



Environmental drivers of parasite load and species richness in introduced parakeets in an urban landscape

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Abstract

Introduced species represent a threat to native wildlife worldwide, due to predation, competition, and disease transmission. Concurrent introduction of parasites may also add a new dimension of competition, i.e. parasite-mediated competition, through spillover and spillback dynamics. Urban areas are major hotspots of introduced species, but little is known about the effects of urban habitat structure on the parasite load and diversity of introduced species. Here, we investigated such environmental effects on the ectoparasite load, richness, and occurrence of spillback in two widespread invasive parakeets, *Psittacula krameri* and *Myiopsitta monachus*, in the metropolitan area of Rome, central Italy. We tested 231 parakeets and found that in both species parasite load was positively influenced by host abundance at local scale, while environmental features such as the amount of natural or urban habitats, as well as richness of native birds, influenced parasite occurrence, load, and richness differently in the two host species. Therefore, we highlight the importance of host population density and habitat composition in shaping the role of introduced parakeets in the spread of both native and introduced parasites, recommending the monitoring of urban populations of birds and their parasites to assess and manage the potential occurrence of parasite-mediated competition dynamics as well as potential spread of vector-borne diseases.

Keywords Ectoparasites · Introduction · *Myiopsitta monachus* · Psittaciformes · *Psittacula krameri* · Urban ecology

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Introduction

Biological invasions are a major driver of global biodiversity loss (Clavero and García-Berthou 2005; Capinha et al. 2015; Bellard et al. 2016) and commonly result in deleterious impacts on native communities (Sakai et al. 2001). Direct impacts, including predation and competition (Welch and Leppanen 2017), are easy to record, whereas indirect effects, such as habitat alteration and parasite/disease transmission, may be more difficult to detect (Mack et al. 2000; Mazza et al. 2014; Bosso et al. 2017; Barbar and Lambertucci 2018).

Parasite-mediated competition—occurring between introduced and native species through the transmission of co-introduced parasites or the spread of native ones (Hudson and Greenman 1998; Sakai et al. 2001)—has attracted much attention in the last decade (Sakai et al. 2001; Dunn and Hatcher 2015; Tuttle et al. 2017). Alien species usually lose a high proportion of their own parasites following introduction to a novel environment, a process described as the “enemy release” (Mori et al. 2015; Mazzamuto et al. 2016). The acquisition of native parasites from the invaded area rarely

compensates for this loss (Torchin and Mitchell 2004; Romeo et al. 2014). Since arthropod ectoparasites parasitising the host's skin, hair, and/or feathers (such as lice, fleas, ticks, and mites) may cause illness and reduced fertility (Booth et al. 1993; Krasnov et al. 2004), the natural enemy loss may facilitate viability and establishment success of an alien species (Colautti et al. 2004). On the other hand, alien parasites that overcome the introduction step may represent a major threat to native species through spillover dynamics and increase competitiveness of introduced vs. native hosts (Kelly et al. 2009; Karamon et al. 2015). Finally, transinfestation (spillback) of introduced species by native parasites may magnify parasite spread and infective power harming native hosts further (Kelly et al. 2009; Mori et al. 2015).

Urban areas often represent hotspots of introduction events (Shochat et al. 2010; Clemants and Moore 2003; van Rensburg et al. 2009; Hernández-Brito et al. 2014; Gaertner et al. 2017), particularly when alien species come from the pet trade (Bowers and Breland 1996; Orchan et al. 2013; Mori et al. 2018) via intentional or accidental release by owners.

The novel environmental condition urban habitats offer expose animal colonisers to contrasting factors, some (such as pollution or vehicle traffic) limiting, others (food provided by humans, warmer temperatures) facilitating their establishment (Golightly Jr et al. 1994; Chapuis et al. 2011; Clergeau and Vergnes 2011). Within this framework, there is increasing attention towards the relationships between wildlife diseases and urban habitats, due to their implications for wildlife conservation and public health (Hofer et al. 2000; Comer et al. 2001; Himswoth et al. 2013; Rothenburger et al. 2017).

Although parasites from the introduced range might counter the spread of an invader, there is little evidence that this occurs in many introduced species. According to the “enemy release hypothesis”, alien species are less infested by parasites and might become invasive by experiencing less regulation from the latter (as well as other factors) than in their native range (Colautti et al. 2004).

Birds are excellent models to test hypotheses on the ecological and evolutionary effects of urbanisation. Many bird species occur in urban cities worldwide (Blair 1996; McKinney 2008; Orchan et al. 2013), so there is a wealth of information about synurbic birds. Urban birds are also usually very responsive to fine-grained habitat characteristics (Jokimäki and Suhonen 1998; Parsons et al. 2006), which makes them suitable models to test the effects of urbanisation at a small scale. Pet bird species are also among the most commonly introduced species in urban areas, especially parrots and parakeets: > 16% of all known species (Menchetti and Mori 2014) have established at least one population outside their native range after introduction.

The monk parakeet *Myiopsitta monachus* (hereafter, MP) and the ring-necked parakeet *Psittacula krameri* (hereafter,

RNP) are the most successful invaders among Psittaciformes (Menchetti and Mori 2014; Turbè et al. 2017). RNP is native to tropical Sub-Saharan Africa (from Senegal to Somalia) and the Indian subcontinent (from Eastern Pakistan to Assam and Manipur: Menchetti and Mori 2014); alien populations occur in Europe, Middle and Far East Asia, Australia, South Africa, USA, and Venezuela (Menchetti and Mori 2014), and introduced populations in Europe are rapidly expanding (Pârâu et al. 2016). MP is native to South America (from Southern Brazil to central-southern Argentina), with alien populations occurring throughout northern and central America, the Caribbean Islands, Eurasia, and Tanzania (Edelaar et al. 2015). European populations of MP are also increasing in both population size and extent of occurrence (Domènech et al. 2003; Mori et al. 2013) (Di Santo et al. 2013). The information available on parakeet ectoparasites is partial or anecdotal, both in their native and invaded ranges (Mori et al. 2015). Both RNP and MP are documented to host a number of parasitic taxa in both ranges (Table S1 in supplementary materials).

