



Universidade de São Paulo

Biblioteca Digital da Produção Intelectual - BDPI

Departamento de Medicina Veterinária Prevenção e Saúde Animal Artigos e Materiais de Revistas Científicas - FMVZ/VPS
- FMVZ/VPS

2012

Ecological implications on the aggregation of *Amblyomma fuscum* (Acari: Ixodidae) on *Thrichomys laurentius* (Rodentia: Echimyidae), in northeastern Brazil

EXPERIMENTAL AND APPLIED ACAROLOGY, DORDRECHT, v. 57, n. 1, pp. 83-90, MAY, 2012
<http://www.producao.usp.br/handle/BDPI/42337>

Downloaded from: Biblioteca Digital da Produção Intelectual - BDPI, Universidade de São Paulo

Ecological implications on the aggregation of *Amblyomma fuscum* (Acari: Ixodidae) on *Thrichomys laurentius* (Rodentia: Echimyidae), in northeastern Brazil

Filipe Martins Aléssio · Filipe Dantas-Torres · Daniel Barreto Siqueira · Marie-Hélène Lizée · Maria Fernanda Vianna Marvulo · Thiago Fernandes Martins · Marcelo Bahia Labruna · Jean Carlos Ramos Silva · Jean-François Mauffrey

Received: 29 September 2011 / Accepted: 4 February 2012 / Published online: 19 February 2012
© Springer Science+Business Media B.V. 2012

Abstract We investigated the *Amblyomma fuscum* load on a pullulating wild rodent population and the environmental and biological factors influencing the tick load on the hosts. One hundred and three individuals of *Thrichomys laurentius* were caught in an Atlantic forest fragment in northeastern Brazil, as part of a longitudinal survey on ticks infesting non-volant small mammals. Ticks ($n = 342$) were found on 45 individuals and the overall mean intensity of infestation was 7.6 ticks per infested rodent. Ticks were highly aggregated in the host population and the negative binomial distribution model provides a statistically satisfactory fit. The aggregated distribution was influenced by sex and age of the host. The microhabitat preference by *T. laurentius* probably increases contact opportunities between hosts and aggregated infesting stages of the ticks and represents important clues about the habitat suitability for *A. fuscum*.

F. M. Aléssio (✉) · M.-H. Lizée · J.-F. Mauffrey
Laboratoire Population Environnement Développement, Université de Provence,
Case 10, 13331 Cedex 3, Marseille, France
e-mail: filipe.aleccio@gmail.com

F. Dantas-Torres
Dipartimento di Sanità Pubblica e Zootecnia, Facoltà di Medicina Veterinaria, Università degli Studi di Bari, Str. Prov. per Casamassima km 3, 70010 Valenzano, Bari, Italy
e-mail: f.dantastorres@veterinaria.uniba.it

D. B. Siqueira · J. C. R. Silva
Departamento de Medicina Veterinária, Universidade Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros, s/n Dois Irmãos, Recife, PE 52171-900, Brazil

M. F. V. Marvulo
Instituto Brasileiro para Medicina da Conservação—Tríade, Rio de Janeiro, RJ, Brazil

T. F. Martins · M. B. Labruna
Departamento de Medicina Veterinária Preventiva e Saúde Animal, Universidade de São Paulo, Av. Prof. Orlando Marques de Paiva, 87, Cidade Universitária São Paulo, São Paulo, SP 05508-270, Brazil

Keywords Ticks · Aggregation · Negative binomial distribution · Atlantic Forest

Introduction

Tick-host associations are driven by complex ecological interactions and tick load dynamic is explained by complementary factors (Brunner and Ostfeld 2008), such as tick life history traits (Daniels and Fish 1990), host sex and age (Zuk and McKean 1996), host behavior (Ostfeld et al. 1996a), and climate conditions (Randolph and Storey 1999). Habitat structure (e.g., vegetation heterogeneity and complexity), also influence tick distribution patterns (Schulze and Jordan 2005). Host species diversity, abundance and distribution are also related to habitat features (August 1983). As vegetation structure is crucial for tick survival and development, habitat suitability for ticks might indirectly be estimated by infested host capture (Guerra et al. 2002).

In this work, we detailed the ecological relationships between the immature stages of the tick *Amblyomma fuscum* and the rodent *Thrichomys laurentius*, the most abundant tick and rodent species of a longitudinal survey on ticks infesting non-volant small mammals in six Atlantic Forest fragments in the Metropolitan Region of Recife, north-eastern Brazil, conducted from December 2007 to March 2009 (Dantas-Torres et al. 2012). In particular, our aims were to evaluate the tick load on this rodent species and to understand the environmental or biological factors influencing the tick load on it.

