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New records of rodent hosts for hard ticks in tropical forests of Yucatán, México: Implications for tick-borne diseases in human-modified landscapes

Nuevos registros de roedores como hospederos de garrapatas en bosques tropicales de Yucatán, México: Implicaciones para las enfermedades transmitidas por garrapatas en paisajes modificados

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Rodents serve as reservoirs for up to 85 zoonotic diseases, some of which can be transmitted by ticks. Ticks of the *Amblyomma* and *Ixodes* genera have been recognized to be associated with 4 rodent species in the Yucatán Peninsula, México. Here, we present new records of rodents acting as hosts for ticks of these genera in tropical forests of Yucatán. Between June 2021–March 2022, Sherman traps were used for rodent capture in the Biocultural State Reserve of Puuc, Yucatán, México. Twelve quadrants with 50 traps each were established in tropical forest sites with varying levels of anthropogenic intervention. Rodents were inspected for ectoparasites, and ticks were collected using entomological forceps and preserved in 70 % ethanol. We captured 160 individuals of 6 rodent species in 5,400 trap nights. The most captured species were *Heteromys gaumeri* (*n* = 60) and *Sigmodon toltecus* (*n* = 44), while the least represented were *Handleyomys rostratus* (*n* = 1). We retrieved 492 ticks, identifying *Amblyomma mixtum*, parasitizing *H. rostratus*, *H. gaumeri*, and *S. toltecus*; *Ixodes cf. Ixodes affinis* parasitizing *H. gaumeri* and *Ixodes* sp. parasitizing *S. toltecus*. We reported, for the first time in México, *H. rostratus* and *S. toltecus* as hosts for *Amblyomma mixtum*. Additionally, we present the first record of *Ixodes affinis* parasitizing *H. gaumeri* and *Ixodes* sp. parasitizing *S. toltecus* in the Yucatán Peninsula. The presence of tick vectors of zoonotic pathogens among rodent reservoirs reflects a latent risk to humans and domestic animals in the region.

Key words: *Amblyomma mixtum*; ectoparasite; *Ixodes*; Maya Forest; pathogens; small mammals; vectors; zoonoses.

Los roedores son reservorios de hasta 85 patógenos zoonóticos, algunos transmitidos por garrapatas. En la Península de Yucatán, México, garrapatas de los géneros *Amblyomma* e *Ixodes* están asociadas a 4 especies de roedores. Aquí presentamos nuevos registros de roedores hospederos para garrapatas de estos géneros en Yucatán. Entre junio 2021–marzo 2022, se utilizaron trampas Sherman para la captura de roedores en la Reserva Estatal Biocultural del Puuc, Yucatán, México. Se establecieron 12 cuadrantes de 50 trampas en sitios con diferente nivel de intervención antrópica. Los roedores fueron inspeccionados por ectoparásitos y las garrapatas fueron colectadas usando pinzas entomológicas y preservadas en etanol al 70 %. Capturamos 160 individuos de 6 especies de roedores en 5,400 noches/trampa. Las especies más capturadas fueron *Heteromys gaumeri* (*n* = 60) y *Sigmodon toltecus* (*n* = 44), y la menos representada fue *Handleyomys rostratus* (*n* = 1). Recuperamos 492 garrapatas identificando a *Amblyomma mixtum*, parasitando a *H. rostratus*, *H. gaumeri* y *S. toltecus*; *Ixodes cf. Ixodes affinis*, parasitando a *H. gaumeri* e *Ixodes* sp. parasitando a *S. toltecus*. Reportamos, por primera vez en México, a *H. rostratus* y *S. toltecus* como hospederos de garrapatas de *Amblyomma mixtum*, y el primer registro de *Ixodes* cf. *Ixodes affinis* en *H. gaumeri* e *Ixodes* sp. en *S. toltecus* en la Península de Yucatán. La presencia de garrapatas vectores de patógenos zoonóticos entre roedores reservorios refleja el riesgo latente de propagación de enfermedades hacia el ser humano y sus animales domésticos en la región.

Palabras clave: *Amblyomma*; ectoparásito; *Ixodes*; patógenos; pequeños mamíferos; Selva Maya; vectores; zoonosis.

