Parasitology Research (2022) 121:1281–1293
https://doi.org/10.1007/s00436-022-07484-w

ARTHROPODS AND MEDICAL ENTOMOLOGY - ORIGINAL PAPER

Factors associated with prevalence and intensity of the northern fowl mite (*Ornithonyssus sylviarum*) in commercial poultry farms of Argentina

Sofía I. Arce[1] · Leandro R. Antoniazzi[2] · Agustín A. Fasano[3] · Darío E. Manzoli[1,3] · Micaela Gomez[4] · Claudia C. Sosa[3] · Martín A. Quiroga[1,5] · Marcela Lareschi[6] · Pablo M. Beldomenico[1,3]

Received: 21 October 2021 / Accepted: 7 March 2022 / Published online: 22 March 2022

Abstract

The haematophagous mite *Ornithonyssus sylviarum* may cause important economic losses in commercial poultry farms whilst also potentially affecting the health of farm workers. The dynamics of this ectoparasite has been linked to several factors, including wild birds, fomites, farm workers, management of hen houses, and host traits. Along two consecutive years, we carried out systematic sampling at three laying hen farms located in Santa Fe province, Argentina, with the aim of identifying factors that may influence *O. sylviarum* prevalence and intensity. We found that the density of feathers around the hen vent area and the presence of Menoponidae lice were negatively associated with mite abundance. We also found that the density of hens in the cages was negatively associated with mite prevalence, suggesting a possible dilution effect, whereas prior reports found a positive association with hen density. In addition, summer was the season with minimum mite prevalences and intensities, contrary to previous studies in northern farms where warm weather appeared to prompt an increase in mite populations. Another factor associated with mite intensity was age, but this effect varied depending on the season, which hints that the association between hen's age and mites is complex. Basic epidemiological knowledge on *O. sylviarum* in poultry farms from South America may aid in a more efficient and integrative approach to its control.

Keywords *Ornithonyssus sylviarum* · *Gallus gallus domesticus* · Hen houses · Macronyssid mites · Host-parasite interactions · South America · Layer hens

Introduction

The northern fowl mite, *Ornithonyssus sylviarum* Canestrini & Fanzago 1877, is a haematophagous mite from the Macronyssidae family (Acari: Mesostigmata: Dermanyssoidea) affecting commercial poultry worldwide. This mite is considered as a pest for laying hens in North America, China, Australia, and Brazil (Murillo and Mullens 2017). Infections by *Ornithonyssus sylviarum* cause anaemia, stress, reduction in feed conversion efficiency, and loss of body weight on their hosts (DeVaney 1979), and thus result in important economic losses to the poultry industry (Mullens et al. 2009). Also, *Ornithonyssus* mites are considered potential vectors of pathogenic viruses and bacteria, including zoonotic pathogens (Reeves et al. 1955; Valiente Moro et al. 2005; Chaisiri et al. 2015; Santillán et al. 2015; Lareschi et al. 2017), posing a threat to poultry farm workers (Teixeira et al. 2020).

Section Editor: Elizabeth Marie Warburton

✉ Pablo M. Beldomenico
pbeldome@fcv.unl.edu.ar

[1] Laboratorio de Ecología de Enfermedades, Instituto de Ciencias Veterinarias del Litoral, Universidad Nacional del Litoral - Consejo Nacional de Investigaciones Científicas Y Técnicas (UNL-CONICET), Esperanza, Argentina

[2] Instituto de Bio Y Geociencias del NOA (IBIGEO), Universidad Nacional de Salta - Consejo Nacional de Investigaciones Científicas Y Técnicas (UNSa-CONICET), Salta, Argentina

[3] Facultad de Ciencias Veterinarias, Universidad Nacional del Litoral (UNL), Santa Fe, Argentina

[4] Facultad de Humanidades Y Ciencias, Universidad Nacional del Litoral (UNL), Santa Fe, Argentina

[5] Departamento de Biología, Universidad Autónoma de Entre Ríos (UADER), Parana, Argentina

[6] Centro de Estudios Parasitológicos Y de Vectores (CEPAVE), CCT - CONICET - La Plata/Universidad Nacional de La Plata, La Plata, Argentina

The life cycle of *O. sylviarum* is short (3–5 days; Sikes and Chamberlain, 1954) which confers this species the ability to rapidly increase their population size (Radovsky 2010). This mite survives off the host for up to 35 days (Chen and Mullens 2008), which facilitates its dispersal and its population continuity inside hen houses in spite of host vacancy once a flock is replaced. Also, in contrast to other Dermanyssoidea, *O. sylviarum* is able to complete its entire life cycle on the host, as its eggs can be laid on the hen feathers (Sikes and Chamberlain 1954). Moreover, given that male offspring of *O. sylviarum* are produced from unfertilised eggs (arrhenotoky), through oedipal mating a population could virtually initiate with as little as one female individual (McCulloch and Owen 2012). Therefore, once a population of *O. sylviarum* is established inside a farm, its eradication becomes extremely challenging.

Although *O. sylviarum* is considered to be a major poultry pest, it is speculated that it became established in hen houses introduced by wild birds, in particular by the synanthropic house sparrow (*Passer domesticus* Linnaeus, 1758), which often nests nearby chicken coops (Murillo and Mullens 2017). Dispersion of mites between flocks and farms has also been ascribed to wild birds (Mullens et al. 2004; McCulloch et al. 2019), as well as to farm workers and fomites (Kells and Surgeoner 1996). According to studies conducted in North America, several factors have been identified associated with the dynamics of this mite on laying hens, including trimming of the beak (Vezzoli et al. 2015), density of hosts (Hall et al. 1978), genetic lines of the hosts (Arthur and Axtell 1982), and stress levels (Hall and Gross 1975).

Whilst *O. sylviarum* is a common parasite of wild birds in North America (Knee and Proctor 2007), the tropical fowl mite, *Ornithonyssus bursa* Berlese 1888, is the predominant mite found in neotropical wild birds (e.g., Aramburú et al. 2003; Mascarenhas et al. 2009; Arrabal et al. 2012; Santillán et al. 2015; Arce et al. 2018). Although *O. bursa* is also present in domestic fowl from Brazil (Reis et al. 1934; Vas 1935; Freire 1968; Oliveira et al. 2020) and Argentina (da Fonseca 1947), evidence suggests that it has been mostly replaced by other Dermanyssinae mite species in laying hens of commercial farm systems (Faccini and Massard 1974; Tucci et al. 1998). Tucci et al. (1998) found either *O. sylviarum* or *Dermanyssus gallinae* DeGeer 1778, or a combination of both, to be present in 74% of the inspected poultry farms in the state of São Paulo, Brazil, in which *O. bursa* was absent. In a more recent study, also in Brazil, Oliveira et al. (2020) found that most inspected hen flocks were parasitised by *O. sylviarum*, followed distantly by *O. bursa* and *D. gallinae*. Furthermore, other studies in Brazil and Argentina determined that despite *O. bursa* being present in nests and wild birds inhabiting hen houses and their surroundings, this species was not found parasitising the hens (Horn et al. 2018; Arce et al. 2020). There are also relatively recent records of *O. sylviarum* parasitising poultry in Colombia (Marín-Gómez and Benavides-Montaño 2007). In Argentinean commercial farms, Doti and Muzureta (1989) reported *O. sylviarum* in the 1980s. This species was also found in a more recent study in central Argentina (Arce et al. 2020). In addition to this, there are records of *O. sylviarum* in wild birds from South America, but these are scarce and seem to be in association to the presence of laying hens (Serafini et al. 2003; Arce et al. 2020) or synanthropic areas (Téllez et al. 2008), which points to a probable recent anthropogenic introduction of this species of mite in this geographic region.

Our knowledge on the occurrence of mesostigmatid mites in commercial poultry farms in South America is still very limited, and studies focusing on ecological or epidemiological aspects in this continent are even more scarce (Tucci et al. 1998; Oliveira et al. 2020). Furthermore, the apparently recent onset of *O. sylviarum* in South American poultry farms poses a particular interest on its epidemiology. Here, we contribute with a longitudinal study that evaluated associations between *O. sylviarum* prevalence and intensity and environmental and host factors in poultry farms from central Argentina.

Material and methods

Characteristics of the sampled farms

Systematic sampling sessions were carried out at three commercial farms located in the centre of Santa Fe province, Argentina. The farms are about 40 km away from each other, in the vicinity of the localities of San Agustín (31°39′S, 60°52′W), San Carlos (31°48′S, 61°3′W), and Humboldt (31°22′S, 61°4′W) (Fig. 1). The region is considered temperate-warm and humid (Castignani 2011). Precipitations are greater in spring and summer (on average, 239-mm fall during the warm seasons), and lowest in winter (on average, 35 mm). The average annual temperature is 18 °C (mean minimum = 14 °C; mean maximum = 25 °C). The mean maximum temperature in summer is 30.3 °C and the mean minimum temperature in winter is 9 °C.