In this work, we assessed arthropod ectoparasite richness and diversity within an area that is part of the invaded range of these parakeet species. Additionally, we also tested whether parasite loads in RNP and MP are related to individual variation and land use.

Materials and methods

Study area

Sample collection took place in the metropolitan area of Rome (41.89° N, 12.49° E, central Italy), a large urban area covering approximately 1300 km². The study area is characterised by a prevalence of urban matrix (~90%), comprising sparse to high-density districts. A total of 1798 public green areas are present in Rome, ranging from small recreational gardens to extensive natural reserves and agro-pastoral areas, covering ca. 40 km² (www.comune.roma.it).

RNPs and MPs are both present in Rome with well-established and large populations since the 1970s (RNP) and 1980s (MP), numbering ca. 6000 and 2500 birds for RNP (Pârâu et al. 2016) and MP (unpublished data), respectively.

Parasite sampling and identification

Arthropod ectoparasites were sampled from individual parakeets of both species admitted to the LIPU Wildlife Rescue Centre in Rome in 2015–2016; for each parakeet brought to the centre by the public, the centre's staff recorded species, age (categorised as adult, subadult, or nestling), sex (for RNPs only, assessed following Butler 2003), location, and cause of admittance. Animals sampled at rescue centres

may provide valuable data on wildlife ecology, distribution, and epidemiology, otherwise difficult to obtain, e.g. due to low success in capturing wild individuals (e.g. Ancillotto et al. 2013; Pyke and Szabo 2018); birds admitted for rescue may though represent a biased picture of parasite abundance and distribution in the free-ranging population of the hosts, i.e. rescued birds may face higher parasite loads and poorer health conditions, which actually led to their capture. No published work has tested differences in parasite loads between wild and rescued birds yet; thus, caution must be taken when interpreting results from this kind of source, but most parakeets admitted in Rome are rescued as a result of injuries due to impacts with infrastructures (e.g. windows) and were otherwise apparently in good body and plumage conditions (Authors, unpublished data). On admission, we visually checked birds and immediately treated them following a fumigation procedure, using a pesticide for veterinary use (NeoForactil® by Formevet; formula: piperonyl butoxide 1%, permethrin 0.3%, tetramethrin 0.2%). Birds were manually sprayed while being singly held in a sterile plastic box (55 × 25 × 20 cm) with small holes on one side for ventilation; 10 min after treatment, the bird was handled over the box, and body and wing feathers were systematically ruffled and inspected. Fumigation procedures are non-invasive and generally allow to collect > 70% of arthropod ectoparasites, being thus recommended for parasite collection on live birds (Clayton and Drown 2001). The parasites were then manually collected from the box and stored in 95% ethanol; lice were slide-mounted in Canada balsam following the protocol by Palma (1978).

We identified parasites using published keys (Siphonaptera: Smit 1983; Whitaker 2007; Mallophaga: Johnson and Clayton 2003; Guimarães 1980; Acarina: Baker 1999; Diptera, Hippoboscidae: Hutson 1984) and consulting reference specimens hosted at the Department of Life Sciences of the Natural History Museum of London. We identified parasites using a stereo microscope (Leica MZ6 C, with 10–100 × lenses) for Hippoboscidae and Siphonaptera and an optical microscope (Olympus BH2 optic microscope equipped with 10–200 × lenses) for Mallophaga and Acarina (Galloway and Lamb 2016).

Overall parasite prevalence was calculated as the proportion of occurrence of a parasite species within the studied host population.

Data on surrounding habitat

We assessed habitat composition within a 1-km radius around the locations where parakeets were rescued by extracting land use composition from land cover IV-level Corine Land Cover 2012 (available from <http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais/corine-land-cover>; Fig. 1). Only birds for which the exact location of rescue was available

(i.e. exact address or site assessed by the person who brought the bird) were included in the dataset. We carried out this analysis using ArcGIS version 9.2 (Environmental Systems Research Institute Inc., Redlands, CA, USA). The surface area we chose was similar to that of the core areas known for introduced parakeets (da Silva et al. 2010; Strubbe and Matthysen 2011). We reclassified habitats into (i) urban areas (buildings and paved roads), (ii) natural and semi-natural habitats (natural vegetation and recreational green areas), and (iii) agricultural areas (orchards and crops).

We estimated an index of parakeet abundance by direct surveys consisting of counts of visual and acoustic contacts with parakeets of both species during 10-min point counts at each location (Ralph et al. 1995). Locations were selected opportunistically within green areas (i.e. recreational urban parks, natural reserves, public villas) as close as possible to the locations from which rescued parakeets came from (the maximum distance between rescue and survey locations was 350 m). Counts took place between 6.00 and 11.00 AM avoiding days with strong wind or heavy rain; each location was visited twice in 2016, once during nesting (February–May), once in the non-nesting season (October–November). The two species of parakeets we focused on are easy to tell apart both visually and acoustically, as they differ in size and plumage markings as well as in vocalisations. Individuals of Alexandrine parakeet *Psittacula eupatria*, also present in Rome (Ancillotto et al. 2016), are so few (1–2 breeding pairs) that their presence had no effect on counts.

We also assessed the species richness of the native breeding bird community through the Rome Atlas of Breeding Birds (Cignini and Zapparoli 1996). In this case, we overlapped rescue locations with the Atlas grid (1 × 1 km cells) and extracted richness value from the grid cells where each rescue site was located.

