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Seasonality of immature stages of *Ixodes loricatus* (Acari: Ixodidae) in the Paraná Delta, Argentina

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ABSTRACT

In this study we analyzed seasonal trends of immature stages of *Ixodes loricatus* parasitizing *Akodon azarae* (Sigmodontinae) in a locality of the Paraná Delta, Buenos Aires, Argentina. The data encompassed two consecutive years and the analysis included the control of potential confounders using Generalized Linear Mixed Models (GLMM) with a negative binomial response. Larvae had within-year differences in abundance, but the peak months differed drastically between both sampling years, indicating that there was no consistent seasonal pattern. Regarding nymphs, a seasonal pattern was first apparent, but it vanished completely when potential confounders were considered, strongly suggesting that the association with season was spurious and caused by the confounders. Our results showed that the occurrence of immature *I. loricatus* in its hosts does not follow a distinct seasonal pattern, and highlight the usefulness of controlling for confounding and statistically assessing consistency between years when establishing tick seasonality.

Introduction

Ixodes loricatus (Acari: Ixodidae) is a three-host tick whose range encompasses central-eastern Argentina, southern Uruguay and Paraguay up to north-eastern Brazil (Guglielmone et al., 2011). Hoogstraal and Aeschlimann (1982) classified *I. loricatus* as a species with strict-total specificity to New World marsupials (Didelphidae), but studies by Nava et al. (2004) and Beldomenico et al. (2005) demonstrated that cricetid rodents of the subfamily Sigmodontinae are crucial to sustain their larvae and nymphs in its southern range. Didelphidae represents the most ancient extant group of marsupials and its origin is South America (Horovitz et al., 2009), while Sigmodontinae are relatively new in the subcontinent, as it has been postulated that they (or their precursors) invaded South America about 5 million years ago (Pliocene) (Pardiñas et al., 2011). This emerging host–parasite relationship consequence of the irruption of Sigmodontinae into South American habitats is of evolutionary importance (Guglielmone and Nava, 2011), but this relationship is not exclusive for *I. loricatus* because related species as *I. luciae* and *I. amarali* are also known for their capacities to infest both Didelphidae and Sigmodontinae (Guglielmone and Nava, 2011; Guglielmone et al., 2011; Guzmán-Cornejo et al., 2012; Saraiva et al., 2012).

Lareschi (1996), Lareschi et al. (2003), Nava et al. (2003, 2004), Beldomenico et al. (2005), Navone et al. (2009) and Colombo et al. (in press) consistently verified that the Sigmodontinae *Akodon azarae* (Rodentia: Cricetidae) is more prone to be infested with *I. loricatus* than other members of this family in the tick southern range. While there is no data on the temporal occurrence of adults, Barros-Battesti et al. (2000) found that immature stages (larvae and nymphs pooled together) showed highest numbers from April to September on Sigmodontinae rodents in southern Brazil, while Beldomenico et al. (2005) found no seasonal trend for larvae and nymphs of *I. loricatus*, although their samples sizes per year and locality were small. However, it should be noted that the study of Barros-Battesti et al. (2000) lasted 18 trapping sessions, and in six of them the number of rodents caught (all species) ranged from 0 to 2, for which their result should be considered inconclusive.

In this study we analyzed the infestation of *A. azarae* with *I. loricatus* in a locality of central Argentina during two consecutive years, under the hypothesis that a seasonal trend will be found analysing a larger set of data for a given locality. The results may be of scientific relevance to understand the ecology of *I. loricatus* with

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implications to other species of *Ixodes* with similar evolutionary pattern.

Materials and methods

Study area

The study area was located in the Estación Experimental Agropecuaria Delta, Instituto Nacional de Tecnología Agropecuaria (INTA), Campana (34°11′ S, 58°50′ W), Buenos Aires, Argentina. The area is in the lower Parana Delta River region, which is the southern extension of the Paranense Province of the Amazonic Phytogeographic Dominion (Cabrera, 1994). The landscape is characterized by levees that surround dry areas as well as temporarily or permanently flooded marshes with the dominance of graminoids and *Erythrina crista-galli* forests (Kandus et al., 2003). Besides, there are areas with *Cortadeira* spp., *Cynodon* spp., and commercial forestations of *Poppulus* spp. and *Salix* spp. The climate is temperate with a mean annual temperature of 16.7 °C and a mean annual rainfall of 1000 mm with an undefined rainy season (Kandus and Malvárez, 2004).