Rodents constitute the most diverse and abundant order of mammals globally, with at least 2,680 species grouped into 35 families and 535 genera (Burgin *et al.* 2018; ASM 2023). This group of organisms is involved in the highest number of zoonoses compared to any other order of terrestrial mammals, as approximately 10 % of rodent species can harbor and transmit various zoonotic pathogens of public health significance (Han *et al.* 2015; Rabiee *et al.* 2018). Worldwide, it is estimated that 244 rodent species can act as reservoirs or hosts for up to 85 zoonotic diseases. In the case of the Americas, specifically in the Neotropical region, 130 rodent species, from 56 genera and 12 families, have been identified as confirmed reservoirs or hosts for 31 zoonoses caused by viruses, bacteria, helminths, and protozoa (Han *et al.* 2016; Rabiee *et al.* 2018; Ibarra-Cerdeña *et al.* 2024).

The transmission of zoonotic diseases can occur through direct or indirect pathways. Direct transmission occurs through contact with the saliva, feces, or urine of rodents or by consuming contaminated water or food (Meerburg *et al.* 2009; Battersby 2015). On the other hand, indirect transmission occurs through the bite of arthropod ectoparasite vectors (*i.e.*, mites, ticks, fleas), which previously fed on the blood of infected rodents (Meerburg *et al.* 2009; Himsworth *et al.* 2013; Selmi *et al.* 2021). Zoonotic diseases with the highest number of rodent hosts are precisely those transmitted indirectly by vectors (Ibarra-Cerdeña *et al.* 2024).

Ticks (Acari: Ixodidae) are hematophagous ectoparasites of terrestrial vertebrates that constitute the second most important group of vectors in the transmission of diseases to humans worldwide, second only to mosquitoes (de la Fuente *et al.* 2008). Diseases transmitted by ticks associated with rodents include Crimean-Congo hemorrhagic fever (Földes *et al.* 2019), caused by viruses; rickettsioses (Sosa-Gutiérrez *et al.* 2016; Helminiak *et al.* 2022), Lyme disease (Krawczyk *et al.* 2020), anaplasmosis (Clark 2012), bartonellosis (Silaghi *et al.* 2016; Schulte Fischedick *et al.* 2016), Q fever, and tularemia (Bártová *et al.* 2020), all bacterial infections; and babesiosis (Obiegala *et al.* 2015), caused by protozoa.

In México, on the Yucatán Peninsula, comprising the states of Campeche, Quintana Roo, and Yucatán, 2 genera of ticks have been recorded on 4 rodent species (Light *et al.* 2020). *Amblyomma* ticks (Koch, 1844) have been found parasitizing Gaumer's spiny pocket mouse (*Heteromys gaumeri* Allen and Chapman, 1897) in the state of Yucatán (Guzmán-Cornejo *et al.* 2011). On the other hand, *Ixodes* ticks (Latreille, 1795) have been found on the big-eared climbing rat (*Ototylomys phyllotis* Merriam, 1901) and the Yucatán deer mouse (*Peromyscus yucatanicus* Allen and Chapman, 1897) in the state of Yucatán (Hoffmann *et al.* 1989; Whitaker and Morales-Malacara 2005) and in Campeche on Gaumer's spiny pocket mouse and the Toltec cotton rat (*Sigmodon toltecus* Saussure, 1860; Ceballos 2014; Light *et al.* 2020). However, knowledge about the ectoparasites associated with the 15 species of small rodents distributed across different habitat types in the Yucatán Peninsula region (Zaragoza-Quintana *et al.* 2016) is still limited. Therefore, our objective in this study was to present new records of rodents acting as hosts for ticks in the tropical forests of Yucatán.

The study was conducted in the central part of the protected area known as the Biocultural State Reserve of Puuc, in the southwestern region of Yucatán, with coordinates ranging from 19° 51' 33.92" – 20° 23' 24.16" N, and 89° 10' 30.42" – 89° 52' 30.12" W (Figure 1). The reserve covers an area of 1,358.49 km² and includes portions of the municipalities of Muna, Santa Elena, Oxkutzcab, Tekax, and Ticul (DOF 2011; INEGI 2017). The main types of vegetation include deciduous lowland forest, deciduous midland forest, and semi-deciduous midland forest (Rzedowski 2006; Essens and Hernández-Stefanoni 2013). These vegetation types are characterized by 50–70 % of tree species losing their foliage during the dry season, from November to April (Flores-Guido and Espejel-Carvajal 1994). The landscape consists of a mosaic of patches of the main vegetation types in different successional stages (anthropogenic impact) following traditional agricultural use (Dupuy *et al.* 2012). The climate in the study area is tropical subhumid with summer rainfall (Aw1), with an average annual temperature of 26 °C and annual precipitation ranging between 900–1100 mm (Flores-Guido and Espejel-Carvajal 1994; Orellana *et al.* 2009).