Data analyses

We ran generalised linear mixed models (GLMMs): count data were modelled with zero-inflated Poisson distribution models; for occurrence data, we ran both binomial and Poisson (with zero inflation) models, as suggested by our sample size and low probabilities (Hodges and Le Cam 1960), selecting the approach that maximised model fit (evaluated by inspecting model R^2); in all cases, zero-inflated distribution models were thus selected. We modelled the following: (i) parasite occurrence, classified as presence (1) or absence (0) for each ectoparasite species; (ii) total parasite load (total number of ectoparasites collected on each parakeet); (iii) ectoparasite species richness (number of species on each parakeet); and (iv) occurrence of spillback (presence (1) or absence (0) of parasites from the native bird community).

We considered parakeet age, sex (only for RNP), and season as fixed factors, amount of habitat categories (as

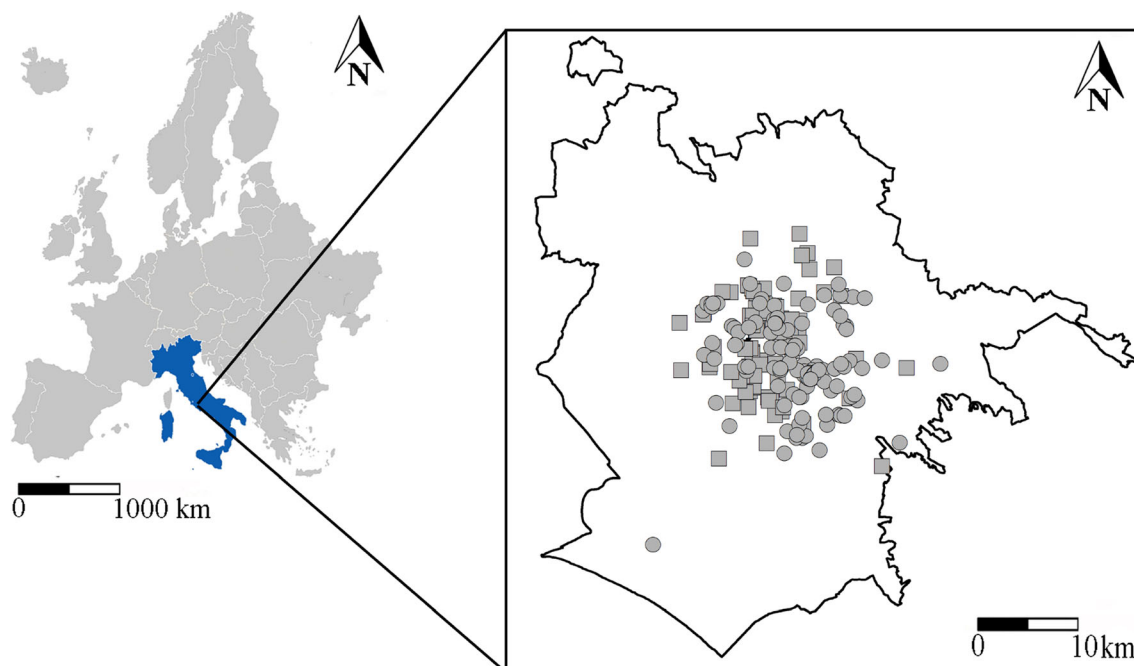


Fig. 1 Locations where parakeets were sampled for arthropod ectoparasites within the metropolitan area of Rome, Italy. Circles: monk-parakeet *Myiopsitta monachus* ($n = 127$); Squares: ring-necked parakeet *Psittacula krameri* ($n = 104$)

percentages), parakeet abundance index (separately for the two species), and native bird richness as covariates and location as a random factor. We performed the analyses with R 3.3.2 (R Core Team 2016), using the *nlme* package (Pinheiro et al. 2014); all presented models are full models.

Results

We collected and identified 1572 ectoparasites belonging to 10 species from 104 RNPs and 127 MPs (Table 1); no ectoparasite species was shared by the two hosts. The most frequent (> 18% of prevalence) and abundant (> 10% of total ectoparasites for each host species) taxa were Ischnoceran chewing lice (RNP: *Neopsittaconirmus lybartota*, *Echinophlopterus tota*; MP: *Paragoniocotes fulvofasciatus*) and the haematophagous mite *Ornithonyssus bursa* (on MP).

Overall, 50.0% of parasite species found on RNP and MP were native to the introduced area, including generalist and widespread bird parasites (e.g. *Dermanyssus gallinae* and three hippoboscids) as well as parasites specialised on mammals (i.e. the squirrel flea *Tarsyopsylla octodecimdentata*).

General parasite prevalence was relatively high, corresponding to 52.8% for RNP and 38.6% for MP. Abundance and prevalence of parasites were significantly correlated with each other at the level of individual parakeets of both species (see Tables S2–5 in supplementary materials), so we pooled together all species' data and used the overall parasite abundance and prevalence.

Responses of parasitological variables to environmental and biological factors differed between the two avian hosts (Table 2). In RNP, parasite presence was influenced by sex ($p < 0.05$) and males were more heavily parasitised. The parakeet abundance index was positively correlated with parasite prevalence, load, and richness in RNP (all $p < 0.001$) and only parasite load in MP ($p < 0.001$).

In the case of RNP, increasing amounts of urbanisation corresponded to higher rates of presence of parasites from the introduced range ($p < 0.05$). In MP, parakeets from more urbanised areas showed a higher prevalence ($p < 0.05$) and were more likely to carry parasites from native species ($p < 0.001$); also, MP parasite richness was positively correlated with the amount of natural habitats ($p < 0.05$). For RNP only, both parasite richness and occurrence of spillback were higher for higher values of species richness of the native bird community (both $p < 0.01$).