Hen houses with manual systems were present in the three farms (but in San Agustín farm only during the first sampling year). Manual systems consisted of hen houses with a capacity to host 7000 to 8600 hens each, which were confined in metal cages that held a maximum of 4 individuals. Battery cages were organised in rows of one (Humboldt farm) or two levels (San Carlos and San Agustín farms), and in the latter case, positioned in a stair step manner. The house walls were made of partial mesh and tarpaulin, which was used to protect the house from the external weather.

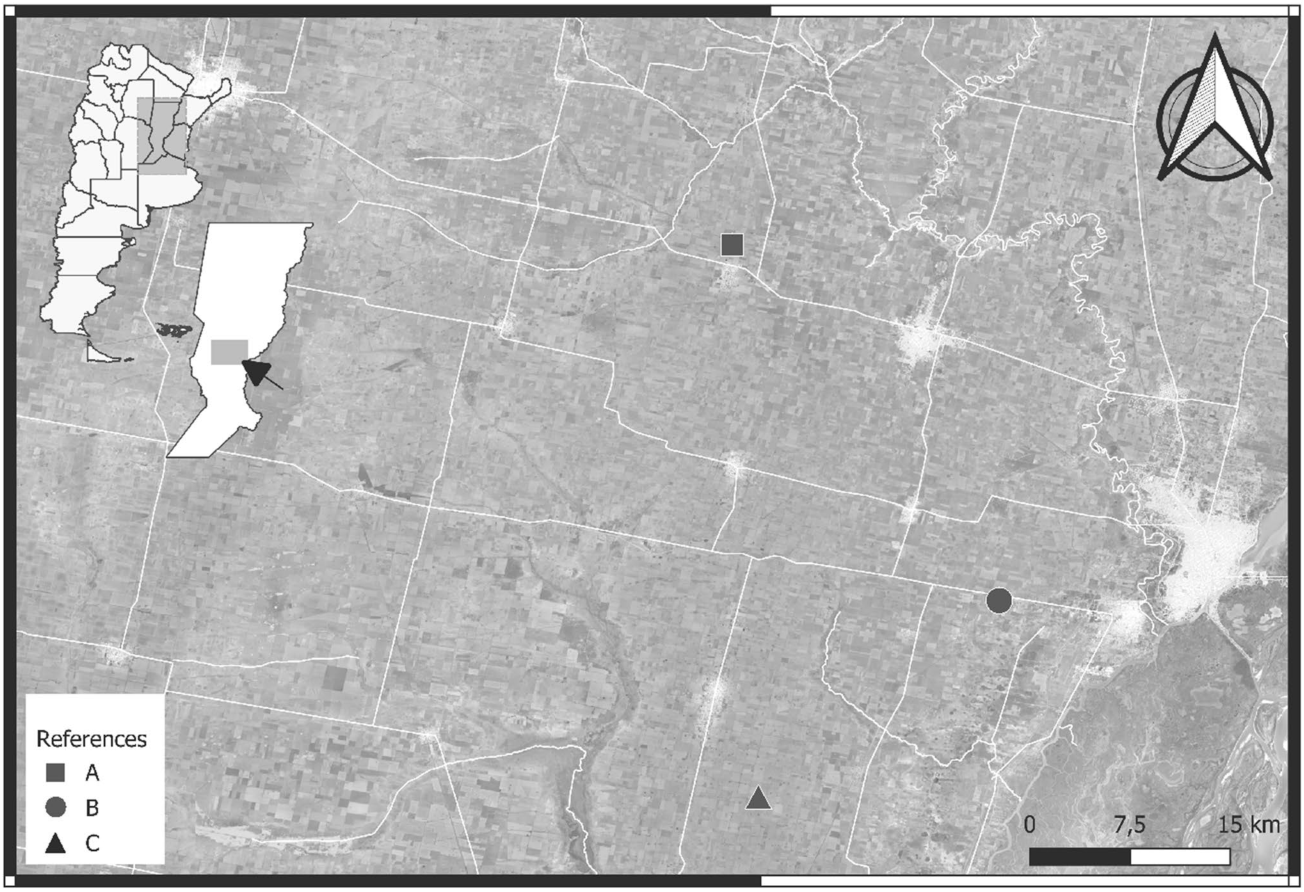

Fig. 1 Location of the three sampled farms. *A* Humboldt farm, *B* San Agustín farm, and *C* San Carlos farm

Hens' manure accumulated beneath the cages, and the frequency of its elimination varied between farms: every 1 to 1.5 months in Humboldt farm, every 4 to 5 months in San Carlos farm, and every 15 to 20 days in San Agustín farm. Water was provided in an automated manner with nipple-type drinkers, and eggs were harvested manually. Food was provided either manually (Humboldt) or with the aid of a trolley pushed by a worker (San Agustín and San Carlos).

In automated systems, which were present in San Carlos and San Agustín farms only, the total capacity of hens was 22,000 and 33,000, respectively. Cages containing hens were distributed in rows of up to six levels of height, and each cage harboured a maximum of 13 hens. The farm house walls were made of solid material, with partial mesh and tarpaulin, which provided better isolation from the external weather and from wild birds than manual ones. Eggs were collected on an automatic treadmill, whilst another treadmill collected faeces every 36 h. An automated trolley provided food, and water provision was also automated with nipple-type drinkers.

In both house systems hens were beak-trimmed. Induced molting was also applied to every flock at approximately 70 weeks of age. In all three farms laying hens arrived at approximately 1 day of age, and were kept in a separate house inside the farm reserved for this purpose, until they were ready to produce eggs (at around 20 weeks of age). In the three farms laying hens belonged to the Hy Line W80 Brown and Hy Line commercial lines, all acquired from the same breeder, except for San Agustín farm, which also incorporated Lohmann LSL-Lite and Lohmann Brown Classic commercial lines from a different breeder.

Data collection

Samples were taken between autumn of 2016 and summer of 2018, completing two sampling years. We aimed at conducting one sampling session per season (as determined by solstices and equinoxes; autumn: 21 March–20 June, winter: 21 June–20 September, spring: 21 September–20 December, summer: 21 December–20 March). All three farms were sampled in each session. Between sampling sessions, there were intervals of 2 to 4 months, and during a single sampling session, intervals amongst farms were in general shorter than 1 month.

Sampling in a hen house was interrupted when the flock was replaced, a period in which hen houses remained empty until a new flock arrived. In Humboldt farm, there was an event of acaricide application, after which sampling was discontinued until the flock was replaced to avoid the confounding effect of this treatment.

In each sampling session, approximately 90 hens were examined per hen house. The sampled hens were equally distributed in three areas within the house: a group of 30 hens in one end of the hen house, 30 in the middle, and 30 on the opposite end of the hen house. In the case of automated houses, three to four randomly selected hens were examined from each cage, whilst in manual systems the totality of the hens in each cage was examined. In houses where there was more than one level of cages, sampling was performed alternating the first row from the floor with the second one.

The three sampled areas within each hen house were marked so that they were followed each sampling session. Hens themselves were not marked in order to minimise disruption of production activities. When more than one hen house was examined in a single day, examiners changed protective clothes and washed plastic boots to minimise dispersion of mites from one hen house to the other.

Variables of interest regarding hosts and their habitat were registered during each sampling session. Whilst examining hens for mites (see below), we also checked for the presence of lice in the vent region. At the beginning of the study, a sample of lice was collected for family identification with the aid of a stereoscopic microscope. The density of hens' feathers in the vent area was registered through a scoring method, classifying the observed density in three levels (from 1, when density was at its highest, to 3, when it was at its lowest). Hens in each sampled cage were counted in order to obtain the density of hens in the cage. The age of the flock in a hen house was also recorded each sampling session.

Sampling procedure protocol was approved by the Ethics and Security in Experimental Work Committee, CONICET Santa Fe (Argentine Council for Research and Technology).

Mite count and identification

The examination of the hens was restricted to the vent region, as it has been demonstrated to be the body region where mites aggregate (Lemke and Kissam 1986). In the first two sampling sessions, we also examined the area beneath one of the wings in a randomly selected proportion of the hens sampled, to take into account that low density of feathers in the vent might result in mites migrating to other body regions (Devaney and Ziprin 1980). As the abundance of mites at these additional areas was very low, only data from the vent area was used.