Between June 2021 and March 2022, Sherman box traps (Tallahassee, Florida) baited with a mixture of oat flakes and vanilla (Krebs 2006) were used for rodent capture in the study area (Figure 1). Three habitat types with different levels of anthropogenic intervention were considered, including mature/conserved forest, secondary/regenerative forest (without human intervention for ≥ 30 years), and agricultural crop sites. In each habitat type, 4 quadrants of 5 x 10 traps were established, with a separation of 10 m between them. Each quadrant was active for 3 consecutive nights during 3 sampling seasons: humid (October-November), sub-humid (June-July) and dry (February-March).

Captured rodents were identified using specialized keys (Reid 2009; Álvarez-Castañeda *et al.* 2017). As part of an alternate study focused on detection of zoonotic pathogens (bacteria and viruses), captured rodents were anesthetized with isoflurane (Sofloran Vet©) and euthanized by either cervical dislocation or overdose of sodium pentobarbital (Pisabental©) via intracardiac injection (AVMA 2020).

During anesthesia, sex, age, reproductive condition, and conventional body measurements (weight, total length, length of tail, foot, and ear) were obtained for each captured individual (Panti-May *et al.* 2012). Additionally, captured rodents were inspected for ectoparasites. Ticks were removed and collected using fine-tipped entomological forceps and preserved in 70 % ethanol. In the laboratory, we classified the life stage of collected ticks and identified adult individuals following the specialized taxonomic keys of Dantas-Torres *et al.* (2019), Guzmán-Cornejo *et al.* (2019), and Nava *et al.* (2019). Subsequently, we calculated the mean intensity of infection (MI) for each rodent species,

