Parasitology Research (2019) 118:399–409
https://doi.org/10.1007/s00436-018-6174-2

ARTHROPODS AND MEDICAL ENTOMOLOGY - ORIGINAL PAPER

Ectoparasite sharing among native and invasive birds in a metropolitan area

Emilano Mori[1] · **Jordi Pascual Sala**[2] · **Niccolò Fattorini**[1] · **Mattia Menchetti**[3,4] · **Tomas Montalvo**[5,6] ·
Juan Carlos Senar[7]

Received: 10 July 2018 / Accepted: 3 December 2018 /

Abstract

Parasite-mediated competition has been reported to be one of the most harmful, although overlooked, impacts that alien species have on native ecosystems. Monk parakeets *Myiopsitta monachus* are successful invaders in Europe, where they have been introduced from South America. Colonial nests of these parrots may also host other species, e.g. the rock pigeon *Columba livia* forma *domestica*. In this work, we analysed the ectoparasite composition of monk parakeets in Barcelona (Spain) and we evaluated their potential role as parasite-mediated competitors, by comparing their parasitic load with that of coexisting rock pigeons. Only two arthropod species were observed on monk parakeets, whereas four species were detected on pigeons. Parakeets were rarely infested by pigeon parasites (prevalence = 0.66%), whereas parakeet mites were recorded more often on pigeons (prevalence = 10.00%). The number of total parasites per bird increased with increasing densities of monk parakeets, both for pigeons and for parakeets. Therefore, overcrowding of birds due to the increasing population of monk parakeets in Barcelona may affect the health status of native pigeons, suggesting a potential role for parasite mediated competition by introduced parakeets. Furthermore, spill-over of alien mites (*Ornithonyssus bursa*) by monk parakeets to rock pigeons should be monitoring as it may affect human health.

Keywords Alien species · *Columba livia* · *Myiopsitta monachus* · Parasite-mediated competition · Spill-back · Spill-over

Introduction

Invasive alien species occupy the ecological niche of native species at an alarming rate and alter the structure and the function of native ecosystems, through hybridisation, competition, predation, parasitism and disease (e.g. Mack et al. 2000; Mazza et al. 2014; Nentwig et al. 2018). Two species may compete one another through the inter-transmission of several parasite species they share (Price et al. 1986; McInnes et al. 2013); therefore, parasites may have a substantial role in biological invasions. When a species establishes new populations outside its natural range, it may spread its own parasites to the invasion range ("spill-over process") and/or be subjected to the infection by local parasites ("spill-back process")

Section Editor: Domenico Otranto

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00436-018-6174-2) contains supplementary material, which is available to authorized users.

✉ Emilano Mori
moriemiliano@tiscali.it

[1] Dipartimento di Scienze della Vita, Università degli Studi di Siena, Via P.A. Mattioli 4, 53100 Siena, SI, Italy

[2] Agència de Salut Pública de Barcelona, Plaza de Lesseps, 1, 08023 Barcelona, Spain

[3] Institut de Biologia Evolutiva (CSIC-Universitat Pompeu Fabra), Barcelona, Spain

[4] Dipartimento di Biologia, Università degli Studi di Firenze, Via Madonna del Piano 6, Sesto Fiorentino, 50019 Florence, Italy

[5] Servei de Vigilància i Control de Plagues Urbanes, Agència de Salut Pública de Barcelona, Av. Príncep d'Astúries 63, 3r 2a, 08012 Barcelona, Spain

[6] CIBER Epidemiology and Public Health, Public Salud Agency of Barcelona, Barcelona, Spain

[7] Museu de Ciències Naturals de Barcelona, Psg. Picasso s/n., 08003 Barcelona, Spain

increasing their spread success (Colautti et al. 2014; Romeo et al. 2014; Mori et al. 2018a). The spill-back process has been long overlooked in biological invasions (Kelly et al. 2009; Romeo et al. 2014), despite growing interest in recent times, mostly involving spill-back that impacts human health (Marsot et al. 2013; Vourc'h et al. 2016). Accordingly, an introduced host infested by native ectoparasites may suffer from these ectoparasite attacks which, in turn, may influence its invasion process (Prenter et al. 2004; Kelly et al. 2009). This cross-infestation may also locally increase the distribution of native parasites, which may in turn alter the dynamics of infestation on native hosts (e.g. Mori et al. 2018a). Among birds, parakeets are widely recorded as alien birds worldwide, with the ring-necked parakeet *Psittacula krameri* and the monk parakeet *Myiopsitta monachus* (hereafter, MP) being the most abundant ones (Menchetti and Mori 2014; Edelaar et al. 2015; Parau et al. 2016; Turbè et al. 2017).

Most colonies of introduced MPs occur in urban areas (Moltoni 1945; Muñoz and Real 2006; Sol et al. 2017), and their ecological impacts have been widely studied (Menchetti and Mori 2014; Reed et al. 2014; Castiglioni et al. 2015; Di Santo et al. 2016; Senar et al. 2016). In America, MPs may kill blue jays *Cyanocitta cristata*, American robins *Turdus migratorius* and house sparrows *Passer domesticus* around colonial nests (MacGregor-Fors et al. 2011), particularly when at very high densities. Conversely, in Europe, where nesting trees are abundant and do not represent a limiting resource, sparrows may use the nests of MPs for breeding (Moltoni 1945; Batllori and Nos 1985). In European countries, harassments by MPs have been observed against jackdaws *Corvus monedula*, hooded crows *Corvus cornix* and common kestrels *Falco tinnunculus* at nesting sites (Dangoisse 2009; Menchetti and Mori 2014; Di Santo et al. 2016). Conversely, MPs frequently share feeding and nesting sites with the feral rock pigeon *Columba livia* forma *domestica* (hereafter, RP) without any apparent competition (Moltoni 1945; Weiserbs and Jacob 1999; Dangoisse 2009; Zocchi et al. 2009; Appelt et al. 2016). Little information is available on ectoparasite loads of MPs, with only a few parasite species reported on them in Italy: the introduced South American louse *Paragoniocotes fulvofasciatus* and tropical blood-eating mite *Ornithonyssus bursa*, as well as the native pigeon louse *Columbicola columbae* and flat flies *Crataerina pallida* and *Ornithophila metallica* (Mori et al. 2015a; Ancillotto et al. 2018). In the native range (South America), the tropical blood-eating mite is abundant on chicks of MP and it has been recorded in a number of synoptic bird species (Aramburù et al. 2003). This parasite has been occasionally spotted also in Europe (Viviano and Bongiorno 2014); its bites may provoke dermatitis, asthma and skin rashes in humans (Orton et al. 2000).

The metropolitan area of Barcelona (Spain) hosts one of the largest, increasing colony of MPs in Europe, coexisting with a number of native bird species and widely observed while foraging together with RPs (Batllori and Nos 1985; Rodríguez-Pastor et al. 2012). Thus, introduced MPs may be prone to spillback from native species. Furthermore, MPs show clustered distributions within European cities, mostly linked to selected nesting plant species (Sol et al. 1997). By contrast, RPs may range for up to 6 km from their nests to reach feeding sites and, therefore, they show a continuous distribution over urban areas (Baldaccini et al. 2000; Rose et al. 2006a; Soldatini et al. 2006).

