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Comprehensive investigation of ectoparasite community and abundance across life history stages of avian host

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Abstract

Fitness consequences of ectoparasitism are expressed over the lifetime of their hosts in relation to variation in composition and abundance of the entire ectoparasite community and across all host life history stages. However, most empirical studies have focused on parasite species-specific effects and only during some life history stages. We conducted a systematic, year-long survey of an ectoparasite community in a wild population of house finches *Carpodacus mexicanus* Müller in south-western Arizona, with a specific focus on ecological and behavioral correlates of ectoparasite prevalence and abundance. We investigated five ectoparasite species: two feather mite genera – both novel for house finches – *Strelkoviacarus* (Analgidae) and *Dermoglyphus* (Dermoglyphidae), the nest mite *Pellonyssus reedi* (Macronyssidae), and the lice *Menacanthus alaudae* (Menoponidae) and *Ricinus microcephalus* (Ricinidae). Mite *P. reedi* and louse *Menacanthus alaudae* abundance peaked during host breeding season, especially in older birds, whereas feather mite abundance peaked during molt. Overall, breeding birds had more *P. reedi* than non-breeders, molting males had greater abundance of feather mites than molting females and non-molting males, and young males had more feather mites than older males. We discuss these results in relation to natural history of ectoparasites under study and suggest that ectoparasites might synchronize their life cycles to those of their hosts. Pronounced differences in relative abundance of ectoparasite species among host's life history stages have important implications for evolution of parasite-specific host defenses.

Introduction

Ectoparasites exert strong selection pressures on avian hosts (Hamilton & Zuk, 1982; Møller, 1990*a*; Loye & Carroll, 1995; Clayton & Moore, 1997) by lowering nestling survival and growth (Møller, 1990*b*; Richner, Oppliger & Christe, 1993; Merino & Potti, 1995; Fitze, Clobert & Richner, 2004), increasing the cost of sexual ornamentation (Pérez-Tris, Carbonell & Tellería, 2002), reducing future reproductive success, and decreasing long-term survival (Brown, Brown & Rannala, 1995; Fitze *et al*., 2004). At the same time, there is substantial variation in extent of parasitism across individuals in host populations (e.g. Goater & Holmes, 1997), and investigations of ecological, physiological and behavioral correlates of ectoparasite distribution, especially across complete life history of the host, is an important starting point for elucidating mechanisms of parasite-mediated natural selection.

Seasonal trends of parasite prevalence and abundance are often associated with the host's annual activities (Rothschild & Clay, 1952; Cook & Beer, 1958; Foster, 1969; Marshall, 1981; Blanco & Frías, 2001; Altizer *et al*., 2004; Dietsch, 2005). Such associations can be driven either by synchronization of reproduction or dispersal of ectoparasites with life history stages of their hosts (Rothschild & Ford, 1964; Foster, 1969; Blanco & Frías, 2001; Dietsch, 2005) or by seasonal changes in host's ectoparasite defense, for example, reproduction and post-breeding molt can impose substantial energetic and immunological costs resulting in a trade-off with ectoparasite defense (Stearns, 1989; Lindström, Visser & Daan, 1993; Møller, 1993, 1994).

Such seasonal trends can be distinct between the sexes of hosts. For example, in males, the costs of post-breeding molt can be compounded by greater energetic requirements of developing sexual ornamentation (e.g. Badyaev & Vleck, 2007), an expenditure that might increase males' susceptibility to greater parasite infestation during molt period compared with females. In addition, sex and age differences in parasite susceptibility have been attributed to differences in behaviors that increase risk of ectoparasite contact and transmission, such as greater time spend on the nest by females of some species or large flocks in juvenile birds or limited behavioral or physiological defense against ectoparasites in juvenile birds (Mohr, 1947; Thompson, 1960*a*,*b*; Marshall, 1971, 1981; Weatherhead & Bennett, 1991; Alonso & Alonso, 1993; Poulin, 1996; Duckworth, Mendonça & Hill, 2001; Morales-Montor *et al*., 2004).

