Estructura annual de edad y reproducción en el ratón con la nariz roja de Caatinga, *Wiedomys pyrrhorhinos* (Rodentia, Sigmodontina)

THERYA, agosto, 2014
Vol.5(2): 509-534
DOI: 10.12933/therya-14-194

Annual age structure and reproduction in the Caatinga red-nosed mouse, *Wiedomys pyrrhorhinos* (Rodentia, Sigmodontinae)

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Introduction: We analyzed the variation in the age structure, sex ratio, proportion of reproductive individuals, age and size at sexual maturity, and litter size in a population of the sigmodont rodent *Wiedomys pyrrhorhinos*. We compared the observed distributions with the monthly rainfall for the same period, to identify the reproductive period and to assess the effects of the rains on the age structure of the population during the ensuing months. We further compared our results with age structure patterns recovered from other documented rodent outbreaks to identify possible causes of a presumptive population outbreak represented by this series.

Methodology: Museum samples had been obtained between July 1953 and February 1955 from 40 sites in Caruaru, Pernambuco, Brazil (Fig. 1, Appendix). Records from a total of 2,280 individuals, 1,834 of which represented by their skulls, were analyzed. Skulls were sorted into seven age classes based on molar eruption and wear (Fig. 3). Monthly rainfall during the entire collecting period (Fig. 2) was analyzed for putative correlations with monthly frequencies of specimens (Figs. 4 and 5) and of indicators of reproductive condition, tabulated for each sex and age class.

Results: Monthly frequency distributions of age classes presented separated and consecutive modal peaks, conforming to an age structured population (Fig. 6). Monthly proportions of pregnant females were highly correlated with the amount of rainfall of the same and of the previous month (Fig. 7), although records of pregnant females were obtained every month between July 1953 and December 1954. Pregnant females were found from age class 2 on. From January to April, 1954, reproductive females belonged to age classes 5 to 7. From May to September a wide range of age classes was documented among pregnant females, and from October to December only those of age classes 2 to 4 were recorded (Fig. 8). Litter size varied throughout the year, with larger averages and ranges at mid-wet season (June-August) (Fig. 10) and was highly correlated with female weight, female length and with the amount of rainfall of the previous 30 days. Higher means in litter size were also in phase with higher proportions of pregnant females and with the age class 1 peak.

Discussion and Conclusion: The population peak occurred four to six months after the rainfall peak (September – November) and was primarily comprised of young adults. After this period, the pregnancy rates were very low, ceasing completely by January, 1955, when most of the individuals belong to older age classes. This shift in age structure from younger to older individuals during population decline indicated that the samples documented an outbreak episode in 1954. This episode was possibly related to the unusual rainfall in November 1953, apparently sufficient to support two closely-spaced breeding seasons, with the second amplifying the effect of the first.

Key words: bionomy, Brazil, breeding season, life history, litter size, outbreak, Pernambuco, population dynamics, pregnancy rate, ratada

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Resumen

Hemos analizado la variación en la estructura etaria, proporción sexual, proporción de individuos reproductivos, edad y grado en la madurez sexual, y el tamaño de la prole en una población del roedor sigmodontino *Wiedomys pyrrhorhinos*, con base en una gran serie de individuos obtenida entre julio de 1953 y febrero de 1955 en Caruaru, Pernambuco, Brasil. Se registraron 2,280 individuos, de los cuales 1,834 están representados por cráneos, los que fueron analizados. Los cráneos fueron agrupados en siete clases de edad basadas en la erupción y desgaste molar. La proporciones mensuales de hembras grávidas tubieron una alta correlación con la cantidad de lluvia del mismo mes y del mes anterior, a pesar de que la variación han sido encontradas también durante la estación seca. El tamaño de la prole varió a lo largo del año, con valores más altos durante mediados de la estación húmeda (junio), y este fue altamente correlacionado al peso, el largo del cuerpo de la hembra y con la lluvia de los 30 días anteriores. Distribuciones de frecuencias mensuales de clases de edad presentaron máximos modales consecutivos y separados, ajustándose a una población estructurada de manera etaria. El máximo poblacional ocurrió de 4 a 6 meses después del máximo de lluvias (septiembre-noviembre) y estaba compuesto primariamente por jóvenes adultos. A partir de ese período, sin embargo, las tasas de gravidez fueron muy bajas, cesando completamente en enero, cuando la mayoría de los individuos pertenecía a clases etarias más viejas. Ese cambio en la estructura etaria, de los más jóvenes a individuos más viejos durante el descenso poblacional, indicó que la muestra disponible sufrió un surto poblacional en 1954. Este episodio fue posiblemente relacionado a un aumento poco común en las lluvias en noviembre de 1953, aparentemente suficiente para soportar dos estaciones reproductivas enmendadas.

Palabras clave: bionomía, Brasil, estación reproductiva, historia de vida, tamaño de camada, brote poblacional, Pernambuco, dinámica poblacional, tasa de preñez, ratada.

Introduction

Patterns of growth rate, age and size at maturity, reproductive investment, litter size, mortality and life span comprise life history traits of a species (MacArthur and Wilson 1967; Roff 1992; Stearns 1992; Dobson and Oli 2007). The evolution of life histories involves trade-offs among these traits (Stearns 1989), which, among other factors, vary across age, size and sex classes (Deevey 1947; Caughley 1966; Goodman 1971; Caswell 2001). Such trade-offs evolve in response to ecological problems, comprising life strategies (Stearns 1976) that ultimately affect population growth and structure by determining different patterns of birth and death of individuals (Cole 1954; Ricklefs 2003).

Small mammals have unique traits in their life history strategies, such as short life span, short gestation time, early reproduction and weaning, and large litter sizes, with altricial young (Gaillard *et al.* 1989; Read and Harvey 1989), allowing quick responses to environmental variation. Therefore, small mammals, and particularly rodents, are often used as models to evaluate the correlation between extrinsic factors and population dynamics (Easterling *et al.* 2000; Wolff and Sherman 2007).

In tropical and arid zones, population fluctuations of small mammals are often related to climate forces, typically rainfall (Lima *et al.* 1999a; Lima *et al.* 1999b; Letnic *et al.* 2005). In the tropics temperatures do not vary notably, and the strongly seasonal pattern of rainfall makes it the most important climatic variable (Nimer 1979), influencing, to a large extent, diverse aspects of the biology of the organisms. In response to this heterogeneous regime, the availability of nutrients also occurs in heterogeneous pulses, influencing the density of primary consumers (Dickman *et al.* 2010; Thibault *et al.* 2010).

Population outbreaks in rodents ("ratadas") are generally correlated with years of unusually high rainfall and/or increased primary production (Jaksic and Lima 2003). The former may include large scale environmental changes as main causes, as many of these changes influence the amount of rainfall (*e. g.* El Niño Southern Oscillations, Lima *et al.* 1999a; Lima *et al.* 1999b; Letnic *et al.* 2005; and North Atlantic Oscillation, Kausrud *et al.* 2008). The later may be related to seed production after long intervals (Jensen 1982), particularly mast-seeding (King 1983; Pathak and Kumar 2000; Jaksic and Lima 2003; Sage *et al.* 2007).

One particular rodent that shows notable population fluctuations is the red-nosed-mouse *Wiedomys pyrrhorhinos* (Wied, 1821), a semi-arboreal species with granivorous-folivorous habits (Streilein 1982a), which is a generally rare (Mares *et al.* 1981) and endemic (Oliveira *et al.* 2003; Gonçalves *et al.* 2005) species in the semi-arid region of northeastern Brazil. Although this species cannot be considered as truly adapted to arid regions, it has the highest urine concentrating capability among Brazilian Sigmodontinae (Strelein 1982b) and presents morphological features that are common among desert rodents such as large auditory bullae, long tail and large eyes (Mares, 1983). Few reports on the natural history of *W. pyrrhorhinos* are available (Moojen 1943; Streilen 1982a; Weigl 2005), so that basic information on bionomy, ecological relations, and demographic patterns still remains unknown or poorly understood.

The availability of an unusually large and well documented series of *W. pyrrhorhinos*, collected during a 20-month period in a limited region in northeastern Brazil, allowed an assessment of the reproduction and age structure of this species and its possible determinants in the semiarid Caatinga. We analyzed the monthly variation in frequencies of relative age classes and reproductive traits and compared the observed distributions with the monthly rainfall for the same period, to identify the reproductive period and to assess the effects of the rains on the age structure of the population during the ensuing months. Furthermore we compared our results with age structure patterns recovered from documented rodent outbreaks to identify possible causes of a presumptive population outbreak represented by this series.