In this work, we aimed at assessing the species composition of the ectoparasite community of MPs in Barcelona and at evaluating their potential role as parasite-mediated competitors, by comparing their ectoparasite load with that of coexisting RPs. According to the "enemy release hypothesis", alien species lose a high proportion of their ectoparasites following the introduction outside their native range (Colautti et al. 2014; Romeo et al. 2014). Thus, it is suggested that they might be more susceptible to native ones (Mori et al. 2015b, 2018a, b). We predicted (i) a higher parasite diversity and higher infestations in native RPs, with respect to introduced MPs. In turn, given the "enemy release hypothesis", we also predicted that spill-back would be much more frequent than spill-over, as a lower diversity in parasite infestations on the introduced host might favour the transmission and spread of native parasites on the "new" host (ii).

Materials and methods

Study area

Our research was carried out within the metropolitan area of Barcelona (north-eastern Spain: Fig. 1). Barcelona covers an area of 102.16 km^2, mostly composed by human settlements and buildings (72.3%). This city is divided into ten districts (Fig. 1), and it hosts one of the largest MP colony in Europe, including over 5000 individuals, with a clustered distribution according to the last census (Senar et al. 2017a; Fig. 1). About 85,000 individuals of feral RPs evenly occur throughout the city (in 2015: Montalvo et al. 2017). The population of ring-necked parakeets is still low in Barcelona (i.e. less than 300 individuals: Senar et al. 2017b), and this parrot species rarely interacts with RPs (Hernández-Brito et al. 2014; Menchetti et al. 2016). Conversely, RPs quite often use abandoned nests of MPs to breed, and then they could easily be infested by their parasites (cf. Moltoni 1945; Ancillotto et al. 2018). As well, few blue-crowned parakeets *Psittacara acuticaudatus* and red-masked parakeets *Psittacara erythrogenys* are also present in Barcelona, but no interaction with native birds has been reported (Santos 2006).

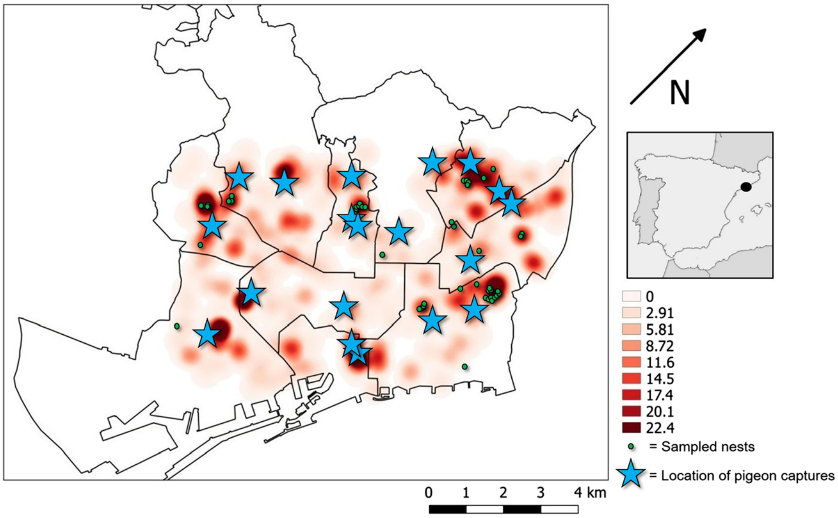


Fig. 1 Location of trees where chicks of MP were sampled in Barcelona ("sample nests"). Location of sites where RPs were captured through compressed air propelled nets are also reported. The heat map (made through the QGIS tool "heatmap") shows the density of trees with MP nests in the city (2015 census: Senar et al. 2017a, b)

Selection of MP nests

We created a shapefile including all trees hosting MP nests through the software QGIS (www.qgis.org. Accessed on 10 April 2017), following the 2015 census (Senar et al. 2017a). Then, we built up a polygon layer encompassing all the MP colonies. We defined as a "colony" every group of individuals nesting in clusters of trees located in a single urban geographic location (square, park, garden, avenue, street): none of the trees were separated by more than 100 m from the nearest one. We excluded from our analyses all the colonies located in the city centre (i.e. Ciutadella Park area): MP population dynamics studies by JCS are ongoing in this area, and we did not want to affect results. As to the other colonies, we first visited them to determine the accessibility to trees and nests. We needed to reach the tree base with a truck crane, and in many parks, gardens, streets and avenues, this was not possible. Furthermore, in some trees, nests were too high or tree branches prevented us to sample them. We then selected a subsample of available colonies spread apart (Fig. 1), so that they were representative for the distribution of the MP in Barcelona (Senar et al. 2017a). The first clutch of MPs in Barcelona usually takes place from March to May–June, and the second one—when parasites for our study were collected—from June to July–August. Parasites were collected from 17 colonies in July.

Sampling methods

In each colony, we checked all the trees with MP nests accessible to the truck crane. For each checked tree, we checked all the chambers of each nest. On July, about one third of all chambers (30%; $n = 149$) was occupied. Some chambers were occupied by RPs, which used the MP nests (Supplementary Material 1). When a chamber occupied by MP or RP chicks was detected, we collected birds alive and we put them in a divided box. Chicks coming from the same chamber were put into the same division of the box, which was assigned to a unique code (Supplementary Material 1). Chicks were distinguished from adults following Navarro and Bucher (1990). Once we finished checking the nests of one tree, birds were checked for parasites and released at the capture point. Furthermore, RPs were also captured using compressed air propelled nets during an ongoing numerical control program of urban birds carried out by the Monitoring and Control of Urban Pests Service (Barcelona City Council) in 18 localities included within all the districts of Barcelona (Fig. 1). Capture areas were selected according to the local density of RPs (Pascual et al. 2015) and also occurred in the surroundings of the highest densities of MPs.

We sampled a total of 178 MPs and 340 RPs: MP chicks came from 58 trees and 68 chambers, located in 17 sampling sites. In 39 chambers, we collected only 1 chick; in 22 chambers, we collected 2 brother chicks; in 11 chambers, we collected 3 chicks; in 9 chambers, we collected 4 chicks; and in 4 chambers, we collected 5 chicks.

Collection and identification of ectoparasites

We collected ectoparasites from the plumage of each captured bird. Individuals were set on a white tray and a pesticide was sprayed on their plumage. After 2 min, the plumage was thoroughly brushed for the collection of ectoparasites. We also applied an electric aspirator throughout the plumage to collect remaining parasites. The feathers of the head, the neck, under the wings, body, legs and cloaca were raised and thoroughly examined with a hand lens. Attached ectoparasites such as mites, which could not be removed by brushing or aspiration, were gently dislodged with tweezers. Collected ectoparasites were counted and preserved in labelled vials, containing 70% alcohol. Parasites were identified using keys (lice, Mallophaga: Johnson and Clayton 2003; mites, Acarina:

Baker 1999; flat flies, Hippoboscidae: Hutson 1984). All identifications were accomplished through examination of samples at stereomicroscope (× 400: Leica DM8000 M).