Data collection

Rodents of the species *A. azarae* were captured from December 2010 to October 2012 in 3-night trapping sessions carried out every 5 weeks. Four trapping grids were set out at each of 4 sites, each grid consisting of squares with 12 Sherman-type live-traps in the corners and 2 Ugglan-type live-traps in the middle of the square, baited with pelleted dog food. Within a site, the grids were at least 200 m apart from each other. The rodents trapped were anesthetized by inhalation of Isoflurane, sacrificed by cervical dislocation, and then conserved in individual plastic bags with ethanol 96°. Rodents were weighed, measured and data of their age, sex and body condition were taken. Their skin was examined in the laboratory with a magnifying lens to recover LL (larvae) and NN (nymphs) of *I. loricatus*. Rodents were determined following Massoia and Fornes (1969) and then confirmed by assessing cranium morphology. Ticks were determined following Marques et al. (2004) and also compared with material deposited in the tick collection of INTA, Estación Experimental Agropecuaria Rafaela, Argentina. All procedures were carried out under the approval of the Dirección de Flora y Fauna de la Provincia de Buenos Aires and the Ethic and Biosafety Committee of the Facultad de Ciencias Veterinarias, Universidad Nacional del Litoral.

Statistical analysis

In order to evaluate the distribution along the year of LL and NN of *I. loricatus*, only data from grids where *I. loricatus* was found were taken into account (10 out of 16 grids). Rodents classified as "juvenile" were excluded from the analysis because they are only present during a few months of the year. LL and NN mean abundance per host was considered separately for the analysis. To establish the presence of a seasonal pattern, the moment of the year was defined using two sinusoidal components (sine and cosine) to reflect a seasonal cycle (SEASON [sin] + SEASON [cos]) (Diggle, 1990). Regular seasonal cycles, including complex wave forms, may be synthesized using sine and cosine, whose frequencies are integer multiples of the fundamental seasonal frequency (Pollock et al., 1999).

The analysis was conducted in three stages. First a statistical description of the response variable (LL or NN) is offered, including prevalence, mean abundance per host and Kappa (κ) index (Hudson et al., 2002) in which 0 represents a total aggregation and 1 a non-aggregation of the ticks. In the second stage, only the raw association between LL or NN per host and SEASON [sin] + SEASON [cos] was evaluated, including the interaction between year and season, the latter to verify that a possible pattern is consistent for both years. "Year 1" consisted of trapping sessions from December 2010 to November 2011, and "Year 2" from December 2011 to October 2012. Because spurious associations may arise as a result of confounding phenomenon (e.g. if males are more parasitized than females, an apparent seasonality will result if the female:male ratio changes along the year), in a third and final stage, we included in the analysis variables deemed a priori as potential confounders, namely "sex", "body condition", "body length", "type of vegetation" (scrubland or implanted forest) and "flooding proneness" (yes/no). This multivariable approach examines the effect of season adjusting for all other independent variables included in the model – e.g. the effect of season for equal values of sex, body condition, etc.

The analyses were conducted with Generalized Linear Mixed Models (GLMM) with a negative binomial response (count of LL or NN), using the *glmmADMB* package of the statistical software R (R Foundation for Statistical Computing, http://www.r-project.org). To control for the lack of independence of observations from the same trapping grid, we included the random intercept "Grid ID". The interactions between season and sampling year were eliminated if unimportant. The criterion used to remove the interaction term was Akaike information criteria (AIC) or, when over-dispersion was present, Quasi-Akaike information criteria (QAIC) (Richards, 2008).

Table 1
Total of *A. azarae* (*A. a.*) trapped in each season, total count of *I. loricatus* (*I. l.*), prevalence (P) and mean larvae (LL) and nymphs (NN).

Year	Ticks	Total *A. a.*	Total *I. l.*	P (%)	Mean
Year 1	Summer				
	LL	16	5	19	0.31
	NN		3	19	0.19
	Autumn				
	LL	40	0	0	0.00
	NN		2	5	0.05
	Winter				
	LL	50	20	12	0.40
	NN		20	12	0.40
	Spring				
	LL	33	16	27	0.48
	NN		18	27	0.55
Year 2	Summer				
	LL	36	26	19	0.72
	NN		11	14	0.31
	Autumn				
	LL	53	35	30	0.66
	NN		4	7	0.07
	Winter				
	LL	15	14	27	0.93
	NN		4	20	0.27
	Spring				
	LL	15	0	0	0.00
	NN		7	40	0.47
Total					

Results

A total of 258 *Akodon azarae* were included in the analyses, 111 were female and 147 male. Table 1 shows the total number of *A. azarae* trapped in each season, total counts of LL and NN, prevalence and mean abundance per host. Tick counts showed aggregated distributions for LL ($\kappa = 0.14$) and NN ($\kappa = 0.16$), and the maximum number of LL and NN found on a host were 37 and 8, respectively. Given this individual with 37 LL was clearly an outlier (the second individual with greatest number of LL had just 10); all analyses were conducted excluding it.

