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The tropical fowl mite, *Ornithonyssus bursa* (Acari: Macronyssidae): environmental and host factors associated with its occurrence in Argentine passerine communities

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Abstract

The tropical fowl mite, *Ornithonyssus bursa*, is a common avian parasite found on diverse bird species worldwide. In the Neotropical region, *O. bursa* is present in wild birds, but it may also infect poultry and bite humans. Little is known about the ecology and epidemiology of this parasite. We conducted a thorough longitudinal study in passerine assemblages from central Argentina, gathering data from six reproductive seasons, with the aim of identifying factors that have a role in driving the occurrence and distribution of *O. bursa* in its natural hosts. We focused on the brood and microhabitat levels, accounting for potential confounders of higher levels. The results hereby presented contribute to our knowledge on the eco-epidemiology of *O. bursa* in natural hosts of the Neotropical region. Among the many variables assessed, nest material and host species appeared to be the most important correlates of *O. bursa* prevalence. Nonetheless, supplementary analyses showed that host species is a stronger predictor than nest material. Moreover, mite burden (parasite intensity) was found to depend on host species, but not on nest material. The association with species depended on nestling age, suggesting that resistance builds up as the nestling develop, but at a different pace depending on the bird species. Brood size was inversely correlated with intensity of parasitism, suggesting a dilution of the parasite burden on each nestling.

Introduction

The tropical fowl mite, *Ornithonyssus bursa* Berlese, 1888 (Acari: Macronyssidae), is a common avian parasite found

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on diverse bird species worldwide (Walter and Proctor 1999). These mites live within the nesting material and feed predominantly on chick's blood throughout their life (Sikes and Chamberlain 1954; Burtt et al. 1991). The life cycle of *O. bursa* encompasses five stages: egg, larva, protonymph, deutonymph, and adult (Sikes and Chamberlain 1954). Adults engorge rapidly and, after a blood meal is completed, the mature female lays her eggs. These eggs can hatch as soon as 1 day after being laid, depending on the surrounding conditions (Sikes and Chamberlain 1954). Among the immature stages, only the protonymph feeds on its host, the deutonymph is a relatively brief, poorly developed, non-feeding stage. This distinctive characteristic of macronyssid mites confers on them a higher reproductive rate compared to closely related families (Radovsky 2010). The full cycle may be completed in only a few days (2 to 10) in the laboratory (Sikes and Chamberlain 1954; El-Kammah et al. 1990), although it is considered to be longer (up to a fortnight) in natural conditions (Powlesland 1977). It is suggested that there is vertical transmission of *O. bursa* in nests:

parents carrying a low level of parasite intensity infect the nest, and then, due to the short life cycle, mite abundance builds up rapidly parasitising the nestlings (Powlesland 1978; Petersen 1979; Møller 2002).

In the Neotropical region, *O. bursa* can infect poultry, causing significant economic losses (Fletchmann 1985; Horn et al. 2018). It also has the potential of biting humans, causing intense itching and painful dermatitis (Baker et al. 1956; Semenas and Angaut Rocha 1998; Jofré et al. 2009). Moreover, as with other mesostigmatid mites (Valiente Moro et al. 2005; Chaisiri et al. 2015), it is considered a potential vector of pathogenic viruses and bacteria (Santillán et al. 2015; Lareschi et al. 2017). Detrimental effects on its natural hosts have been demonstrated, such as impairment in chick growth and development (Berggren 2005) or nest abandonment (Moss and Carmin 1970; Møller 1990).

Increasing our knowledge on the ecology and epidemiology of this parasite is of interest to the poultry industry, public health, and bird conservation. The existing literature on the subject is extremely limited and outdated. Powlesland (1978) found that the prevalence and abundance of *O. bursa* showed a positive correlation with the progress of the breeding season in starlings (*Sturnus vulgaris* Linnaeus, 1758) from New Zealand. Berggren (2005) found that both nestling age and humidity of the microhabitat around the nest were positively correlated with *O. bursa* prevalence on chicks of New Zealand's robin (*Petroica australis longipes* Lesson & Garnot, 1827). Also, field studies showed that climate variability affects natural populations of the tropical fowl mite parasitising barn swallows (*Hirundo rustica* Linnaeus, 1758) in northern Europe (Møller 2009). A few other studies have focused on other macronyssid species, reporting that mite occurrence varied depending on factors related to the environment and the host. Darolová et al. (1997) found that parasite loads of mites of the species *Ornithonyssus sylviarum* Canastrini and Fanzago, 1877, and *Dermanyssus hirundinis* Hermann, 1804 (Acari: Dermanyssidae), were negatively associated with male bird quality in penduline tits (*Auriparus flaviceps* Sundevall, 1850) from central Europe. Garvin et al. (2004) found that the temporal distribution of *O. sylviarum* was correlated with the breeding season of its main host, the grey catbird (*Dumetella carolinensis* Linnaeus, 1766), in the USA. Mazgajski (2007) found that the presence of old nest material in nestboxes used by the European starling had an impact on *O. sylviarum* abundance. In addition, laboratory studies showed that *O. sylviarum* is very sensitive to fluctuations in temperature and humidity (Chen and Mullens 2008; Halbritter and Mullens 2011). All these studies independently show that the dynamics of macronyssid mites is strongly influenced

by the environment and by the host. However, there is a paucity of studies that assess such influence in an integrative manner and at multiple scales, especially in natural environments.

Here, we conducted a thorough longitudinal study in two breeding passerine assemblages, aiming to identify the major factors driving the abundance and distribution of *O. bursa* in its natural hosts. We focused on the brood and microhabitat levels, accounting for variables of higher levels that may act as potential confounders.