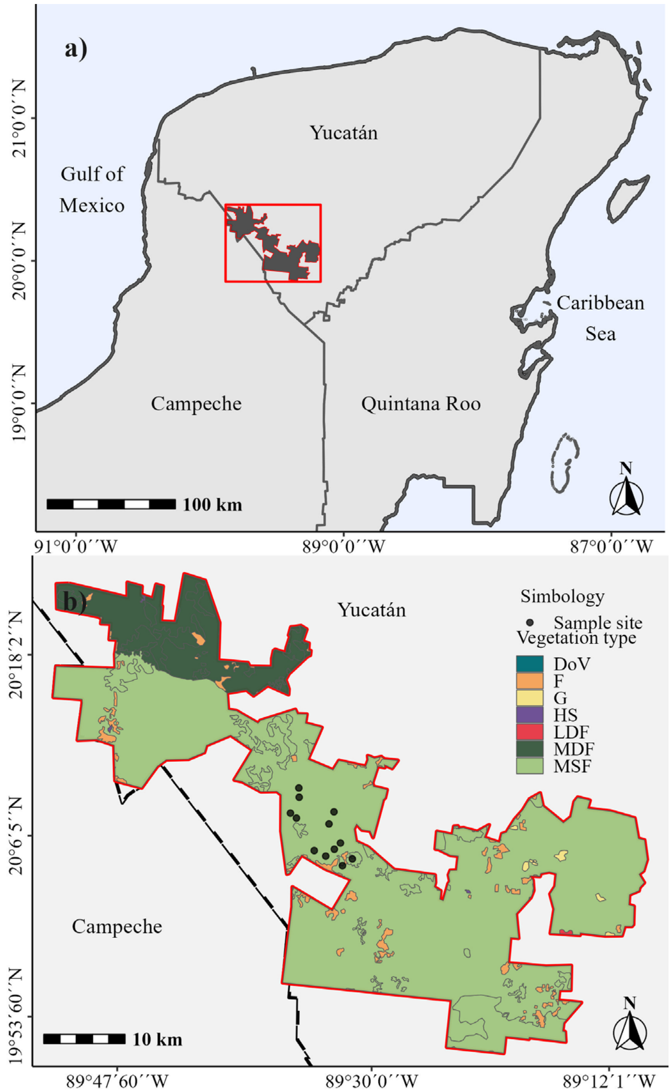

Figure 1. a) Macro-location of the study area in the central part of the Biocultural State Reserve of Puuc, on the Yucatán Peninsula, México and b) spatial location of the trapping sites with Sherman traps (black circles) within the reserve polygon (red line). In the figure, we depict the state division (dotted line) and vegetation types based on publicly available information on Land Use and Vegetation (s VII) from the National Institute of Statistics and Geography (INEGI), accessible for free at https://www.inegi.org.mx/temas/usosuelo/#Descargas. The land use and vegetation types are described as follows: DoV, Area devoid of vegetation; F, Farmland; G, Grasslands; HS, Human settlements; LDF, Low deciduous forest; MDF, Tropical medium deciduous forest; MSF, Tropical medium subdeciduous forest.

defined as the total number of a tick species divided by the number of infected hosts, and the tick infestation prevalence as the proportion of infected hosts, with one or more individuals of a particular tick species, divided by the number of examined hosts and multiplied by 100 to express it as a percentage (Bush *et al.* 1997).

The rodent hosts specimens and their parasites were deposited in the Mammal (CINMMC 404–564) and Parasite collections (CINMPC 1404–1564), respectively, of the Departamento de Ecología Humana of the Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV) Unidad Mérida (Yucatán, México).

During the physical containment and manipulation of organisms, we followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research and education (Sikes *et al.* 2016) and the procedure indicated by the American Veterinary Medical Association (Underwood *et al.* 2013; AVMA 2020). Specimen collections were done under collecting permit number SGPA/DGVS/3941/19, issued by the General Direction of Wildlife of México under the name of C. N. Ibarra-Cerdeña.

We achieved a sampling effort of 5,400 trap nights and captured 160 rodents, representing 3 families, 6 genera, and 6 species (Table 1). The most frequently captured rodent was Gaumer's spiny pocket mouse (*H. gaumeri*, *n* = 60), followed by the Toltec cotton rat (*S. toltecus*, *n* = 44), the big-eared climbing rat (*O. phyllotis*, *n* = 27), and the house mouse (*Mus musculus*, *n* = 26). The least represented species were the pygmy rice rat (*Oligoryzomys fulvescens, n* = 2) and the big-eared harvest mouse (*Handleyomys rostratus*, *n* = 1). Considering the habitat type, farmland sites accounted for 56.9 % (*n* = 91) of captures, followed by preserved forest sites (23.1 %, *n* = 37), and secondary forest (20.0 %, *n* = 32). The species *H. rostratus* was only present in preserved forest, while *M. musculus* was only captured in farmland sites. On the other hand, *H. gaumeri* and *S. toltecus* were present in all habitat categories, although the highest number of *S. toltecus* captures (*n* = 41) occurred in farmland sites (Table 1).

Table 1. Overall number of rodent captures (*N*) and by habitat condition, as well as the number of host individuals infested (*n*) by larvae and adult ticks (Acari: Ixodidae), their infestation prevalence, and mean intensity of infection (MI) in tropical forests in southern Yucatán, México. The prevalence value, estimated as prevalence = (*n*/*N*)*100, is expressed as a percentage and denoted in parentheses. * First record of this rodent species as a host for *Amblyomma* ticks in México; + First record of this rodent species as a host for *Ixodes* sp. ticks in the Yucatán Peninsula.

		Tropical forest condition				**Number of individuals infested (*n*) by ticks (prevalence %)**			**Mean intensity of infection (MI)**		
Family	**Species**	**Preserved**	**Regenerative**	**Farmland**	**Total (*N*)**	**Larvae**	***Amblyomma mixtum***	***Ixodes***	**Larvae**	***Amblyomma mixtum***	***Ixodes***
Heteromyidae	*Heteromys gaumeri*	23	14	23	60	34 (56.7)	5 (8.3)	6 (10.0)+	4.0	1.4	1.0
Cricetidae	*Handleyomys rostratus*	1	-	-	1	1 (100)	1 (100)*	-	2.0	1.0	-
	Oligoryzomys fulvescens	-	1	1	2	2 (100)	-	-	1.5	-	-
	Sigmodon toltecus	1	2	41	44	37 (84.1)	6 (13.6)*	13 (29.5)+	5.7	1.5	2.6
	Ototylomys phyllotis	12	15	-	27	15 (55.6)	-	-	5.5	-	-
Muridae	*Mus musculus*	-	-	26	26	5 (19.2)	-	-	1.0	-	-