Material and Methods

Origin of Data and Data Assembling. The samples analyzed in this study were obtained by the Serviço Nacional de Peste (SNP, National Plague Service, Ministry of Education and Health, Brazil) during a small mammal inventory carried out under the guidance of João Moojen, from June 1951 to February 1955 (Oliveira and Franco 2005). The specimens were deposited in the Museu Nacional (MN/UFRJ), in Rio de Janeiro, either as skin and skull specimens, or as skulls alone.

Study Area. Samples were obtained from the Caruaru region of the state of Pernambuco, northeastern Brazil (Fig. 1). This region is influenced geologically by the Planalto da Borborema, which determines orographic rainfall (Tabarelli and Santos 2004), and eventually favors the occurrence of "brejos de altitude", evergreen rainforest islands surrounded by typical Caatinga (Andrade-Lima 2007; Fig. 1).

Falling within the semi-arid Caatinga, the Caruaru region does not show the extreme climatic characteristics typical of this domain (Nimer 1979). Normals average (1930-1960) for annual rainfall was 511.8 mm (DNOCS 1972), seasonally distributed throughout the year in the typical autumn-winter pattern of the eastern region of Brazil. This data indicates that the dry season in Caruaru extends from September to January (Nimer 1979).

Sampling Localities. The most detailed reference to the locality of collection is the name of the "sítio" (= site), a former land division still recognized locally in the rural areas of northeastern Brazil. The choice of a specific site for sampling was determined by previous detection of human cases of bubonic plague (Oliveira and Franco 2005).

Around the focus site, all sites within a radius of 6 km were consecutively sampled in subsequent months. This sampling design, originally intended to allow detection of possible differences in the mammals' compositions of plague positive and negative sites, eventually allowed the comparison of subsequent month frequencies without the putative bias caused by oversampling the same site.

Rainfall Databases. Mean monthly rainfall and 30-year monthly means (normals) for Caruaru (Station PE-14-CARUARU, Rio Ipojuca Watershed, -8° 14′ 18″ S, -35° 55′ 17″ W, elev. 557m) were available from Departamento Nacional de Obras Contra as Secas (DNOCS, 1972) for the period 1931 to 1960. Daily rainfall from 1951 to 1955 was available from the Departamento Nacional de Águas e Energia Elétrica (DNAEE) and the Divisão de Controle de Recursos Hídricos (DCRH), Ministério das Minas e Energia, Pluviometric station #835009, situated at -8° 17′ S, -35° 58′ W, elevation 545 m. Both stations were located in the region that includes the collecting sites (Fig. 1), outside Caruaru city limits, and are situated at the same general elevation, supporting the reliability of their data for the study area.

Preparatory Analyses. All documented information about the collecting was available from individual file cards, which included, among other not used here, data on the locality of collection, date of capture and death, collector name, length of head-body (HB) and weight (W), sex and reproductive condition – for females if pregnant or not, and if so the number of embryos, and for males if testes showed vascularization.

Records came from a wide range of sampling sites throughout the sampling period (Appendix). Of the total sample of *Wiedomys pyrrhorhinos* from the Caruaru region (2,395 records), 2,280 were actively collected by hand or with forceps, 31 by traps, and for 84 records the capture method was unrecorded. Because a relatively small fraction of the specimens has been obtained using trapping methods, almost exclusively during a different period from those obtained by active methods, to avoid possible bias in the estimation of month frequencies due to the collecting method, our analysis was restricted to the specimens obtained by the active methods, obtained from July 1953 to February 1955.

Specimen data was used to identify potential bias in the monthly sampling effort, by comparing raw specimen numbers per month, number of sites worked, number of days worked per site (as revealed from the analysis of original file cards including the capture dates of all specimens collected), and mean daily captures per site per month (Appendix). Number of days worked by each active collector and respective number of specimens captured were also calculated.

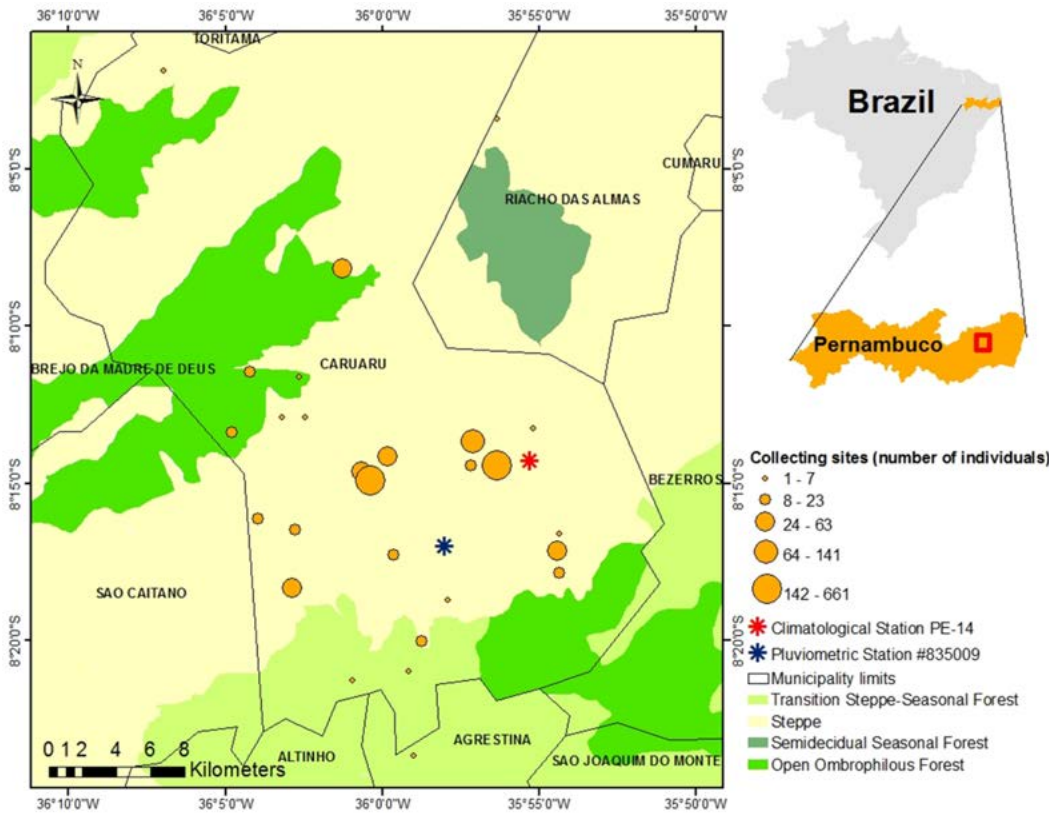

Figure 1. Location of main collected sites in the Caruaru region and their respective abundance of specimens and local vegetation types, as defined by RADAMBRASIL (1983).

We found no correlation between the number of collectors working and the number of specimens captured in each month, but found a significant correlation ($P < 0.01$) between the number of days worked by each collector and the respective number of captured specimens. This result suggested that the differences in monthly frequencies might be influenced by the number of days worked in each month by each collector.

To correct this possible sampling bias we computed the average daily capture rate per month, dividing the total number of captured individuals by the total number of days worked in all sites in each month. In order to compare this adjusted number to the absolute monthly frequencies, we then multiplied the average daily capture rate by the mean number of days by month worked in the best sampled year (1954, 19 days/month). We noticed that only rarely more than one site was sampled by the same collector in a given day, so, to simplify the computation of worked days, we considered two sites sampled by the same collector in a same day as two different days.

Frequency analyses that did not require a comparable collecting effort across months, such as the monthly frequencies of reproductive individuals relative to the number of sexually mature ones, as well as the monthly frequencies of litter sizes, were not adjusted by collector effort.

Age Classification, The skulls of 1834 specimens were examined and aged on the basis of molar eruption and wear.

Reproductive Data. Reproductive status of females was based only on the number of embryos. No information was available about placental scars or lactating tissue, consequently the number of reproductive females is likely an underestimate. Following Cerqueira (2005) and Krebs (2013) the number of embryos was taken as reflective of litter size. Females and males were considered sexually mature only from the minimum age and size (as inferred by body length and weight, Cerqueira *et al*. 1989) documented respectively in pregnancy or with testes vascularization (Krebs 2013).

Since Sigmodontinae gestation periods range from 23 to 30 days (Carpenter 1975; Eisenberg and Redford 1999; Vercruysse *et al*. 2006), the total amount of rainfall in the 30 days prior to the capture was considered for each pregnant female.

Analyses. Absolute and relative monthly frequencies of specimens and their indicators of reproductive condition, were tabulated for each sex and age class. Bar graphs of monthly rainfall during the entire collecting period were analyzed for putative correlations between the reproductive frequencies and that determinant of primary production.