Materials and methods

Data collection

Data originated from systematic fieldwork carried out along six reproductive seasons of the avian hosts (spring and summer months): 2008/2009, 2009/2010, 2012/2013, 2013/2014, 2014/2015, and 2015/2016. In the first two sampling seasons, data was gathered in two sites, and only in one of them afterwards. The study sites were a natural reserve belonging to Universidad Nacional del Litoral (all sampling years; "Reserva M. Vet. Martín de la Peña"; 60° 55′ W, 31° 23′ S) and a private natural area of similar characteristics (reproductive seasons 2008/2009 and 2009/2010; "Mihura"; 60° 47′ W, 31° 30′ S). The area sampled in both sites was fixed at 40 ha. Both sites are located alongside "El Salado" river, in the centre of Santa Fe province (Argentina). They are considered relics of "El Espinal" biogeographic province and contain similar biological communities.

For this study, we focused on five bird species, which are common at the study area, and are known to be hosts of *O. bursa* (Arrabal et al. 2012): *Furnarius rufus* Gmelin, 1788, *Sicalis flaveola* Linnaeus, 1766, *Phacellodomus ruber* Vieillot, 1817, *Phacellodomus sibilatrix* Sclater, 1879, and *Pitangus sulphuratus* Linnaeus, 1766. All five species are altricial and breed in enclosed nests with a breeding chamber covered with grass (de la Peña 2015). In the case of *S. flaveola*, the species utilises the mud, oven-like nests built by *F. rufus*, either earlier in the same reproductive season or in previous ones. On the other hand, the nest of the *Phacellodomus* species are built by each species and are similar in structure and material (de la Peña 2015), although for *P. ruber* the wood sticks with which it is built are usually slightly thicker and less woven than in the nests of *P. sibilatrix*. *Pitangus sulphuratus* nests are mainly made of woven grass and its chamber is less isolated from the environment than the rest of the species involved in the analysis (de la Peña 2015). Three times a week, the study areas were thoroughly surveyed to look for nests of potential hosts, starting from the 21st of September (the start of spring, which was

considered as week 1 of the study) until the end of the summer or beginning of autumn.

Nestlings were examined from hatching until they were absent from the nests. Mite abundance on each nestling was registered following a scoring method: 0 = no mites; 1 = 1–15 mites; 2 = 15–30 mites; 3 = 30 or more mites. Nests were sampled at least once a week. At times when they were sampled more than one time a week, one of the repeated samples obtained in a given week was randomly selected to make the sampling effort even.

Parasite diagnosis

A sample of the mites observed on nestlings was collected with forceps or cotton swabs and stored in 96% alcohol for later identification. In the laboratory, they were cleared in lactophenol and then mounted on microscope slides in Hoyer's medium (Krantz 1971). Mite identification was assessed with the aid of an optic microscope, following Baker et al. (1956), Micherdzinski (1980), and Radovsky (2010) (representative sampled mite in Fig. 1). This coincided with the identification previously carried out in the same community (Arrabal et al. 2012).

Statistical analysis

Although records were taken from individual nestlings, the study unit was the whole brood at a given time (brood$_i$-week$_{ti}$), as $O.$ $bursa$ is not a permanent parasite and spends a large proportion of its life dwelling among the nest material. Therefore, the measurements obtained for the nestlings of a brood at a given week were averaged.

The statistical analysis was divided into two parts: first, the prevalence of $O.$ $bursa$ on sampled broods each week of study (presence/absence of $O.$ $bursa$) and, second, the intensity of the parasitism by $O.$ $bursa$ on infected broods each week, as estimated by the average of the scores given to individual nestlings (notice that negative brood-weeks were not considered in this second analysis).

The independent variables of interest were selected based upon the literature. An a priori exploratory analysis of the data was also utilised as a first approach to eliminate co-lineal variables (see details in Table 1). The variables of interest were related to the microhabitat level of the nest, but also included variables of higher hierarchical levels, as they may act as confounders. At the microhabitat level, the variables selected were: parental brood species (host species), species that built the nest (nest builder), external material of the nest (nest material), brood size, presence of parasitic nestlings (i.e. *Molothrus bonariensis* Gmelin, 1789 and *Tapera naevia* Linnaeus, 1766), nestlings development (as approximated by status of the feather development of a randomly selected nestling of the brood), number of times the nest was previously used and nest support (tree species). A quadratic term was added for continuous variables to check for non-linearity.

Fig. 1 **a** Image of a female *Ornithonyssus bursa* from the present survey, taken with an optic microscope. **b** Detail of the ventral shield, arrows to accentuate *st3* position inside the shield. **c** Detail of the last portion of the dorsal shield, showing the typical shape of *O. bursa*
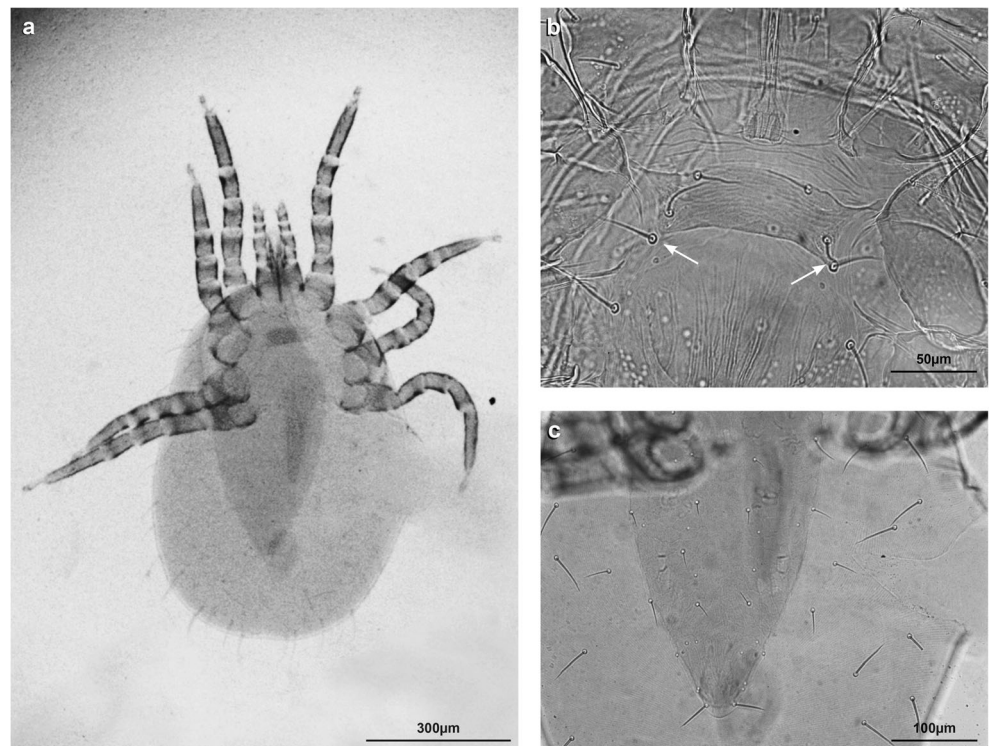
Table 1 Variables of interest included in the analysis. Variables selected for model construction after exploratory assessment are shown in bold