We collected 492 ticks from the 160 captured rodents. In 3 rodent species, we only recovered (*n* = 91) ticks in immature stages: *M. musculus*, *O. fulvescens*, and *O. phyllotis*. No nymph-stage ticks were found, and larvae represented 89 % (*n* = 438) of all the collections. The infestation by larvae was found in all 6 species of captured rodents and the prevalence of tick larvae infection in rodents was 58.8 % (Table 1). The highest prevalence values were for *O. fulvescens* and *H. rostratus* (100 %, both), followed for *S. toltecus* (84.1 %), *H. gaumeri* (56.7 %), and *O. phyllotis* (55.6 %). Meanwhile the lowest prevalence value was for *M. musculus* (19.2 %). The 3 species with the highest mean intensity of infection were *S. toltecus* (MI = 5.7), *O. phyllotis* (MI = 5.5), and *H. gaumeri* (MI = 4.0; Table 1).

On the other hand, the adult ticks, all females, represented 11 % (*n* = 54) of all the collections. Among adult ticks, we identified *A. mixtum* (*n* = 17), parasitizing *H. rostratus*, *H. gaumeri*, and *S. toltecus*; and *Ixodes cf. Ixodes affinis* (*n* = 37), parasitizing *H. gaumeri* and *Ixodes* sp. parasitizing *S. toltecus* (Figure 2). The infection prevalence for *A. mixtum* was 100 % for *H. rostratus*, 13.6 % for *S. toltecus*, and 8.3 % for *H. gaumeri*; for *Ixodes* ticks, the prevalence was 27.3 % for *S. toltecus* and 10.0 % for *H. gaumeri* (Table 1). The mean intensity of infection by ticks of *A. mixtum* was MI = 1.5 for *S. toltecus*, MI = 1.4 for *H. gaumeri*, and MI = 1.0 for *H. rostratus*. Meanwhile, the mean intensity by ticks of *Ixodes* sp. was MI = 2.6 for *S. toltecus* and *Ixodes cf. Ixodes affinis* MI = 1.0 for *H. gaumeri* (Table 1).

According to the habitat condition, no pattern was found regarding the prevalence of tick infestation in any of the stages (Table 2). However, the mean intensity of infection observed in *A. mixtum* for *H. gaumeri* (MI = 3.0) and *Ixodes* sp. for *S. toltecus* (MI = 2.6) were higher when compared with preserved and secondary forests. Mean intensity of infection, considering larval ticks, showed that the higher value occurred in regenerative forests for *O. phyllotis* (MI = 7.0) as well as in farmland for *S. toltecus* (MI = 6.0; Table 2). On the other hand, no apparent pattern was found that related tick infestation according to seasonal variation (Table 3).

The presence of *Amblyomma* ticks on *Heteromys gaumeri* has been previously documented in the state of Yucatán at the genus level, but the species was not identified (Guzmán-Cornejo *et al.* 2011; Light *et al.* 2020). In this study, we identified the species *Amblyomma mixtum* on *H. gaumeri*, and for the first time, we report the genus *Amblyomma* for *H. rostratus* and *S. toltecus*, specifically identifying *Amblyomma mixtum* on these species as well. *Amblyomma mixtum* is a generalist tick species widely distributed throughout North América and northern South América (Aguilar-Domínguez *et al.* 2021). Other *Amblyomma* species collected from rodents in Yucatán include *Amblyomma maculatum*, previously documented on the agouti (*Cuniculus paca*; Arana-Guardia *et al.* 2015) and in *Handleyomys* in Tabasco (Light *et al.* 2020). These ticks are also known to feed on dogs, equines, opossum and bovines (Rodríguez-Vivas *et al.* 2016; Dzul-Rosado et al. 2021; García-Rejón *et al.* 2021). Additionally, *Ambly-*

Table 2. Prevalence and mean intensity of tick (Acari: Ixodidae) infestation in rodents according to habitat conditions in tropical forests of southern Yucatán, México. The prevalence value, calculated as prevalence = (n/N) * 100, is expressed as a percentage and denoted in parentheses.