Discussion

Despite having been long overlooked in studies focused on biological invasions (Kelly et al. 2009), spillback (parasite transmission from native to alien hosts) has recently gained attention, particularly when posing health risks to humans or pets (Marsot et al. 2013; Mazza et al. 2014; Vourc'h et al. 2016). In most cases, invasive species lose their parasitic load during their establishment in new territories (Vila' et al. 2005; Mori et al. 2015; Mazzamuto et al. 2016), but in the case of

Table 1 Arthropod ectoparasites recorded for monk (*Myiopsitta monachus*) and ring-necked (*Psittacula krameri*) parakeets admitted at a wildlife rescue centre in Rome, Italy, numbers of collected parasites and of positive parakeets, place of origin of parasites (IN, invaded range; NV, native range) and corresponding natural hosts. RNP, ring-necked parakeet *Psittacula krameri* ($n = 104$); MP, monk parakeet *Myiopsitta monachus* ($n = 127$)

Host	Parasite species	N parasites	N positive parakeets	Origin	Natural host
RNP	<i>Neopsittaconirmus lybartota</i>	718	50	NV	Old World parrots
	<i>Echinophlopterus tota</i>	103	29	NV	<i>Psittacula</i> parrots
	<i>Dermanyssus gallinae</i>	17	6	NV	Generalist
	<i>Tarsyopsylla octodecimentata</i>	4	2	IN	<i>Sciurus vulgaris</i>
	<i>Ornithomyia avicularia</i>	1	1	IN	Generalist
MP	<i>Paragoniocolotes fulvofasciatus</i>	360	35	NV	Neotropical parrots
	<i>Ornithonyssus bursa</i>	345	23	NV	Generalist
	<i>Columbicola columbae</i>	8	2	IN	Columbiformes
	<i>Crataerina pallida</i>	1	1	IN	Generalist (<i>Apus apus</i> in particular)
	<i>Ornithophila metallica</i>	1	1	IN	Generalist

introduced parakeets, the “enemy release hypothesis” is not supported (Colautti et al. 2004) at least at the population level. In fact, our sample showed a relatively rich ectoparasite diversity (Mori et al. 2015; this work), comparable to that found in the native ranges of the two hosts (e.g. Aramburú et al. 2003; Briceño et al. 2017; Price et al. 2003), yet at the individual level, most parakeets hosted 0–2 parasite species each (see Fig. S1 in supplementary materials). We found that ectoparasite load in the two introduced parakeet species varied in species composition and infestation magnitude according to host’s traits (sex and age), as well as to environmental factors. The specific prevalence and load of the most common ectoparasite species in our sample was lower than in the native range, at least for MP (the prevalence of *P. fulvofasciatus* in our study was 27.7 vs. 45.7% in Briceño et al. 2017). Despite their frequent co-occurrence in the study area as well as across their invaded ranges, RNP and MP shared neither native nor invasive parasite species.

Being potentially subjected to spillover dynamics, introduced parakeets represent good candidates for parasite-mediated competition with native birds, as also suggested by preliminary assessments of their parasite community (Mori et al. 2015). Yet, the low prevalence at the population level and the small numbers of native parasites per parakeet though highlight that parasite mediated-competition with native birds is still unlikely to occur significantly, and caution is recommended in inferring large-scale interspecific interactions.

Male RNP hosted more parasite species than females, as seen in other vertebrates (e.g. Uller and Olsson 2003; Krasnov et al. 2005; Owen et al. 2009); testosterone may have a role in impairing male immune response, resulting in lower resistance to parasites (Poulin 1996). Furthermore, testosterone level is strongly associated to conspicuous plumage colourations in birds, which is under strong sexual selection by females (Folstad and Karter 1992; Heylen and Matthysen

2008; Escallón et al. 2017). While a colourful plumage is associated with a higher reproductive success, the associated hormonal levels might reduce immunological defence (Roberts et al. 2004), including male bird resistance to parasites (Evans et al. 2000). Parasite distribution on hosts is filtered not only by the ability of parasites to persist on different hosts, but also by the frequency of encounters between hosts and parasites, as described by the host-compatibility and host-encounter concept suggested by Combes (1991). Thus, male parakeets may be subjected to higher parasite loads also due to their higher mobility, e.g. by spending more time out of the nest and/or moving over longer distances to reach their foraging areas.

The amount of urban settlements surrounding sites where RNP and MP were collected influenced the probability of parakeets to host native parasites (spillover). However, the low numbers of parakeets hosting parasites from the invaded range suggest that this aspect warrants confirmation. In urban environments, contacts between parakeets and synurbic native birds, such as domestic pigeons *Columba livia* var. *domestica*, are frequent (Dangoisse 2009; Di Santo et al. 2016; Le Louarn et al. 2016). Not only do pigeons host high numbers of parasite species (Ferman et al. 2010; Delgado and French 2012), but they also forage (Clergeau and Vergnes 2011) and nest (Batllori and Nos 1985; Hernández-Brito et al. 2014) together with parakeets. Parasite prevalence increased in MP in areas dominated by urban settlements, possibly because of poorer health conditions of birds in more urbanised, polluted (Fry 1995) urban districts. Parasite richness in this species was also lower in areas characterised by a greater extent of natural habitat.