On each hen, the examination was performed with the aid of a headlight and forceps to separate the feathers. Time of examination was set to be approximately 2 min for each individual hen. A qualitative score from 1 to 5 was used to estimate mite abundance. This score was based on the one reported by Mullens et al. (2009), slightly modified, as follows: 0: no visible mites, 1: very low intensity (1–10 counted mites), 2: low intensity (approximately 11–50 counted mites), 3: moderate intensity (approximately 51–100 estimated mites), 4: moderate to high intensity (approximately 101–500 estimated mites, mites in clumps), and 5: high to very high intensity (approximately 501 estimated mites or more, mites in clumps and abundant frass). In the case of low mite scores (1 to 2), estimation of mites was performed by individually counting them at first glance in order to minimise possible error as mites can rapidly move on the host's surface. When mite score was moderate to high (3–5), we obtained an approximate mite load, and other cues to its abundance were also considered (mites in clumps, presence of abundant frass). In order to minimise error, the score was assessed by only one examiner (SI Arce) in all sampling sessions. Also, before the sampling period included in the present analysis, there was an additional sampling session for training and adjustment purposes.

A sample of mites was collected from parasitised hens found during each sampling session that, once in the laboratory, were cleared with lactophenol and mounted on microscope slides in Hoyer's medium (Krantz 1978). They were identified under an optic microscope following Radovsky (2010). For further details regarding data collection and mite identification, see Arce et al. (2020).

Statistical analysis

Statistical analysis was divided into two parts, according to the response variable assessed: prevalence (proportion of parasitised hens) and intensity of parasitism (1–5 score of mite abundance). Both analyses were performed using the software R 3.6.0 (The R Project for Statistical Computing; http://www.rproject.org) fitting Generalised Linear Mixed Models (GLMM). The fixed effect variables are described in Table 1. The random effects were the identification code of each sampled area inside the hen house (three per hen house) nested within the hen house identification, and, independently, the sampling session number. These random effects were included to take into account the lack of independence of data points collected from the same area/farm and at the same sampling session. For the prevalence models, where the response variable was dichotomic (presence/absence), the function "glmmTMB" with the binomial family distribution from the package glmmTMB was used. In the case of the intensity models, as the response variable was ordinal (5 levels of mite intensity), the function "clmm" from the ordinal package was

Table 1 Variables of interest and relevant interactions included in the statistical analysis

Variable	*Levels*	*Description*
Lice	Presence Absence	Presence or absence of chewing lice (family Menoponidae) in the vent region
Feathers	1 2 3	Score indicating the density of feathers in the vent region. 1: high density, 2: intermediate density, 3: low density
Age	Count (discrete)	Age of the hens in months
Age^2	Count (discrete)	Quadratic term of the age of hens in months
Density hens	Count (continuous)	Density of hens in the cage as number of hens per square meter
Density hens^2[a]	Count (continuous)	Quadratic term of the density of hens in the cage as number of hens per square meter
System	Automated Manual	Production system of the poultry house. Automated: six floors of cages on top of each other, collection of eggs and faeces done by automatic treadmills, and automatic provision of food, manual: battery cages of one or two rows (one on top of the other in a stair steps manner), collection of piles of faeces, collection of eggs, and provision of food done by workers
Farm	San Carlos (SCA) San Agustín (SAG) Humboldt (HUM)	Sampled poultry farms
Season	Summer Autumn Winter Spring	Sampled seasons
Year	I II	Sampled years. I: from autumn 2016 to summer 2017, II: from autumn 2017 to summer 2018
Relevant interactions		*Set of models*
Density hens × system		Prevalence models including SCA, SAG, and HUM farms, and intensity models
Density hens^2 × system		Prevalence models including SCA, SAG, and HUM farms, and intensity models
Year × season		Prevalence models including SCA, SAG, and HUM farms, and intensity models
Age × season		Prevalence models including SCA, SAG, and HUM farms, and intensity models
Age^2 × season		Prevalence models including SCA, SAG, and HUM farms, and intensity models
Farm × system		Prevalence models with subset SCA and SAG farms

used (Christensen 2019). In this case, variables “age” and “density” were scaled for model convergence purposes.

Models were selected following the Akaike Information Theory approach following Burnham and Anderson (2004). In this regard, a stepwise manner was used for model comparison through the Akaike Information Criteria (AIC). The model weight was calculated for a group of best performing models: the best fitting model (the one with the least AIC value) and the ones with a difference in AIC of a maximum of 5 units from the best one. This group of models was sorted according to their weight, and an average model was obtained using a subgroup of models that amounted to 0.9 cumulative weight. In order to reach an average model from this subgroup of selected models, a multimodel inference was performed using the weighted mean of the models’ coefficients and standard errors (Burnham and Anderson 2004). For each term of the average model, a confidence interval was calculated ($\alpha = 0.05$), and they were considered significant if they did not include the 0.

Given that Humboldt farm lacked representation of automated production system, an additional analysis was performed to assess for the interaction between farm and poultry house production system on mite prevalence. For this purpose, a set of models were obtained using a subset of the data that only included San Agustin and San Carlos farms. These generalised mixed models also had the same random effects as the previous ones, and included the fixed effect variables presented in Table 2. They were also constructed using the function “glmmTMB” with the binomial family distribution, found in the package glmmTMB. In this case, model selection was based on AIC, and the model with the least AIC was considered the best fitted model.

Results

A total of 199 female mites from the three farms and both automated and manual hen house systems were used for morphological examination under lens, of which the totality

Table 2 Variables of interest for the average model for *O. sylviarum* prevalence

	Estimate	Std. error	2.5%	97.5%	*P* value
Intercept	**− 16.210**	**7.804**	**− 31.511**	**− 0.910**	**0.038**
Lice (present)[a]	**− 3.449**	**0.502**	**− 4.432**	**− 2.465**	**< 0.001**
Feathers (level 2)[b]	**− 1.409**	**0.202**	**− 1.806**	**− 1.013**	**< 0.001**
Feathers (level 3)[b]	**− 4.449**	**1.052**	**− 6.511**	**− 2.387**	**< 0.001**
Age	1.537	0.978	− 0.380	3.454	0.116
Age^2	− 0.043	0.030	− 0.101	0.015	0.148
Density hens	0.260	0.275	− 0.279	0.800	0.344
Density hens^2	**− 0.014**	**0.007**	**− 0.027**	**0.000**	**0.049**
Season (autumn)[c]	0.892	7.499	− 13.810	15.594	0.905
Season (winter)[c]	11.581	7.547	− 3.216	26.378	0.125
Season (spring)[c]	**15.022**	**7.378**	**0.557**	**29.487**	**0.042**
System (manual)[d]	− 0.166	3.099	− 6.240	5.909	0.957
Farm (SCA)[e]	**4.077**	**1.243**	**1.639**	**6.514**	**0.001**
Farm (HUM)[e]	**3.178**	**1.509**	**0.219**	**6.137**	**0.035**
Year (II)[f]	**− 2.136**	**0.704**	**− 3.515**	**− 0.756**	**0.002**
Age: season (autumn)[c]	0.475	1.003	− 1.491	2.440	0.636
Age: season (winter)[c]	− 0.590	1.001	− 2.552	1.372	0.555
Age: season (spring)[c]	− 1.316	0.982	− 3.241	0.610	0.180
Age^2: season (autumn)[c]	− 0.021	0.030	− 0.081	0.039	0.489
Age^2: season (winter)[c]	0.003	0.031	− 0.057	0.063	0.921
Age^2: season (spring)[c]	0.033	0.030	− 0.026	0.092	0.268
Density hens: system (manual)[d]	− 0.271	0.352	− 0.962	0.420	0.442
Density hens^2: system (manual)[d]	0.009	0.007	− 0.005	0.023	0.218

Significant coefficients in bold ($\alpha = 0.05$)

[a] Compared to absent (reference for lice)

[b] Compared to level 1 (reference for feather)

[c] Compared to summer (reference season)

[d] Compared to automated (reference system)

[e] Compared to farm SAG (reference farm)

[f] Compared to year I (reference year)

was identified as *Ornithonyssus sylviarum*. All lice examined belonged to the family Menoponidae (suborder Amblycera).

Out of 3571 observations, 793 hens were found parasitised by *O. sylviarum* at a given time (overall prevalence of 22.2%). The best models for prevalence from which the average model was constructed are shown in Table S1 of Supplementary Material. The average model (Table 2) shows that the prevalence of mites was negatively associated with presence of lice (Fig. 2) and lower densities of feathers around the vent area (Fig. 3). The density of hens in a cage had a negative effect on mite prevalence (Fig. 4). Spring was the season with the highest prevalence, and this difference is significant in comparison to summer, when the lowest prevalence was observed (Fig. 5). San Agustin farm had the lowest prevalence of mites in comparison to the other two farms (Fig. 6), and during the first sampling year the prevalence was higher than during the second year (Fig. 7).

The subset of models to assess the effect of the interaction between farms and production system were constructed using 2964 observations from San Carlos and San Agustín farms. In the selected model (Table 3), the interaction between hen house system and farm was significant, indicating inconsistency of the association with production system. In San Carlos, the manual house had greater prevalence than the automated one, whereas in San Agustin the opposite was observed (Fig. 8).