Materials and methods

We selected data obtained in one of the six Atlantic Forest fragments included in the aforementioned study (Dantas-Torres et al. 2012), i.e., the Estação Ecológica de Tapacurá (8°2'12.48"S, 35°11'41.12"W), a 382 ha Atlantic Forest reserve located in the municipality of São Lourenço da Mata. The climate of this area is tropical and humid, with a mild dry season from September to February. The native vegetation, which surrounds the dam of the Tapacurá River (394 ha), is typical of the Atlantic Forest (Andrade and Rodal 2004). The landscape mosaic around this seasonal semi-deciduous forest fragment is composed basically by subsistence farming and sugar cane monoculture.

In the study area, four missions of five consecutive trapping nights were conducted every 3 months, in March, June, September and December. Animals were captured (license ICMBio/SISBIO, n° 11854-1 and n° 11854-2) by living traps established in four transects of 20 trapping stations each. Ticks were collected manually and directly placed into vials (individualized per host) containing 70% ethanol.

Microhabitat characterization and structure is adapted from Freitas et al. (2002) and Pardini et al. (2005). Habitat characterization was based on 7 variables explained in Table 1 (Freitas et al. 2002). In each trapping station, variables were measured on 5 points of a 36 m², the center and the cardinal points. At each point, plant, litter, rock and canopy were measured using a square wooden frame (50 × 50 cm) divided into 100 open wire meshed squares. OBSTR 1, 2, and 3 were measured with the frame held vertically at 3 heights (0.5, 1, and 1.5 m), as the observer stands at the central stake pointing the frame to each of the other four points. The obstruction percentage was then measured only in the 3 m range between the frame and the stake (for more details, see Freitas et al. 2002).

Table 1 Microhabitat variables measured at the trap stations, based on Freitas et al. (1980)

Variables	Description
Plant	Plant cover on the ground (%)
Litter	Litter cover on the ground (%)
Rock	Rock cover on the ground (%)
Canopy	Canopy cover
OBSTR 1	Obstruction at 0–0.5 m high
OBSTR 2	Obstruction at 0.5–1.0 m high
OBSTR 3	Obstruction at 1.0–1.5 m high

Forest structure was described using foliage density and stratification (Pardini et al. 2005), and was measured using a 5 m graduated stick settled in the center of the square to help establish an imaginary vertical column until the canopy. Each foliage contact with the stick was recorded by its inferior and superior heights. Cumulative height of foliage is an indication of foliage density and was calculated for the following strata: (0–1, 1–5, 5–10, 10–15, >15 m) (Pardini et al. 2005).

In order to verify the aggregated distribution of *A. fuscum* in the population of *T. laurentius*, a goodness of fit test was performed with “MASS” and “vcd” packages of the R software (R Development Core Team 2009). The frequency distribution of this parasite was analyzed by maximum likelihood for goodness of fit to negative binomial distribution. The fit of the data to the negative binomial distribution was compared to the fit to the Poisson distribution, in effect acting as null random distribution (Shaw et al. 1998), using Akaike’s information criterion (AIC). Non-parametric correlation tests (Spearman rank correlation—rs) were performed between microhabitat and vegetation structure variables and presence/absence of *T. laurentius* on the 80 trapping stations using PAST software (Hammer et al. 2001).

Results and discussion

Over the four capture sessions and 4,005 trap-nights of sampling effort, a total of 103 specimens of *T. laurentius* were captured and examined for the presence of ticks. Ticks were found on 45 hosts (43.3%). Only immature stages ($n = 342$) of *A. fuscum* were found. Of these, 48.5% were larvae ($n = 166$) and 51.8% were nymphs ($n = 176$). *T. laurentius* trapped in the Estação Ecológica de Tapacurá was recently described as a new host for *A. fuscum* (Martins et al. 2009). The overall mean intensity of infestation was 7.6 ticks per infested host. The highest infestation rate was 68 ticks on an adult male of *T. laurentius*. Ticks were commonly found in groups attached to the ears of the hosts.

Ticks were highly aggregated on the host population. The 31% ($n = 14$) most heavily infested *T. laurentius* (intensity of infestation higher than the mean, i.e., ≥ 8) harbored 79% of the nymphs ($n = 139$) and 78.3% of the larvae ($n = 130$) collected. Two adult males of *T. laurentius* were caught carrying respectively 43 and 29 nymphs suggesting that after molting, the nymphs, like the larvae, may also display an aggregated distribution (Ostfeld et al. 1996b).