		Number of individuals infested (*n*) by ticks (prevalence %)			**Mean intensity of infection (MI)**		
Tropical forest condition	**Species**	**Larvae**	***Amblyomma mixtum***	***Ixodes***	**Larvae**	***Amblyomma* mixtum**	***Ixodes***
Preserved	*Heteromys gaumeri*	13 (56.5)	2 (8.7)	3 (13.0)	5.1	1.0	1.0
	Handleyomys rostratus	1 (100)	1 (100)	-	2.0	1.0	-
	Oligoryzomys fulvescens	-	-	-	-	-	-
	Sigmodon toltecus	1 (100)	-	-	1.0	-	-
	Ototylomys phyllotis	6 (50.0)	-	-	3.3	-	-
	Mus musculus	-	-	-	-	-	-
Regenerative	*Heteromys gaumeri*	8 (57.1)	2 (14.3)	1 (7.1)	1.4	1.0	1.0
	Handleyomys rostratus	-	-	-	-	-	-
	Oligoryzomys fulvescens	1 (100)	-	-	2.0	-	-
	Sigmodon toltecus	2 (100)	-	1 (50.0)	2.0	-	3.0
	Ototylomys phyllotis	9 (60.0)	-	-	7.0	-	-
	Mus musculus	-	-	-	-	-	-
Farmland	*Heteromys gaumeri*	13 (56.5)	1 (4.3)	1 (4.3)	4.5	3.0	1.0
	Handleyomys rostratus	-	-	-	-	-	-
	Oligoryzomys fulvescens	1 (100)	-	-	1.0	-	-
	Sigmodon toltecus	34 (82.9)	6 (14.6)	11 (26.8)	6.0	1.5	2.6
	Ototylomys phyllotis	-	-	-	-	-	-
	Mus musculus	5 (19.2)	-	-	1.0	-	-

omma inornatum has been reported on *Sigmodon* rodents in Durango and Guerrero (Light *et al.* 2020) and on various wildlife species in the state of Yucatán (Arana-Guardia *et al.* 2015; García-Rejón *et al.* 2021; López-Pérez *et al.* 2022).

Amblyomma ticks are important vectors of pathogens of zoonotic diseases as carriers of bacteria of the genera *Anaplasma*, *Ehrlichia*, and *Rickettsia* (Trout-Fryxell *et al.* 2017; Rochlin and Toledo 2020; Lippi *et al.* 2021). In Yucatán, *Rickettsia felis* has been reported in 6 rodent species, including *H. gaumeri* and *S. toltecus* (Panti-May *et al.* 2015). The first reports of human cases of spotted fever attributed to *R. felis* were diagnosed in Yucatán (Zavala-Velazquez *et al.* 2000). Similarly, wildlife with tick infestations has been found to be infected with rickettsias in various municipalities of Yucatán (Ojeda-Chi *et al.* 2019; Canto-Osorio *et al.* 2020).

In the case of *Ixodes* ticks, our findings represent the first records of these ticks in Yucatán, identifying 2 species: *Ixodes* cf. *Ixodes affinis* on *H. gaumeri* and an unidentified species, *Ixodes* sp., on *S. toltecus*. Within the Yucatán Peninsula, the presence of the genera *Ixodes* has been previously recognized in both host species only in the state of Campeche (Ceballos 2014; Light *et al.* 2020). In México, *Ixodes eadsi* and *Ixodes sinaloa* have been reported parasitizing rodents of the family Heteromyidae (Guzmán-Cornejo *et al.* 2023), and *Ixodes minor* has been reported on rodents of the genus *Sigmodon* (Light *et al.* 2020).

Ixodes ticks are known to harbor pathogens of the genera *Anaplasma*, *Borrelia*, *Ehrlichia*, *Coxiella*, *Babesia*, and *Rickettsia* (Biggs *et al.* 2016; Rochlin and Toledo 2020; Moraga-Fernández *et al.* 2023). Notably, *Ixodes* cf. *Ixodes affinis*, the tick species we collected on *H. gaumeri*, has been found infected with *Rickettsia* sp. *cf. Rickettsia monacensis* on a white-tailed deer in Campeche, México. This bacterium is a member of the Spotted Fever Group described in the Old World and is considered pathogenic to humans (Sánchez-Montes *et al.* 2021). In another study, *Ixodes affinis* was found infected with a *Rickettsia endosymbiont* on a hunting dog (Dzul-Rosado *et al.* 2023). These 2 studies highlight the significance of *Ixodes cf. Ixodes affinis* as a vector of *Rickettsia*, with the potential to amplify the transmission of disease agents between different hosts at the wildlife-domestic interface in human-modified landscapes.