Statistical analyses

We investigated differences in parasites load using generalised linear mixed models (GLMMs; Zuur et al. 2009). We considered the number of specimens of each arthropod species counted per examined host individual, i.e. including not infested hosts. In turn, we modelled 5 different indicators, i.e. our response variables: (i) the overall number of parasite specimens, (ii) the number of specimens of *O. bursa*, (iii) the number of specimens of *C. columbae*, (iv) the number of specimens of *C. bidentatus* and (v) the number of specimens of *P. canariensis* counted in each sampled bird. We modelled our indicators using negative binomial errors (link: log), which are suited for count data as well as can handle potential overdispersion (Zuur et al. 2009). Statistical analyses were performed following the information-theoretic approach (Burnham and Anderson 2002), by evaluating multiple candidate models for each indicator. Global models included all the biologically meaningful fixed effects which could influence our response variables.

We investigated the variation in the number of parasite specimens counted on host individuals according to the following, potential influencing factors: host species (two levels: RP vs MP; reference category: RP), MP density (continuous variable: number of breeding pairs/5 m^2), extent of urban green area (continuous, in hectares) and sampling date (continuous, Julian day). In addition, we included three interaction terms as potential influencing predictors: the interaction between the host species and the extent of urban areas, the interaction between the host species and the density of MPs as well as the interaction between the host species and the sampling date, to test whether host-specific effects on parasites load may occur. Modelling the number of *C. columbae*, *C. bidentatus* and *P. canariensis* in relation to host species and relevant interactive effects was not necessary, since these parasites were mostly found in RPs, without infesting MPs (Supplementary Material 1). Thus, for these arthropod species, we analysed a subsample of the total dataset, by considering the sampled RPs only, to assess how they vary in relation to monk parakeet density, green area extent and sampling date, as predictors.

The number of parasites is expected to be associated for those host individuals which share the same nesting chamber, as well as for those living in the same nesting tree/urban green area, likely showing a hierarchical spatial autocorrelation. In turn, each model included crossed and nested random effects among/within nesting trees and nesting areas. In detail, we included the following: (i) the sampling nesting chamber as a random intercept nested within the nesting tree, to account for repeated counts of parasites on birds sharing the same nesting chamber; (ii) the nesting tree as a random intercept nested within the nesting green area, to account for repeated counts of parasites on birds living in the same nesting tree; and (iii) nesting areas as a random intercept, to account for repeated measures within and between different urban green areas. Consequently, hierarchical random structure of our models should allow to handle potential spatial autocorrelation of response variables (Zuur et al. 2009).

Continuous predictors were centred to improve the interpretability of models' main effects and interactions (Schielzeth 2010). Multicollinearity among covariates was tested for each full model by calculating the variance inflation factor (VIF) for all the predictors. All VIF values were < 2, indicating no multicollinearity (Zuur et al. 2009). VIFs were calculated through the R package *car* (Fox and Weisberg 2011). Model selection was performed following the minimum Akaike's Information Criterion, corrected for small samples (AICc: Burnham and Anderson 2002). For each response variable, all alternative models were ranked and weighted from the global model. Models with ΔAICc ≥ 2 of the best model, as well as models with an AICc value greater than that of any simpler, nested alternative were not selected. For each response variable, coefficients of predictors, 95% confidence intervals and variance of random effects were estimated for the top-ranked model. Significance of predictors was assessed by checking whether 95% confidence intervals included 0. Model selection and GLMMs were performed through the R packages *MuMIn* (Bartoń 2012) and *lme4* (Bates et al. 2015), respectively. Validation of the best models was made by visual inspection of residual patterns (Zuur et al. 2009), as well as by calculating and testing the dispersion variance factor (cf. Zuur et al. 2009; Bolker 2018) through the R package *sjstat* (Lüdecke 2018).

Results

We obtained 1805 ectoparasites from 173 out of 178 MPs, belonging to 2 species (Table 1; see also Supplementary Material 1 for detailed information on sampled individuals) and 2463 ectoparasites from 339 out of 340 sampled pigeons, belonging to 4 species (Table 1). Parasite load did not change significantly among birds able and unable to fly ($\chi^2_{RP} = 1.43$, $p = 0.18$; $\chi^2_{MP} = 0.09$, $p = 0.73$); thus, we pooled together the relevant data.

MPs showed a higher prevalence for *O. bursa* with respect to RPs, which showed the highest prevalence for the other parasites species (Table 1). In particular, no *C. bidentatus* and *P. canariensis* were found in MPs, while only 2 out of 178 sampled MPs were infected by *C. columbae* (Table 1).

Table 2 shows the selected models. No overdispersion was detected in our best models ($\phi_{\text{overall no. of parasites}} = 0.8056$,

Table 1 Ectoparasite load assessed on monk parakeets (MPs) and rock pigeons (RPs) in Barcelona (n = number of chicks sampled; A = alien, N = native)

Parasite species (typology, origin)	Chicks infested		Mean ± SE no. parasite specimens/chick	
	MP ($n = 178$) (%)	RP ($n = 340$) (%)	MP ($n = 178$)	RP ($n = 340$)
Ornithonyssus bursa (Mite, A)	97.19	10	10.01 ± 1.08	0.44 ± 0.09
Columbicola columbae (Louse, N)	1.12	90.29	0.13 ± 0.10	3.71 ± 0.17
Campanulotes bidentatus (Louse, N)	0	58.82	Nil	1.61 ± 0.12
Pseudolynchia canariensis (Flat fly, N)	0	70.88	Nil	1.48 ± 0.07

$\chi^2 = 409.2238$, $p = 0.9995$; $\phi_{\text{no. of } O.\ bursa} = 0.3517$, $\chi^2 = 178.6589$, $p = 0.9995$; $\phi_{\text{no. of } C.\ columbae} = 0.7083$, $\chi^2 = 235.1649$, $p = 1$; $\phi_{\text{no. of } C.\ bidentatus} = 0.5860$, $\chi^2 = 195.1310$, $p = 1$; $\phi_{\text{no. of } P.\ canariensis} = 0.6468$, $\chi^2 = 215.3843$, $p = 1$; Table 3). Overall, the number of parasites counted in a bird was higher in RPs and increased with the MP density whichever the host species (Table 3a; Fig. 2a). The number of *O. bursa* specimens counted was higher in MPs, decreased through sampling period (Table 3b; Fig. 3) and was influenced by the interaction between the host bird species and MP density; *O. bursa* increased with MP density for MPs, but not for RPs (Table 3b; Fig. 2b). As to ectoparasites infesting RPs only (*C. columbae*, *C. bidentatus* and *P. canariensis*), all the arthropod species showed an increase of the specimens counted with increasing density of MPs (Table 3c, d, e; Fig. 4). No response variable was influenced by the extent of urban green areas (Tables 2 and 3).