In the case of *T. laurentius*, the negative binomial distribution provides a statistically satisfactory fit (respectively $\chi^2 = 40.18$; $p < 0.001$) indicating that *A. fuscum* distribution shows significant aggregation (Fig. 1). The estimated distribution parameters were

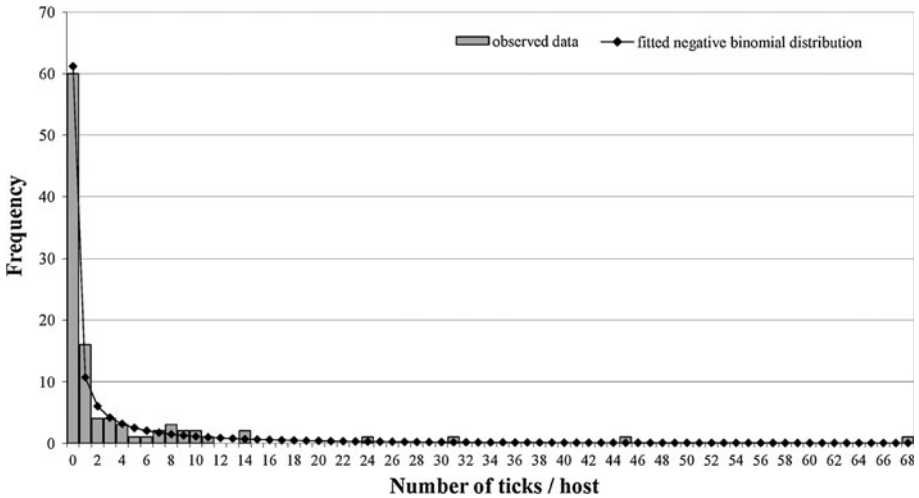


Fig. 1 Observed *Amblyomma fuscum* frequency distribution on the host population and expected negative binomial distribution

$\mu = 3.2571$ and $k = 0.1844$. The value of k , smaller than 1, indicates a quite large degree of aggregation. Moreover, when nymphs and larvae distribution are analyzed separately, they can be fitted by negative binomial distribution either.

The negative binomial distribution and the Poisson distribution both provide statistically satisfactory fits (respectively $\chi^2 = 40.18$; $p < 0.001$ and $\chi^2 = 900.18$; $p < 0.001$). But, based on the AIC, the negative binomial distribution provides a better fit than the Poisson distribution [AIC (negbin) = 395.01 and AIC (poisson) = 1253.02].

Aggregation is considered a general law of parasite ecology (Poulin 2007) and has been demonstrated in many tick-small mammal associations worldwide (Brunner and Ostfeld 2008; Nava et al. 2011; Stanko et al. 2007). In South America, particularly in Argentina, many *Amblyomma* ticks (e.g., *A. parvum*, *A. tigrinum*, *A. triste*) were found in aggregated distribution on rodent hosts (Nava et al. 2006, 2009, 2011). In Brazil, tick aggregation has not been commonly measured in studies of tick-small mammal relationship (Barros-Battesti et al. 2000; Bittencourt and Rocha 2003; Bossi et al. 2002). But, as both prevalence and the mean number of ticks per host, in overall, correlate negatively with aggregation (Poulin 2007), the low prevalence of infestation of ticks observed in that studies may indicate that this phenomenon is more widespread on small mammal hosts.

The proportion of infested hosts was significantly different between sex ($\chi^2 = 5.564$, $df = 1$, $p < 0.05$) and for adults and juveniles ($\chi^2 = 8.979$, $df = 1$, $p < 0.05$) (Table 2). Overall, there were more infested adults and males than juveniles and females, respectively. Considering the ages separately, there were proportionally more infested adult males than adult females ($\chi^2 = 8.574$, $df = 1$, $p < 0.05$), whereas there was no difference between the number of infested juvenile males and females. In adults, the males were 4.15 times infested as much as females, and 2.6 times in juveniles (Table 2). Sexual bias in tick infestation on rodents might be related to home range (Sonenshine and Stout 1968). With a larger home range than females, males have more opportunities to be infested (Ostfeld et al. 1996a). This pattern might be true for *T. laurentius* as males are documented to cruise on a larger home range than females (Streilen 1982).