We conducted a systematic, year-long survey of ectoparasites in a native population of house finches *Carpodacus mexicanus* Müller, with a specific focus on ecological and behavioral correlates of ectoparasite prevalence and abundance. Though several ectoparasites have been documented in house finches (Thompson *et al*., 1997; Stoehr *et al*., 2000; Hartup *et al*., 2004; Badyaev *et al*., 2006), this is the first study to examine the entire ectoparasite community across the host's main life history stages in the native habitat. Further, by capitalizing on complete recaptures of birds in our study, we minimize association between capture probability and parasitism inherent in the studies of parasitism in wild animals. First, we describe the diversity of ectoparasites in the study population, and provide a first description for this host of two ectoparasite genera. Second, we examine ectoparasite abundance and prevalence in relation to host phenology, life history, age and sex. We discuss these results in relation to the evolution of parasite-resistance strategies.

Materials and methods

House finches were studied in a resident native population in south-western Arizona in Pima County, in 2003–2006. As a part of larger monitoring, resident birds were trapped year-round at seven permanent feeding stations with large walk-in traps three to four times a week. At first capture, birds were marked with a unique combination of one aluminum and three colored plastic rings. The capture protocol assured systematic recaptures of most birds in the population; more than 90% of adult resident birds are recaptured within 3.5 months (detailed protocols and study site description in Badyaev & Oh, 2008). To identify breeders and non-breeders during breeding season in March–July, pairing associations and nest-initiation behavior were closely followed for the entire population as described in Oh & Badyaev (2008). Based on breeding records, resident birds were assigned to hatch-year (HY), after-hatch year or after-second year. Post-breeding molt in this population lasts from June to November (Badyaev & Vleck, 2007) and individuals captured during this time were examined for the presence of molting feathers. In HY birds before the first molt, sex was determined molecularly. We collected 50 μL of blood by brachial venipuncture, extracted DNA by standard salt extraction protocol, and amplified the CHD1 genes on the sex chromosomes.

On each trapping day, six to 12 birds were selected at random from 30 to 60 captured birds and placed in specialized fumigation jars for 10 min with a cotton ball soaked with 0.4 mL chloroform, followed by systematic thorough ruffling of feathers in order to exterminate and detach ectoparasites, particularly those on the inside of feather quills (Fowler & Cohen, 1983; Wheeler & Threlfall, 1986). Each bird's head, neck, wing, breast, back, rump and tail feathers were ruffled by hand over a 21.6×27.8 cm paper and contents were added to the jar. The filter paper in the bottom of each jar was removed, the jar was swabbed with a cotton swab and all contents were added to the filter paper that was placed in a small zipper-closure plastic bag. The bag was then examined under the dissecting microscope without being opened. In lice, only nymph and adult stages were identified to the species. We sampled between 80 and 100 birds per month. Chloroform was more efficient at detaching lice than ether, ethyl acetate and CO_2 (see also Visnak & Dumbacher, 1999), and fumigation jars removed 56–95% of ectoparasites (see also Fowler & Cohen, 1983; Poiani, 1992). Ectoparasites were identified and counted under a Leica MZ 12.5 (Leica Microsystems Inc., Bannockburn, IL, USA) dissecting microscope at $\times 12.5$ magnification, without prior knowledge of host identity or characteristics, and photos of all ectoparasites were taken with a Leica DC 300 7.2 megapixel digital camera with sizes standardized with a ruler. Mite and lice samples were critical-point dried in a Polaran 3600, coated with 60 nm gold in a Hummer 6.2 by Anatech Ltd (Hayward, CA, USA), and photographed with Polaroid Type 55 PN film under a Philips 515 scanning electron microscope.

Here we report data collected in a continuous 12-month period from April 2005 to March 2006 from a total of $n = 1010$ fumigated birds ($n = 587$ males and 423 females). Data collected before 2005 were used to assign age categories. Prevalence of a given ectoparasite species was defined as the percent of hosts sampled that had at least one parasite. For ectoparasites that peaked in prevalence and abundance during host breeding season (*Pellonyssus reedi* and both lice), the significance of age was assessed only during March–July.