Microhabitat-level variables

Variable (code if needed)	Levels	Description
Host species (host sp)	*Pitangus sulphuratus* *Phacellodomus ruber* *Phacellodomus sibilatrix* *Furnarius rufus* *Sicalis flaveola*	The five predominant host species parasitized by *O. bursa*
Nest builder	*Furnarius rufus* *Pitangus sulphuratus* *Phacellodomus ruber* *Phacellodomus sibilatrix*	Species that built the nest (*S. flaveola* occupies *F. rufus* nests)
Nest material	Mud Grass Wood sticks	Construction material of the nest: mud: *F. rufus* and *S. flaveola*. grass: *Pi. sulphuratus*. wood sticks: *P. ruber* and *P. sibilatrix*.
Age category	1–7	Age categorised according to feather development. 1: absence of feathers; 2: rachis emergence; 3: developed rachis; 4: vane emergence from the rachis; 5: more developed vane; 6: feather almost completely developed (except tail); 7: feathers developed almost on the whole body (but might be less developed in tail), nestling ready to fledge.
Brood size	Count	Number of nestlings in the nest
Parasitic bird	Presence Absence	Presence or absence of parasitic bird in the brood (*Molothrus bonariensis* or *Tapera naevia*)
Nest use by the same species (nest use sp)	Discrete	Number of times the nest was used by the same species. Exploratory analysis showed this variable to be better predictor than 'nest used by any species' (below).
Nest use by any species	Discrete	Number of times the nest was used by any species
Forest type	*Tessaria sp.* *Aspidosperma quebracho blanco* *Celtis tala* *Geoffroea decorticans* *Gleditsia triachantos* *Prosopis sp.* *Geoffroea decorticans / Gleditsia triacanthos* *Gleditsia triachantos / other species* *Geoffroea decorticans / Prosopis sp.* *Successional mixture (dense area composed of a mixture of Tessaria sp., Geoffrea decorticans, Gleditsia triachantos, others)*	Predominant tree species surrounding the nest (higher stratum)
Support	*Aspidosperma quebracho blanco* *Celtis tala* *Geoffroea decorticans* *Gleditsia triachantos* *Prosopis sp.* *Sapium haematospermum*	Tree species on which the nest was built

Community-level variables

Variable (code if needed)	Levels	Description
Area	Reserva Mihura	Studies sites
Year	8 9 12 13 14 15	Year in which the reproductive season begins. Year 8 corresponds to reproductive season "2008–2009", year 9 to "2009–2010", year 12 to "2012–2013", year 13 to "2013–2014", year 14 to "2014–2015" and year 15 to "2015–2016"
Week	Continuous	Groups of 7 consecutive days, starting the count each season on September 21st
Rain$_{(week—2)}$	Continuous	Sum of precipitation (mm) during the 2 weeks before the sample was taken
Mean temperature$_{(week—2)}$	Continuous	Mean temperature (°C) during the 2 weeks before the sample was taken
Maximum temperature$_{(week—2)}$	Continuous	Weekly maximum temperature (°C) 2 weeks before the sample was taken
Minimum temperature$_{(week—2)}$ (min temp)	Continuous	Weekly minimum temperature (°C) 2 weeks before the sample was taken
Furnarius rufus abundance$_{(week—2)}$	Continuous	Abundance of *F. rufus* nests 1 month before the sample was taken
Sicalis flaveola abundance1$_{(week—2)}$	Continuous	Abundance of *S. flaveola* nests 1 month before the sample was taken
Passerine nest abundance$_{(week—2)}$ (Pass nest)	Continuous	Abundance of Passerine nests 1 month before the sample was taken

Table 2 Number of sampled bird broods (N), prevalence of *O. bursa* (P), mean intensity (I_{mean}), and maximum intensity (I_{max}) by host species and year (breeding season)