Abundance of conspecific parakeets significantly increased total parasite load in both parakeet species, parasite richness, and prevalence in RNP only. Parakeets are highly social, form long-term pair bonds, and often nest, roost, and forage

Table 2 Effect of biological and environmental factors and individual characteristics on the arthropod ectoparasite community of ring-necked parakeet *Psittacula krameri* (RNP, $n = 104$) and monk parakeet *Myiopsitta monachus* (MP, $n = 127$) from the metropolitan area of Rome (Italy) tested with generalised linear mixed models. Spillover, presence of parasites naturally occurring on native species present in the invaded range: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s., not significant; NA, not applicable

Model	Variable contribution (estimate \pm standard error) and significance									
	Species	Response	R^2 and p	Age	Sex	Season	Abundance	%urban	%green	%agricultural
RNP	Parasite presence	0.48**	-5.33 \pm 1.12 n.s.	1.71 \pm 0.95*	1.85 \pm 1.86 n.s.	4.88 \pm 0.99***	3.55 \pm 7.72 n.s.	-4.45 \pm 4.63 n.s.	2.74 \pm 0.42 n.s.	0.90 \pm 10.30 n.s.
	Parasite load	0.33**	-2.45 \pm 3.71 n.s.	0.03 \pm 0.88 n.s.	1.87 \pm 2.31 n.s.	1.03 \pm 0.18***	0.65 \pm 1.41 n.s.	0.79 \pm 0.85 n.s.	0.09 \pm 0.71 n.s.	0.19 \pm 0.18 n.s.
	Parasite richness	0.49**	-3.91 \pm 3.75 n.s.	-1.23 \pm 3.36 n.s.	3.01 \pm 3.22 n.s.	1.03 \pm 0.71***	0.65 \pm 0.04 n.s.	-0.79 \pm 0.86 n.s.	0.93 \pm 0.74 n.s.	0.75 \pm 0.09*
MP	Spillover	0.27*	3.32 \pm 1.18 n.s.	4.54 \pm 1.08 n.s.	4.95 \pm 5.61 n.s.	4.96 \pm 5.10 n.s.	9.74 \pm 1.21*	1.60 \pm 2.53 n.s.	4.13 \pm 6.30 n.s.	3.16 \pm 0.93**
	Parasite presence	0.12*	1.22 \pm 1.28 n.s.	NA	2.98 \pm 1.61 n.s.	3.21 \pm 2.11 n.s.	9.15 \pm 1.72*	2.10 \pm 2.10 n.s.	4.32 \pm 2.22 n.s.	1.91 \pm 1.35 n.s.
	Parasite load	0.28**	5.32 \pm 6.11 n.s.	NA	0.98 \pm 1.21 n.s.	2.32 \pm 0.81***	0.98 \pm 1.01 n.s.	0.85 \pm 0.85 n.s.	1.16 \pm 0.67 n.s.	1.98 \pm 0.81 n.s.
	Parasite richness	0.18*	1.34 \pm 1.75 n.s.	NA	1.56 \pm 0.42 n.s.	1.03 \pm 0.71 n.s.	0.65 \pm 0.04 n.s.	-1.39 \pm 0.06*	0.93 \pm 0.74 n.s.	1.95 \pm 1.89 n.s.
	Spillover	0.55**	3.32 \pm 1.18 n.s.	NA	4.95 \pm 5.61 n.s.	4.96 \pm 5.10 n.s.	1.74 \pm 0.21***	1.60 \pm 2.53 n.s.	-4.53 \pm 2.30 n.s.	3.16 \pm 5.63 n.s.

socially, sometimes with large numbers which often engage in mutual preening (Forshaw 2010). Higher parakeet densities may therefore enhance parasite transmission through an increased inter-individual contact frequency and not be counterbalanced by increased preening rates (Møller et al. 1993).

RNPs from areas characterised by a higher species richness of native birds showed a higher parasite species richness and were more likely to host native parasites. Of the two parakeet species, introduced RNPs interact more often with native bird species than MPs: according to published work, with 36 native species for the former (Hernández-Brito et al. 2014; Covas et al. 2017; Mori et al. 2017) and 12 for the latter (MacGregor-Fors et al. 2011; Appelt et al. 2016; Di Santo et al. 2016). Sporadic aggressive interactions may also occur between RNPs and MPs (Hernández-Brito et al. 2014), yet the two species did not share any parasite species in our study. All these behaviours increase spillover chances, with parasites moving from the native host to the parakeet in the course of the interaction. RNP is more mobile than MP, travelling longer daily distances and being a more efficient disperser (Butler 2003), all factors that increase the probability of encounter between parakeets and parasites; the lower mobility of MP, whose activity is closely centred around the large communal nests built by the species (da Silva et al. 2010), may also explain the stronger relationship between land use and parasites in this species, when compared to RNP.

In South America, infestation of MP by *Paragoniocolles fulvofasciatus* and *Ornithonyssus bursa* was considerable in chicks and decreased in fledged juveniles (Aramburú et al. 2003). Nesting sites may represent important “hubs” for spillover-spillover dynamics, as many ectoparasites overwinter in nesting holes and dens (Cox et al. 1999) where they may colonise novel hosts of the same site (both of the same species and belonging to different taxa) in the following year or season (e.g. Onstad and McManus 1996; Ancillotto et al. 2014).

Parasites may play a substantial role in parakeet invasion success, but evidence of the actual impact on parakeet fitness due to ectoparasites has yet to be found; further investigations are also needed to assess whether parasites introduced along with parakeets may colonise and spread among native species, with potential implications for parasite-mediated competition. Our results indicate that the role of these birds in spreading parasites may also be influenced by landscape composition, since natural and urban habitats represent important factors in promoting parasitic infestations. Vector-borne diseases, especially those transmitted by mites and ticks, raise concern because they may affect both wildlife and human health in urban contexts (Orton et al. 2000; Pisanu et al. 2018); thus, the virological and bacteriological monitoring of parakeet parasites may increase public awareness and address future policies on the management of these invaders.