Table 2 Tick-host infestation indices, according to sex and age classes of *Thrichomys laurentius*, in the Estação Ecológica de Tapacurá, State of Pernambuco, 2008

	Total			Juveniles				Adults				
	<i>N</i>	INF (%)	<i>T</i> (%)	<i>Ma</i>	<i>N</i>	INF (%)	<i>T</i> (%)	<i>Ma</i>	<i>N</i>	INF (%)	<i>T</i> (%)	<i>Ma</i>
M	46	26 (56.5)	250 (73.1)	5.4	18	5 (27.7)	16 (80)	0.8	28	21 (75)	234 (72)	8.3
F	57	19 (33.3)	92 (26.9)	1.6	14	2 (14.3)	4 (20)	0.3	43	17 (39.5)	88 (27.3)	2.0
Total	103	45 (43.7)	342		32	7 (21.8)	20		71	38 (53.5)	322	

N number of trapped individuals, *INF* (%) number and percentage of infested hosts, *T* (%) number and percentage of collected ticks, *Ma* mean abundance, *M* males, *F* females

Table 3 Seasonality of captures of *Thrichomys laurentius* and number of ticks encountered at the Estação Ecológica de Tapacurá, São Lourenço da Mata municipality, Pernambuco, Brazil

Missions	Number of <i>T. laurentius</i>		Number of <i>A. fuscum</i>		
	Infested	Trapped	Larvae	Nymphs	Larv + nymph
March (1)	13	25	50	35	85
June (2)	14	31	75	54	129
September (3)	11	26	30	25	55
December (4)	7	21	11	62	73
<i>p</i> (χ^2)	0.82 (ns)	0.58 (ns)	<0.01	<0.01	<0.01
Wet (1 + 2)	27	56	125	89	214
Dry (3 + 4)	18	47	41	87	128
<i>p</i> (χ^2)	0.45 (ns)	0.38 (ns)	<0.01	0.01	0.33 (ns)
Total	45	103	166	176	342

No differences were found between the number of captured and infested hosts, as well as the prevalence rates, among trapping sessions (Table 3). However, the number of ticks collected varied among trapping sessions ($\chi^2 = 23.8$, $df = 3$, $p < 0.001$). We can hypothesize that host population being relatively constant, the variation of the number of ticks collected was the result of either ticks demography or other environmental variables. As far as tick population is concerned, the largest number of ticks ($n = 129$) was observed in June and the lowest ($n = 55$) in September. The larval population increased from March to June and decreased until December, reaching the lowest number of individuals ($n = 11$). The population of nymphs followed the same pattern as larvae, but it increased in December, with its greatest number of individuals ($n = 62$), eventually a result of synchronization in molting. The χ^2 tests on the abundance of larvae and nymphs, in proportion to the numbers of hosts captured, give us a clue on the seasonal variation of the tick population (see Table 3). The tick abundance was higher than expected in June and December due to larval abundance in June and nymphal abundance in December. A lower tick abundance in March and September was the consequence of low larval population in March and low larval and nymphal populations in September. In overall, larvae were significantly more abundant in the wet season ($\chi^2 = 16.2$, $df = 1$, $p < 0.001$), whereas the nymphs were proportionally more abundant in the dry season ($\chi^2 = 6.5$, $df = 1$, $p < 0.01$). In the tropics, where there are no large variations in environmental conditions such as average temperatures and photoperiod, all tick stages are active during the year in

continuous overlapping generations. Decreases of the abundance of tick stages take place generally during the dry season (Randolph 2004) which is consistent with our general results. A long-term study with monthly captures is then needed to address more accurately the seasonal population fluctuations of both ticks and hosts.

Trichomys laurentius occurrence (without discrimination according to infestation) is positively correlated to PLANT ($r_s = 0.25$, $p < 0.05$) and vegetation in the 1–5 m strata ($r_s = 0.25$, $p < 0.05$), and negatively correlated with CANOPY ($r_s = -0.29$, $p < 0.05$), and strata >15 m ($r_s = -0.301$, $p < 0.05$). As far as infested *T. laurentius* are concerned, their presence is positively correlated with the 1–5 m strata ($r_s = 0.31$, $p < 0.05$) and negatively with the strata >15 m ($r_s = -0.24$, $p < 0.05$).