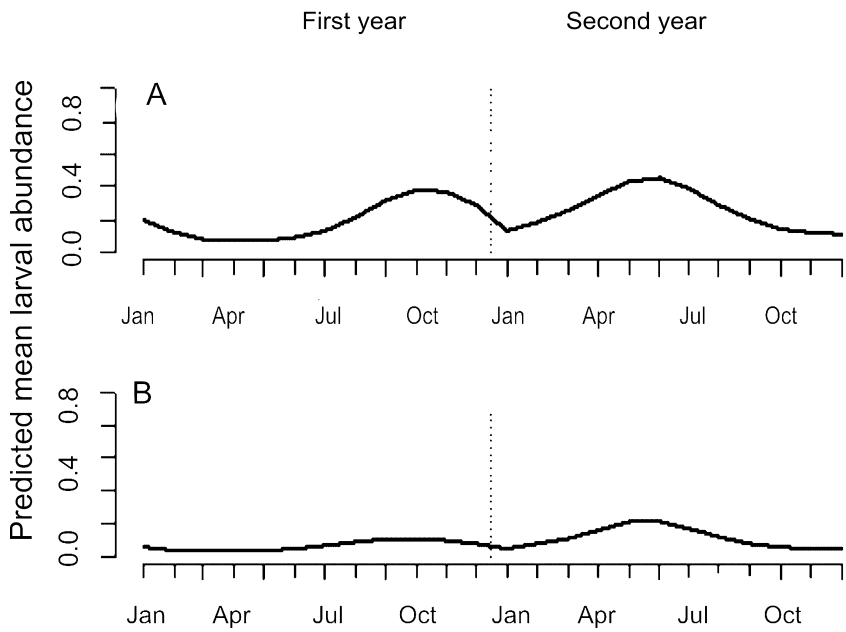

Fig. 1. Mean larval abundance per host by month and sampling year, as simulated by the generalized linear mixed models. (a) Model with only season and year as explanatory variables; (b) model including potential confounders (simulation for a 10 cm-long *A. azarae* male with average body condition in a grid placed in native grassland within a site not prone to flooding).

Larvae

The model that only evaluated the interaction between season and sampling year showed that the interaction term was significant, which establishes that the within-year variability was different in both years. In the first year, there was a peak in larval mean abundance per host in October – November, whereas in the second year, this peak was observed in May – June (Table 2 and Fig. 1A). When the potential confounders were included in the analysis, the interaction term was still significant, and the peaks remained in the same months within each year (Table 2 and Fig. 1B). It is noteworthy that the within-year variability was not large.

Nymphs

The model that only evaluated the interaction between season and sampling year showed that the interaction term was not significant (ΔAIC = −2.84; removing the term improves the model), indicating that the pattern was not different between sampling years. There was a significant association with SEASON [sin] (Table 3 and Fig. 2A), with a peak around October – November. However, when potential confounders were included in the analysis, the association with SEASON [sin] disappeared, even when the non-significant potential confounders were removed from the model (Table 3 and Fig. 2B).

Of the potential confounders assessed, the association with proneness to flooding was highly significant and consistent for both larvae (Table 2) and nymphs (Table 3); the tick mean abundance per host was much greater in sites prone to periodical flooding. The association with "body length" was significant only for nymphs: its mean abundance increases with a greater body length (Table 3), while "body condition", "sex" and "type of vegetation" have no major influence on *I. loricatus* infestation of *A. azarae*.

Discussion

Barros-Battesti et al. (2000) suggested that the immature stages of *I. loricatus* follow a seasonal pattern, as they found greater abundance from April to September. Their study, however, was flawed due to several reasons: the data did not include at least two complete years, their sample size was too small and the analysis did not control for potential confounders. Our results do not support the hypothesis that immature stages of *I. loricatus* follow a seasonal pattern. However, there were apparent patterns consisting

Table 2
Generalized linear mixed models showing the association between larval mean abundance per host and sinusoidal components describing a seasonal cycle by year in the first model. The second model includes potential confounders.