Monthly abundance was calculated as mean number of ectoparasites per host in a particular month, and Type III general linear models were used to assess significance of season (sampling date), age ('young' indicating birds ≤ 1 year and 'older' indicating birds > 1 year), sex and the interaction among these factors on abundance of each ectoparasite species. A second model included breeding status (breeder, non-breeder), sampling date and sex, while a third model incorporated molting status ('molting' indicating birds with ≥ 1 molting feather and 'non-molting' indicating birds without molting feathers). To achieve normal distribution, ectoparasite abundance was transformed into ratios with arcsine and log transformations applied for each species separately. Mean abundance and standard errors for each group were tested with non-parametric Kruskal–Wallis tests and presence/absence of ectoparasites was tested within groups using χ^2 tests. All analyses were conducted with SAS 9.13 (SAS, 1989).

Results

Parasite species diversity

Of 1010 birds, 29.1% ($n = 171$) of all males and 21.7% ($n = 92$) of all females had ectoparasites. Of the 171 males, 87% ($n = 149$) had one, 12% ($n = 20$) had two and 1% ($n = 2$) had three species of ectoparasites. Of the 92 females, 92% ($n = 85$) had one and 8% ($n = 7$) had two ectoparasite species. We found five species of ectoparasites (Fig. 1, Table 1) – three species of mites, *P. reedi* Zumpt and Patterson

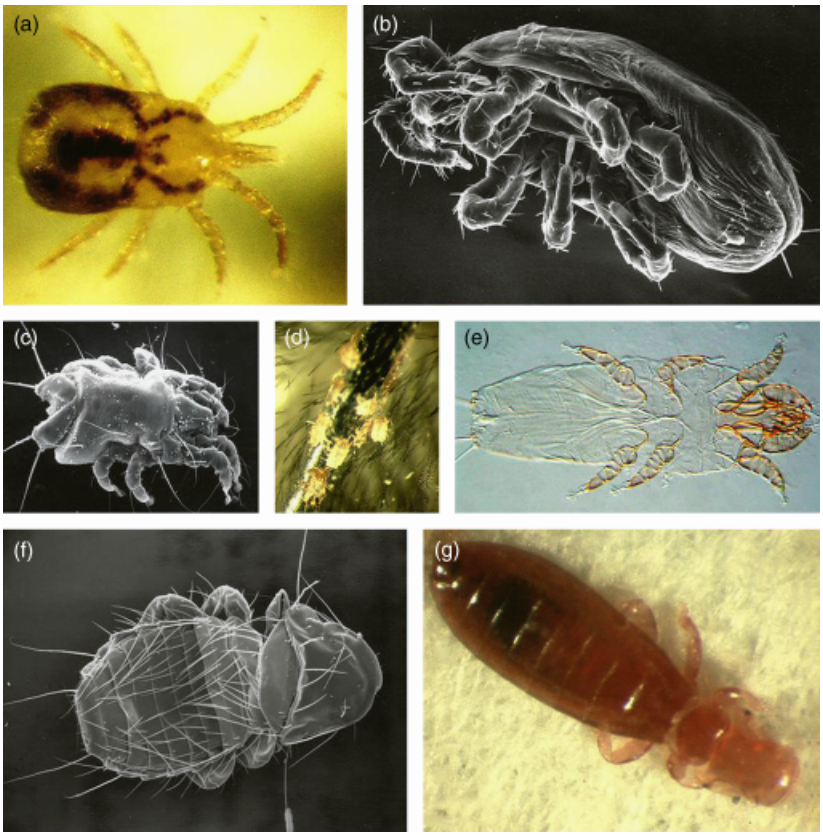

Figure 1 Ectoparasites of house finches in a native population in south-western Arizona. (a, b) *Pellonyssus reedi*, a hematophagous nest mite, (c) *Strelkoviacarus* sp., a feather mite, (d) several *Strelkoviacarus* on calamus of pin-feather, (e) *Dermoglyphus* sp., a feather quill mite, (f) louse species *Menacanthus alaudae* and (g) louse species *Ricinus microcephalus*. (*Dermoglyphus* photo by Heather Proctor, all other photos by T. Hamstra.)