Discussion

The "enemy release hypothesis" (Colautti et al. 2014) suggests that alien species lose most of their ectoparasites after the introduction process in new areas (Romeo et al. 2014; Mori et al. 2015b; Mazzamuto et al. 2016). Therefore, parasite-mediated by alien species has been for long overlooked in studies on biological invasions. Despite this, some parasites may survive the introduction event, and attention on this topic recently increased, particularly when involving human health and wellness (for a review, see Mazza et al. 2014). MP chicks are infested by more ectoparasites in their native range (Aramburù et al. 2003), with respect to the introduced one. Only one species, the tropical fowl mite *O. bursa*, occurred with a high prevalence in our sample. Mite prevalence in MP was high in areas dominated by urban settlements, most likely because of bird health conditions within polluted urban districts (Haag-Wackernagel 2005; Delgado and French 2012), as well as of parakeet overcrowding in urban areas (Rodríguez-Pastor et al. 2012). Conversely, native European parasites are very rare (lice) or totally absent (flat flies) on MPs, with only few pigeon lice *C. columbae* observed, discarding the hypothesis of spill-back occurrence. Thus, despite overcrowding, parakeets are poorly vulnerable to native parasite attacks (see Masello et al. 2018). In Europe, RPs host a high number of parasite species (i.e. up to 10–23 species of ecto-and endo-parasites), particularly in urban areas

Table 2 Result of models selection: best models and models with $\Delta AIC_c < 2$, each with K, AIC_c value, ΔAIC_c and weight. Response variables are intended per sampled chick. All the models run also include crossed and nested random intercepts (see "Materials and methods")

Dataset	Response variable	Models retained (fixed effects)	K	AIC_c	ΔAIC_c	Weight
Monk parakeets and rock pigeons ($n = 518$)	No. of parasite specimens	host species + MP density + green area extent + host species × MP density	10	3107	0	0.390
		host species + MP density + green area extent	9	3107.1	0.11	0.371
		host species + MP density + host species × MP density	9	3108	0.97	0.239
	No. of *O. bursa* specimens	host species + MP density + Julian day + host species × MP density	10	1561.8	0	0.613
		host species + Julian day	8	1562.7	0.92	0.387
Rock pigeons ($n = 340$)	No. of *C. columbae* specimens	MP density + green area extent	8	1523.5	0	0.51
		MP density	7	1523.5	0.01	0.49
	No. of *C. bidentatus* specimens	MP density	7	1097.3	0	1
	No. of *P. canariensis* specimens	MP density	7	970.8	0	1

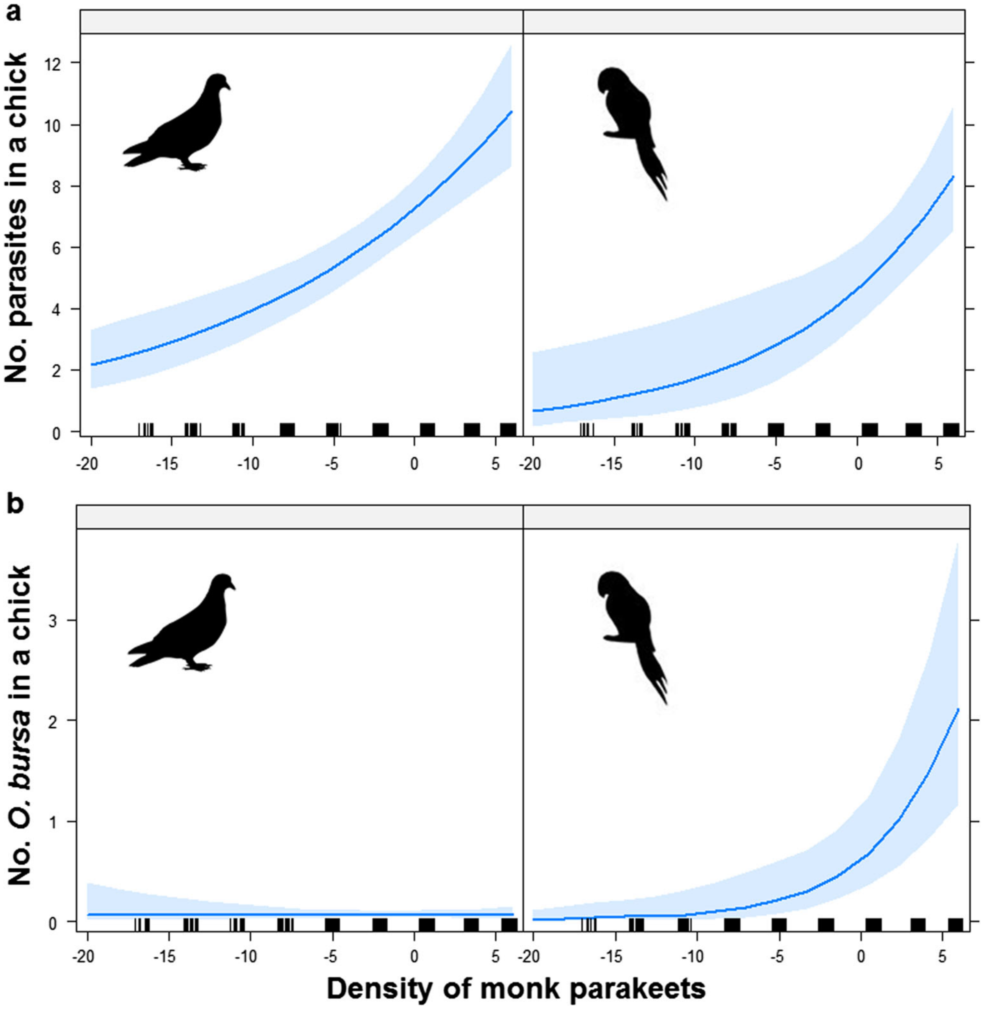
Table 3 Parameters estimated (B: coefficient; CI: 95% confidence interval; ϕ: variance dispersion factor; variance of random factors) for the top-ranked models of ectoparasites counted in RP and MP chicks. Continuous predictor are centred. The reference category of host species is RP. Predictors whose 95% CIs do not include 0 are shown in bold

Response variable	Predictor	B	95% CI
a) No. parasite specimens ϕ = 0.8056 (nesting chamber : nesting tree) variance = 0.1800 (nesting tree) variance = 0.0059 (nesting tree : nesting area) variance = 0.0070 (nesting area) variance < 0.0000	**intercept**	**1.9811**	**1.8840; 2.0783**
	host species (MP)	**-0.4559**	**-0.7105; -0.2011**
	MP density	**0.0608**	**0.0449; 0.0767**
	green area extent	0.0170	-0.0020; 0.0361
	host species (MP) : MPs density	0.0380	-0.0125; 0.0885
b) No. *O. bursa* specimens ϕ = 0.3517 (nesting chamber : nesting tree) variance = 1.3400 (nesting tree) variance < 0.0000 (nesting tree : nesting area) variance < 0.0000 (nesting area) variance = 3.2600	**intercept**	**-2.7613**	**-3.6889; -1.8337**
	host species (MP)	**2.2684**	**1.1163; 3.4205**
	MPs density	-0.0009	-0.1263; 0.1244
	Julian day	**-0.0601**	**-0.0928; -0.0275**
	host species (MP) : MPs density	**0.2077**	**0.0141; 0.4013**
c) No. *C. columbae* specimens ϕ = 0.7083 (nesting chamber : nesting tree) variance = 0.1270 (nesting tree) variance < 0.0000 (nesting tree : nesting area) variance < 0.0000 (nesting area) variance = 0.1330	**intercept**	**1.2369**	**1.0852; 1.3886**
	MP density	**0.0494**	**0.0254; 0.0734**
	green area extent	0.0348	-0.0115; 0.0811
d) No. *C. bidentatus* specimens ϕ = 0.5860 (nesting chamber : nesting tree) variance = 0.2866 (nesting tree) variance < 0.0237 (nesting tree : nesting area) variance < 0.0097 (nesting area) variance = 0.4348	intercept	0.1437	-0.1334; 0.4207
	MP density	**0.0741**	**0.0321; 0.1160**
e) No. *P. canariensis* specimens ϕ = 0.6468 (nesting chamber : nesting tree) variance < 0.0000 (nesting tree) variance < 0.0000 (nesting tree : nesting area) variance < 0.0000 (nesting area) variance = 0.2890	**intercept**	**0.3343**	**0.1201; 0.5485**
	MP density	**0.0803**	**0.0447: 0.1159**