Intensity models were constructed using 783 observations, from which nearly half of them (47.6%) corresponded to the lowest level of mite intensity, 24.3% to the second level, 16.1% to the third level, 9.3% to the fourth level, and 2.6% to the highest level. The best selected models for intensity can be found in Table S2 of Supplementary Material. For this analysis only Humboldt and San Carlos farms are represented, given that San Agustin farm had very few parasitised hens, generating an imbalanced structure of the data.

The average model (Table 4), based on the best 44 top models, shows that the presence of Menoponidae lice had a significant negative effect on the intensity of mites. The

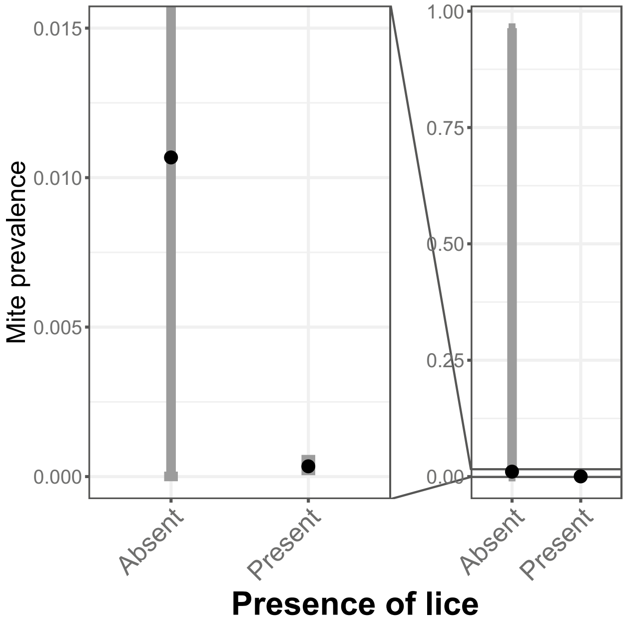

Fig. 2 Association between presence of lice in the vent region and prevalence of mites as predicted by the prevalence average model. Variables that are not depicted in this prediction were set as follows: numerical variables (hen density in a cage and age) were set at its mean, feather density was set at level 1, season was set at summer, house system was set at automated, farm was set at San Agustín, and sampling year was set at year I

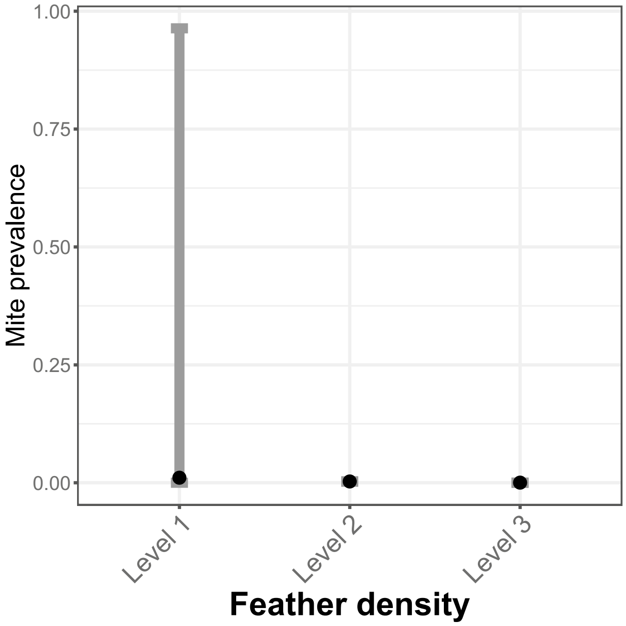

Fig. 3 Association between feather density in the vent area and prevalence of mites as predicted by the prevalence average model. Variables that are not depicted in this prediction were set as follows: numerical variables (hen density in a cage and age) were set at its mean, lice were set at absent, season was set at summer, house system was set at automated, farm was set at San Agustín, and sampling year was set at year I

interaction between season and year was significant, indicating that there was no consistent seasonal pattern for mite intensity. The intensity was lowest in summer in both years, but it was as low in winter in the second year of sampling. Also, the effect of age was not consistent as it varied depending on the season.

Discussion

To our knowledge, this is the first comprehensive longitudinal study assessing potential drivers of prevalence and intensity of parasitic mesostigmatid mites in commercial poultry systems of the Neotropical region.

Ornithonyssus sylviarum is mainly found on the hen vent area, where denser downy feathers and a thicker feather coat favour optimal humidity and temperature conditions for this species fitness (DeVaney 1986; Halbritter and Mullens 2011). Mites have been observed to move vertically on feathers, positioning at different height on feather rachis and barbules, hypothetically, to regulate atmospheric conditions at which they are exposed. What is more, feathers are also needed for *O. sylviarum* to complete its life cycle, as they are utilised as substrate for oviposition (Halbritter and Mullens 2011). Therefore, the inverse correlation between feather

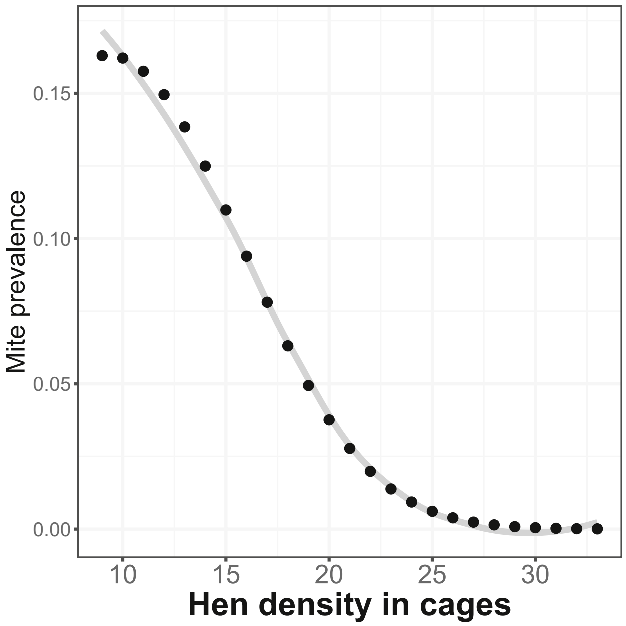

Fig. 4 Association between the density of hens in cages and the prevalence of mites as predicted by the prevalence average model. Variables that are not depicted in this prediction were set as follows: age was set at its mean, lice were set at absent, feather density was set at level 1, season was set at summer, house system was set at automated, farm was set at San Agustín, and sampling year was set at year I

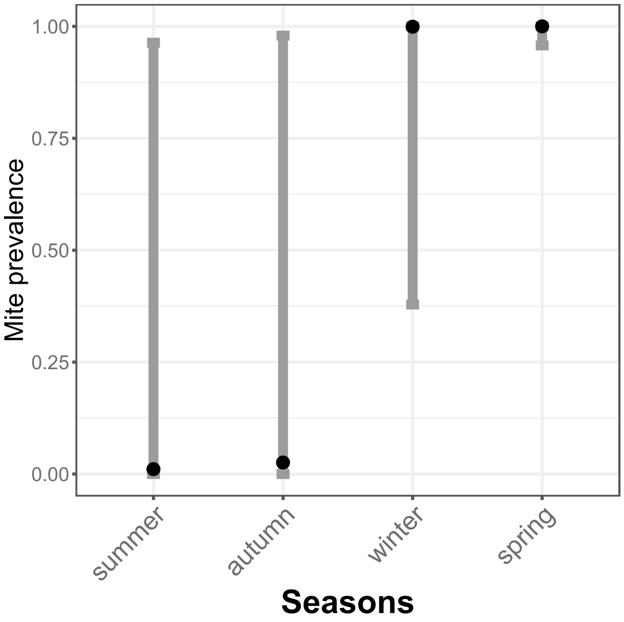

Fig. 5 Association between the seasons and the prevalence of mites as predicted by the prevalence average model. Variables that are not depicted in this prediction were set as follows: numerical variables (hen density in a cage and age) were set at its mean, lice were set at absent, feather density was set at level 1, house system was set at automated, farm was set at San Agustín, and sampling year was set at year I