Future investigations will have to look at the potential effects of parasites on individual fitness and behaviour of both introduced parakeets and native birds in urban areas, as well as search for parasite spillover from parakeets to native birds, assessing its effects on individual and population fitness.

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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.

References

- Ancillotto L, Serangeli MT, Russo D (2013) Curiosity killed the bat: Domestic cats as bat predators. *Mammalian Biology - Zeitschrift für Säugetierkunde* 78 (5):369–373
- 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. *Parasitol Res* 113:3909–3912
- Ancillotto L, Strubbe D, Menchetti M, Mori E (2016) An overlooked invader? Ecological niche, invasion success and range dynamics of the Alexandrine parakeet in the invaded range. *Biol Invasions* 18:583–595
- Appelt CW, Ward LC, Bender C, Fasanello J, van Vossen BJ, Knight L (2016) Examining potential relationships between monk parakeets (*Myiopsitta monachus*) and avian communities in an urban environment. *Wilson J Ornith* 128:556–566
- Aramburu R, Calvo S, Alzugaray ME, Cicchino A (2003) Ectoparasitic load of monk parakeet (*Myiopsitta monachus*, Psittacidae) nestlings. *Ornit Neotrop* 14:415–418
- Baker AS (1999) Mites and ticks of domestic animals: an identification guide and information source. The Stationary Office, London
- Barbar F, Lambertucci SA (2018) The roles of leporid species that have been translocated: a review of their ecosystem effects as native and exotic species. *Mam Rev* <https://doi.org/10.1111/mam.12126>
- Batllori X, Nos R (1985) Presencia de la cotorrta gris (*Myiopsitta monachus*) y de la cotorrta de collar (*Psittacula krameri*) en el Area Metropolitana de Barcelona. *Misc Zool* 9:407–411
- Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. *Biol Lett* 12:20150623
- Blair RB (1996) Land use and avian species diversity along an urban gradient. *Ecol Appl* 6:506–519
- Booth DT, Clayton DH, Block BA (1993) Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proc R Soc Lond B* 253:125–129
- Bosso L, De Conno C, Russo D (2017) Modelling the Risk Posed by the Zebra Mussel *Dreissena polymorpha*: Italy as a Case Study. *Environ Manag* 60(2):304–313
- Bowers MA, Breland B (1996) Foraging of gray squirrels on an urban-rural gradient: use of the GUD to assess anthropogenic impact. *Ecol Appl* 6:1135–1142
- Briceño C, Surot D, González-Acuña D, Martínez FJ, Fredes F (2017) Parasitic survey on introduced monk parakeets (*Myiopsitta monachus*) in Santiago, Chile. *Rev Bras Parasitol Vet* 26:129–135
- Butler CJ (2003) Population biology of the introduced Rose-ringed Parakeet *Psittacula krameri* in the UK. Doctoral dissertation, University of Oxford: Oxford
- Capinha C, Essl F, Seebens H, Moser D, Pereira HM (2015) The dispersal of alien species redefines biogeography in the Anthropocene. *Science* 348:1248–1251
- Chapuis JL, Obolenskaya E, Pisanu B, Lissovsky A (2011) Datasheet on *Tamias sibiricus*. CABI, Invasive Species Compendium, Wallingford
- Cignini B, Zapparoli M (1996) Atlante degli uccelli nidificanti a Roma. Fratelli Palombi Editori, Roma
- Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends Ecol Evol* 20:110
- Clayton DH, Drown DM (2001) Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). *J Parasitol* 87: 1291–1300
- Clemants SE, Moore G (2003) Patterns of species diversity in eight northeastern United States cities. *Urban Habitats* 1:4–16
- Clergeau P, Vergnes A (2011) Bird feeders may sustain feral Rose-ringed parakeets *Psittacula krameri* in temperate Europe. *Wildl Biol* 17: 248–252
- Colausti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecol Lett* 7: 721–733
- Combes C (1991) Evolution of parasite life cycles. In: Toft C, Aeschlimann A, Bolis L (eds) Parasite–host associations: coexistence or conflict? Oxford University Press, Oxford, pp 62–82
- Comer JA, Paddock CD, Childs JE (2001) Urban zoonoses caused by *Bartonella*, *Coxiella*, *Ehrlichia*, and *Rickettsia* species. *Vector Borne Zoonotic Dis* 1:91–118
- Covas L, Senar JC, Roque L, Quesada J (2017) Records of fatal attacks by rose-ringed parakeets *Psittacula krameri* on native avifauna. *Rev Catal Ornit* 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
- da Silva AG, Eberhard JR, Wright TF et al (2010) Genetic evidence for high propagule pressure and long-distance dispersal in monk parakeet (*Myiopsitta monachus*) invasive populations. *Mol Ecol* 19: 3336–3350
- Dangoisse G (2009) Étude de la population de Conures veuves (*Myiopsitta monachus*) de Bruxelles-Capitale. *Aves* 46:57–69
- Delgado VCA, French K (2012) Parasite–bird interactions in urban areas: current evidence and emerging questions. *Landsc Urban Plan* 105: 5–14
- Di Santo M, Vignoli L, Battisti C, Bologna MA (2013) Feeding activity and space use of a naturalized population of monk parakeet, *Myiopsitta monachus*, in a Mediterranean urban area. *Rev Ecol Terre Vie* 68:275–282
- 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
- Domènech J, Carrillo J, Senar JC (2003) Population size of the Monk Parakeet (*Myiopsitta monachus*) in Catalonia. *Rev Cat Ornit* 20:1–9
- Dunn AM, Hatcher MJ (2015) Parasites and biological invasions: parallels, interactions, and control. *Trends Parasitol* 31:189–199
- Edelaar P, Roques S, Hobson EA (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
- Escallón C, Becker MH, Walke JB, Jensen RV, Cormier G, Belden LK, Moore IT (2017) Testosterone levels are positively correlated with cloacal bacterial diversity and the relative abundance of Chlamydiae in breeding male rufous-collared sparrows. *Funct Ecol* 31:192–203
- Evans MR, Goldsmith AR, Norris SR (2000) The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). *Behav Ecol Sociobiol* 47:156–163