Table 1 Description of ectoparasite species found on house finches in south-western Arizona population over 12-month period

Species/genus	Type	# Range per host	Mean size of ectoparasite (mm)	Biology/natural history
Pellonyssus reedi	Nest mite	M 0–27 F 0–69	0.56	Pierces host skin to obtain blood, found on other passerines, temporary parasite, adapted to nest environment
Strelkoviacarus sp.	Feather mite	M 0–18 F 0–6	0.28	Feeds on uropygial gland oil, may or may not damage feathers, not known if permanent parasite
Dermoglyphus sp.	Feather mite	M 0–11 F 0–10	0.40	Feeds on fluids from papillae of feathers, lives inside quills, can damage feathers, not known if permanent parasite
Menacanthus alaudae	Louse	M 0–35 F 0–7	1.00	Chews on developing feather tips to obtain blood, permanent parasite
Ricinus microcephalus	Louse	M 0–15 F 0–10	3.40	Pierces host skin to obtain blood, host-specific, permanent parasite

The range in abundance of each observed ectoparasite by host sex (M, male; F, female).

(Macronyssidae), *Strelkoviacarus* sp. Dubinin (Analgidae, Anomalginae) and *Dermoglyphus* sp. Robin and Mégnin (Dermoglyphidae), the latter two recorded for the first time in the house finch, and two species of chewing lice (order Phthiraptera, suborder Amblycera), *Menacanthus alaudae* Schrank (Menoponidae) and *Ricinus microcephalus* Kellogg (Ricinidae). Details of the five ectoparasites are given in Table 1. The specificity of these ectoparasites varies: *P. reedi* parasitizes several families of passerines (Burley, Tidemann & Halupka, 1991; Szabó *et al*., 2002) and one cuckoo species (Lindholm, Venter & Ueckermann, 1998), *M. alaudae* parasitizes at least two families of passerines (Price, 1977), while *R. microcephalus* is species-specific (Nelson, 1972; Price, 1977). Hosts of *Strelkoviacarus* are from orders Passeriformes and Coraciiformes, while those of *Dermoglyphus* are passerines, pigeons (Wehr, 1952; OConnor *et al*., 2005) and hummingbirds (Atyeo & Gaud, 1979). *Pellonyssus reedi* is a hematophagous, temporary parasite adapted to the nesting environment. Both *M. alaudae* and *R. microcephalus* are also hematophagous, and, as lice, are permanent ectoparasites (although only nymph and adult stages are present in some seasons, see below). *Strelkoviacarus* probably feeds on