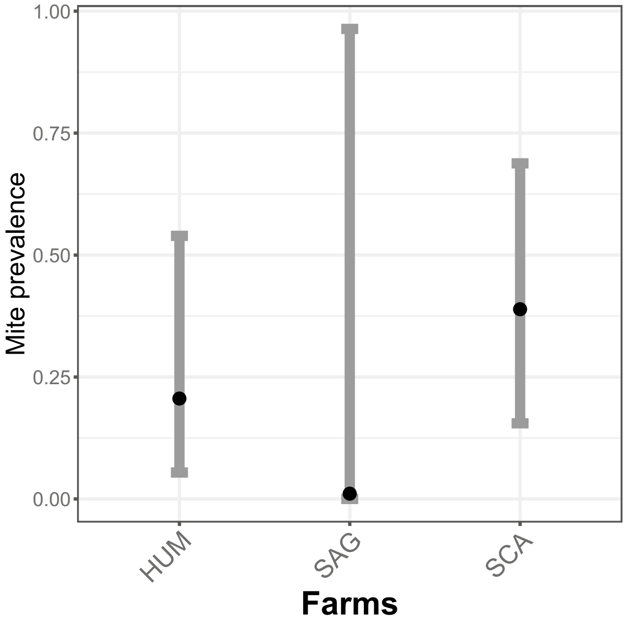

Fig. 6 Association between the farms and the prevalence of mites as predicted by the prevalence average model. Variables that are not depicted in this prediction were set as follows: numerical variables (hen density in a cage and age) were set at its mean, lice were set at absent, feather density was set at level 1, season was set at summer, house system was set at automated, and sampling year was set at year I

density in the vent region and mite prevalence (statistically significant) and intensity (almost significant) observed in the present analysis makes biological sense. Furthermore, there were no mites found in hens that ranked in the lowest category of feather density in the vent area. Feather characteristics, such as length, have also been linked to mite abundance in previous studies (DeVaney and Beerwinkle 1980; DeVaney 1986). Trimming of hens' feathers in specific body regions has even been suggested as a possible alternative method for mite abundance control in farms, as it has not been linked to a reduction on egg production (Nakamae et al. 1996). Alternatively, selection of hens with less feathers in the vent area should be considered by breeders to generate a biotype less prone to *O. sylviarum* infection.

According to our analysis, the presence of Menoponidae lice on the vent region had a negative effect on both prevalence and intensity of *O. sylviarum*. Chen et al. (2011) also found that the presence of a Monoponidae louse, *Menacanthus stramineus* Nitzsch 1818, in the vent region had a detrimental effect on *O. sylviarum* populations. In their trial, mites only persisted on hens infested by lice for a short period of time and at a low-intensity level. However, the exclusion of mites by the presence of lice on hens is not ubiquitous, as some studies have found mixed infections and eggs from both lice and *O.*

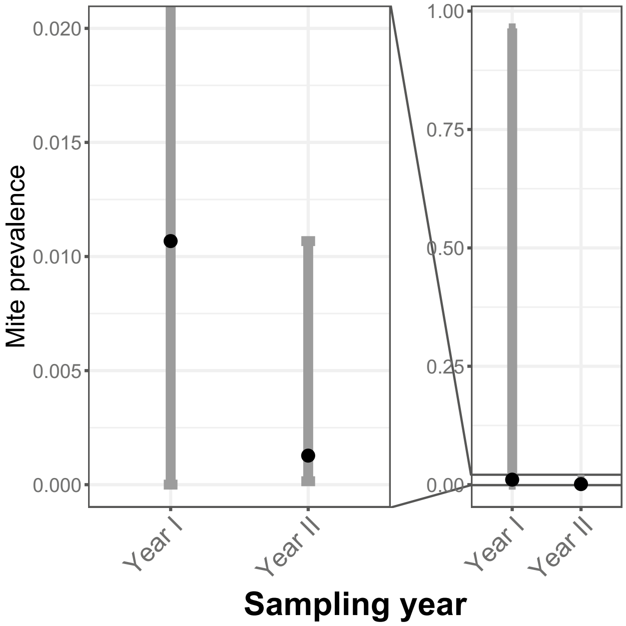

Fig. 7 Association between the sampling year and the prevalence of mites as predicted by the prevalence average model. Variables that are not depicted in this prediction were set as follows: numerical variables (hen density in a cage and age) were set at its mean, lice were set at absent, feather density was set at level 1, season was set at summer, farm was set at San Agustín, and house system was set at automated

Table 3 Variables of interest for the best model for *O. sylviarum* prevalence in SCA and SAG farms

	Estimate	Std. error	2.5%	97.5%	*P* value
Intercept	**−13.650**	**2.748**	**−19.036**	**−8.265**	**< 0.001**
Lice (present)[a]	−2.029	1.110	−4.204	0.145	0.067
Feathers (level 2)[b]	**−1.343**	**0.204**	**−1.742**	**−0.943**	**< 0.001**
Feathers (level 3)[b]	**−4.214**	**1.050**	**−6.271**	**−2.156**	**< 0.001**
Age	**1.516**	**0.209**	**1.105**	**1.926**	**< 0.001**
Age^2	**−0.038**	**0.004**	**−0.047**	**−0.030**	**< 0.001**
Season (autumn)[c]	**14.041**	**2.476**	**9.189**	**18.893**	**< 0.001**
Season (winter)[c]	**17.044**	**3.159**	**10.853**	**23.235**	**< 0.001**
Season (spring)[c]	**9.964**	**2.219**	**5.615**	**14.313**	**< 0.001**
Density hens	−0.048	0.111	−0.266	0.169	0.663
Density hens^2	**−0.006**	**0.003**	**−0.012**	**−0.001**	**0.020**
System (manual)[d]	**−5.527**	**1.385**	**−8.241**	**−2.813**	**< 0.001**
Farm (SCA)[e]	1.738	1.000	−0.223	3.698	0.082
Year (II)[f]	**−4.721**	**0.759**	**−6.209**	**−3.234**	**< 0.001**
Age: season (autumn)[c]	**−0.695**	**0.157**	**−1.002**	**−0.387**	**< 0.001**
Age: season (winter)[c]	**−0.823**	**0.177**	**−1.169**	**−0.476**	**< 0.001**
Age: season (spring)[c]	**−0.363**	**0.129**	**−0.615**	**−0.110**	**0.005**
Density hens: system (manual)[d]	**0.144**	**0.040**	**0.065**	**0.223**	**< 0.001**
System (manual)[d]: farm (SCA)[e]	**5.862**	**1.293**	**3.329**	**8.396**	**< 0.001**

Significant coefficients in bold ($\alpha = 0.05$)

[a] Compared to absent (reference for lice)

[b] Compared to level 1 (reference for feather)

[c] Compared to summer (reference season)

[d] Compared to automated (reference system)

[e] Compared to farm SAG (reference farm)

[f] Compared to year I (reference year)

sylviarum on the same feathers (de Figuereido et al. 1993; do Carmo Rezende et al. 2016). As Menoponidae lice feed mainly on feather barbules (Crutchfield and Hixson 1943), it seems logical that the damaged feather structure left by chewing louse populations could alter the conditions needed by mites to colonise and establish (Axtell and Arends 1990; Chen et al. 2011). Resource limitation imposed by the presence of lice seems to be the most plausible explanation behind this relationship; nevertheless, further studies should focus on the mechanism behind it. Other type of interactions between these two ectoparasites could be taking place, such as an interplay with the host's immune response (Graham 2008; Chen et al. 2011). In the present study, we have not reached an identification of lice to the species level. It should be noted that not all species of hen lice have the vent area as their preferable host body region (Trivedi et al. 1991); however, at least some of them might migrate to the lower abdomen when their hosts are beak-treamed (like the ones involved in this study), as Chen et al. (2011) have demonstrated in the case of *M. stramineus*. Assessing the community of lice on different areas of the hens' body could further broaden our knowledge regarding the interaction between poultry ectoparasites.

Our results showed that mite prevalence and intensity were lowest in summer. Despite the fact that a certain level of climatic isolation is maintained inside hen houses, fluctuations amongst seasons tend to occur, and their range depends on various factors concerning hen house structure and hen cage disposition (Daghir 2008). Contrary to our results, a previous study found the lowest abundance of *O. sylviarum* during cold seasons (Mullens et al. 2000). Nevertheless, this study was based on poultry systems from the Northern hemisphere, and therefore, the observed differences could be due to climate regionality and structural differences in hen houses, such as ventilation systems. Perhaps optimal weather conditions for mite populations might occur in different seasons depending on the region. Although hens are homeothermic, heat stress is reached at certain ambient temperature and humidity values. This generates failure in their thermoregulation, causing the body temperature to increase at its core and surface (Chang et al. 2018). Under laboratory conditions, hatching of *O. sylviarum* eggs is dependent mainly on temperature, finding the peak in