- 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 de Miscellània Zoològica* 8:1–8
- Folstad I, Karter AJ (1992) Parasites, bright males, and the immunocompetence handicap. *Am Nat* 139:603–622
- Forshaw JM (2010) Parrots of the world. Helm Field Guides, Christopher Helm Editions, London
- Fry DM (1995) Reproductive effects in birds exposed to pesticides and industrial chemicals. *Environ Health Perspect* 103:165
- Gaertner M, Wilson JR, Cadotte MW, MacIvor JS, Zenni RD, Richardson DM (2017) Non-native species in urban environments: patterns, processes, impacts and challenges. *Biol Invasions* 19:3461–3469
- Galloway TD, Lamb RJ (2016) Chewing lice (Phthiraptera: Amblycera and Ischnocera) infesting woodpeckers and sapsuckers (Aves: Piciformes: Picidae) in Manitoba, Canada. *Can Entomol* 148:520–531
- Golightly Jr RT, Faulhaber MR, Sallee KL, Lewis JC (1994) Food habits and management of introduced red fox in southern California. *Proceedings of the Sixteenth Vertebrate Pest Conference* 21
- Guimarães LR (1980) Ischnocera (Mallophaga) infesting parrots (Psittaciformes). IV. Genus *Echinophlopterus* Ewing, 1927. *Papeis avulsos de zoologia*
- 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
- Heylen DJA, Matthysen E (2008) Effect of tick parasitism on the health status of a passerine bird. *Funct Ecol* 22:1099–1107
- Himsworth CG, Parsons KL, Jardine C, Patrick DM (2013) Rats, cities, people, and pathogens: a systematic review and narrative synthesis of literature regarding the ecology of rat-associated zoonoses in urban centers. *Vector Borne Zoonotic Dis* 13:349–359
- Hodges JL, Le Cam L (1960) The Poisson approximation to the Poisson binomial distribution. *Ann Math Stat* 31:737–740
- Hofer S, Gloor S, Müller U et al (2000) High prevalence of *Echinococcus multilocularis* in urban red foxes (*Vulpes vulpes*) and voles (*Arvicola terrestris*) in the city of Zürich, Switzerland. *Parasitology* 120:135–142
- Hudson P, Greenman J (1998) Competition mediated by parasites: biological and theoretical progress. *Trends Ecol Evol* 13:387–390
- Hutson AM (1984) Keds, Flat-flies and Bat-flies: Diptera, Hippoboscidae and Nycteribiidae. Royal Entomological Society of London, London
- Johnson KP, Clayton DH (2003) The biology, ecology, and evolution of chewing lice, vol 24. Illinois Natural History Survey Special Publication, Champaign, pp 449–476
- Jokimäki J, Suhonen J (1998) Distribution and habitat selection of wintering birds in urban environments. *Landsc Urban Plan* 39:253–263
- Karamon J, Larska M, Jasik A, Sell B (2015) First report of the giant liver fluke (*Fascioloides magna*) infection in farmed fallow deer (*Dama dama*) in Poland—pathomorphological changes and molecular identification. *Bull Vet Inst Pulawy* 59:339–344
- Kelly DW, Paterson RA, Townsend CR, Poulin R, Tompkins DM (2009) Parasite spillback: a neglected concept in invasion ecology? *Ecology* 90:2047–2056
- Krasnov BR, Shenbrot GI, Khokhlova IS, Allan Degen A (2004) Relationship between host diversity and parasite diversity: flea assemblages on small mammals. *J Biogeogr* 31:1857–1866
- Krasnov BR, Morand S, Hawlena H, Khokhlova IS, Shenbrot GI (2005) Sex-biased parasitism, seasonality and sexual size dimorphism in desert rodents. *Oecologia* 146:209–217
- Le Louarn M, Couillens B, Deschamps-Cottin M, Clergeau P (2016) Interference competition between an invasive parakeet and native bird species at feeding sites. *J Ethol* 34:291–298
- 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 Biodiversidad* 82:1053–1056
- Mack RN, Simberloff D, Mark Lonsdale W, 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
- 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 et al (2016) Poor parasite Community of an invasive alien Species: macroparasites of Pallas’s squirrel in Italy. *Ann Zool Fenn* 53:103–112
- McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst* 11:161–176
- 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
- Møller AP, Dufva R, Allander K (1993) Parasites and the evolution of host social behavior. *Adv Study Behav* 22:60405–60402
- Mori E, Di Febbraro M, Foresta M, Melis P, Romanazzi E, Notari A, Boggiano F (2013) Assessment of the current distribution of free-living parrots and parakeets (Aves: Psittaciformes) in Italy: a synthesis of published data and new records. *Ital J Zool* 80:158–167
- Mori E, Ancillotto L, Groombridge J, Howard T, Smith VS, Menchetti M (2015) Macroparasites of introduced parakeets in Italy: a possible role for parasite-mediated competition. *Parasitol Res* 114:3277–3281
- Mori E, Ancillotto L, Menchetti M, Strubbe D (2017) “The early bird catches the nest”: possible competition between scops owls and ring-necked parakeets. *Anim Conserv* 20:463–470
- Mori E, Zozzoli R, Menchetti M (2018) The invasion of “Chip ‘n Dale”: global distribution and status of introduced Siberian chipmunks *Eutamias sibiricus*. *Mammal Rev.* <https://doi.org/10.1111/mam.12117>
- Onstad DW, McManus ML (1996) Risks of host range expansion by parasites of insects. *BioScience* 46:430–435
- Orchan Y, Chiron F, Shwartz A, Kark S (2013) The complex interaction network among multiple invasive bird species in a cavity-nesting community. *Biol Invasions* 15:429–445
- Orton DI, Warren LJ, Wilkinson JD (2000) Avian mite dermatitis. *Clin Exp Dermatol* 25:129–131
- Owen JP, Delany ME, Cardona CJ, Bickford AA, Mullens BA (2009) Host inflammatory response governs fitness in an avian ectoparasite, the northern fowl mite (*Ornithonyssus sylviarum*). *Int J Parasitol* 39:789–799
- Palma RL (1978) Slide-mounting of lice: a detailed description of the Canada balsam technique. *N Z Entomol* 6:432–436
- Pârâu LG, Strubbe D, Mori E et al (2016) Rose-ringed Parakeet *Psittacula krameri* populations and numbers in Europe: a complete overview. *Open Ornithol J* 9(1):1–13