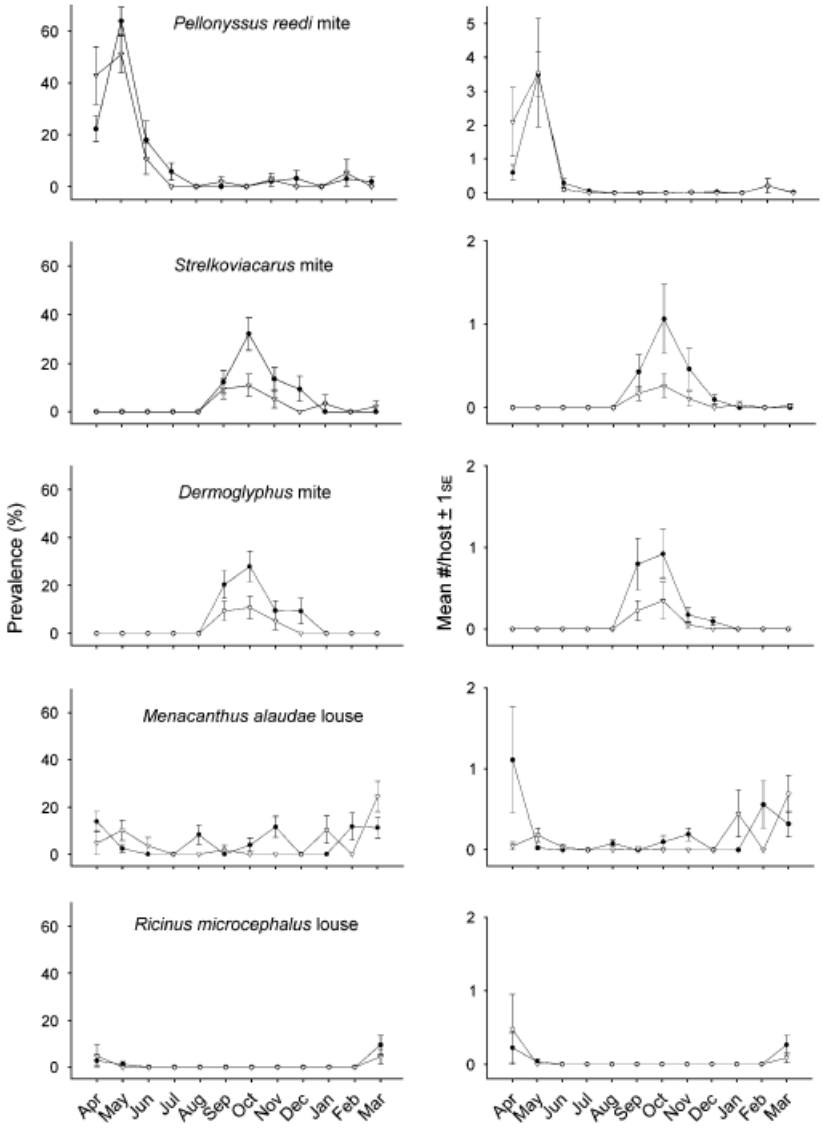

Figure 2 Seasonal trends in prevalence and abundance of five ectoparasite species of house finches in south-western Arizona. Left column: Seasonal trends in prevalence in $n = 1010$ house finches. Shown is percent of birds (± 1 SE) each month with parasites (by host sex). Right column: Seasonal trends in abundance of ectoparasites. Shown is mean number (± 1 SE) of ectoparasites per bird, by host sex. Solid circles are male hosts and open triangles are female hosts.

uropygial gland oil (Proctor, 2003) and lives on the outside of feathers, *Dermoglyphus* feeds on fluids from the papillae at the base of feathers and lives inside quills (Proctor, 2003).

General patterns of distribution and abundance

In both host sexes, prevalence and abundance were the highest in May for nest mite *P. reedi*, in October for both feather mites, and in March–April for the lice *R. microcephalus* and *M. alaudae* (Fig. 2). Over the 12-month period, the abundance of ectoparasites varied with season (sampling date: $F = 42.26$, $P < 0.01$ for *P. reedi*; $F = 3.71$, $P < 0.05$ for *Strelkoviacarus*; $F = 11.28$, $P < 0.01$ for *M. alaudae*, but not for *Dermoglyphus* $F = 2.92$, $P < 0.1$ or *R. microcephalus* $F = 0.13$, NS, $n = 664$) and host age (sampling date × age interaction, $F = 10.19$ for *P. reedi*, $F = 3.95$ for *M. alaudae* and $F = 4.29$ for *R. microcephalus*, all P's < 0.05, interaction not significant for *Strelkoviacarus*: $F = 1.19$ and *Dermoglyphus*: $F = 0.11$). There were no differences in overall ectoparasite abundance between the sexes (all F's < 1.3, all P's > 0.1; Fig. 2). Older birds had greater abundance of *P. reedi* compared with young birds ($F = 10.25$, $P < 0.001$). Young birds had more louse *M. alaudae* than older birds ($F = 3.97$, $P < 0.05$, $n = 664$), especially in males, while older birds had more louse *R. microcephalus* ($F = 4.29$, $P < 0.05$, $n = 664$; Fig. 3). Louse *R. microcephalus* was present at very low numbers and only in older birds ($n = 3$ females and 8 males; Fig. 3).

Breeding season

During breeding season (March–July), feather mites *Strelkoviacarus* and *Dermoglypus* were not detected. The abundance of nest mite *P. reedi* increased as breeding season progressed (sampling date: $F = 16.73$, $P < 0.001$, $n = 363$