As vegetation structure is crucial for tick survival and development (Estrada-Peña 2001), habitat quality for ticks might indirectly be estimated by infested host capture (Boyard et al. 2008; Guerra et al. 2002). Despite the lack of information on life history traits for *A. fuscum* we found that habitat preferences of *T. laurentius* are biologically relevant for this tick's biology. Abundance of ground vegetation helped to maintain lower temperatures, protecting the litter layers from sun heat (Schulze and Jordan 2005) while the trapped moisture in the litter prevents drying for immature stages and provides a stable temperature for larval development (Sonenshine and Mather 1994).

The microhabitat selection by *T. laurentius* may indicate that this rodent species use open habitat hiding in dense ground or shrubby vegetation. In dense canopy covering, the understory is often clear which might explain the absence of *T. laurentius*. In Brazil, this species is also known to be adapted to xeric rocky and bushy areas (Reis and Pessôa 2004). Finding in Tapacurá fragment a large *T. laurentius* population suggests that this species locally display a large ecological range. Because fields frequently used by cattle and horses surround this area, *T. laurentius* might act as an epidemiological bridge (Boyard et al. 2008, Paziewska et al. 2010) between forested environments and open ones.

Shrubby and opened areas might also be the preferred habitat for boa snakes (*Boa constrictor*) (Pontes et al. 2008), one of the most important hosts of adult stages of *A. fuscum* in Brazil and, particularly, in the Estação Ecológica de Tapacurá (Dantas-Torres et al. 2008). Thereby, engorged female ticks would find ideal conditions to lay eggs and, consequently, the hatched larvae would be more successful in finding small mammals, their primary hosts.

In conclusion, this study demonstrates that the aggregated burden of *A. fuscum* on *T. laurentius* is related to host sex and age. Moreover, microhabitat selection by *T. laurentius* probably increases contact opportunities between hosts and aggregated infesting stages of *A. fuscum*. Due to the ease of *T. laurentius* capturing and to the high infestation rates observed in the study area, *A. fuscum*–*T. laurentius* relationship can become a powerful model for studying the ecology of species and population dynamics and for generating testable predictions for further studies.

Acknowledgments Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq (grant 478.229/2007-0 to JCRS), Institut de Recherche pour le Développement (IRD), Alβan Program fellowship to FMA, Instituto Brasileiro para Medicina da Conservação—Triade.

References

- Andrade K, Rodal MJ (2004) Fisionomia e estrutura de um remanescente de floresta estacional semidecidual de terras baixas no nordeste do Brasil. *Rev Bras Bot* 27:463–474
- August PV (1983) The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* 64:1495–1507