(Ferman et al. 2010; Delgado and French 2012; Mori et al. 2018b). Accordingly, in our sample, RPs showed a higher number of ectoparasites and a higher arthropod species-richness, with respect to MPs, thus fulfilling our prediction (i). Furthermore, 10.00% of sampled RPs were infested by O. bursa, a typical parasite of MPs, indicating that spill-over process was common differently from spill-back, therefore providing evidence to the opposite of our prediction (ii). This may be due to the nature of the ectoparasites. On one side, lice are often highly-specific to their host species (Johnson and Clayton 2003), thus explaining why pigeon lice infesting RPs are rare on MPs. On the other side, acarid mites, as those detected on alien MPs, may develop in a wild array of bird host species, thus potentially infesting native bird species, e.g. RPs (Baker 1999). Being wide-ranging birds (Rose et al. 2006a), RPs may spread *O. bursa* over large areas (i.e. over 150 ha: Baldaccini et al. 2000; Rose et al. 2006a, b; Soldatini et al. 2006), thus increasing the transmission risk of this mite and posing a further risk to human health (Orton et al. 2000; Mori et al. 2018b). Bites of *O. bursa* may affect human health, provoking dermatitis, asthma, severe irritations and skin rashes in humans (Orton et al. 2000). *Ornithonyssus bursa* is frequently found on a number of bird species in tropical and subtropical areas (Mori et al. 2018b), where it is reported as a vector of viruses affecting both wild birds and poultry activities (Santillán et al. 2015). This parasite has also been occasionally found in Europe (Viviano and Bongiorno 2014), where several alien populations of MPs occur (Edelaar et al. 2015).

We showed that the number of total parasites on each sampled bird (both MPs and RPs) increased with increasing density of birds (both MPs and RPs), whereas the size of green areas did not influence it. This finding supports the hypothesis that introduced MPs might represent good candidates for parasite-mediated competition with native birds (Mori et al. 2015a; Ancillotto et al. 2018). In details, ectoparasites load was higher on RPs with respect to MPs, furtherly confirming our prediction (i). Where the density of MPs is the highest (cf. Fig. 1), RPs increase their susceptibility also to their native ectoparasites, which may affect their health status. This may be due to the fact that RPs and MPs use to feed on the same areas, often on the same trophic resources (Carrillo-Ortiz

Fig. 2 Relationship between density of MPs (breeding pairs/5 m^2, mean-centred $\bar{x}$ = 16.6125) and **a** the overall number of ectoparasite specimens and **b** the number of *O. bursa* specimens counted in RPs (left panels) and MPs (right panels) chicks. Lines and bands show predicted values and 95% confidence intervals estimated by GLMMs



2009; Menchetti and Mori 2014; Di Santo et al. 2016), which might elicit interspecific competition and, in turn, susceptibility to ectoparasite attack (cf. Lafferty and Holt 2003; Tschirren et al. 2007).

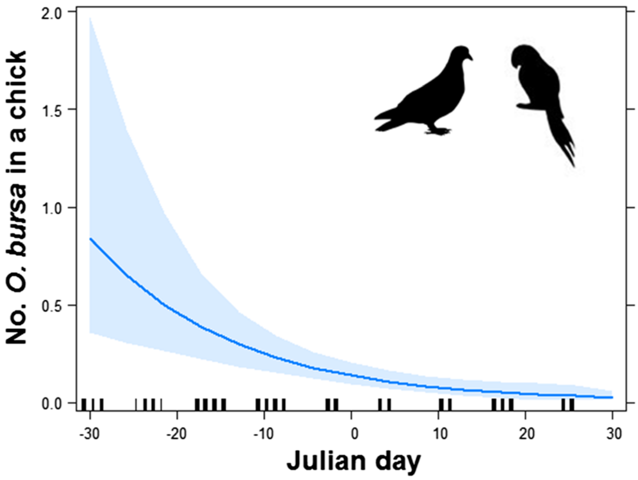


Fig. 3 Relationship between Julian day (mean-centred $\bar{x}$ = 216.7066) and the number of *O. bursa* specimens counted in host chicks. Lines and bands show predicted values and 95% confidence intervals estimated by GLMMs

The number of mites per bird was higher on MPs than on RPs, although it increased with increasing density of MPs only, i.e. of their specific host, but not of RPs. In our sample, infestations by *O. bursa* decreased with increasing date, thus providing support to the fact that this mite is linked to nests and to unfledged chicks, while leaving birds when near to flight (cf. Aramburù et al. 2003; Mori et al. 2018b).

MPs use to share their colonial nests with other species both in the native range (e.g. with jabirus *Jabiru mycteria* and RPs: Burger and Gochfeld 2005; Nores 2009) and in the introduced one (e.g. with Italian sparrows *Passer italiae*, RPs, introduced sacred ibis *Threskiornis aethiopicus*, white storks *Ciconia ciconia* and jackdaws *Corvus monedula*: Moltoni 1945; Castiglioni et al. 2015; Gioele Grandi and Jordi Pascual, personal observations). Thus, we suggest that the risk of virus/parasite transmission to native birds would occur. Accordingly, contacts between MPs and other synurbic birds may occur both at feeding and at nesting sites (e.g. Dangoisse 2009; MacGregor-Fors et al. 2011; Di Santo et al. 2016), despite being more uncommon than