Nest material	Host species	Year 8	Year 9	Year 12	Year 13	Year 14	Year 15	Total per species
Mud	*F. rufus*: N ($P\%$; I_{mean}; I_{max})	28 (56.5%; 1.55; 3)	46 (57.6%; 1.63; 3)	6 (66.7%; 1.50; 2)	11 (31.7%; 1.00; 2)	6 (16.7%; 3.00; 3)	7 (17.9%; 2.11; 3)	104 (50.0%; 1.61; 3)
	S. flaveola: N ($P\%$; I_{mean}; I_{max})	43 (36.8%; 1.25; 3)	53 (63.2%; 1.01; 3)	0	0	19 (43%; 0.89; 3)	15 (51.1%; 1.01; 2)	130 (50.1%; 1.06; 3)
Wood sticks	*P. ruber*: N ($P\%$; I_{mean}; I_{max})	19 (11.4%; 0.53; 1)	18 (28.2%; 0.92; 2)	5 (0%; -; -)	8 (0%; -; -)	6 (0%; --; -)	6 (8.3%; 0.33; 0.33)	62 (12.5%; 0.78; 2)
	P. sibilatrix: N ($P\%$; I_{mean}; I_{max})	34 (5.9%; 0.92; 2)	39 (18.6%; 0.76; 1.5)	4 (0%; -; -)	23 (7.2%; 0.25; 1)	12 (0%; -; -)	15 (0%; -; -)	127 (8.6%; 0.78; 2)
Grass	*Pi. sulphuratus*: N ($P\%$; I_{mean}; I_{max})	23 (24.6%; 0.95; 3)	45 (23.7%; 1.06; 3)	1 (0%; -; -)	7 (0%; -; -)	10 (0%; -; -)	8 (18.8%; 0.63; 1)	94 (20.0%; 1.01; 3)
Total per year ($P\%$; I_{mean}; I_{max})		147 (28.2%; 1.29; 3)	201 (41.3%; 1.20; 3)	16 (25.0%; 1.50; 2)	49 (10.5%; 0.92; 2)	53 (17.3%; 1.26; 3)	51 (21.4%; 1.10; 3)	517 (29.7%; 1.05; 3)

P prevalence was estimated by calculating the percentage of broods that were parasitised at a given week. Notice that because broods were repeatedly sampled on a weekly basis, some weeks a given brood could be positive, and others negative, while the denominator used was brood-week

The selected confounding variables were the reproductive season (year in which it starts), the season week (since the 21st September), and mean minimum temperature 2 weeks previously (Table 1), the latter being selected from various climatic factors assessed a priori. In addition, the abundance of active nests of all potential hosts (all passerines in the sampling area) 1 month previously was also included in the analysis. The lag of 2 weeks for the climatic factor was established in relation to the approximate duration of a female *O. bursa*'s life cycle, so that the climatic variable would have exerted effects on at least one generation. A lag of 1 month was established for the abundance of hosts, as breeding a brood lasts from 2 to 3 weeks. Relevant two-way interactions were also included in the analysis.

Statistical analyses were conducted using the software R (The R Project for Statistical Computing; http://www.r-project.org), fitting Generalised Linear Mixed Models (GLMM), with brood ID as a random effect. In the case of the prevalence study, the 'glmmadmb' function of the *glmmADMB* package was used with a binomial distribution, with the presence/absence of *O. bursa* as the response variable; while for the mite intensity analysis, the 'glmer' function of the *lme4* package was used, with a Poisson distribution. In the case of the latter, a transformation of the response variable was needed, i.e. the score was multiplied by 10 and then rounded, to meet the conditions of the link family distribution.

Model selection was done following an information theory approach, as described by Burnham and Anderson (2002), where a stepwise manner was utilised for model comparison through Akaike information criteria (AIC) in the case of the prevalence analysis, and AICc (second order information criteria corrected for small samples; Burnham and Anderson 2002) in the case of the intensity analysis, due to a reduction in the sample size. Highly correlated variables were not included in the same model (e.g. nest builder, nest material and host species). The subgroup of best performing models was selected, consisting of those with a maximum of ΔAIC or ΔAICc of 5 units from the best fitting model, and their weights were calculated. These models were ordered according to their weights, and the top models were selected as the ones that reached 0.9 cumulative weight. A multimodel inference was performed using the weighted mean of the coefficients and its standard error, reaching an average model from the top models (Burnham and Anderson 2002). The confidence interval ($\alpha = 0.05$) of each term of the average model was obtained, and terms were considered significant if they did not include the 0.

Additionally, a set of simpler models were obtained dividing the dataset by nest material, as follows: nests made of wood sticks (with *Ph. ruber* and *Ph. sibilatrix* as the host species) and nests made of mud (with *F. rufus* and *S. flaveola* as host species) (*P. sulphuratus* was excluded from these analyses as the composition of its nests are unique compared with the rest of the main hosts). This was done to compare the effect of the host species on the prevalence in cases where the nest material was not different. Following the same criteria

described above, the best fitting model within each subset was selected using AIC.

Results

Descriptive statistics

In the six breeding seasons that encompassed this study, a total of 517 broods of five species were weekly monitored. Overall, 29.7% of the broods were parasitised by *O. bursa* at a given time, being the mean abundance score 1.05. The highest prevalences and intensities were observed in the species that use oven-like mud nests: *F. rufus* and *S. flaveola*. The number of broods sampled by year, prevalences, and intensities for each host species is shown in Table 2.

Prevalence models

This analysis was conducted with a total of 1033 observations, which represented 517 broods. The best models showing the variables associated with prevalence of parasitism by *O. bursa* on broods at a given week are shown in Supplementary material S1. The average model (Table 3) shows that, at a young age, the prevalence is

highest in *F. rufus*, followed by *S. flaveola*, with the rest of the host species less likely to be parasitised by *O. bursa*. The interaction between the nestlings' age and their species was consistently significant (Fig. 2). The prevalence of *O. bursa* increased as nestlings developed, but this phenomenon was accentuated in the case of *Pi. sulphuratus* and both *Phacellodomus* spp. The quadratic term of age category was negatively associated with the prevalence of *O. bursa*, which indicates that, in the case of *F. rufus* and *S. flaveola*, the prevalence reached a maximum and then descended as the chicks advanced their development.

Even though models containing nest material instead of host species appeared among the selected models and the term was significant, where oven-like mud nests (built by *F. rufus* and also occupied by *S. flaveola*) had much higher prevalence than the rest, only one of the 19 selected models had nest material, compared to 18 that had host species.

The rest of the variables of the microhabitat levels were either not significant (number of times the nest was used, brood size, presence of a parasitic nestling), or not even included in the selected models (support, nest builder).