Frequency distributions were portrayed for: 1) the absolute and adjusted numbers of specimens collected by month, as recorded in the original file card; 2) the absolute and adjusted numbers of specimens collected by month, as represented by the available voucher skulls; 3) the relative frequencies of specimens collected by month, by sex; 4) the absolute numbers of specimens of collected by month, by age class; 5) the relative frequencies of pregnant females collected by month; 6) the relative frequencies of pregnant females, by each age class; 7) the relative frequencies of males with vascularized testes collected by month; and 8) the absolute numbers of embryos in the uteri.

Descriptive statistics (mean, mode, minimum and maximal values) were calculated for body length and weight for samples of males and females (for both reproductive and non-reproductive individuals) of each age class, and also for litter size by month.

Spearman Rank Correlation was used to assess the significance of correlations between the monthly proportion of pregnant females and the total rainfall for the previous month. This analysis was also used to assess the correlation between litter size and: 1) total rainfall in the previous month, 2) mother's age, 3) mother's weight, and 4) mother's HB length. An Exact Binomial test was used to assess sex ratio variation by age classes among months. Descriptive statistics, as well as statistical tests were implemented using routines written in the software R (R Development Core Team, 2013). Histograms and bar charts portraying frequency distributions and other graphic data were implemented in Excel®.

Results

Rainfall pattern in Caruaru region. Compared to the normal precipitation pattern from 1931 to 1960, higher than average rainfall was recorded in June and November 1953, from May to July 1954, and during January and February 1955. The periods from January to April in 1953 and 1954 were drier than average (Fig. 2). Annual rainfall varied from a maximum of 418.3 mm in 1951 to a minimum of 165.3mm the following year.

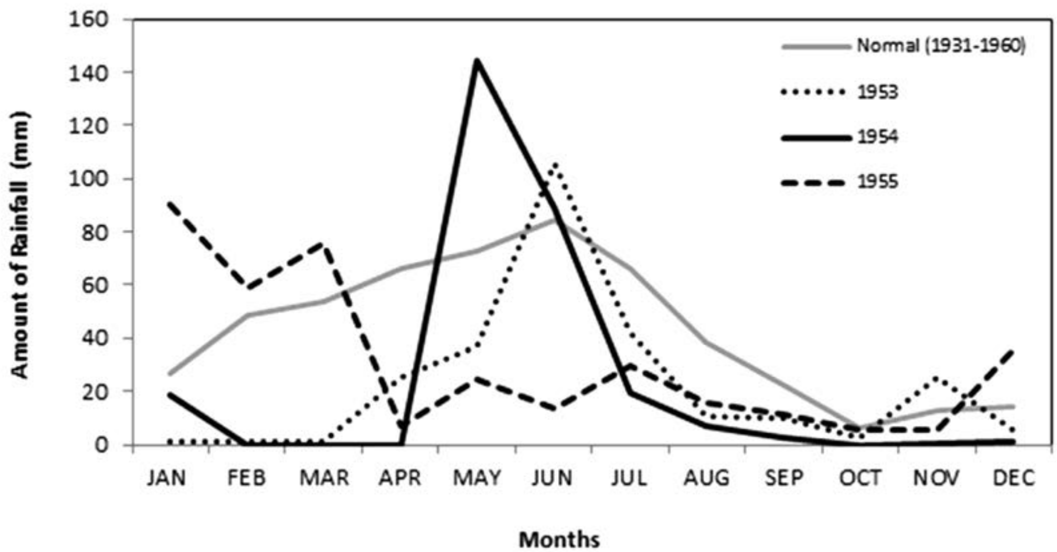

Figure 2. Monthly total rainfall (mm) from Rio Ipojuca Watershed (Station PE-14-Caruaru), Caruaru, Pernambuco, Brazil, for 1953 to 1955, and normal curve for the period of 1931-1960 (data from DNOCS, 1972).

Age classes. Skulls were allocated to one of the following relative age classes, defined on the basis of the following landmarks in molars wear and eruption of the third molar (Fig. 3):

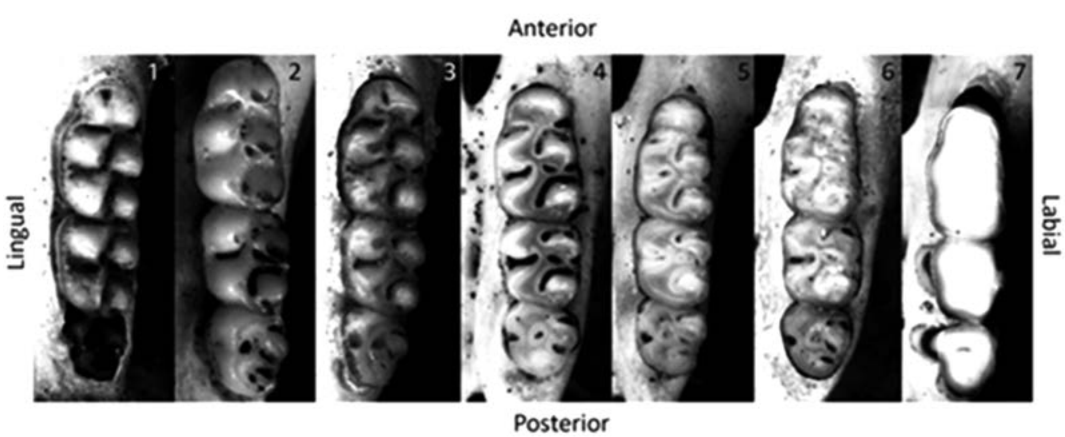

Figure 3. Examples of occlusal surfaces of upper molars illustrating the seven relative age classes of *Wiedomys pyrrhorhinos* from Caruaru Pernambuco, Brazil, used in the present study. Age class 1 (MN72801), age class 2 (MN61039), age class 3 (MN61420), age class 4 (MN61043), age class 5 (MN72794), age class 6 (MN60956) and age class 7 (MN72856).

Age class 1: 1st and 2nd molars erupted and unworn; 3rd molar in the alveolus.

Age class 2: 1st and 2nd molars erupted and unworn; 3rd molar on the occlusal plane, unworn.

Age class 3: 1st, 2nd and 3rd molars with initial wear, isolated dentine visible on protocone, paracone, hipocone and metacone.

Age class 4: 1st, 2nd and 3rd molars with moderate wear, islands of dentine of the protocone, paracone, metacone and hipocone interconnected by the dentine of the median mure.

Age class 5: 1st, 2nd and 3rd molars with moderate wear, islands of dentine of the protocone, paracone, metacone and hipocone interconnected by the dentine of the median mure, lingual cusps very worn.

Age class 6: 1st, 2nd and 3rd molars very worn, islands of dentine of the protocone, paracone, metacone and hipocone interconnected by the dentine of the median mure, lingual and labial cusps very worn.

Age class 7: 1st, 2nd and 3rd molars completely worn, no internal enameled component discernible, cusps indistinct in relation to the folds, minimum enamel thickness.

Analyses of frequency distributions. Monthly frequencies in 1954 reveal population size at its minimum in May, and a gradual growth from this month on, reaching the highest peak in October and then decreasing until December. By January, 1955, the population achieved another high peak, but collecting activities ended by February, 1955. The comparison between monthly frequency distributions based on the whole sample and on samples adjusted for collecting effort (Fig. 4), showed similar patterns, especially in the best sampled year, 1954, which showed minimum frequency in May and maximum in October. In both distributions, a tendency of decrease can be seen from October on, with a slight increase in January, 1955.

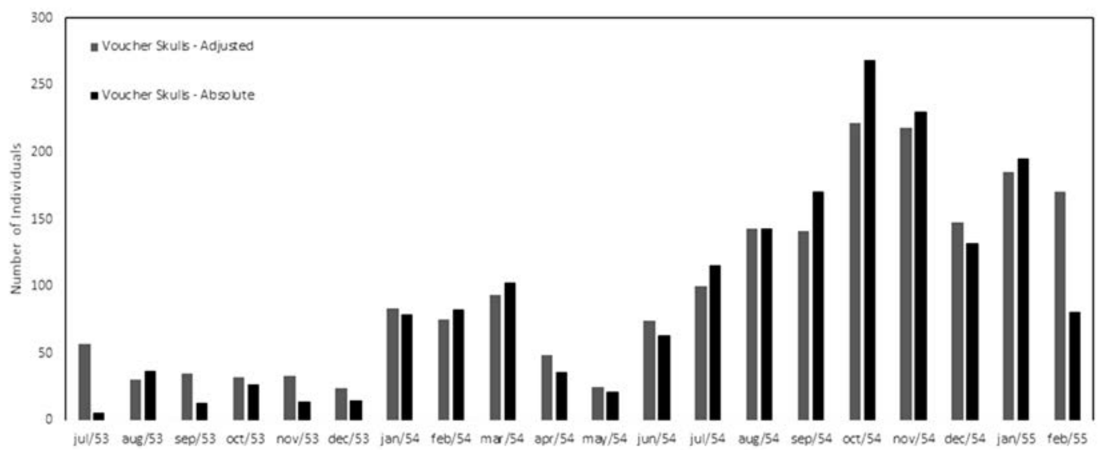

Figure 4. Absolute (black bars) and sampling effort-adjusted frequencies (grey bars) of voucher skulls of *Wiedomys pyrrhorhinos* collected by from July 1953 to February 1955 in Caruaru, Pernambuco, Brazil.