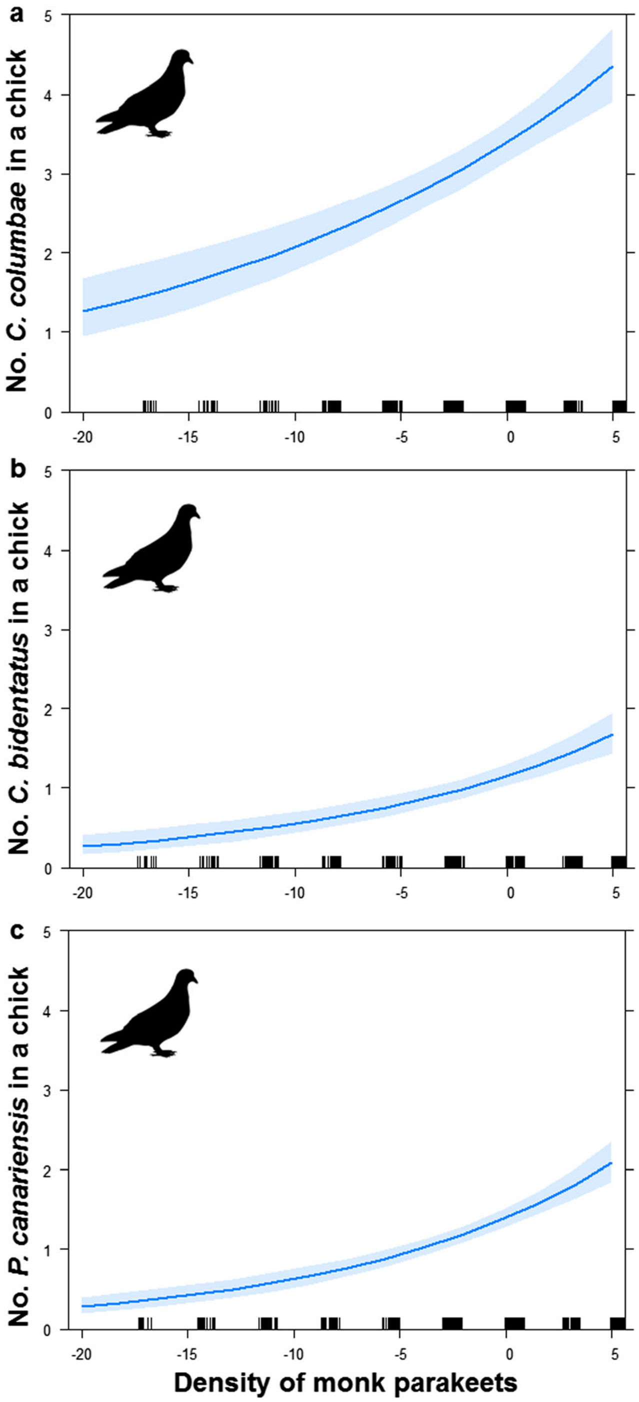


Fig. 4 Relationship between density of MPs (breeding pairs/5 m^2, mean-centred $\bar{x} = 17$) and the number of specimens of **a** *C. columbae*, **b** *C. bidentatus* and **c** *P. canariensis* counted in rocky pigeon chicks. Lines and bands show predicted values and 95% confidence intervals estimated by GLMMs

those between native birds and invasive ring-necked parakeets (Menchetti et al. 2016; Covas et al. 2017).

Furthermore, colonial nests are used by MPs as roosts outside the breeding period (Moltoni 1945; Hyman and Pruett-Jones 1995; Postigo et al. 2017). Arthropod ectoparasites often overwinter in nesting holes and dens (Cox et al. 1999; Ancillotto et al. 2014). Thus, they may affect chicks of the same chamber in the following breeding season independently from the species they belong to (Aramburú and Campos Soldini 2008). Commensalism and syntopy between native and alien species increased the frequency of inter-individual contact, thus enhancing ectoparasite load and sharing. Even if only neutral interactions have been reported between MPs and RPs (Nores 2009; Di Santo et al. 2016), diet overlap and feeding/nesting/roosting site sharing may result in interspecific competition. The invasion success of the MP (e.g. Hobson et al. 2017; Postigo et al. 2017) may be favoured by the low species richness in arthropod they are infested with. Conversely, infested RPs may exponentially spread arthropod infestations and vector-borne diseases even outside metropolitan areas. RPs may increase the spread of vector-borne diseases brought by MP mites, as they may affect both wildlife (e.g. other MPs) and human health in urban and periurban contexts (Mori et al. 2018b).

In light of all these considerations, and also given the impacts of MPs to local agriculture (Senar et al. 2016), management actions should be rapidly taken into account following the European guidelines (Crowley et al. 2017; Carboneras et al. 2018; Crowley et al. 2018;). Further research should be deserved to analyse the effects of parasites on the fitness of native birds (e.g. house sparrows and tits *Parus major* and *Cyanistes caeruleus:* cf. Lymbery et al. 2014) and the importance of spill-back by MPs in other invaded areas. Special attention should also be paid to vector-borne disease, especially those transmitted by *O. bursa* to native vertebrates, humans included (Orton et al. 2000; Mori et al. 2018b).

Acknowledgements Birds were handled and ringed with the permission of Institut Català d'Ornitologia and the Environment Department of the Generalitat de Catalunya. We also wish to acknowledge the support provided by COST European Cooperation in Science and Technology Actions ES1304 "ParrotNet" for the development of this manuscript. The contents of this manuscript are the authors' responsibility and neither COST nor any person acting on its behalf is responsible for the use that may be made of the information contained herein. D. Beal and V. Sfondrini kindly took the time to read our manuscript and improve English language and syntax. Two anonymous reviewers greatly improved our first draft with useful comments.

Author contributions JCS, JP and EM conceived the idea and wrote most of the paper. TM, JP and JCS collected the parasites; EM and MM identified the parasites of monk parakeets. NF performed the statistical analyses and wrote the relevant part of the manuscript, as well as participated in writing the last draft.

Funding information The present study was funded by CGL-2016-79568-C3-3-P research project to JCS from the Spanish Research Council (Ministry of Economics and Competiveness).

Compliance with ethical standards

All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest The authors declare that they have no conflict of interest.

Data statement All the data we used are included within the paper, in tables or figures. Further information may be asked by email to the corresponding author, by whom it may concern.

References

Ancillotto L, Mazza G, Menchetti M, Mori E (2014) Host specificity of the badger's flea (*Paraceras melis*) and first detection on a bat host. Paras Res 113:3909–3912

Ancillotto L, Studer V, Howard T, Smith VS, McAlister E, Beccaloni J, Manzia F, Renzopaoli F, Bosso L, Russo D, Mori E (2018) Environmental drivers of parasite load and species richness in introduced parakeets in an urban landscape. Paras Res 117:3591–3599

Appelt CW, Ward LC, Bender C, Fasenella J, Van Vossen BJ, Knight L (2016) Examining potential relationships between exotic monk parakeets (*Myiopsitta monachus*) and avian communities in an urban environment. Wilson J Ornit 128:556–566

Aramburú RM, Campos Soldini MP (2008) Presencia de *Psitticimex uritui* (Hemiptera: Cimicidae) en nidos de caserote *Pseudoseisura lophotes* (Passeriformes: Furnariidae) en la provincia de Entre Ríos. Revista Soc Entomol Argentina 67:131–133

Aramburù RM, Calvo S, Alzugaray ME, Cicchino A (2003) Ectoparasitic load of monk parakeet (*Myiopsitta monachus*) nestlings. Ornitologia Neotropical 14:415–418

Baker AS (1999) Mites and ticks of domestic animals: an identification guide and information source. The Stationary Office, London

Baldaccini NE, Giunchi D, Mongini E, Ragionieri L (2000) Foraging flights of wild rock doves (*Columba l. livia*): a spatio-temporal analysis. It. J Zool 67:371–377

Bartoń K (2012) MuMIn: multi-model inference. R package version 1.15.6. https://cran.r-project.org/web/packages/MuMIn. Accessed: 22 May 2018

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Soft 6:1–48

Batllori X, Nos R (1985) Presencia de la cotorrita gris (*Myiopsitta monachus*) y de la cotorrita de collar (*Psittacula krameri*) en el Area Metropolitana de Barcelona. Miscell Zool 9:407–411

Bolker BM (2018) Overdispersion. http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#testing-for-overdispersioncomputing-overdispersion-factor. Accessed: 7 October 2018

Burger J, Gochfeld M (2005) Nesting behavior and nest site selection in monk parakeets (*Myiopsitta monachus*) in the Pantanal of Brazil. Acta Ethol 8:23–34

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York

Carboneras C, Genovesi P, Vilà M, Blackburn TM, Carrete M, Clavero M, D'hondt M, Orueta JF, Gallardo B, Geraldes P, Gonzàlez-Moreno P, Gregory RD, Nentwig W, Paquet JY, Pysek P, Rabistsch W, Ramirez I, Scalera R, Tella JL, Walton P, Wynde R (2018) A prioritised list of invasive alien species to assist the effective implementation of EU legislation. J Appl Ecol 55:539–547