In the additional models where data are grouped and analysed separately according to the material of the nest, running independent models for wood sticks (Table 4) and mud

Table 3 Variables of interest for the average model for *O. bursa* prevalence. Variables selected for model construction after exploratory assessment are shown in bold and indicate the variables of interest at a microhabitat level and the significant coefficients are underlined

	Estimate	Std. error	2.50%	97.50%	*p* value
(Intercept)	1.161	1.004	− 0.808	3.131	0.250
Host sp (*P. ruber*) [a]	**− 4.667**	**0.922**	**− 6.476**	**− 2.858**	**< 0.001**
Host sp (*P. sibilatrix*) [a]	**− 5.247**	**0.872**	**− 6.959**	**− 3.535**	**< 0.001**
Host sp (*Pi. sulphuratus*) [a]	**− 5.533**	**0.851**	**− 7.204**	**− 3.863**	**< 0.001**
Host sp (*S. flaveola*) [a]	**− 2.093**	**0.674**	**− 3.416**	**− 0.770**	**0.002**
Age cat	**0.568**	**0.264**	**0.050**	**1.087**	**0.031**
Age cat^2	**− 0.067**	**0.028**	**− 0.121**	**− 0.013**	**0.017**
Nest use sp	− 0.622	0.345	− 1.300	0.055	0.071
Age cat: Host sp. (*P. ruber*) [a]	**0.403**	**0.183**	**0.043**	**0.762**	**0.027**
Age cat: Host sp. (*P. sibilatrix*) [a]	**0.450**	**0.156**	**0.144**	**0.756**	**0.004**
Age cat: Host sp. (*Pi. sulphuratus*) [a]	**0.505**	**0.146**	**0.219**	**0.791**	**0.001**
Age cat: Host sp. (*S. flaveola*) [a]	**0.166**	**0.118**	**− 0.065**	**0.397**	**0.160**
Parasitic bird (presence)	**0.516**	**0.461**	**− 0.388**	**1.421**	**0.266**
Brood size	− 0.110	0.120	− 0.345	0.125	0.365
Nest material (wood sticks) [b]	**− 3.615**	**0.582**	**− 4.758**	**− 2.473**	**< 0.001**
Nest material (grass) [b]	**− 4.058**	**0.669**	**− 5.372**	**− 2.745**	**< 0.001**
Age cat: Nest material (wood sticks) [b]	**0.290**	**0.115**	**0.064**	**0.516**	**0.012**
Age cat: Nest material (grass) [b]	**0.380**	**0.133**	**0.119**	**0.641**	**0.004**
Week	1.432	0.307	0.831	2.034	< 0.001
Week^2	− 0.976	0.223	− 1.414	− 0.537	< 0.001
Temp min	− 0.012	0.057	− 0.124	0.100	0.844
Nest pass	0.223	0.167	− 0.105	0.550	0.183
Year 9 [c]	1.359	0.323	0.724	1.993	< 0.001
Year 12 [c]	0.764	0.872	− 0.947	2.475	0.388
Year 13 [c]	− 0.323	0.601	− 1.501	0.856	0.603
Year 14 [c]	0.053	0.553	− 1.033	1.140	0.930
Year 15 [c]	0.570	0.518	− 0.446	1.586	0.275
Area (Reserva) [d]	− 0.731	0.293	− 1.306	− 0.155	0.013

[a]: Compared to *F. rufus* (reference host); [b]: compared to mud (reference nest material); [c]: compared to year 8 (breeding season 2008/2009, reference year); [d]: compared to 'Mihura' (reference area)
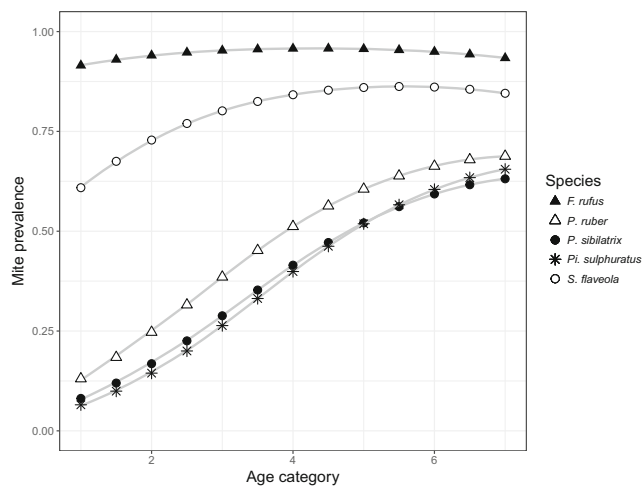
Fig. 2 Relationship between age category and mite prevalence by host species, as predicted by the average model for prevalence. For this prediction, the variables not depicted were set at its median or mean, parasitic bird set as absent, year as 8 and area as 'Mihura'

(Table 5), the host species is shown to be very relevant when nest material remains the same (Fig. 3). In the case of nests made of wood sticks, *P. ruber* showed a higher prevalence than *P. sibilatrix* (odds ratio = 4.85), while for nests made of mud, *F. rufus* showed a higher prevalence than *S. flaveola* (odds ratio = 9.05).

Infection intensity models

In the case of the intensity models, a total of 306 observations from 205 broods were used. The best models showing the variables associated with infection intensity by *O. bursa* on infected broods each week (estimated by the average of the scores given to individual nestlings) can be found in Supplementary material S2. The average model (Table 6) shows that host species had an impact on the intensity of *O. bursa*. At a young age, *P. ruber* had the highest mite burdens followed by *Pi. sulphuratus*, *F. rufus*, *S. flaveola*, and, lastly,

P. sibilatrix. Only in the case of *S. flaveola* the mite intensity was statistically significant in comparison to *F. rufus*.

The interaction between the species and age of the nestlings was significant. In the case of *Pi. sulphuratus* and *S. flaveola*, it showed a more accelerated increase in the intensity of *O. bursa* as the nestlings developed than the rest of the species involved in the analysis (Fig. 4). In the case of *S. flaveola*, it even surpassed the burdens found on *F. rufus* at an older age. On the other hand, brood size was inversely correlated to the mean intensity of parasitism of the brood and this phenomenon was of equal proportions for all species studied (Fig. 5).