Sex ratio. Sex ratio in the total sample was skewed toward females (1:0.84, $P < 0.01$). However, only the samples from the mid-year months (June to September) were significantly female-biased (Fig. 5). Since this could also be explained by variation in the age structure of the population during the year, sex ratios for each age class were also analyzed separately (Table 1) revealing that younger classes (1-3) were composed primarily of females, and older classes (4-7) exhibited a more balanced sex ratio, but the sex ratio was significantly biased toward females, albeit marginally, only in the age class 2 sample.

Monthly frequency distributions by age classes. The monthly distributions of individuals by age classes formed modal patterns, with peaks in subsequent months for consecutive age classes (Fig. 6). These peaks are clear as far as age class 4, but less recognizable after that, possibly due to the lower sample sizes of older age classes. To enable comparison with frequency patterns of other age classes, the last two age classes were combined.

Age class 1 individuals were nearly all recorded from June to November, with the class peak in July. Age class 2 individuals were recorded during a similar period. The bulk of this class was collected between August and November, with the peak of frequencies in October. Age class 3 individuals were recorded in almost every month, but records between April and July were scarce, and increased from August on, with the peak of the class in November. Age class 4 was more abundant between September and March, and its peak occurred in January, 1955. Age classes 5 and 6 + 7 were also recorded all year long, with peaks respectively in February, June and July.

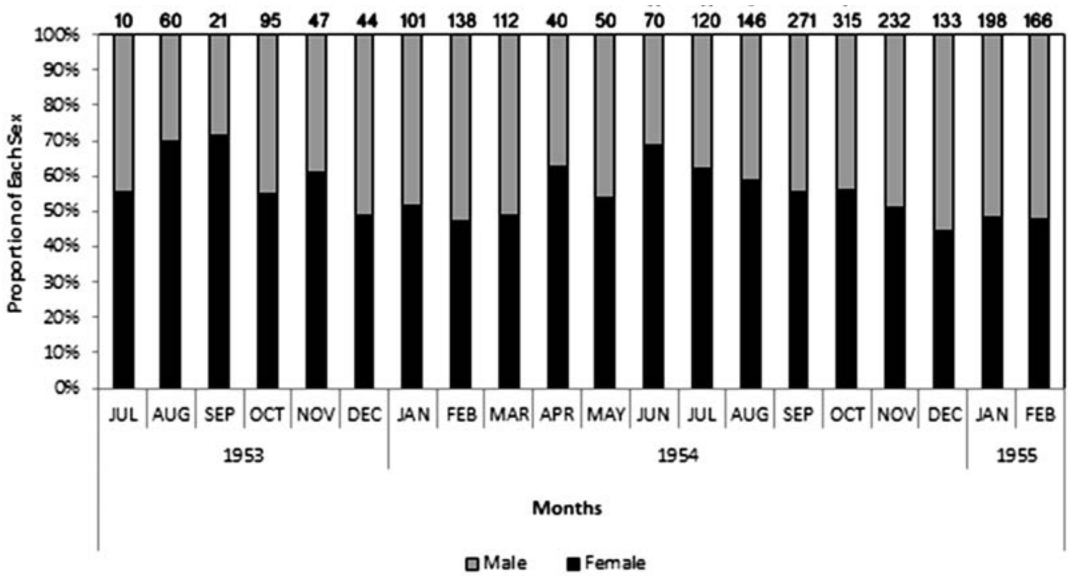

Figure 5. Relative frequencies of each sex of *Wiedomys pyrrhorhinos* collected by month, from July 1953 to February 1955 in Caruaru, Pernambuco, Brazil. Numbers above chart indicate the total number of individuals of a particular month. Asterisks refer to *P*-value for the Exact Binomial test: ** -0.002 < *P* < 0.01; * -0.02 < *P* < 0.05.

Analyses of reproductive traits: pregnant females. Pregnant females were captured uninterruptedly from July 1953 to December 1954. The months that presented more than 20% of females pregnant were August and November, 1953, and between May and September, 1954, which showed the highest proportions, with up to 50 % of females pregnant (Fig. 7). Proportions decreased considerably by October, and by December, 1954, the last pregnant individuals were recorded. Monthly proportions of pregnant females were highly correlated with the amount of rainfall of the same month, as well as with the previous month ($P < 0.01$): the peak of August, 1953, occurred two months after the peak in rainfall in June of the same year; likewise, the slight increase in the proportion of pregnant females in February, 1954 occurred after above normal rainfall recorded in November 1953 and January 1954, and after a dry period that extended from August to October, 1953.

Of the 134 pregnant females, only 108 had skulls available to provide an age estimate.

When analyzed with respect to the age composition among months, an age structured pattern emerges in 1954: from January to April all reproductive females belonged to age classes 5 to 7; in May individuals from age classes 4, 5 and 7 were recorded; from June to September reproductive females were of all classes 2 to 7, and from October to December, only those of age classes 2, 3 and 4 were recorded (Fig. 8). The pattern observed in 1953 is similar to the one observed in 1954, with the peak in reproduction (August) representing all reproductive age classes.

No female was found pregnant at a younger age than class 2, or with less than 100 mm HB or 30 g (Table 2). Females of this and higher age classes and sizes were considered to be potentially mature; therefore, of the 512 potentially mature females, 19.1% were recorded as pregnant.

Analyses of reproductive traits: Males with Vascularized Testes. Similarly to the female pattern, no male with this reproductive evidence was found at age class 1. Nevertheless, minimum size for sexually mature male individuals of age class 2 was 83 mm HB and 20 g (Table 2). Males of this and higher age classes and sizes were considered to be sexually mature; of the 659 potentially mature males, 636 were recorded with testes vascularized. Therefore, the monthly frequency distribution of males with vascularized testes reached 96.5% and was not concordant with the monthly distribution of pregnant females (Fig. 9). In addition, differently from the pattern observed for pregnant females, there is no prevalence of an age class in the monthly frequencies of reproductive males, and the age structure of potentially mature individuals closely followed that of the total sample (Fig. 6).

Table 1. Absolute frequencies of male and females by age classes and sex-ratio (percent female) of *Wiedomys pyrrhorhinos* in Caruaru, Pernambuco. Total Voucher Skulls: number of males and females with voucher skulls available for age classification. Total File Cards: total number of males and females, based on information of original file cards. Asterisks refer to the significance of *p*-values of the Exact Binomial test for sex-ratio: ** $0.002 < P < 0.01$; * $0.02 < P < 0.05$; ns: $P > 0.05$, n. s. not significant.

Age Class	Males	Females	%F	*p*-value
1	71	86	0.55	ns
2	127	169	0.57	*
3	232	234	0.50	ns
4	153	189	0.55	ns
5	72	87	0.54	ns
6	42	36	0.46	ns
7	39	32	0.45	ns
Total Voucher Skulls	736	833	0.53	*
Total File Cards	843	971	0.54	**

Litter size. Overall mean litter size was 5.6 and ranged from 2 to 11embryos, 4 embryos being the most frequent litter size. The number of embryos varied considerably among months (Table 3; Fig. 10). In 1953, August litters (*n* = 8) varied from 2 to 8 embryos, with 5 and 6 being the most frequent; from September to December, almost all litters recorded had 4 embryos (*n* = 1, 6, 3 and 1 litters, respectively). The year of 1954 presented a wider variation in mean litter sizes. In January, litters varied between 3 and 4 embryos; in February and March all litters had 4 embryos; in April, litters varied between 4 and 6 embryos; in May, between 2 and 8 embryos; in June, between 4 and 11 (the largest number recorded), with 8 being the most frequent; in July litters varied from 5 to 8 embryos, 6 and 8 being the most frequent; August recorded the largest amplitude, from 2 to 10 embryos, those with 6 being the most frequent; September litters varied from 2 to 8 embryos, with 5 being the most frequent; in October, 4 litters were recorded, with 3 to 6 embryos; in November only one litter was recorded, with 7 embryos, and in December two litters, with 4 and 5 embryos. Average number of embryos per parturition was lower at the beginning of the year (3.7), reached its peak in June (7.2) and declined until December.