Carrillo-Ortiz J (2009) Dinámica de poblaciones de la cotorra de pecho gris (*Myiopsitta monachus*) en la ciudad de Barcelona. PhD Thesis. University of Barcelona, Barcelona

Castiglioni R, Azzola C, Capelli F, Biancardi C (2015) Aspetti ecologici e riproduttivi del parrocchetto monaco (*Myiopsitta monachus* Boddaert, 1783) in una colonia in provincia di Bergamo. XVIII Congresso Italiano di Ornitologia, Caramanico Terme (Pescara), 17–20 September 2015, 17

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2014) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7:721–733

Covas L, Senar JC, Roqué L, Quesada J (2017) Records of fatal attacks by Rose-ringed parakeets *Psittacula krameri* on native avifauna. Revista Catalana d'Ornitologia 33:45–49

Cox R, Stewart PD, Macdonald DW (1999) The ectoparasites of the European badger, *Meles meles*, and the behavior of the host-specific flea, *Paraceras melis*. J Insect Behav 12:245–265

Crowley SL, Hinchliffe S, McDonald RA (2017) Conflict in invasive species management. Front Ecol Environ 15:133–141

Crowley SL, Hinchliffe S, McDonald RA (2018) The parakeet protectors: understanding opposition to introduced species management. J Environ Manag 229:120–132. https://doi.org/10.1016/j.jenvman.2017.11.036

Dangoisse G (2009) Étude de la population de Conures veuves (*Myiopsitta monachus*) de Bruxelles-Capitale. Aves 46:57–69

Delgado CA, French K (2012) Parasite–bird interactions in urban areas: current evidence and emerging questions. Landsc Urban Plan 105:5–14

Di Santo M, Battisti C, Bologna MA (2016) Interspecific interactions in nesting and feeding urban sites among introduced monk parakeet (*Myiopsitta monachus*) and syntopic bird species. Ethol Ecol Evol 29:138–148

Edelaar P, Roques S, Hobson EA, Gonçalves da Silva A, Avery ML, Russello MA, Senar JC, Wright TF, Carrete M, Tella JL (2015) Shared genetic diversity across the global invasive range of the monk parakeet suggests a common restricted geographic origin and the possibility of convergent selection. Mol Ecol 24:2164–2176

Ferman LM, Peter HU, Montalti D (2010) A study of feral pigeon *Columba livia* var. in urban and suburban areas in the city of Jena, Germany. Arxius Misc Zool 8:1–8

Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. SAGE, Thousand Oaks, USA

Haag-Wackernagel D (2005) Parasites from feral pigeons as a health hazard for humans. Ann Appl Biol 147:203–210

Hernández-Brito D, Carrete M, Popa-Lisseanu AG, Ibáñez C, Tella JL (2014) Crowding in the city: losing and winning competitors of an invasive bird. PLoS One 9:e100593

Hobson EA, Smith-Vidaurre G, Salinas-Melgoza A (2017) History of nonnative monk parakeets in Mexico. PloS ONE 12:e0184771

Hutson AM (1984) Keds, flat-flies and bat-flies: Diptera, Hippoboscidae and Nycteribiidae. Royal Entomological Society of London, London

Hyman J, Pruett-Jones S (1995) Natural history of the monk parakeet in Hyde Park, Chicago. Wilson Bull 3:510–517

Johnson KP, Clayton DH (2003) The biology, ecology, and evolution of chewing lice. Illinois Nat Hist Surv Special Public 24:449–476

Kelly DW, Paterson RA, Townsend CR, Poulin R, Tompkins DM (2009) Parasite spillback: a neglected concept in invasion ecology? Ecology 90:2047–2056

Lafferty KD, Holt RD (2003) How should environmental stress affect the population dynamics of disease? Ecol Lett 6:654–664

Lüdecke D (2018) sjstats: Statistical functions for regression models. R package version 0.17.1. Available online at https://cran.r-project.org/package=sjstats. Accessed 07 Sept 2018

Lymbery AJ, Morine M, Kanani HG, Beatty SJ, Morgan DL (2014) Co-invaders: the effects of alien parasites on native hosts. Int J Parasitol 3:171–177

MacGregor-Fors I, Calderón-Parra R, Meléndez-Herrada A, López-López S, Schondube JE (2011) Pretty, but dangerous! Records of non-native monk parakeets (*Myiopsitta monachus*) in Mexico. Rev Mex Biodiv 82:1053–1056

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Marsot M, Chapuis JL, Gasqui P, Dozières A, Massèglia S, Pisanu B, Ferquel B, Vourc'h G (2013) Introduced Siberian chipmunk (*Tamias sibiricus barberi*) contribute more to Lyme borreliosis risk than native reservoir rodents. PLoS One 8:e55377

Masello JF, Martínez J, Calderón L, Wink M, Quillfeldt P, Sanz V, Theuerkauf J, Ortiz-Catedral L, Berkunsky I, Brunton D, Díaz-Luque JA, Hauber ME, Ojeda V, Barnaud A, Casalins L, Jackson B, Mijares A, Rosales R, Seixas G, Serafini P, Silva-Iturriza A, Sipinski E, Vásquez RA, Widmann P, Widmann I, Merino S (2018) Can the intake of antiparasitic secondary metabolites explain the low prevalence of hemoparasites among wild Psittaciformes? Parasit Vectors 11:357

Mazza G, Tricarico E, Genovesi P, Gherardi F (2014) Biological invaders are threats to human health: an overview. Ethol Ecol Evol 26:112–129

Mazzamuto MV, Pisanu B, Romeo C, Ferrari N, Preatoni D, Wauters LA, Chapuis JL, Martinoli A (2016) Poor parasite community of an invasive alien species: macroparasites of Pallas's squirrel in Italy. Ann Zool Fennici 53:103–112

McInnes CJ, Coulter L, Dagleish MP, Deane D, Gilray J, Percival A, Willoughby K, Scantlebury M, Marks N, Graham D, Everest DJ, McGoldrick M, Rochford J, McKay F, Sainsbury AW (2013) The emergence of squirrel pox in Ireland. Anim Conserv 16:51–59

Menchetti M, Mori E (2014) Worldwide impact of alien parrots (Aves Psittaciformes) on native biodiversity and environment: a review. Ethol Ecol Evol 26:172–194

Menchetti M, Mori E, Angelici FM (2016) Effects of the recent world invasion by ring-necked parakeets *Psittacula krameri*. In: Angelici FM (ed) Problematic wildlife. A cross-disciplinary approach. Springer, New York, pp 253–266

Moltoni E (1945) Pappagalli in libertà nei giardini pubblici di Milano e loro nidificazione in colonia in associazione con il passero. Riv It Ornitol 15:98–106

Montalvo T, Pascual J, Senar JC, Peracho V (2017) Colom roquer *Columba livia*. In: Anton M, Herrando S, García D, Ferrer X, Parés M, Cebrian R (eds) Atles dels ocells nidificants de Barcelona. Barcelona. Ajuntament de Barcelona, Barcelona, pp 90–91

Mori E, Ancillotto L, Groombridge J, Howard T, Smith VS, Menchetti M (2015a) Macroparasites of introduced parakeets in Italy: a possible role for parasite-mediated competition. Paras Res, 114:3277–3281