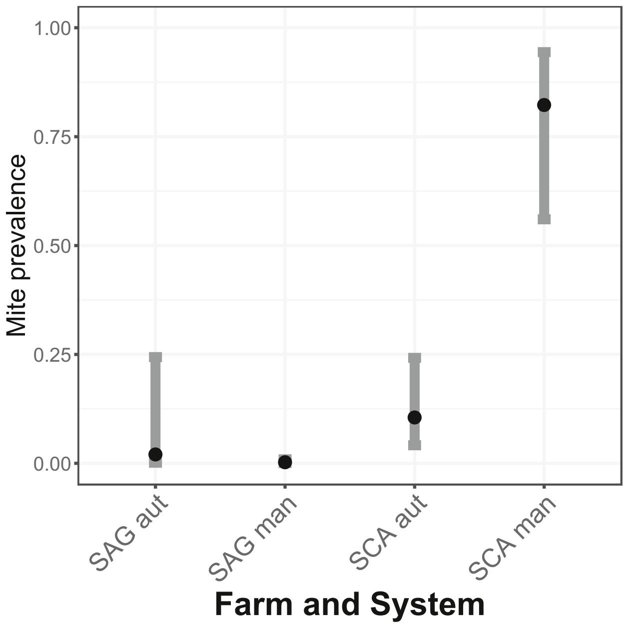

Fig. 8 Association between the farm and type of management system with the prevalence of mites as predicted by the prevalence average model for San Agustín and San Carlos farms. Variables that are not depicted in this prediction were set as follows: numerical variables (hen density in a cage and age) were set at its mean, lice were set at absent, feather density was set at level 1, season was set at summer, and sampling year was set at year I

hatching success at 30 °C, although at higher temperature the effect is reversed (Crystal 1985). As an alternative explanation, wild bird behaviour could vary according to weather conditions, food availability and their reproductive period, coming into contact with hens during certain seasons more frequently than others, and consequently, facilitating mite transmission and dispersal. Further studies are needed to enquire about this difference in seasonal patterns and environmental conditions within hen houses, as it is pertinent for control interventions.

Previous studies have shown more abundant *O. sylviarum* populations in cages with higher hen density (Hall et al. 1978; Arthur and Axtell 1982; Mullens et al. 2000). Our results showed that at high densities the prevalence starts to decrease rapidly. At higher numbers of hens in a cage the contact rate between them becomes greater, resulting in a higher mite transmission. However, there is possibility of a dilution effect taking place at high densities (Richner and Heeb 1995). This was documented also for another *Ornithonyssus* mite, *O. bursa*, on wild bird nestlings. The probability of mite occurrence on a nestling was lower at greater brood sizes (Arce et al. 2018). The dilution hypothesis is also reinforced by the results of the intensity model, in which, although not significant, both lineal and quadratic terms of density had a negative effect on mite intensity. An alternative explanation to the association between mite abundance and the hen density is a differential investment in resistance induced by social stress at higher densities. Social stress increases levels of corticosterone in the blood of hens, which in turn has been associated with higher efforts to resist *O. sylviarum* (Hall and Gross 1975; Hall et al. 1979).

San Agustin farm was the one with the lowest prevalence. This farm was the only one in which there was no acaricide treatment applied, nor were wild bird nests removed from hen houses (pers. obs.). Likewise, the fact that there was an interaction between farms and type of management system suggests that additional factors not assessed in the present analysis are having an influence on mite occurrence. There could be intrinsic factors differently distributed amongst hen houses that may be behind variation in mite abundance between them, such as hens' race or genetic lines (Burg et al. 1988; Owen et al. 2008), cleaning frequency of hen houses and work material (Hall and Gross 1975; Oliveira et al. 2020), presence of rodents that can potentially act as accidental hosts of *O. sylviarum* (Miller and Price 1977), wild bird species associated to the farm and their mite abundance, and permeability of hen houses to them (McCulloch et al. 2019; Arce et al. 2020), or the level of infestation of pullets prior to its transfer to laying hen house facilities (Kells and Surgeoner 1997), amongst others.

Overall, the present study emphasises the inherent complexity underneath the dynamics of parasitic mesostigmatid mite populations in commercial poultry houses, where several factors and their interactions have an impact on the abundance of *O. sylviarum* on hens. Interestingly, the components of abundance (intensity and prevalence) seem to be affected differently by some of the explanatory variables explored (e.g., farm, year, density of feathers are only significant for prevalence models although not for intensity). This highlights the relevance of analysing both epidemiological traits separately, as other studies on drivers of parasitism have found as well (e.g., Oppliger et al. 1998; Blersch et al. 2021; Bommarito et al. 2022).

Future studies are needed to better define the impact and mechanism behind some of the drivers of mite abundance exposed here. The relationship between mites and lice in poultry facilities has not been deeply explored, but the antagonistic interaction that is suggested here and in other studies suggest that leaving lice-infested flocks untreated may contribute to control *O. sylviarum*. Further investigation of this interaction and its costs and benefits is warranted to improve management practices involving parasite control.

The presence of *O. sylviarum* in South American farms has been noted relatively recently (Doti and Muzureta 1989; Tucci et al. 1998). Therefore, basic knowledge on the epidemiology of this pest and its economic importance in commercial poultry farms in this region is needed to aim at an effective control. Furthermore, based on the known

Table 4 Variables of interest for the average model for *O. sylviarum* intensity

	Estimate	Std. error	2.5%	97.5%	*P* value
Threshold coefficients					
1|2	3.659	4.146	–4.468	11.785	0.378
2|3	5.041	4.149	–3.092	13.173	0.224
3|4	6.443	4.154	–1.700	14.585	0.121
4|5	**8.326**	**4.160**	**0.172**	**16.480**	**0.045**
Variable coefficients					
Lice (present)[a]	**–1.629**	**0.667**	**–2.936**	**–0.321**	**0.015**
Feathers (level 2)[b]	–0.659	0.347	–1.338	0.020	0.057
Age	9.268	7.704	–5.832	24.367	0.229
Age^2	–2.973	3.432	–9.700	3.754	0.386
Density hens	–2.204	4.479	–10.982	6.574	0.623
Density hens^2	–1.883	3.246	–8.246	4.479	0.562
Season (spring)[c]	6.600	3.786	–0.821	14.021	0.081
Season (autumn)[c]	8.089	7.061	–5.751	21.929	0.252
Season (winter)[c]	**7.299**	**2.631**	**2.142**	**12.456**	**0.006**
System (manual)[d]	0.013	2.182	–4.265	4.290	0.995
Farm (HUM)[e]	–0.182	0.540	–1.241	0.877	0.736
Year (II)[f]	–1.171	0.803	–2.744	0.402	0.145
Age: season (autumn)[c]	–12.701	14.071	–40.279	14.876	0.367
Age: season (winter)[c]	**–7.354**	**2.142**	**–11.553**	**–3.156**	**0.001**
Age: season (spring)[c]	–5.935	7.005	–19.665	7.796	0.397
Age^2: season (autumn)[c]	4.117	7.573	–10.726	18.961	0.587
Age^2: season (winter)[c]	**–3.190**	**0.954**	**–5.060**	**–1.320**	**0.001**
Age^2: season (spring)[c]	–0.039	3.903	–7.690	7.611	0.992
Density hens: system (manual)[d]	5.232	8.062	–10.569	21.033	0.516
Density hens^2: system (manual)[d]	–4.056	5.638	–15.107	6.995	0.472
Year (II)[f]: season (spring)[c]	–2.105	3.107	–8.195	3.984	0.498
Year (II)[f]: season (autumn)[c]	–1.515	3.116	–7.622	4.593	0.627
Year (II)[f]: season (winter)[c]	**–6.003**	**1.602**	**–9.144**	**–2.862**	**<0.001**

Significant coefficients in bold ($\alpha = 0.05$)

[a] Compared to absent (lice reference)

[b] Compared to level 1 (reference feather)

[c] Compared to summer (reference season)

[d] Compared to automated (reference system)

[e] Compared to farm SCA (reference farm)

[f] Compared to year I (reference year)

widespread mite resistance to chemical treatments (Mullens et al. 2004), and the increasing concern on toxicity (Murillo and Mullens 2017), commercial egg production could benefit from an evidence-based integrative approach to mite control.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00436-022-07484-w.

Acknowledgements We would like to thank the owners of the poultry farms for giving us permission to use their flocks to conduct this study. We would also like to thank Valeria Corbalán and Silvina Sorroche for the assistance during the field work and Exequiel Furlan for creating the map with field site locations.

Author contribution All authors read and approved the final manuscript.

Idea of article by Pablo M. Beldomenico; data collection by Sofia I. Arce, Agustín Fasano, Claudia Sosa, Micaela Gomez, and Leandro R. Antoniazzi; draft preparation by Sofia I. Arce and Pablo M. Beldomenico; review and editing by all authors; and funding acquisition by Pablo M. Beldomenico and Martín A. Quiroga.

Funding This study was funded by the Argentine Council for Research and Technology, CONICET (www.conicet.gob.ar, Grant No. PIP 11220130100561CO), and by Universidad Autónoma de Entre Ríos (Res. 370–15).