Additionally, rodents harbor several bacteria that use ticks as vectors. In the Yucatán Peninsula, *Borrelia burgdorferi s.l.*, the etiological agent of Lyme disease, has been reported in several rodent species: in the state of Quintana Roo, it has been described in *H. gaumeri* (Rodríguez-Rojas *et al.* 2020), and in Yucatán, in synanthropic species *M. musculus* and the black rat (*Rattus rattus*; Solís-Hernández *et al.* 2016). In Yucatán, cases of babesiosis in children attributed to *Babesia microti* have been detected (Peniche-Lara *et al.* 2018), whose competent reservoir is the white-footed mouse (*Peromyscus leucopus*; Hersh *et al.* 2012), a species native to the Yucatán Peninsula (Zaragoza-Quintana *et al.* 2016).

In the present study, tick infestation in the larval stage was observed in all 6 host rodent species. Small mammals are considered an important group for feeding tick larvae (Lindsø

Table 3. Prevalence and mean intensity of tick (Acari: Ixodidae) infestation in rodents according to habitat seasonality in tropical forests of southern Yucatán, México. The prevalence value, calculated as prevalence = (n/N) * 100, is expressed as a percentage and denoted in parentheses.

			Number of individuals infested (*n*) by ticks (prevalence %)			**Mean intensity of infection (MI)**		
Season	**Species**	**Captured (*N*)**	**Larvae**	***Amblyomma mixtum***	***Ixodes***	**Larvae**	***Amblyomma mixtum***	***Ixodes***
Humid	*Heteromys gaumeri*	17	14 (82.4)	1 (5.8)	2 (11.7)	2.2	1.0	1.0
(Oct–Nov)	*Handleyomys rostratus*	-	-	-	-	-	-	-
	Oligoryzomys fulvescens	2	2 (100)	-	-	1.5	-	-
	Sigmodon toltecus	10	8 (80.0)	4 (40.0)	1 (10.0)	6.0	1.3	1.0
	Ototylomys phyllotis	8	4 (50.0)	-	-	1.5	-	-
	Mus musculus	4	1 (25.0)	-	-	1.0	-	-
Sub-humid	*Heteromys gaumeri*	20	5 (25.0)	1 (5.0)	2 (10.0)	8.8	1.0	1.0
(Jun–Jul)	*Handleyomys rostratus*	-	-	-	-	-	-	-
	Oligoryzomys fulvescens	-	-	-	-	-	-	-
	Sigmodon toltecus	17	15 (88.2)	-	9 (52.9)	4.4	-	3.0
	Ototylomys phyllotis	6	5 (83.3)	-	-	10.2	-	-
	Mus musculus	18	5 (27.8)	-	-	1.0	-	-
Dry	*Heteromys gaumeri*	23	15 (65.2)	3 (13.0)	2 (8.7)	4.1	1.7	1.0
(Feb–Mar)	*Handleyomys rostratus*	1	1 (100)	1 (100)	-	2.0	1.0	-
	Oligoryzomys fulvescens	-	-	-	-	-	-	-
	Sigmodon toltecus	17	14 (82.4)	2 (11.7)	2 (11.7)	6.8	2.0	1.5
	Ototylomys phyllotis	13	6 (46.2)	-	-	4.3	-	-
	Mus musculus	4	2 (50.0)	-	-	1.0	-	-

et al. 2023), as larvae commonly feed on wild rodents, unlike adult ticks that tend to prefer larger mammals (Paziewska *et al.* 2010; Esser *et al.* 2016). Additionally, the contribution of pathogens from rodents to the infection of larvae has been documented. For instance, in Europe, it was found that 89.0 % of *Ixodes ricinus* larvae infected with *Borrelia burgdorferi s.l.* had fed on rodents (Hofmeester *et al.* 2016).

Land use change was related to a higher mean intensity of infection for *A. mixtum* and larvae. Ticks are susceptible to the climatic conditions of their habitat, although susceptibility to temperature and desiccation can vary according to species and stage (Needham and Teel 1991). Ticks of the genus *Ixodes*, such as *Ixodes scapularis*, have low tolerance to desiccation and tend to be more present in forested habitats and thickets with dense vegetation. In contrast, *Amblyomma americanum* has generalist habits that allow it to occupy grassland habitats and environments subject to human disturbance (Diuk-Wasser *et al.* 2021; Mathisson *et al.* 2021).