Litter size was not correlated with female age. However, litter size was highly correlated with female weight ($P < 0.001$), female HB length ($P < 0.01$) and with the amount of rainfall of the previous 30 days ($P < 0.001$).

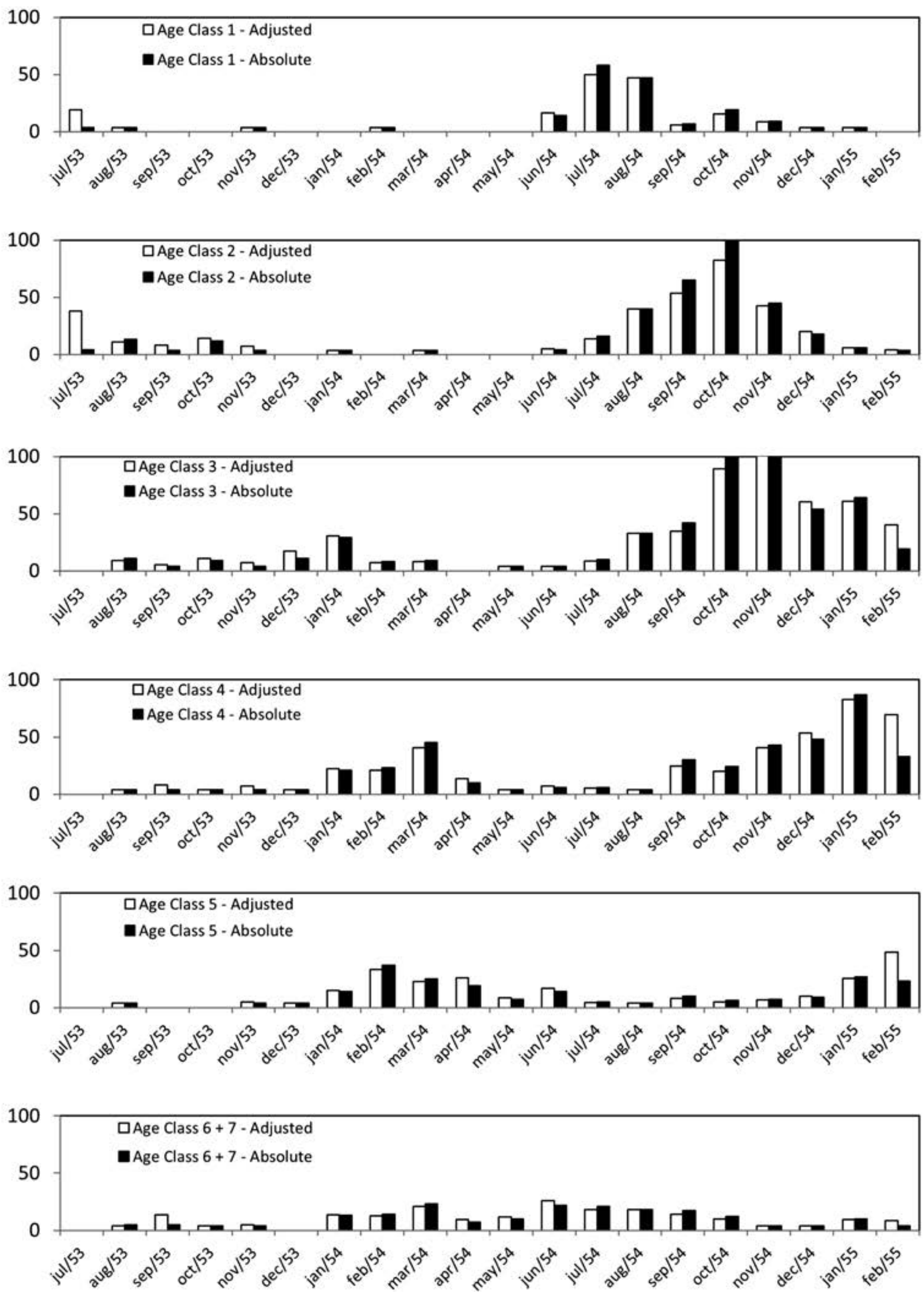

Figure 6. Absolute and adjusted frequencies of individuals of *Wiedomys pyrrhorhinos* in each age class by month, from July 1953 to February 1955 in Caruaru, Pernambuco, Brazil.

Discussion

The use of museum specimens is unusual in studies of population dynamics, yet crucial bionomic information can be gleaned if detailed collection data is taken, including number of embryos and the reproductive status of males. Museum specimens allow the analysis of molar wear for age determination, usually a limitation in studies of live specimens.

A possible confounding factor in the determination of demographic patterns to be revealed by analysis of frequency data might be the method used to age specimens. Molar wear may be affected by many variables, like quality and type of food, soil type or even individual differences related to development and behavior (Oliveira *et al.* 1998; Hillson 2005). Because all samples in this study were from the same region, we regard geographic variation in molar wear, as well as possible differences related to the environment, to be negligible.

Another question that may arise in a study based on the removal of specimens is whether the sampling in one month might affect the number of individuals to be recorded in subsequent months to an extent that would obscure or confound demographic patterns to be revealed by frequency data.

Two characteristics of the dataset do not support such a conclusion. First, the samples in months of low densities both in 1953 and in 1954 have in general been assembled from a large number of sites (Appendix), which were usually sampled for a few days in each month. In addition, even during the period of higher densities between September and November, 1954, in which few sites were sampled for longer periods, sampling in consecutive months was carried out in different sites. Lastly, the increasing amount of specimens collected in the last months of sampling, is regarded here as evidence that the continuous removal of specimens by the SNP sampling in the Caruaru region, and in the same sites, did not result in a significant decrease in the population of *Wiedomys pyrrhorhinos* during the sampling period.

Wiedomys pyrrhorhinos is a rare species in museum collections, and the sample from SNP deposited in MN/UFRJ represents an exception. Nevertheless, this species has been identified by means of photographs as the only species involved in a rodent outbreak related to a bamboo mast-seeding episode that occurred in 2002 in Formosa do Rio Preto, state of Bahia, Brazil (A. Almeida [*pers. comm.*]). Nearly 95% of *W. pyrrhorhinos* specimens obtained during the SNP survey were hand collected. The scarcity of this species in collections might be, at least in part, due to the limitations of trapping methods traditionally used to capture this species. According to specimen data most specimens were collected in nests, often located in hedges made of “Aveloz” (*Euphorbia tirucalli*, Euphorbiaceae), an exotic bush. Collection of individuals of *W. pyrrhorhinos* in nests had also been noted by Streilein (1982a) and this species is often recorded using abandoned bird nests (Bocchiglieri *et al.* 2012). Active collecting by hand thus may have unintentionally biased results with searchers looking preferentially in more predictable spots, such as inside or near nests, more probably of females and/or their offspring. Analysis of sex ratio suggests that the sampling may have been biased toward females, especially during the breeding season.

Age structure. The monthly frequency distributions of samples classified by molar wear (Fig. 6) provided clear evidence of an age structured population, with modal peaks for subsequent age classes separated and consecutive. The pattern of subsequent peaks revealed by the frequency distributions of age classes may also be indicative of the duration of each age class. Weaning for most Cricetinae rodents occurs at approximately 21 days (Millar 1977), an age at which the young are probably able to leave the nest and forage. These emergent juveniles might be those classified as age class 1 in the present study, with frequency peaks in July. The frequency peak of the next age class, 2, is in October, suggesting an interval of three months between landmarks defining these classes. The difference of frequency peaks of age class 2 and age class 3 (November) is one month, and between age class 3 and age class 4 are two months, indicating that age class 1, 2, 3 and 4 individuals would be respectively around one, four, five and seven months old. The peak of age class 5 (February) occurs one month after the peak of age class 4. The peaks of oldest age classes (6 and 7) are less well defined (June and July, respectively). The maximum life span of age class 7 individuals in the wild is about a year and a half, since the youngest individuals appear in July and the eldest are recorded in until December. In captivity, an individual has lived for 3.9 years (Weigl 2005).