Other variables were present among the top models, but they were not significant (age category quadratic term, presence of a parasitic nestling, number of times a nest was used, support). Type of nest and nest material were not selected.

Discussion

A few reports have documented *O. bursa* in Argentina (Aramburú et al. 2003; Arrabal et al. 2012; Santillán et al. 2015). Nevertheless, to our knowledge, this is the first study in the Neotropical region that focuses on finding associations between putative drivers of parasitism and the intensity and prevalence of *O. bursa*.

Although *O. bursa* is a nest dweller and lays its eggs within the nest material (Sikes and Chamberlain 1954; Powlesland 1978), our results show that the host species might be of more importance on the prevalence and intensity of *O. bursa* than the nest's traits. This was found even in species of the same genus that build similar nests, as with species of *Phacellodomus*, but also in unrelated species (*F. rufus* and *S. flaveola*) that occupy the same nest. This consistent result contradicts the findings of Fend'a and Schniererová (2004), where mite fauna (including *O. sylviarum*) was found to be more dependent of the nest material structure than the host species. On the other hand, these results are in concordance

Table 4 Best selected model for species in which the nest is made of wood sticks. The terms in bold indicate the variables of interest at a microhabitat level and the significant coefficients are underlined

	Estimate	Std. Error	2.50%	97.50%	*p* value
(Intercept)	− 3.908	1.113	− 6.089	− 1.726	< 0.001
Host sp (*P. sibilatrix*) [a]	**− 1.579**	**0.735**	**− 3.018**	**− 0.139**	**0.031**
Week	0.459	0.302	− 0.132	1.051	0.129
Year 9 [b]	1.495	0.692	0.139	2.851	0.030
Year 12 [b]	− 13.747	564.810	− 1120.755	1093.260	0.982
Year 13 [b]	− 1.267	1.028	− 3.282	0.748	0.220
Year 14 [b]	− 12.437	216.23	− 436.240	411.366	0.958
Year 15 [b]	− 1.871	1.424	− 4.662	0.920	0.190
Area (Reserva) [c]	1.797	0.776	0.276	3.319	0.020

[a]: Compared to *P. ruber* (reference host); [b]: compared to year 8 (breeding season 2008/2009, reference year); [c]: compared to 'Mihura' (reference area)

Table 5 Best selected model for species in which the nest is made of mud. The terms in bold indicate the variables of interest at a microhabitat level and the significant coefficients are underlined

	Estimate	Std. Error	2.50%	97.50%	p value
(Intercept)	3.260	0.728	1.833	4.688	< 0.001
Host sp (*S. flaveola*) [a]	**−2.203**	**0.547**	**−3.276**	**−1.131**	**0.018**
Nest use sp	**−0.994**	**0.419**	**−1.815**	**−0.172**	**< 0.001**
Week	1.985	0.381	1.237	2.732	< 0.001
Week^2	−1.361	0.273	−1.897	−0.825	< 0.001
Year 9 [b]	1.654	0.409	0.853	2.455	0.016
Year 12 [b]	2.761	1.152	0.503	5.020	0.796
Year 13 [b]	0.212	0.773	−1.303	1.727	0.052
Year 14 [b]	1.248	0.643	−0.012	2.508	0.036
Year 15 [b]	1.338	0.640	0.083	2.593	< 0.001
Area (Reserva) [c]	−1.537	0.402	−2.325	−0.750	< 0.001

[a]: Compared to *F. rufus* (reference host); [b]: compared to year 8 (breeding season 2008/2009, reference year); [c]: compared to 'Mihura' (reference area)

with those of Moreno et al. (2009), in which differences in nest material of the same and different host species was not associated with the prevalence of another hematophagous mite, *Dermanyssus gallinoides* Moss, 1966 (Acari: Dermanyssidae). Characteristics associated with host species other than host nest composition were also found to be more important for *D. gallinoides* abundance in Cantarero et al. (2013).

Brood size was found to have a negative effect on mites count in the intensity models. This might be explained by a dilution effect of the parasite load per nestling as the number of nestlings in a brood increases

(Richner and Heeb 1995). Although Richner and Heeb (1995) noted that this pattern is more suited for long-cycled ectoparasites (duration of cycle similar to the time it takes for its host to fledge), our finding for *O. bursa* might be explained by the fact that in natural conditions, *O. bursa*'s life cycle may be longer than it is in laboratory conditions, closer to the period of time nestlings stay in the nest (Powlesland 1978). This result is consistent with other studies that investigated the intensity of mesostigmatid mites, arriving at the same predictions stated by Richner and Heeb (1995) for long-cycled ectoparasites (e.g. Darolová et al. 1997; Berggren 2005; Mazgajski