- Barros-Battesti DM, Yoshinari NH, Bonoldi VL, de Castro Gomes A (2000) Parasitism by *Ixodes didelphidis* and *I. toricatus* (Acari: Ixodidae) on small wild mammals from an Atlantic Forest in the State of São Paulo, Brazil. *J Med Entomol* 37:820–827
- Bittencourt EB, Rocha CF (2003) Host-ectoparasite specificity in a small mammal community in an area of Atlantic rain forest (Ilha Grande, State of Rio de Janeiro), southeastern Brazil. *Mem Inst Oswaldo Cruz* 98:793–798
- Bossi DE, Linhares AX, Bergallo HG (2002) Parasitic arthropods of some wild rodents from Juréia-Itatins Ecological Station, state of São Paulo, Brazil. *Mem Inst Oswaldo Cruz* 97:959–963
- Boyard C, Vourc'h G, Barnouin J (2008) The relationships between *Ixodes ricinus* and small mammal species at the woodland–pasture interface. *Exp Appl Acarol* 44:61–76
- Brunner JL, Ostfeld RS (2008) Multiple causes of variable tick burdens on small-mammal hosts. *Ecology* 89:2259–2272
- Daniels TJ, Fish D (1990) Spatial distribution and dispersal of unfed larval *Ixodes dammini* (Acari: Ixodidae) in southern New York. *Environ Entomol* 19:1029–1033
- Dantas-Torres F, Oliveira-Filho EF, Soares FAM, Souza BOF, Valença RBP, Sa FB (2008) Ticks infesting amphibians and reptiles in Pernambuco, northeastern Brazil. *Rev Bras Parasitol Vet* 17:218–221
- Dantas-Torres F, Aléssio FM, Siqueira DB, Mauffrey JF, Marvulo MFV, Martins TF, Moraes-Filho J, Camargo MCGO, Nicoletti D'Auria SG, Labruna MB, Silva JCR (2012) Exposure of small mammals to ticks and rickettsiae in Atlantic Forest patches in the metropolitan area of Recife, north-eastern Brazil. *Parasitology* 139:83–91
- Freitas SR, Cerqueira R, Vieira MV (2002) A device and standard variables to describe microhabitat structure of small mammals based on plant cover. *Braz J Biol* 62:795–800
- Guerra M, Walker E, Jones C, Paskewitz S, Cortinas MR, Stancil A, Beck L, Bobo M, Kitron U (2002) Predicting the risk of lyme disease: habitat suitability for *Ixodes scapularis* in the North Central United States. *Emerg Infect Dis* 8:289–297
- Hammer O, Harper DAT, Ryan D (2001) PAST: paleontological statistics software package for education and data analysis. *Palaentol Electron* 4:9
- Martins TF, Dantas-Torres F, Nieri-Bastos FA, Marcili A, Siqueira DB, Aléssio FM, Mauffrey JF, Marvulo MF, Silva JC, Labruna MB (2009) Host records for the immature stages of the South american tick, *Amblyomma fuscum* (Acari: Ixodidae). *Entomol News* 120:370–374
- Nava S, Mangold AJ, Guglielmone AA (2006) The natural hosts for larvae and nymphs of *Amblyomma neumanni* and *Amblyomma parvum* (Acari: Ixodidae). *Exp Appl Acarol* 40:123–131
- Nava S, Mangold AJ, Guglielmone AA (2009) Seasonal distribution of larvae and nymphs of *Amblyomma tigrinum* Koch, 1844 (Acari: Ixodidae). *Vet Parasitol* 166:340–342
- Nava S, Mangold AJ, Mastropaolo M, Venzal JM, Fracassi N, Guglielmone AA (2011) Seasonal dynamics and hosts of *Amblyomma triste* (Acari: Ixodidae) in Argentina. *Vet Parasitol* 181:301–308
- Ostfeld RS, Hasler KR, Cepeda OM (1996a) Temporal and spatial dynamics of *Ixodes scapularis* (Acari: Ixodidae) in a rural landscape. *J Med Entomol* 33:90–95
- Ostfeld RS, Miller MC, Hazler KR (1996b) Causes and consequences of ticks (*Ixodes scapularis*) burdens on white-footed mice (*Peromyscus leucopus*). *J Mammal* 77:266–273
- Pardini R, de Souza SM, Braga-Neto R, Metzger JP (2005) The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic Forest landscape. *Biol Conserv* 124:253–266
- Paziewska A, Zwolinska L, Harris PD, Bajer A, Sinski E (2010) Utilization of rodent species by larvae and nymphs of hard ticks (Ixodidae) in two habitats in NE Poland. *Exp Appl Acarol* 50:79–91
- Pontes JAL, Figueiredo JP, Pontes RC, Rocha CFD (2008) Snakes from the Atlantic rain forest area of Serra do Mendanha, in Rio de Janeiro state, southeastern Brazil: a first approximation to the taxocenosis composition. *Braz J Biol* 68:601–608
- Poulin R (2007) Evolutionary ecology of parasites, 2nd edn. Princeton University Press, Princeton
- Randolph SE (2004) Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology* 129:S37–S65
- Randolph SE, Storey K (1999) Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. *J Med Entomol* 36:741–748
- Reis SF, Pessôa LM (2004) *Thrichomys apereoides*. *Mammal Species* 3(4):1–5
- Schulze TL, Jordan RA (2005) Influence of meso- and microscale habitat structure on focal distribution of sympatric *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae). *J Med Entomol* 42:285–294
- Shaw DJ, Grenfell BT, Dobson AP (1998) Patterns of macroparasite aggregation in wildlife host populations. *Parasitology* 117:597–610

- Sonenshine DE, Mather TN (1994) Ecological dynamics of tick-borne zoonoses. Oxford University Press, USA
- Sonenshine DE, Stout J (1968) Tick burdens in relation to spacing and range of hosts in *Dermacentor variabilis*. J Med Entomol 5:49–52
- Stanko M, Krasnov BR, Miklisova D, Morand S (2007) Simple epidemiological model predicts the relationships between prevalence and abundance in ixodid ticks. Parasitology 134:59–68
- Streilen KE (1982) The ecology of small mammals in the semiarid Brazilian Caatinga. III. Reproductive biology and population ecology. Ann Carnegie Mus 51:251–269
- R Development Core Team (2009) R: a language and environment for statistical computing, Vienna, Austria. Available at: <http://www.R-project.org>
- Zuk M, McKean KA (1996) Sex differences in parasite infections: patterns and processes. Int J Parasitol 26:1009–1024