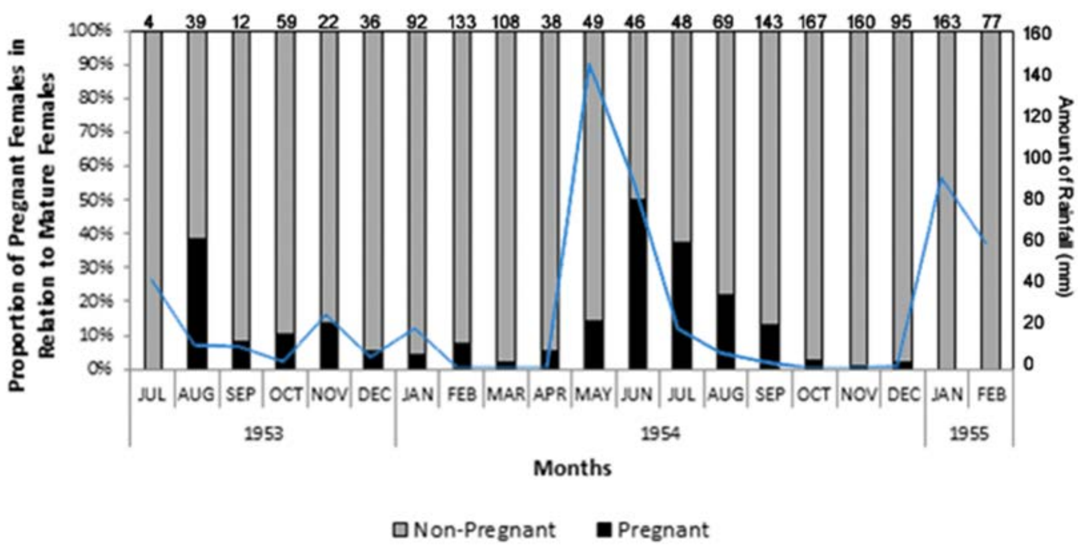

Figure 7. Relative frequencies of pregnant females of *Wiedomys pyrrhorhinos* by month, from July 1953 to February 1955, and monthly rainfall for the same period in Caruaru, Pernambuco, Brazil. Numbers above chart indicate total number of individuals of a particular month.

Sexual maturity and reproductive individuals. Considering the age and size of pregnant females, sexual maturity is reached only when the third molar reaches the occlusal plane (age class 2), and when females reach 100 mm HB length and 30 g.

Observations of six captive females made by E. Maliniak (*pers. comm.* in Eisenberg and Redford 1999:445) indicate that pregnancy in *Wiedomys pyrrhorhinos* starts at the age of 83 days. Therefore, age class 2 females should be at least 83 days old. This value is in agreement with our absolute age estimation.

Males with vascularized testes had at least the third upper molar reaching the occlusal plane (age class 2). Biggers (1966) noticed that only the presence of spermatozoa in the epididymes – information that was not recorded in SNP dissections – would be indicative of reproduction. Since the necessary conditions for spermatogenesis depend on a thermorregulation mechanism directly related to testicular vascularization (Grant and Paulyng-Wright 1971), a condition that has only been identified from age class 2 on, the information obtained from SNP data at least permits ruling out age class 1 males as sexually mature.

Sample	Measurement	AC 1	AC 2	AC 3	AC 4	AC 5	AC 6	AC 7
Total	HB	75.7 (165)	97.4 (348)	104.3 (579)	107.0 (449)	110.3 (266)	111.6 (121)	113.3 (119)
	W	13.0 (165)	31.0 (348)	37.0. (578)	38.0 (449)	41.0 (266)	42.9 (121)	45.0 (118)
Pregnant females	HB	-	109.8 (12)	112.3 (21)	112.0 (16)	115.4 (28)	115.4 (18)	116.2 (18)
	W	-	48.0 (12)	50.0 (21)	53.0 (16)	50.0 (28)	50.5 (18)	48.1 (18)
Non-pregnant females	HB	76.1 (91)	97.5 (195)	103.6 (284)	106 (244)	109.8 (128)	111.3 (51)	114.5 (49)
	W	13.0 (91)	31.0 (195)	36.0 (283)	37.0 (244)	41.0 (128)	42.0 (51)	45.9 (49)
Males	HB	75.2 (74)	97.2 (141)	105.0 (274)	108.0 (189)	110.9 (110)	111.9 (52)	112.1 (52)
	W	12.0 (74)	30.0 (141)	38.0 (274)	40.0 (189)	41.0 (110)	43.0 (52)	44.0 (51)

Table 2. Means for head and body length (HB, in millimeters) and weight (W, in grams), by age class (AC), for the total sample and for samples of pregnant females, non-pregnant females and males separately. In parentheses, the sample size.

Although males and females reach sexual maturity at age class 2, in which males are smaller than females, by age class 3 males are already larger (Table 2). This might be related to differences in energy allocation towards reproduction over growth (Stamps 1993), to increased growth rates in males or even to natural/sexual selection (Lande 1980), allowing females to extend their growth period.

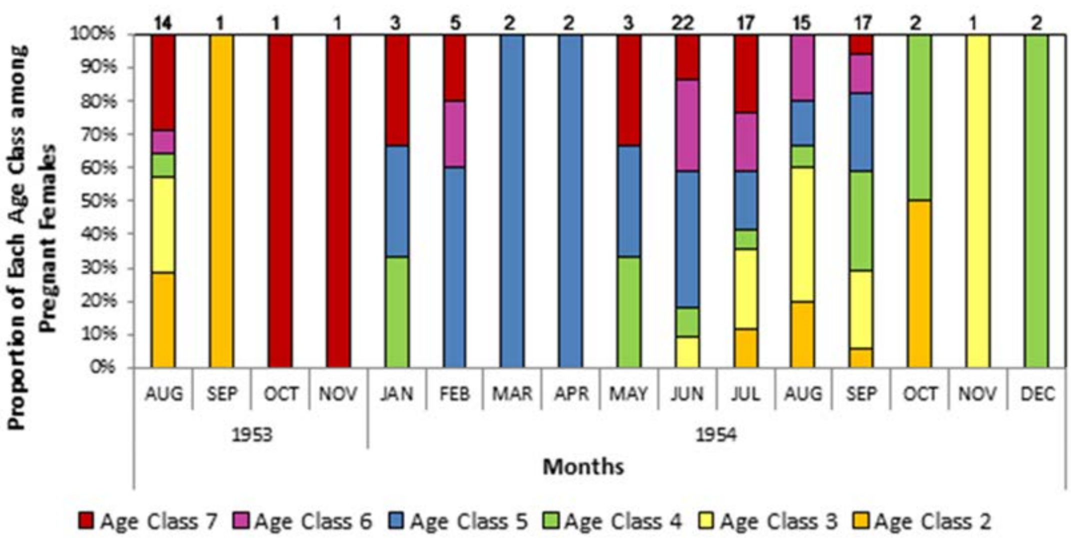

Figure 8. Relative frequencies of pregnant females of *Wiedomys pyrrhorhinos* in each age class, by month, from August 1953 to December 1954 in Caruaru, Pernambuco, Brazil. Numbers above chart indicate total number of individuals of a particular month. Colors in each bar refer to the proportions of each size class among the pregnant females per month.

Breeding season. Breeding season is defined as the period in which reproductive events occur: oestral cycle, fecundation, pregnancy, nursing and weaning (Cerqueira 2005).

When no information on weaning period exists, the breeding season can be estimated from the first and last months in which pregnant females are captured in any given year (Cerqueira *et al.* 1989). Although females were found pregnant in every month throughout most of the sampled period, higher relative frequencies of pregnant females occurred in August, 1953, and between June and August, 1954. During these periods, pregnant females of all reproductive ages were recorded. We thus regarded these periods as the breeding seasons, which were coincident with the late wet season in Caruaru in these two years.

The highest proportion of pregnant females, most of them belonging to older classes (5 to 7), was observed when the population was at its lowest monthly frequency (Figs. 4 and 7). In contrast, when the population was at its highest monthly frequency, the proportion of pregnant females was lowest, most of them belonging to younger classes (2 to 4).

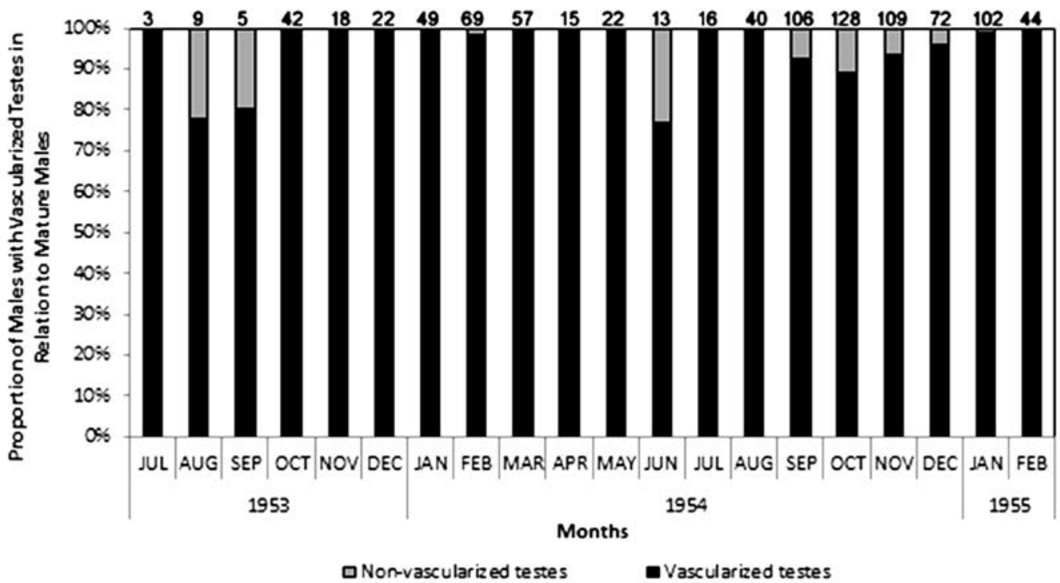

Figure 9. Relative frequencies of males with vascularized testes of *Wiedomys pyrrhorhinos* by month, from July 1953 to February 1955 in Caruaru, Pernambuco, Brazil. Numbers above chart indicate total number of individuals of a particular month.