Availability of data and material Detailed data will be made available upon request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

References

Aramburú R, Calvo S, Alzugaray M, Cicchino A (2003) Ectoparasitic load of monk parakeet (*Myopsitta monachus*, Psittacidae) nestlings. Ornitologia Neotropical 14:415–418

Arce SI, Manzoli DE, Saravia-Pietropaolo MJ et al (2018) The tropical fowl mite, *Ornithonyssus bursa* (Acari: Macronyssidae): environmental and host factors associated with its occurrence in Argentine passerine communities. Parasitol Res 117:3257–3267. https://doi.org/10.1007/s00436-018-6025-1

Arce SI, Monje LD, Antoniazzi LR et al (2020) Mesostigmatid mites (Acari: Mesostigmata) at the domestic-wildlife interface: poultry and passerine birds of central Argentina. Vet Parasitol 284:109203. https://doi.org/10.1016/j.vetpar.2020.109203

Arrabal JP, Manzoli DE, Antoniazzi LR et al (2012) Prevalencia del ácaro *Ornithonyssus bursa* Berlese, 1888 (Mesostigmata: Macronyssidae) en un ensamble de aves (Passeriformes) de bosques del centro de la Provincia de Santa Fe, Argentina. Rev Ibero-Latinoam Parasitol 71:172–178

Arthur FH, Axtell RC (1982) Northern fowl mite population development on laying hens caged at three colony sizes. Poult Sci 62:424–427

Axtell RC, Arends JJ (1990) Ecology and management of arthropod pests of poultry. Annu Rev Entomol 35:101–126

Blersch R, Bonnell TR, Barrett L, Henzi SP (2021) Seasonal effects in gastrointestinal parasite prevalence, richness and intensity in vervet monkeys living in a semi-arid environment. J Zool 314:163–173. https://doi.org/10.1111/jzo.12877

Bommarito C, Wahl M, Thieltges DW et al (2022) Biotic and abiotic drivers affect parasite richness, prevalence and abundance in *Mytilus galloprovincialis* along the Northern Adriatic Sea. Parasitology:1–9. https://doi.org/10.1017/S0031182021001438

Burg JG, Collison CH, Mastro AM (1988) Comparative analysis of precipitating antibodies in White Rock and Fayoumi hens injected with bovine serum albumin or crude mite extract with resulting effects on northern fowl mite, *Ornithonyssus sylviarum* (Acari: Macronyssidae) population densities. Poult Sci 67:1015–1019. https://doi.org/10.3382/ps.0671015

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304. https://doi.org/10.1177/0049124104268644

Castignani H (2011) Zonas Agroeconómicas Homogéneas Santa Fe. Estudios socioeconómicos de la sustentabilidad de los sistemas de producción y recursos naturales. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, p 61

Chaisiri K, McGarry JW, Morand S, Makepeace BL (2015) Symbiosis in an overlooked microcosm: a systematic review of the bacterial flora of mites. Parasitology 142:1152–1162. https://doi.org/10.1017/S0031182015000530

Chang Y, Wang XJ, Feng JH et al (2018) Real-time variations in body temperature of laying hens with increasing ambient temperature at different relative humidity levels. Poult Sci 97:3119–3125. https://doi.org/10.3382/ps/pey184

Chen BL, Haith KL, Mullens BA (2011) Beak condition drives abundance and grooming-mediated competitive asymmetry in a poultry ectoparasite community. Parasitology 138:748–757. https://doi.org/10.1017/S0031182011000229

Chen BL, Mullens BA (2008) Temperature and humidity effects on off-host survival of the northern fowl mite (Acari : Macronyssidae) and the chicken body louse (Phthiraptera: Menoponidae). Vet Entomol 101:637–646

Christensen RHB (2019) Ordinal–regression models for ordinal data. R package version 2019.12–10. Accessed 31 Jul 2020

Crutchfield CM, Hixson H (1943) Food habits of several species of poultry lice with special reference to blood consumption. Fla Entomol 26:63–66. https://doi.org/10.1093/besa/16.4.185b

Crystal MM (1985) Hatching of northern fowl mite eggs held at different temperatures and humidities. J Parasitol 71:122–124. https://doi.org/10.2307/3281992

da Fonseca F (1947) A monograph of the genera and species of Macronyssidae Oudemans, 1936 (synom.: Liponissidae Vitzthum, 1931) (Acari). Proc Zool Soc Lond 118:249–334

Daghir NJ (2008) Poultry production in hot climates. Cromwell Pres, Trowbrige

de Figuereido SM, Guimaraes JH, Gama NMSQ (1993) Biologia e ecologia de malófagos (Insecta: Phthiraptera) em aves de postura de granjas industriais. Rev Bras Parasitol Vet 2:45–51

DeVaney JA (1986) Effects of different feather lengths in the vent area of White Leghorn hens on northern fowl mite populations. Poult Sci 65:452–456. https://doi.org/10.3382/ps.0650452

Devaney JA (1979) The effects of the northern fowl mite, *Ornithonyssus sylivarium*, on egg production and body weight of caged white Leghorn hens. Poult Sci 58:191–194

DeVaney JA, Beerwinkle KR (1980) A nonchemical method of controlling the northern fowl mite, *Ornithonyssus sulviarum* (Canestrini and Fanzago), on caged White Leghorn hens. Poult Sci 59:1226–1228. https://doi.org/10.3382/ps.0591226

DeVaney JA, Ziprin RL (1980) Detection and correlation of immune responses in White Leghorn chickens to northern fowl mite, *Ornithonyssus sylviar*um (Canestrini and Fanzago), Populations. Poult Sci 59:34–37

do Carmo Rezende L, Martins NRDS, Teixeira CM et al (2016) Epidemiological aspects of lice (Menacanthus species) infections in laying hen flocks from the State of Minas Gerais Brazil. Br Poult Sci 57:44–50. https://doi.org/10.1080/00071668.2015.1127893

Doti F, Muzureta A (1989) Ensayo a campo con flumetrina pour-on en Argentina contra ácaros de la subfamilia Dermanyssinae – nuevo método de control de ectoparásitos en la gallina. Vet Argent 6:122

Faccini JLH, Massard CL (1974) Nota sobre a ocorrência de *Ornithonyssus sulviarum* (Canestrini & Fanzago) (Mesostigmata: Mascronyssidae) em Gallus gallus no Brasil. Arq Univ Fed Rural Rio De Janeiro 4:39–40

Freire J (1968) Fauna parasitária riograndense III. Coelho, cobaia, galinha doméstica, galinha d'Angola, peru, pombo, avestruz. Rev Med Vet São Paulo 3:251–267

Graham AL (2008) Ecological rules governing helminth-microparasite coinfection. Proc Natl Acad Sci U S A 105:566–570. https://doi.org/10.1073/pnas.0707221105

Halbritter DA, Mullens BA (2011) Responses of *Ornithonyssus sylviarum* (Acari: Macronyssidae) and *Menacanthus stramineus* (Phthiraptera: Menoponidae) to gradients of temperature, light, and humidity, with comments on microhabitat selection on chickens. J Med Entomol 48:251–261. https://doi.org/10.1603/ME10198

Hall ARD, Gross WB (1975) Effect of social stress and inherited plasma corticosterone levels in chickens on populations of the Northern fowl mite, *Ornithonyssus sylviarum*. J Parasitol 61:1096–1100

Hall RD, Gross WB, Turner EC (1979) Population development of *Ornithonyssus sylviarum* (Canestrini and Fanzago) on Leghorn roosters inoculated with steroids and subjected to extremes of social interaction. Vet Parasitol 5:287–297

Hall RD, Turner EC, Gross WB (1978) Effect of cage densities on northern fowl mite populations in commercial caged-layer operations. Poult Sci 57:564–566

Horn TB, Granich J, Körbes JH et al (2018) Mite fauna (Acari) associated with the poultry industry in different laying hen management systems in Southern Brazil: a species key. Acarologia 58:140–158. https://doi.org/10.24349/acarologia/20184233

Kells SA, Surgeoner GA (1996) Dispersion of northern fowl mites, *Ornithonyssus sylviarum*, between poultry facilities via infested eggs from layer and breeder flocks. J Agric Urban Entomol 13:265–274

Kells SA, Surgeoner GA (1997) Sources of northern fowl mite (*Ornithonyssus sylviarum*) infestation in Ontario egg production facilities. J Appl Poult Res 6:221–228. https://doi.org/10.1093/japr/6.2.221

Knee W, Proctor H (2007) Host records for *Ornithonyssus sylviarum* (Mesostigmata: Macronyssidae) from birds of North America (Canada, United States, and Mexico). J Med Entomol 44:150–154. https://doi.org/10.1603/0022-2585(2007)44

Krantz GW (1978) A manual of acarology. Oregon State University, Corvellis

Lareschi M, Cicuttin GL, De Salvo MN et al (2017) The tropical fowl mite *Ornithonyssus bursa* (Acari: Mesostigmata: Macronyssidae) parasitizing the European starling *Sturnus vulgaris* (Aves: Passeriformes: Sturnidae), an invasive bird in central Argentina. An approach to the bacterial fauna of this mite. Rev Mex Biodiversidad 88:454–458. https://doi.org/10.1016/j.rmb.2017.03.022