Fig. 3 Relationship between mite prevalence and **a** species of hosts that use oven-like mud nests (*F. rufus* and *S. flaveola*) or **b** species of hosts whose nests are made of wood sticks (*P. ruber* and *P. sibilatrix*). Predictions correspond to outcomes of the model fitted for these species. For this prediction, variables not depicted were set at its median or mean, parasitic bird set as absent, year as 8 and area as 'Mihura'
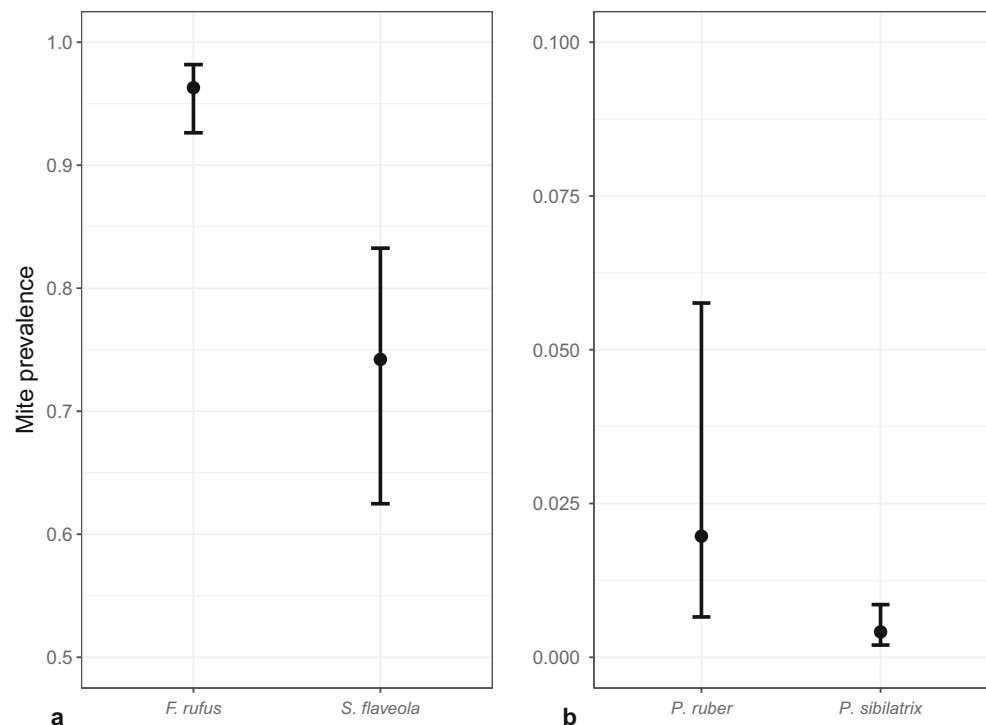
Table 6 Variables of interest in the average model for the intensity for *O. bursa*. The terms in bold indicate the variables of interest at a microhabitat level and the significant coefficients are underlined

	Estimate	Std. Error	2.50%	97.50%	p value
(Intercept)	3.023	0.279	2.475	3.570	< 0.001
Host sp (*P. ruber*) [a]	**0.410**	**0.687**	**−0.940**	**1.760**	**0.562**
Host sp (*P. sibilatrix*) [a]	**−0.880**	**0.450**	**−1.767**	**0.006**	**0.050**
Host sp (*Pi. sulphuratus*) [a]	**−0.307**	**0.331**	**−0.958**	**0.344**	**0.360**
Host sp (*S. flaveola*) [a]	**−0.536**	**0.226**	**−0.981**	**−0.091**	**0.018**
Age cat	**0.007**	**0.035**	**−0.061**	**0.075**	**0.852**
Age cat ^ 2	**−0.019**	**0.028**	**−0.074**	**0.036**	**0.508**
Brood size	**−0.195**	**0.051**	**−0.295**	**−0.095**	**< 0.001**
Nest use sp	**−0.147**	**0.125**	**−0.393**	**0.100**	**0.242**
Parasitic bird (present)	**0.128**	**0.136**	**−0.140**	**0.396**	**0.352**
Support Geoffroea [b]	**0.016**	**0.216**	**−0.409**	**0.442**	**0.946**
Support Gledittsia [b]	**0.209**	**0.325**	**−0.430**	**0.848**	**0.531**
Support Prosopis [b]	**0.324**	**0.217**	**−0.104**	**0.751**	**0.136**
Support Sapium [b]	**0.414**	**0.342**	**−0.260**	**1.087**	**0.228**
Support Tala [b]	**−0.686**	**0.449**	**−1.570**	**0.198**	**0.127**
Age cat: Host sp. (*P. ruber*) [a]	**0.080**	**0.101**	**−0.118**	**0.278**	**0.437**
Age cat: Host sp. (*P. sibilatrix*) [a]	**0.056**	**0.121**	**−0.182**	**0.294**	**0.656**
Age cat: Host sp. (*Pi. sulphuratus*) [a]	**0.501**	**0.105**	**0.295**	**0.707**	**< 0.001**
Age cat: Host sp. (*S. flaveola*) [a]	**0.190**	**0.053**	**0.085**	**0.295**	**< 0.001**
Brood size: Host sp. (*P. ruber*) [a]	**−0.396**	**0.215**	**−0.818**	**0.026**	**0.065**
Brood size: Host sp. (*P. sibilatrix*) [a]	**0.107**	**0.187**	**−0.262**	**0.476**	**0.579**
Brood size: Host sp. (*Pi. sulphuratus*) [a]	**−0.199**	**0.127**	**−0.449**	**0.051**	**0.117**
Brood size: Host sp. (*S. flaveola*) [a]	**0.066**	**0.071**	**−0.074**	**0.206**	**0.358**
Week	0.139	0.076	−0.010	0.288	0.067
Weeks ^ 2	−0.067	0.056	−0.176	0.041	0.234
Nest pass	0.017	0.038	−0.058	0.092	0.668
Temp min	−0.003	0.044	−0.090	0.084	0.950
Area (Reserva) [c]	−0.174	0.115	−0.401	0.052	0.130

[a]: compared to *F. rufus* (reference host); [b]: compared to *Aspidosperma quebracho blanco*; [c]: compared to 'Mihura' (reference area)

2007). Further studies focusing on *O. bursa*'s life cycle in different contexts might help unravel this conundrum.