Females born late in the reproductive season (September) would reach sexual maturity at the beginning of the following year, since young pregnant females (age classes 2 and 3) were not found in the first months of the year. Those born in the late reproductive season would only reproduce in the next breeding season. On the other hand, females born shortly before the breeding season (May) would be apt to reproduce in the same season, since they would reach age class 2 about 80 days later (around August). This might still be dependent of the abundance of food during the rainy season, enabling young females to gain the necessary fat for reproduction (Williams 1966; Bronson 1985).

The ability to reproduce in the same season in which it was born is found in a variety of desert rodents (McCulloch and Inglis 1961; Speth *et al*. 1968; Smith and Jorgensen 1975; Conley *et al*. 1977; Cerqueira *et al*. 1989) and contributes to the potential of the population to respond quickly to favorable conditions.

Males with vascularized testes were also detected throughout the entire year (Fig. 9). Differently from the female pattern, the monthly frequency distribution was very homogeneous, with almost all sexually mature males in each month showing this pattern. Bronson (1985) hypothesized that for male mammals it might be advantageous to be always ready to reproduce, despite the potential higher mortality of this strategy. According to this author, if females may occasionally be reproductive during challenging times, males should not present seasonal decline in their reproductive potential.

Pregnant females were mainly found in the wet season, but were also recorded in the dry season, a presumptive unfavorable period (Fig. 7). The age composition of these outlier reproductive females clearly reflects the age structure of the population, with those of the first months of the year being old individuals, while those of the last months of the year were younger. The rare records of age class 1 individuals between January and March 1954, are indicative of their low densities, since few females were pregnant in this period. These findings are in accordance with those of Streilein (1982a), who reported *W. pyrrhorhinos* reproducing even during long periods of water stress.

This author considered it a "hit or miss" strategy, in which females give birth whenever possible with the possibility that future conditions will allow their offspring to survive.

Continuous breeding is highly expensive energetically, since chances of offspring survival are low, but enables populations to endure harsh times and to respond even to a small amount of rainfall.

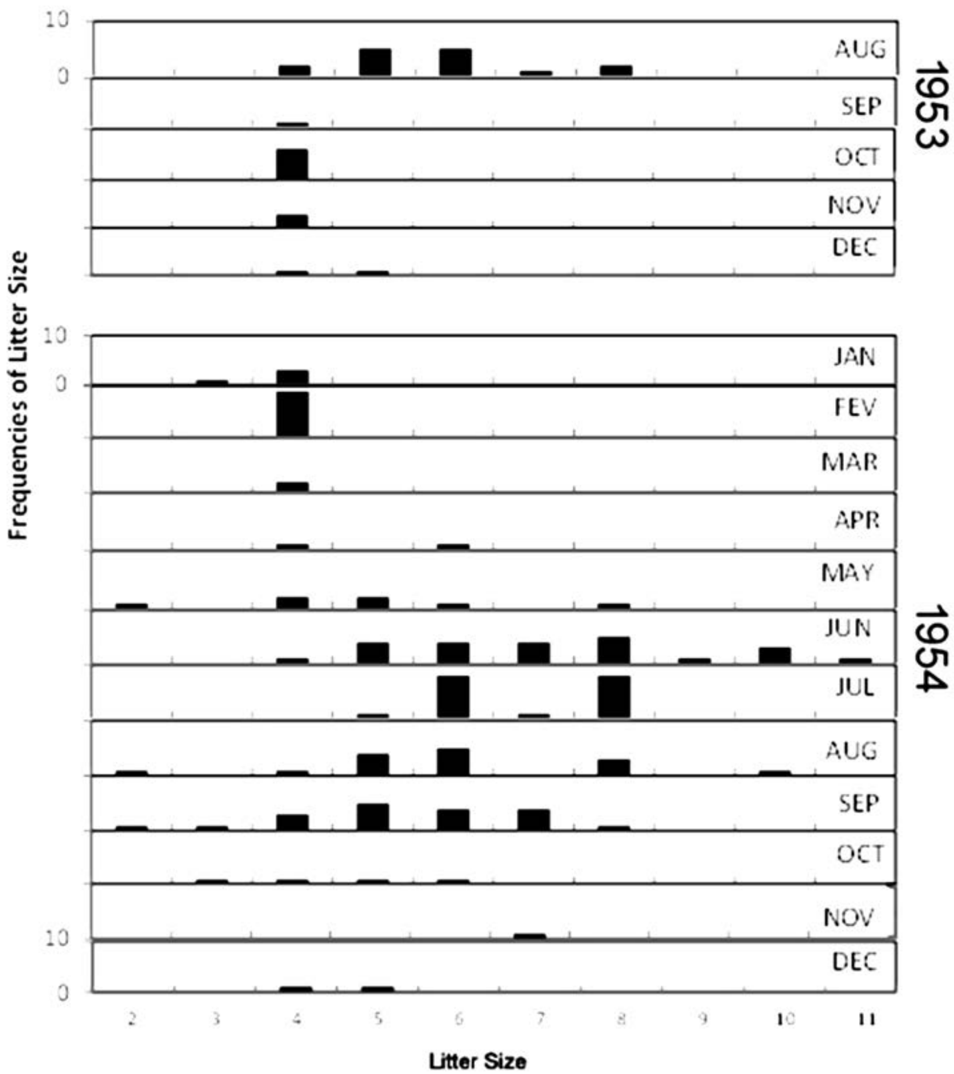

Figure 10. Monthly absolute frequencies of embryos in the uterus (range 2 to 11) of *Wiedomys pyrrhorhinos,* from August 1953 to December 1954 in Caruaru, Pernambuco, Brazil.

Litter size variation. Litter sizes ranged from 2 to 11 pups per litter, with mean 5.6 and mode 4 (Table 3). Moojen (1943) reported a mean litter of 5 embryos for *Wiedomys pyrrhorhinos* and Streilen (1982a) found a mean litter size of 3.8, ranging from 1 to

6. According to Lack (1948; 1954), the most frequent litter size is the most successful litter size. He also hypothesized that species have an optimum mean litter size and the surplus of individuals will probably perish, normally due to inadequate parental care.

Throughout the year, litter size was highly variable, reaching its greatest values (and averages) during the mid and late-wet season (June-August; Fig. 6). Higher means in litter size were in phase with higher proportions of pregnant females and with the age class 1 peak. Inter-season variation in litter size has been observed in other rodents (*Microtus,* Hamilton 1937; *Dicrostonyx,* Braestrup 1941). Lack (1954) associated such variation with better conditions to raise young, eventually favoring higher litter size means.

Table 3. Summarized reproductive data, by age class, of *Wiedomys pyrrhorhinos* from Caruaru, Pernambuco.

Age Class	2	3	4	5	6	7
Mean Litter Size	5.3	6.1	5.1	5.5	6.4	5.2
Most Frequent Litter Size	5	5	2	3	4	4 and 5
Range of Litter Size	2 to 8	4 to 10	4 to 11	2 to 10	3 to 10	2 to 8
Proportion of Pregnant Females	8%	19.7%	15.1%	28%	17.4%	11.6%

Rainfall, reproduction and population irruption. The monthly proportions of pregnant females closely followed the rainfall pattern, with the proportional peak occurring one to two months after the highest peak of rainfall. Monthly frequency of pregnant females and litter sizes were highly and positively correlated to the precipitation of the previous month, favoring an increase in population two months after the rainfall peak of May 1954.

The population peak occurred between September and November 1954, four to six months after the rainfall peak in May 1954 (Fig. 3). The question that arises is whether the peak recorded in 1954 represented the ordinary annual fluctuation of densities in the wild population of *W. pyrrhorhinos* in Caruaru, or constituted a true outbreak peak.

