,982.3 kg (USD$ 763.8), siendo los más perjudiciales los roedores, las aves y en menor grado los osos. También se recomendó el uso de espantapájaros y la limpieza del barbecho en los alrededores de cada parcela (Morales 2003).

Castellanos *et al.* (2011) sugieren varias medidas específicas para contrarrestar las interacciones del oso con el ganado vacuno en la región de Cosanga (Ecuador), en base a una investigación detallada en la zona. Una de ellas, es considerar la posibilidad de uniformizar las razas de ganado que se crían, por la raza Brahman, debido a que no se registraron eventos de su depredación. Otra, es no conceder permisos para la explotación de las lauráceas, ya que se encontró una estrecha relación del oso con esta familia: alimentación, refugio y marcaje. Esta recomendación también podría extenderse a otras áreas en el Perú, como Machu Picchu, en donde Peyton (1987) también observó esta relación.

Asimismo, existen diversas experiencias y conocimientos que se han producido en otros países relacionados con otros úrsidos que podrían tomarse en cuenta. En Noruega, se encontró un mayor riesgo de depredación por el oso pardo a las ovejas que llevaban campanas, ya que de alguna manera los primeros asociaron su sonido con el alimento (Knarrum *et al.* 2006). En Bolivia, este uso fue recomendado por Nallar *et al.* (2008) para alertar a los dueños de los movimientos bruscos del ganado debido a algún depredador, en especial por la noche. Será importante tomar en cuenta las condiciones del lugar para analizar el uso de este método. En Borneo, para el oso solar, se aplicó tiabendazol a los frutos de los huertos que fueron visitados por los osos, con el fin de repelerlos al relacionar a los frutos con un mal sabor (Fredriksson 2005). En la India, para el oso negro asiático, se recomendó el uso de cercas de alambre con tiras de plástico (Chauhan 1999). En Venezuela, en un área aledaña al Parque Nacional Sierra de la Culata, para mantener seguro al ganado vacuno, se usó cerco eléctrico, obteniendo buenos resultados iniciales (Vineyard y Torres 2004); sin embargo en el Perú, su aplicación es poco probable por los limitados recursos económicos de los campesinos.

Chauhan (1999) aconsejó el uso de algunos repelentes clásicos para mamíferos, como la capsaicina (componente activo de los pimientos picantes), el isotiocinato de alilo (esencia de mostaza), benzoato de denatonio y otros amargantes. La capsaicina es utilizada eficazmente en EE.UU. para repeler a los osos negros y pardos en los encuentros con humanos (Hunt 1984 en Clarkson y Stirling 1994). Este conocimiento se podría ajustar a la realidad de las comunidades del Perú, sembrando alrededor de los cultivos, bajo la supervisión de botánicos, barreras de vegetación que posean olores repelentes para los osos e ir probando su efectividad en la reducción de los daños. En la comunidad de El Chairo (Bolivia), para repeler de sus cultivos mixtos de yuca, walusa, maíz y plátano a aves y mamíferos, se utiliza como métodos tradicionales de control, el orín y la siembra de plantas de ají y flores junto con los cultivos (Morales 2003).

En algunos países del centro y sur de Europa, y en Asia, se han utilizado por milenios a los perros pastores como un medio eficaz de protección del ganado de los depredadores (Rigg 2001). En EE.UU., este método de vigilancia se introdujo en la década de 1970, teniendo muy buenos resultados en la actualidad, reduciendo la depredación de ovejas en un 11 % a 100 %, dependiendo del lugar (Gehring *et al.* 2010 en Urbigkit y Urbigkit 2010). Además, los perros mantienen distantes a algunos animales que ocasionan daños a los cultivos, como los venados (Otstavela *et al.* 2009). El uso de perros entrenados de las razas Karelians y Akitas, ha sido anteriormente sugerido para disminuir la depredación del oso andino (Castellanos *et al.* 2011). Se podría explorar en el Perú, la idoneidad de los perros entrenados para la prevención de los daños de grandes carnívoros.

Hay que tomar en consideración que el oso andino puede tornarse agresivo para el hombre cuando es perturbado en un evento de depredación, al querer defender su presa. Además de los dos casos comentados en este estudio, Castellanos (2002) también reportó este comportamiento en dos ocasiones en Cosanga (Ecuador). Por ello, es sumamente importante recomendar a los pobladores, no interrumpir un evento de depredación o carroñeo.