- Parsons H, Major RE, French K (2006) Species interactions and habitat associations of birds inhabiting urban areas of Sydney, Australia. *Austral Ecol* 31:217–227
- Pinheiro J, Bates D, DebRoy S, Sarkar D (2014) nlme: linear and non-linear mixed effects models. R package version 3.1–117. Available at <http://CRAN.R-project.org/package=nlme>
- Pisanu B, Laroucau K, Aaziz R et al (2018) *Chlamydia avium* detection from a Ring-necked parakeet (*Psittacula krameri*) in France. *J Exot Pet Med*. <https://doi.org/10.1053/j.jepm.2018.02.035>
- Poulin R (1996) Sexual inequalities in helminth infections: a cost of being a male? *Am Nat* 147:287–295
- Price RD, Hellenthal RA, Palma RL (2003) World checklist of chewing lice with host associations and keys to families and genera. In: Price RD, Hellenthal RA, Palma RL, Johnson KP, Clayton DH (eds) *The chewing lice: world checklist and biological overview*. Illinois Natural History Survey Special Publication, Champaign-Urbana, pp 1–448
- Pyke GH, Szabo JK (2018) Conservation and the 4 Rs, which are rescue, rehabilitation, release, and research. *Conserv Biol* 32:50–59
- R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Wien
- Ralph CJ, Sauer JR, Droege S (1995) Monitoring bird populations by point counts. Gen. Tech. Rep. PSW-GTR-149. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany
- Roberts ML, Buchanan KL, Evans MR (2004) Testing the immunocompetence handicap hypothesis: a review of the evidence. *Anim Behav* 68:227–239
- Romeo C, Wauters LA, Ferrari N, Lanfranchi P, Martinoli A, Pisanu B, Preatoni DG, Saino N, Russo D (2014) Macroparasite fauna of alien grey squirrels (*Sciurus carolinensis*): composition, variability and implications for native species. *Plos One* 9(2) e88002
- Rothenburger JL, Himsworth CH, Nemeth NM, Pearl DL, Jardine CM (2017) Environmental factors and zoonotic pathogen ecology in urban exploiter species. *EcoHealth* 14:630–641
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE et al (2001) The population biology of invasive species. *Annu Rev Ecol Syst* 32:305–332
- Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH (2010) Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience* 60:199–208
- Smit FGAM (1983) Key to the genera and subgenera of Ceratophyllidae. In: Traub R, Rothschild M, Haddow J (eds) *The Rothschild collection of fleas. The Ceratophyllidae*. British Museum (Nat. Hist.), London, pp 1–36
- Strubbe D, Matthysen E (2011) A radiotelemetry study of habitat use by the exotic Ring-necked Parakeet *Psittacula krameri* in Belgium. *Ibis* 153:180–184
- Torchin ME, Mitchell CE (2004) Parasites, pathogens, and invasions by plants and animals. *Front Ecol Environ* 2:183–190
- Turbè A, Strubbe D, Mori E et al (2017) Assessing the assessments: evaluation of four impact assessment protocols for invasive alien species. *Divers Distrib* 23:297–307
- Tuttle LJ, Sikkil PC, Cure K, Hixon MA (2017) Parasite-mediated enemy release and low biotic resistance may facilitate invasion of Atlantic coral reefs by Pacific red lionfish (*Pterois volitans*). *Biol Invasions* 19:563–575
- Uller T, Olsson M (2003) Prenatal exposure to testosterone increases ectoparasite susceptibility in the common lizard (*Lacerta vivipara*). *Proc R Soc Lond B Biol Sci* 270:1867–1870
- van Rensburg BJ, Peacock DS, Robertson MP (2009) Biotic homogenization and alien bird species along an urban gradient in South Africa. *Landsc Urban Plan* 92:233–241
- Vila M, Maron JL, Marco L (2005) Evidence for the enemy release hypothesis in *Hypericum perforatum*. *Oecologia* 142:474–479
- Vourc'h G, Abrial D, Bord S, Jacquot M, Maseglier S, Poux V, Pisanu B, Bailly X, Chapuis JL (2016) Mapping human risk of infection with *Borrelia burgdorferi* sensu lato, the agent of Lyme borreliosis, in a periurban forests in France. *Ticks Tick Borne Dis* 5:644–652
- Welch JN, Leppanen C (2017) The threat of invasive species to bats: a review. *Mammal Rev* 47(4):277–290
- Whitaker AP (2007) Fleas (Siphonaptera). In: Royal Entomological Society, Spencer KA (eds) *Handbook for the identification of British insects*. Entomological Society of London, London