Boonstra (1994) proposed that over a cycle, a rodent population would be characterized by a shift in age structure from younger to older individuals during declines. He listed the following aspects that would indicate that the age structure would have changed: variation in length of the breeding season, replacement of the entire breeding population from one year to the next, and major changes in the age of sexual maturity over a cycle.

The age structure of the *Wiedomys pyrrhorhinos* population during the peak months (September – November, 1954) was primarily (nearly 80%) composed by young adults (age classes 2 and 3; Fig. 6). From September on, however, the pregnancy rates were very low, ceasing completely by January 1955, when around 60 % of the individuals belonged to age classes 4 to 7.

Pregnant females were recorded in all months between July 1953 and December 1954 (Fig. 7). It is possible that the rainfall recorded in November, 1953, and in January, 1954, in a period that otherwise was very dry in both years, was sufficient to support two closely-spaced breeding seasons, with the second one amplifying the effect of the first, leading to the outbreak recorded in September – November. Such a pattern has been observed for rodents in other parts of the world, and would explain outbreaks as resulting from favorable weather or food conditions for one or two seasons (Pearson 2002). In the present study, we restricted the analysis of possible determinants of the outbreak to the rainfall effects, which is traditionally regarded as the most important variable in arid and semi-arid regions (Bronson 1985; Streilein 1982c). This is in accordance with studies that have shown that precipitation can influence rodent population dynamics through primary production (Shenbrot and Krasnov 2001; Letnic and Dickman 2006).

Food accumulation favors fat accumulation which triggers reproduction (Frisch 1988). Havstad *et al*. (2006) and Whitford (2002) concluded that it also favors successful weaning of the young. In semi-arid ecosystems, like the Caatinga, after rainfall triggers germination, nutrients are abundant and females can expend energy in producing more pups per litter, as large litters demand greater energy expenditures during lactation (Mattingly and McClure 1982; Millar 1987; Glazier 1985).

Although the years of 1954 and 1955 (years of ENSO events, "La Niña") were not particularly rainy with respect to 30-year normals, the total rainfall for May 1954 was higher than average in spite of the previous three months of complete drought. It is possible that above average rainfall in this month may have produced an increase in primary production leading to the increase in the litter size of *Wiedomys pyrrhorhinos,* producing the outbreak recorded later in that year. Thus, in years in which ENSO actually raises rainfall above average, *W. pyrrhorhinos* might experience other outbreaks.

Acknowledgements

A preliminary version of this study was submitted as a monograph by G. Sobral in partial fulfillment of the requirements for a BSc. Degree in Biology at Universidade Federal do Rio de Janeiro. We thank committee members R. Cerqueira, D. Fernandes and L. Lorini for their critical reading of the monograph and for several suggestions that contributed to this article. We are also indebted to three anonymous referees and the editor for their critical reading of a previous version of this manuscript. The authors would like to thank C. Braga, L. Coutinho, A. Pavan, F. Carrasco, F. Caramaschi, L. Drummond, G. Guilhon, T. Miranda and S. M. Franco for their help with the digitalization of SNP file cards and with several aspects of this study. We are particularly grateful to C. Braga for discussions on the SNP sampling and for drawing the map in Figure 1. M. Castro kindly provided the Spanish translation of the abstract. We dedicate this work to the SNP collectors, especially to Abdias P. da Silva, whose effort in assembling the large collection of *Wiedomys* from Caruaru made this study possible. This study was supported by research fellowships from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) to J. A. Oliveira (processes 306935/2010-4 and 308271/2013-0) and by undergraduate (Programa Institucional de Bolsa de Iniciação Científica, Pibic/CNPq/UFRJ) and graduate (Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro, FAPERJ) fellowships to G. Sobral.

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Sometido: 19 de febrero de 2014
Revisado: 25 de mayo de 2014
Aceptado: 4 de junio de 2014
Editor asociado: Robert Owen
Diseño gráfico editorial: Gerardo Hernández

Appendix

Total number of hand collected specimens by year, by month and by site in the Caruaru region, number of days worked by month in each site, and mean number of specimens collected by day in each month and each site. Abbreviations: Faz.: Fazenda (=Farm), St.: Site.

Month/Site	Number of specimens collected	Number of days worked	Mean number of specimens collected by day
1954	**1725**		
JANUARY	**101**	**18**	**5.6**
Faz. Cajá de Preguiça	17	2	8.5
Faz. Serraria	7	2	3.5
St. Água Branca	21	2	10.5
St. Gravata Assu	13	5	4.3
St. Lagoa do Algodão	1	1	1
St. Maria Clara	4	1	4
St. Preguiça	25	4	6.3
St. Várzea da Picada	13	1	13
FEBRUARY	**138**	**21**	**6.6**
Faz. Angico	3	1	3
St. Campo Novo	9	1	9

Continue...

Month/Site	Number of specimens collected	Number of days worked	Mean number of specimens collected by day
St. Capim	8	2	4
St. Gravata Assu	19	2	8.5
St. Jacaré	2	1	2
St. Malhada das Caveiras	24	4	6
St. Maria Clara	24	2	12
St. Pitiá de Capim	6	2	3
St. Preguiça	8	1	8
St. Riachão de G. Ferreira	7	1	7
St. Várzea da Picada	11	1	11
St. Vasco	17	3	5.6
MARCH	**112**	**21**	**5.3**
Faz. Angico	3	1	3
Faz. Encruzilhada	13	1	13
St. Água Branca	13	1	13
St. Banana	1	1	1
St. Brejo Novo	1	1	1
St. Campo Novo	8	1	8
St. Capim	2	1	2
St. Gravata Assu	21	3	7
St. Lagoa de Pedra	10	2	5
St. Maria Clara	12	4	3
St. Preguiça	19	2	9.5
St. Terra Vermelha	4	2	2
St. Vasco	5	1	5
APRIL	**40**	**14**	**2.9**
Faz. Serraria	1	1	1
St. Água Branca	6	3	2
St. Capim	1	1	1
St. Capivara	1	1	1
St. Gravata Assu	1	1	1
St. Maria Clara	1	1	1
St. Olho D'água do Boi	10	2	5
St. Preguiça	8	2	4
St. Queimada do Uruçu	1	1	1
St. Vasco	10	1	10
MAY	**50**	**16**	**3.1**
Faz. Angico	8	3	2.6
St. Banana	2	1	2
St. Capim	1	1	1
St. Gravata Assu	20	5	4
St. Lagoa de Pedra	1	1	1
St. Maria Clara	1	1	1

Continue...

Continue...

Month/Site	Number of specimens collected	Number of days worked	Mean number of specimens collected by day
St. Preguiça	3	1	3
St. Serrote do Boi	2	1	2
St. Vasco	12	2	6
JUNE	**70**	**16**	**4.4**
Faz. Angico	3	1	3
St. Água Branca	8	1	8
St. Capim	17	3	5.6
St. Gravata Assu	18	3	6
St. Maria Clara	11	3	3.7
St. Serrote do Boi	5	1	5
St. Vasco	8	4	2
JULY	**119**	**22**	**5.4**
Faz. Igarlandia	4	1	4
St. Alto do Moura	12	3	4
St. Barra de Taquara	27	3	9
St. Capim	13	2	6.5
St. Gravata Assu	16	2	8
St. Maria Clara	8	2	4
St. Pitiá de Capim	12	3	4
St. Preguiça	1	1	1
St. Serrote do Boi	16	3	5.3
St. Várzea da Picada	6	1	6
St. Vasco	4	1	4
AUGUST	**146**	**19**	**7.7**
St. Capim	59	6	9.8
St. Chicuru	8	1	8
St. Gravata Assu	31	4	7.8
St. Maria Clara	29	5	5.8
St. Pitiá de Capim	12	2	6
St. Vasco	7	1	7
SEPTEMBER	**270**	**23**	**11.7**
Faz. Angico	8	1	8
St. Capim	34	3	11.3
St. Gravata Assu	214	16	13.4
St. Maria Clara	14	3	4.83
OCTOBER	**315**	**23**	**13.7**
St. Capim	151	11	13.7
St. Gravata Assu	15	1	15
St. Maria Clara	143	10	14.3
St. Serra da Quiteria	6	1	6
NOVEMBER	**232**	**20**	**11.6**

Continue...

Continue...

Month/Site	Number of specimens collected	Number of days worked	Mean number of specimens collected by day
St. Capim	186	17	10.9
St. Maria Clara	46	3	15.3
DECEMBER	**132**	**17**	**7.8**
St. Capim	132	17	7.8
1955	**281**		
JANUARY	**197**	**20**	**9.9**
St. Capim	32	4	8
St. Maria Clara	165	16	10.31
FEBRUARY	**84**	**9**	**9.3**
St. Campo De Sementeira	7	1	7
St. Maria Clara	77	8	9.6