La cacería del oso andino está registrada en todas las regiones políticas donde se distribuye el oso andino en el Perú, esta es motivada principalmente por las interacciones cultivo–oso y ganado–oso (Peyton 1980; Figueroa 2008; Figueroa *et al.* 2013). Debido al aumento de la frontera agrícola y ganadera, el territorio del oso disminuye rápidamente y con esto, la posibilidad de las interacciones se eleva (Peyton 1999). Las costumbres tradicionales de las comunidades en la agricultura y ganadería se encuentran muy arraigadas, por lo que el planteamiento de cambios drásticos no será fácilmente acogido por ellos. La alternativa más realista es la aplicación de técnicas de mitigación de daños acorde con las condiciones de cada lugar, en la que el campesino pueda darse cuenta que la prevención le originará una mayor ganancia económica y una mejor calidad de vida para su familia. Este es uno de los principales temas de investigación, donde se deberían dirigir los recursos económicos estatales y privados, para la conservación de la especie.

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Resumen

Introducción: El oso andino *Tremarctos ornatus* fue cazado durante la época incaica por ser considerado como un animal dañino, depredador de vicuñas y guanacos. Posteriormente, con la llegada de los españoles, el ganado vacuno traido por ellos, proporcionó una nueva y abundante fuente de alimento para los osos. Esto conllevó a fortalecer la percepción de los pobladores hacia el oso como depredador, sin tener en cuenta que también podría tratarse de eventos carroñeros. Asimismo, se extendieron los cultivos de maíz en donde el oso también aprovechó de estos. En la actualidad se siguen reportando estas interacciones. El presente trabajo busca, en base a entrevistas a los campesinos, obtener información sobre cómo, cuándo y dónde se producen estas interacciones, así como el de conocer su percepción sobre la especie. Asimismo, se discute el conocimiento de estas interacciones en otros úrsidos y las experiencias de mitigación en otros países.

Metodología: Entre los años 2002 y 2008 se visitaron 50 comunidades de 12 regiones del Perú, ubicadas en áreas aledañas o en las zonas de amortiguamiento de 16 áreas protegidas con registros de presencia del oso andino. Se realizaron 310 entrevistas personales, principalmente a cazadores, agricultores y ganaderos. Se aplicó una entrevista semi–estructurada, en la que se preguntó básicamente: fecha, hora, lugar y tipo de interacción (ganado o cultivo), tipo de registro (observación, rastros), especie de cultivo consumido o animal depredado, descripción del evento (ingresaron osos solitarios o en grupos, edades de los osos, etc.) y motivo de la cacería.

Resultados: Se obtuvieron 86 registros de la cacería del oso en 66 poblados de las 16 áreas protegidas evaluadas. El 60.8 % señaló que cazan al oso por considerarlo perjudicial por alimentarse de los cultivos (48.5 %) y atacar al ganado (42.2 %). Se reportaron 12 cultivos consumidos, siendo el maíz el principal ($n = 150$, 93.3 %); y cinco especies de ganado, siendo el vacuno el más frecuentemente depredado ($n = 131$, 95.9 %). La frecuencia y años de ataques fue muy variable, realizados mayormente por los machos adultos solitarios. Trece personas aseguraron haber presenciado un total de diez eventos de ataque, dando una descripción detallada, mientras que tres personas comentaron observar comportamientos de carroñeo.

Discusión y conclusiones: El ingreso del oso a los cultivos de maíz es un evento oportunista, debido a que es un alimento con altos niveles de energía y proteínas, y fácil de acceder principalmente en las áreas adyacentes a los bosques premontanos y montanos. Por otro lado, si bien existen investigaciones que confirman la depredación del ganado vacuno en Venezuela, Colombia, Ecuador y Bolivia, en el Perú aún no se ha hecho un estudio al respecto. Sin embargo, 13 personas proporcionaron información muy detallada de sus observaciones, las cuales coincidieron con otras investigaciones en otros países, lo que confirmaría que esta depredación también se da en el Perú. Debido a que ambos hechos son un fuerte motivo de la cacería del oso andino, será importante realizar diversas investigaciones para conocer las causas por los que algunos osos depredan ganado e ingresan a los cultivos. Asimismo, se deberá de trabajar conjuntamente con las comunidades para plantear medidas de mitigación acorde con las condiciones de cada lugar que busquen reducir estas interacciones y por lo tanto la cacería de la especie.

Palabras clave: cacería, conservación, depredación de ganado, consumo de cultivos, mitigación, oso andino

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