The specificity patterns of each tick species could explain the higher intensity of infection by *A. mixtum* in disturbed habitats and the lower infestation by *Ixodes*. Immature stage ticks, like larvae, feed opportunistically (Esser *et al.* 2016). Therefore, we attribute the high mean intensity of infection found in this host to the high dominance and competitiveness of *Sigmodon* rats in farmlands (Cruz *et al.* 2010), as well as their higher capture rate in these conditions.

The variability in tick infestation according to seasonality appears to be influenced by the specificity of each species and the stage of the ticks. We recognize that an annual sampling design, coupled with more detailed identification of individuals (Randolph 1975; Kollars *et al.* 2000), could provide more robust results and clarify the specific patterns of each group, as well as the relationships between hosts.

Our results represent the first record of *H. rostratus* and *S. toltecus* as hosts of any *Amblyomma* species in México, and the first report of any *Ixodes* species on *H. gaumeri* and *S. toltecus* in the Yucatán Peninsula. The presence of vector ticks and the circulation of zoonotic pathogens among reservoir rodents reflect a latent risk of disease spread to humans and domestic animals in the region, making it a significant public and animal health concern. This risk may be exacerbated by the fact that both *H. gaumeri* and *S. toltecus* are predominantly found in human-modified landscapes, inhabiting agricultural areas and even rural households and backyards associated with secondary forests, where contact between rodent ectoparasites and humans is possible (Cimé-Pool *et al.* 2007; López-Cancino *et al.* 2015; Peniche-Lara *et al.* 2015; Panti-May *et al.* 2015, 2018; Canché-Pool *et al.* 2022).

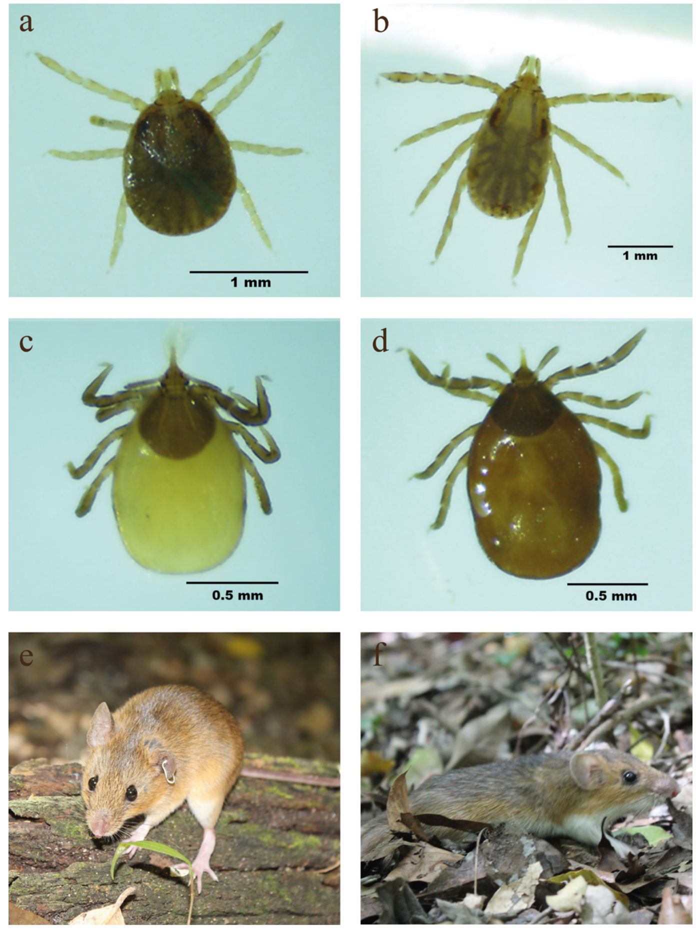

Figure 2. Female ticks (Acari: Ixodidae), adults, collected on rodent hosts in tropical forests of Yucatán, México: a) *Amblyomma mixtum* on *Heteromys gaumeri*; b) *Amblyomma mixtum* on *Handleyomys rostratus*; c) *Ixodes cf. Ixodes affinis* on *H. gaumeri*; d) *Ixodes* sp. on *Sigmodon toltecus*. Two rodent hosts in the study area: e) *Handleyomys rostratus* and f) *Heteromys gaumeri*. Images available at cibarra@cinvestav.mx.

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