Lemke LA, Kissam JB (1986) The status of northern fowl mite research: how far have we come? J Agric Entomol 3:255–264

Marín-Gómez SY, Benavides-Montaño JA (2007) Parásitos en aves domésticas (*Gallus domesticus*) en el Noroccidente de Colombia. Vet Zootec 1:43–51

Mascarenhas CS, Coimbra MAA, Müller G, Brum JGW (2009) Ocorrência de *Ornithonyssus bursa* (Berlese, 1888) (Acari: Macronyssidae) em flhotes de *Megascops choliba* (orujinha-do-mato) e *Pitangus sulphuratus* (bem-te-vi), no Rio Grande do Sul, Brasil. Rev Bras Parasitol Vet 18:69–70. https://doi.org/10.4322/rbpv.01804013

McCulloch JB, Jeb P, Hinkle NC et al (2019) Genetic structure of northern fowl mite (Mesostigmata : Macronyssidae) populations among layer chicken flocks and local house sparrows (Passeriformes: Passeridae). J Med Entomol:1–9.https://doi.org/10.1093/jme/tjz136

McCulloch JB, Owen JP (2012) Arrhenotoky and oedipal mating in the northern fowl mite (*Ornithonyssus sylviarum*) (Acari: Gamasida: Macronyssidae). Parasit Vectors 5:281. https://doi.org/10.1186/1756-3305-5-281

Miller WV, Price FC (1977) The avian mite, *Ornithonyssus sylviarum*, on mammalian hosts with references to transmission to poultry. J Parasitol 63:417. https://doi.org/10.2307/3279990

Mullens BA, Hinkle NC, Szijj CE (2000) Monitoring northern fowl mites (Acari: Macronyssidae) in caged laying hens: feasibility of an egg-based sampling system. J Econ Entomol 93:1045–1054

Mullens BA, Owen JP, Kuney DR et al (2009) Temporal changes in distribution, prevalence and intensity of northern fowl mite (*Ornithonyssus sylviarum*) parasitism in commercial caged laying hens, with a comprehensive economic analysis of parasite impact. Vet Parasitol 160:116–133. https://doi.org/10.1016/j.vetpar.2008.10.076

Mullens BA, Velten RK, Hinkle NC et al (2004) Acaricide resistance in northern fowl mite (*Ornithonyssus sylviarum*) populations on caged layer operations in southern California. Poult Sci 83:365–374. https://doi.org/10.1093/ps/83.3.365

Murillo AC, Mullens BA (2017) A review of the biology, ecology, and control of the northern fowl mite, *Ornithonyssus sylviarum* (Acari: Macronyssidae). Vet Parasitol 246:30–37. https://doi.org/10.1016/j.vetpar.2017.09.002

Nakamae H, Kishi S, Fujisaki K et al (1996) Effect of trimming feathers off abdominal and crural tracts of the hen on parasitism of mites. Jpn Poult Sci 33:377–382

Oliveira TM, Teixeira CM, Rezende LC et al (2020) Epidemiologia e avaliação de risco associado à presença de ácaros hematófagos em galpões de granjas avícolas de postura. Arq Bras Med Vet Zootec 72:2148–2156

Oppliger A, Clobert J, Lecomte J et al (1998) Environmental stress increases the prevalence and intensity of blood parasite infection in the common lizard *Lacerta vivipara*. Ecol Lett 1:129–138. https://doi.org/10.1046/j.1461-0248.1998.00028.x

Owen JP, Delany ME, Mullens BA (2008) MHC haplotype involvement in avian resistance to an ectoparasite. Immunogenetics 60:621–631. https://doi.org/10.1007/s00251-008-0314-2

Radovsky FJ (2010) Revision of genera of the parasitic mite family Macronyssidae. Indira Publishing House, West Bloomfield

Reeves WC, Hammon WM, Doetschmann WH et al (1955) Studies on mites as vectors of western equine and St. Louis encephalitis viruses in California. Am J Trop Med Hyg 4:90–105

Reis J, Reis ASS, Nóbrega P (1934) Moléstias de aves observadas em Sao Paulo. Arq Inst Biol 5:41–49

Richner H, Heeb P (1995) Are clutch in birds and brood size patterns shaped by ectoparasites? Oikos 73:435–441. https://doi.org/10.2307/3545973

Santillán MÁ, Grande JM, Liébana MS et al (2015) New hosts for the mite *Ornithonyssus bursa* in Argentina. Med Vet Entomol 29:439–443. https://doi.org/10.1111/mve.12129

Serafini PS, Anjos LD, Arzua M et al (2003) First report of *Ornithonyssus sylviarum* (Acari: Macronyssidae) on black vulture (*Coragyps atratus*) nestlings from Brazil. Rev Bras Parasitol Vet 12:92–93

Sikes RK, Chamberlain RW (1954) Laboratory observations on three species of bird mites. J Parasitol 40:691–697

Teixeira CM, de Oliveira TM, Soriano-Araújo A et al (2020) *Ornithonyssus sylviarum* (Acari: Macronyssidae) parasitism among poultry farm workers in Minas Gerais State, Brazil. Ciencia Rural 50:1–7. https://doi.org/10.1590/0103-8478cr20190358

Téllez ML, Sordo C, Ruiz A et al (2008) Dermatosis por ácaros de palomas. Primer reporte de la presencia de *Ornithonyssus sylviarum* en el Perú. Folia Dermatol Peru 19:63–68

Trivedi MC, Rawat BS, Saxena AK (1991) The distribution of lice (Phthiraptera) on poultry (*Gallus domesticus*). Int J Parasitol 21:247–249. https://doi.org/10.1016/0020-7519(91)90016-Z

Tucci EC, Guimarães JH, Bruno TV et al (1998) Ocorrencia de ácaros hematófagos em aviários de postura no estado de Sao Paulo. Rev Bras Parasitol Vet 7:71–78

Valiente Moro C, Chauve C, Zenner L (2005) Vectorial role of some dermanyssoid mites (Acari, Mesostigmata, Dermanyssoidea). Parasite 12:99–109

Vas Z (1935) Ectoparasitas de animaes domesticos observados no estado de S. Paulo. Arq Inst Biol 6:29–33

Vezzoli G, Mullens BA, Mench JA (2015) Relationships between beak condition, preening behavior and ectoparasite infestation levels in laying hens. Poult Sci 94:1997–2007. https://doi.org/10.3382/ps/pev171

Terms and Conditions

Springer Nature journal content, brought to you courtesy of Springer Nature Customer Service Center GmbH (“Springer Nature”).

Springer Nature supports a reasonable amount of sharing of research papers by authors, subscribers and authorised users (“Users”), for small-scale personal, non-commercial use provided that all copyright, trade and service marks and other proprietary notices are maintained. By accessing, sharing, receiving or otherwise using the Springer Nature journal content you agree to these terms of use (“Terms”). For these purposes, Springer Nature considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the relevant terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). For Creative Commons-licensed articles, the terms of the Creative Commons license used will apply.

We collect and use personal data to provide access to the Springer Nature journal content. We may also use these personal data internally within ResearchGate and Springer Nature and as agreed share it, in an anonymised way, for purposes of tracking, analysis and reporting. We will not otherwise disclose your personal data outside the ResearchGate or the Springer Nature group of companies unless we have your permission as detailed in the Privacy Policy.

While Users may use the Springer Nature journal content for small scale, personal non-commercial use, it is important to note that Users may not:

1. use such content for the purpose of providing other users with access on a regular or large scale basis or as a means to circumvent access control;
2. use such content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval , sponsorship, or association unless explicitly agreed to by Springer Nature in writing;
4. use bots or other automated methods to access the content or redirect messages
5. override any security feature or exclusionary protocol; or
6. share the content in order to create substitute for Springer Nature products or services or a systematic database of Springer Nature journal content.

In line with the restriction against commercial use, Springer Nature does not permit the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Springer Nature journal content cannot be used for inter-library loans and librarians may not upload Springer Nature journal content on a large scale into their, or any other, institutional repository.

These terms of use are reviewed regularly and may be amended at any time. Springer Nature is not obligated to publish any information or content on this website and may remove it or features or functionality at our sole discretion, at any time with or without notice. Springer Nature may revoke this licence to you at any time and remove access to any copies of the Springer Nature journal content which have been saved.

To the fullest extent permitted by law, Springer Nature makes no warranties, representations or guarantees to Users, either express or implied with respect to the Springer nature journal content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Springer Nature that may be licensed from third parties.

If you would like to use or distribute our Springer Nature journal content to a wider audience or on a regular basis or in any other manner not expressly permitted by these Terms, please contact Springer Nature at

onlineservice@springernature.com