Term	Coefficients	Standard error	*P*-value
Model 1:			
Response = *Ixodes loricatus* larval abundance			
Independent variables = season [sin] + Year + Season [cos] + Season [sin]*Year 1 + Season[cos]*Year 1			
Random intercept = "Grid ID"			
Intercept	−1.464	0.542	0.007
Season [sin]	−0.682	0.392	0.082
Year (1)[d]	−0.332	0.405	0.412
Season [cos]	−0.006	0.382	0.987
Sine*Year 1[d]	1.351	0.536	0.012
Year 1*Cosine[d]	0.544	0.556	0.328
Model 2:			
Response = *Ixodes loricatus* larval abundance			
Independent variables = Flooding proneness + Sex + Body length + Vegetation + Body condition + Season [sin] + Year + Season [cos] + Season [sin]*Year + Season [cos]*Year			
Random intercept = "Grid ID"			
Intercept	−2.988	3.221	0.353
Flooding proneness[a]	1.973	0.739	0.008
Sex[b]	0.615	0.374	0.100
Body length	0.111	0.305	0.716
Vegetation[c]	0.457	0.793	0.564
Body condition	−0.181	0.193	0.345
Season [sin]	−0.814	0.386	0.035
Year (1)[d]	−0.446	0.417	0.285
Season [cos]	−0.056	0.412	0.891
Sine*Year 1[d]	1.126	0.559	0.044
Year 1*Cosine[d]	0.582	0.585	0.319

[a] Reference level: not flooded.
[b] Reference level: female.
[c] Reference level: implanted forest.
[d] Reference level: Year 2.

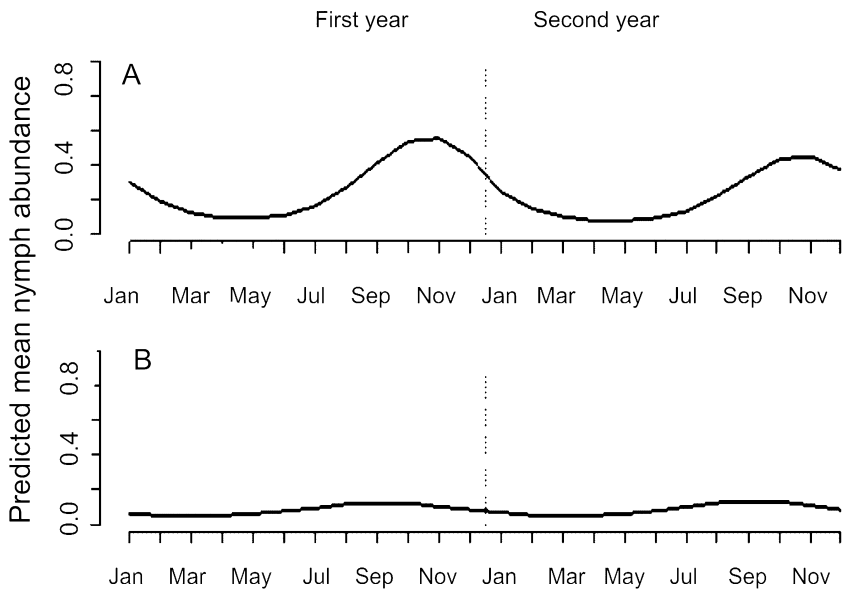

Fig. 2. Mean nymph abundance per host by month and sampling year, as simulated by the generalized linear mixed models. (a) Model with only season and year as explanatory variables; (b) model including potential confounders (simulation for a 10 cm-long *A. azarae* male with average body condition in a grid placed in native grassland within a site not prone to flooding.

Table 3
Generalized linear mixed models showing the association between nymph mean abundance per host and sinusoidal components describing a seasonal cycle by year. The second model includes all potential confounders considered and the third one only the significant ones.