Mori E, Sforzi A, Menchetti M, Mazza G, Lovari S, Pisanu B (2015b) Ectoparasite load in the crested porcupine *Hystrix cristata* Linnaeus, 1758 in Central Italy. Paras Res 114:2223–2229

Mori E, Pisanu B, Zozzoli R, Solano E, Olivieri E, Sassera D, Montagna M (2018a) Arthropods and associated pathogens from native and introduced rodents in Northeastern Italy. Paras Res, 117:3237–3243

Mori E, Meini S, Strubbe D, Ancillotto L, Sposimo P, Menchetti M (2018b) Do alien free-ranging birds affect human health? A global summary of known zoonoses. In: Mazza G, Tricarico E (eds) Invasive species and human health. CABI Editions, Wallingford, pp 120–129

Muñoz AR, Real R (2006) Assessing the potential range expansion of the exotic monk parakeet in Spain. Divers Distrib 12:656–665

Navarro JL, Bucher EH (1990) Growth of monk parakeets. Wilson Bull 102:520–525

Nentwig W, Bacher S, Kumschick S, Pyšek P, Vilà M (2018) More than "100 worst" alien species in Europe. Biol Invasions 6:1611–1621

Nores M (2009) Use of active monk parakeet nests by common pigeons and response by the host. Wilson J Ornith 121:812–815

Orton DI, Warren LJ, Wilkinson JD (2000) Avian mite dermatitis. Clin Experim Derm 25:129–131

Parau LG, Strubbe D, Mori E, Menchetti M, Ancillotto L, van Kleunen A, White RL, Hernàndez-Brito D, Le Louarn M, Clergeau P, Albayrak T, Franz D, Braun MP, Schroeder J, Wink M (2016) Rose-ringed parakeet *Psittacula krameri* populations and numbers in Europe: a complete overview. Open Orn J 9:1–13

Pascual J, Riba D, Senar JC (2015) Cens de la poblacio de coloms i altres aus urbanes a Barcelona 2015. Museu de Ciencies Naturals de Barcelona. Agencia de Salut Publica de Barcelona Editions, Barcelona

Postigo JL, Shwartz A, Strubbe D, Muñoz AR (2017) Unrelenting spread of the alien monk parakeet *Myiopsitta monachus* in Israel. Is it time to sound the alarm? Pest Manag Sci 73:349–353

Prenter J, MacNeil C, Dick JT, Dunn AM (2004) Roles of parasites in animal invasions. Trends Ecol Evol 19:385–390

Price PW, Westoby M, Rice B, Atsatt PR, Fritz RS, Thompson JN, Mobley K (1986) Parasite mediation in ecological interactions. Annu Rev Ecol Syst 17:487–505

Reed JE, McCleery RA, Silvy NJ, Smeins FE, Brightsmith DJ (2014) Monk parakeet nest site selection of electric utility structures in Texas. Landsc Urb Plann 129:65–72

Rodríguez-Pastor R, Senar JC, Ortega A, Faus J, Uribe F, Montalvo T (2012) Distribution patterns of invasive Monk parakeets (*Myiopsitta monachus*) in an urban habitat. Anim Biodiv Cons 35:107–117

Romeo C, Wauters LA, Ferrari N, Lanfranchi P, Martinoli A, Pisanu B, Preatoni DG, Saino N (2014) Macroparasite fauna of alien grey squirrels (*Sciurus carolinensis*): composition, variability and implications for native species. PLoS One 9:e88002

Rose E, Nagel P, Haag-Wackernagel D (2006a) Spatio-temporal use of the urban habitat by feral pigeons. Behav Ecol Sociobiol 60:242–254

Rose E, Haag-Wackernagel D, Nagel P (2006b) Practical use of GPS-localization of feral pigeons *Columba livia* in the urban environment. Ibis 148:231–239

Santillán MA, Grande JM, Liébana MS, Martínez P, Díaz LA, Bragagnolo LA, Solaro C, Galmes MA, Sarasola JH (2015) New hosts for the mite *Ornithonyssus bursa* in Argentina. Medical Vet Entomol 29:439–443

Santos DM (2006) Fichas de aves introducidas en España. Grupo de Aves Exóticas (SEO/BirdLife). http://www.seo.org/?grupodeavesexoticas [Accessed on 10th July 2014]

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol 1:103–113

Senar JC, Domènech J, Arroyo L, Torre I, Gordo O (2016) An evaluation of monk parakeet damage to crops in the metropolitan area of Barcelona. Anim Biodivers Conserv 39:141–145

Senar JC, Montalvo T, Pascual J, Arroyo L (2017a) Cotorra de pit gris *Myiopsitta monachus*. In: Manton M, Herrando S, García D, Ferrer X, Parés M, Cebrian R (eds) Atles dels ocells nidificants de Barcelona. Ajuntament de Barcelona, Barcelona, pp 136–137

Senar JC, Montalvo T, Pascual J, Arroyo L (2017b) Cotorra de Kramer *Psittacula krameri*. In: Manton M, Herrando S, García D, Ferrer X, Parés M, Cebrian R (eds) Atles dels ocells nidificants de Barcelona. Ajuntament de Barcelona, Barcelona, pp 128–129

Sol D, Santos DM, Feria E, Clavell J (1997) Habitat selection by the monk parakeet during colonization of a new area in Spain. Condor 99:39–46

Sol D, Gonzàlez-Lagos C, Lapiedra O, Dìaz M (2017) Why are exotic birds so successful in urbanized ecosystems? In: Murgui E, Hedblom M (eds) Ecology and conservation of birds in urban environments. Springer Editions, New York, pp 75–89

Soldatini C, Mainardi D, Baldaccini NE, Giunchi D (2006) A temporal analysis of the foraging flights of feral pigeons (*Columba livia* f. *domestica*). Ital J Zool 73:83–92

Tschirren B, Bischoff LL, Saladin V, Richner H (2007) Host condition and host immunity affect parasite fitness in a bird-ectoparasite system. Funct Ecol 21:372–378

Turbè A, Strubbe D, Mori E, Carrete M, Chiron F, Clergeau P, Gonzalez-Moreno P, Le Louarn M, Luna A, Menchetti M, Nentwig W, Parau LG, Postigo JL, Rabitsch W, Senar JC, Tollington S, Vanderhoeven S, Weiserbs A, Shwartz A (2017) Assessing the assessments: evaluation of four impact assessment protocols for invasive alien species. Divers Distrib 23:297–307

Viviano E, Bongiorno MR (2014) Avian mite dermatitis: an Italian case indicating the establishment and spread of *Ornithonyssus bursa* (Acari: Gamasida: Macronyssidae) (Berlese, 1888) in Europe. Int J Dermat 54:795–799

Vourc'h G, Abrial D, Bord S, Jacquot M, Masseglia S, Poux V, Pisanu B, Bailly X, Chapuis JL (2016) Mapping human risk of infection with *Borrelia burgdoferi* sensu lato, the agent of Lyme borreliosis, in a periurban forests in France. Ticks Tick-Borne Dis 5:644–652

Weiserbs A, Jacob JP (1999) Etude de la population de perriche jeune-veuve *Myiopsitta monachus* à Bruxelles. Aves 36:207–223

Zocchi A, Battisti C, Santoro R (2009) Note sul pappagallo monaco, *Myiopsitta monachus*, a Roma (Villa Pamphili). Riv Ital Ornitol 78:135–137

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York