Population of mites in the nest increased from hatching and beyond the first half of the brood development, which is consistent with results found in previous studies for mesostigmatid mites, where mite prevalence and intensity increased as a brood progressed (Mašán 1997; Berggren 2005). Nevertheless, the reduction in mite prevalence and intensity at more advanced age categories for some of the species might be associated with an increase of host resistance, be it

Fig. 4 Relationship between age category and mite intensity for each species as predicted by the average model for intensity. Dashed line corresponds to predictions for *Pi. sulphuratus* beyond possible values taken by the response variable (> 30). For this prediction, variables not depicted were set at its median or mean, parasitic bird set as absent, year as 8 and area as 'Mihura'
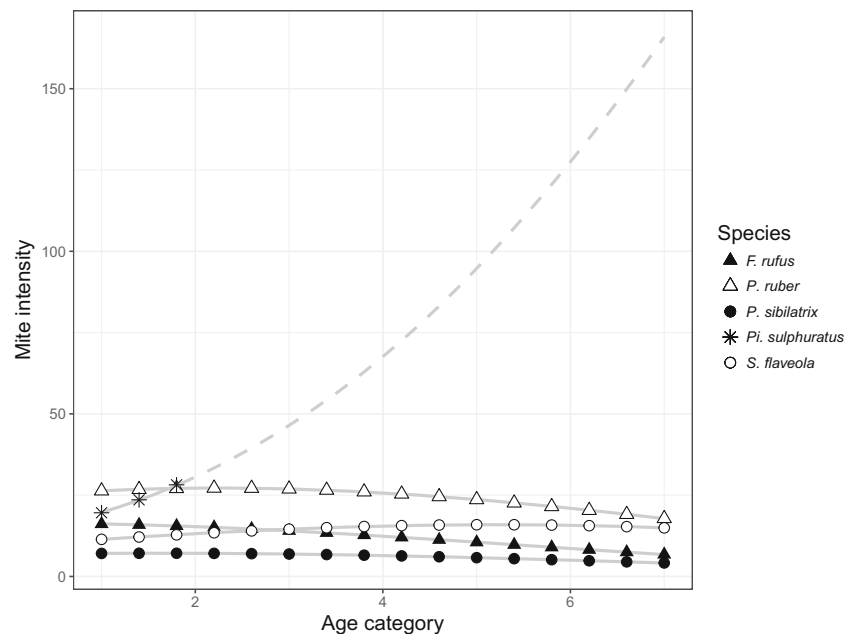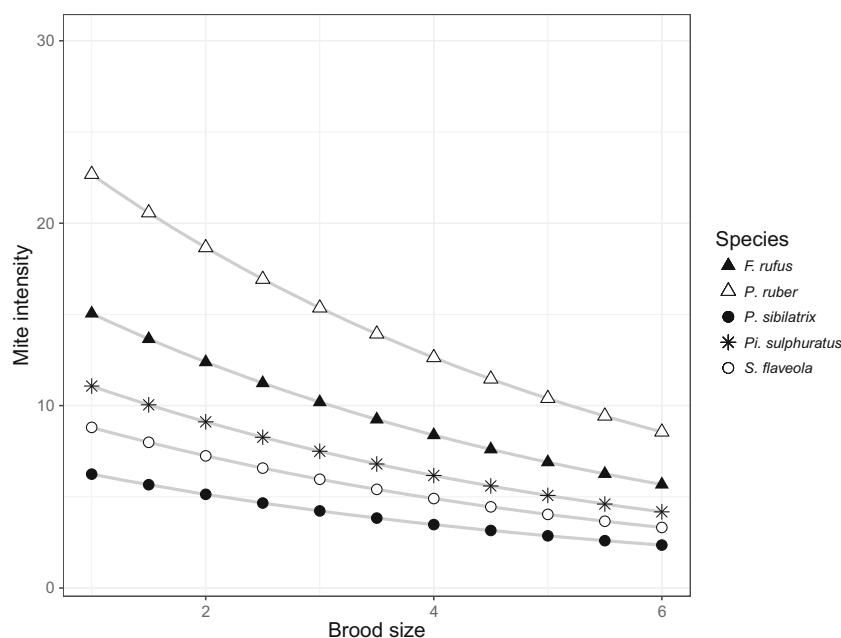
Fig. 5 Relationship between brood size and mite intensity as predicted by the average model for intensity. For this prediction, the variables not depicted were set at its median or mean, parasitic bird set as absent, year as 8 and area as 'Mihura'

immunocompetence (Apanius 1998; Roulin et al. 2007) or behavioural resistance (i.e. preening; Powlesland 1978), which might appear at different developmental stages for each species, as suggested by the significant interactions found in our analyses. Although the possibility of a detection bias due to the difficulty of noticing the presence of mites among developed feathers cannot be ruled out (Moyer et al. 2002), the chance of it being the reason for observing this interaction seems attenuated by the fact that the mite intensity begins to decay on most species before the stage at which the plumage begins to be dense enough to reduce the chances of mite detection (sixth age category).

It is interesting that the species that had the highest prevalences of *O. bursa* infection (*F. rufus* and *S. flaveola*) were not the ones that presented the highest intensities of parasitism (*P. ruber* and *Pi. sulphuratus*). Prevalence of a given generalist parasite in a multi-host context depends, first, on an encounter filter (parasite exposure) and, second, on the performance of host defences (resistance and tolerance) (Manzoli et al. 2018). Differences in exposure, resistance, and tolerance among different hosts shape the distribution of a given parasite, determining its prevalence and intensity in each host (Bauchau 1998; Manzoli et al. 2018). Although further studies are necessary to arrive at accurate conclusions regarding resistance and tolerance, the results presented here suggest that nestlings of the species that presented a high prevalence of *O. bursa* in this study might have a high encounter rate, but also high resistance. On the other hand, species with less prevalence indicate less exposure to the parasite, while higher intensities in them might reflect either less resistance or more tolerance. In studies comparing defence strategies against *O. bursa*, the impact on fitness and parasite exposures between different

hosts may contribute to an explanation of these findings, and would also establish the differential outcomes resulting from parasitising different hosts, both for the host (virulence) and the parasite (transmission).

Compliance with ethical standards

All procedures conducted in this study comply with the current National and Provincial laws, and were approved by the Universidad Nacional del Litoral Bioethics Committee.

Competing interests The authors declare that they have no competing interests.

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