Term	Coefficients	Standard error	*P*-value
Model 1:			
Response = *Ixodes loricatus* nymph abundance			
Independent variables = Season [sin] + Season [cos] + Year			
Random intercept = "Grid ID"			
Intercept	−1.698	0.422	<0.001
Season [sin]	0.791	0.292	0.007
Season [cos]	0.476	0.295	0.106
Year (1)[d]	0.206	0.406	0.612
Model 2:			
Response = *Ixodes loricatus* nymph abundance			
Independent variables = Flooding proneness + Sex + Body length + Vegetation + Body condition + Season [sin] + Year + Season [cos]			
Random intercept = "Grid ID"			
Intercept	−2.495	3.675	0.009
Flooding proneness[a]	1.768	0.511	<0.001
Sex[b]	0.531	0.405	0.190
Body length	0.607	0.331	0.066
Vegetation[c]	0.158	0.582	0.786
Body condition	0.066	0.189	0.727
Season[sin]	0.131	0.337	0.697
Year (1)[d]	−0.054	0.414	0.897
Season [cos]	0.480	0.303	0.113
Model 3:			
Response = *Ixodes loricatus* nymph abundance			
Independent variables = Flooding proneness + Sex + Body length + Vegetation + Body condition + Season [sin] + Year + Season [cos]			
Random intercept = "Grid ID"			
Intercept	−9.207	3.280	0.005
Flooding proneness[a]	1.751	0.532	<0.001
Body length	0.653	0.320	0.041
Season [sin]	0.189	0.323	0.559
Season [cos]	0.450	0.275	0.101

[a] Reference level: not flooded.
[b] Reference level: female.
[c] Reference level: implanted forest.
[d] Reference level: Year 2.

of intra-annual differences in the mean abundance per host that are not to be taken as seasonality. In the case of larvae, the within-year differences differed drastically between both sampling years, indicating that there is no consistent seasonal pattern. We highlight the importance of testing this statistically by including the interaction term with year. Regarding nymphs, a seasonal pattern with peaks in October – November and troughs in April – May was first apparent, which vanished completely when potential confounding factors were considered, strongly suggesting that the association with season was spurious.

Many tick species present seasonal patterns in their life cycles (e.g. Kollars et al., 2000; Labruna et al., 2002; Randolph et al., 2002; Ogden et al., 2005; Nava et al., 2008, 2009a, 2011; Egyed et al., 2012). One exception is *Amblyomma tigrinum*, as shown in Nava et al. (2009b). The authors speculated that the cycle of *A. tigrinum* is regulated by temperature with no occurrence of diapause but quiescence, a characteristic that may also apply to *I. loricatus*.

Of the potential confounders assessed, the association with proneness to flooding is opposite to what was reported by Beldomenico et al. (2005), who found that the prevalence was much greater in highlands than in lowlands. However, in their sample, *A. azarae* (the preferred host for immature stages of *I. loricatus*) was mostly found in highlands, whereas lowlands were dominated by species less prone to be infested by *I. loricatus* (*Scapteromys aquaticus* and *Oxymycterus rufus*). A plausible explanation of the greater abundance of *I. loricatus* in flooding-prone sites is that the marsupial *Lutreolina crassicaudata*, which is one of the main hosts of *I. loricatus* (Guglielmone et al., 2011) and is observed in the study area (Flores et al., 2007), prefers flooded microhabitats (Cajal, 1981; Massoia et al., 2000), where habitats are shared with *A. azarae* and the most probably nidicolous *I. loricatus*.

Host body size may also influence the parasite burdens (Krasnov et al., 2005; Poulin and George-Nascimento, 2007; Brunner and Ostfeld, 2008; Patterson et al., 2008), but it is not a universal phenomenon (Debárbora et al., in press). Nymphs of *I. loricatus* were prone to be more abundant on larger hosts but this characteristic was not found for larval infestation on *A. azarae*, but the reasons for differential host usage of larvae and nymphs remain unclear. Sex and body conditions have been found to influence prevalence and levels of parasitism in different host – parasites association, but

again these facts are not universal as discussed in Debárbora et al. (in press), and sex was found to be irrelevant for infestation of subadult stages of *I. loricatus* on *A. azarae* confirming previous results reported by Beldomenico et al. (2005). The same applies to body condition in coincidence with findings on another Neotropical tick, *Amblyomma dubitatum* (Debárbora et al., in press).

In brief, no seasonality of larvae and nymphs of *I. loricatus* have been found on a riparian locality in Argentina and the level of infestation on its main host was basically independent of the hosts factors analyzed (body size for nymphal infestation excluded). Their presence/abundance is hypothetically related to a lack of seasonality of adult *I. loricatus* ticks, which should be a focus for further studies on the ecology of *I. loricatus*. Our results highlight the usefulness of controlling for confounding and statistically assessing consistency between years when establishing tick seasonality, as well as the importance of analyzing multiple-year data to assess consistency of an apparent seasonal pattern.

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