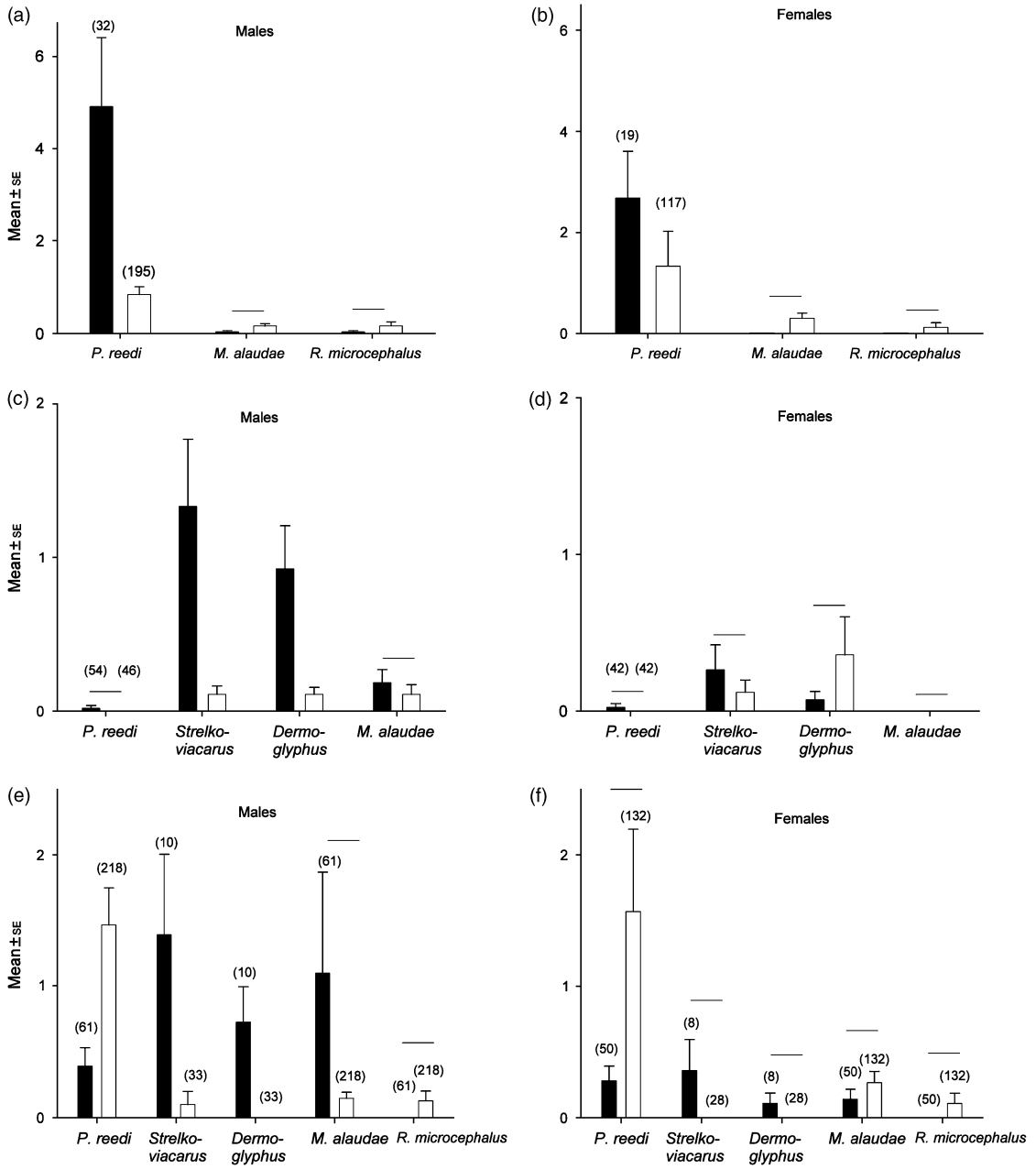

Figure 3 Ectoparasite abundance (mean number per bird ± SE) in relation to (a, b) breeding season, (c, d) molt season and (e, f) age of hosts. (a) Breeding males (black bars) compared with non-breeding males (white bars), and (b) breeding females (black bars) compared with non-breeding females (white bars). Feather mites *Strelkoviacarus* and *Dermoglyphus* were not detected during breeding season. (c) Molting males (black bars) compared with non-molting males (white bars), and (d) molting females (black bars) compared with non-molting females (white bars). Louse *Ricinus microcephalus* was not detected during molt season. (e) Young males (black bars) compared with older males (white bars) during breeding season (March–July) for *Pellonyssus reedi*, *Menacanthus alaudae* and *R. microcephalus*, and for molt season (June–November) for feather mites *Strelkoviacarus* and *Dermoglyhus*, and (f) young females (black bars) compared with older females (white bars) for same time periods. Numbers in parentheses indicate sample sizes, lines above bars indicate no difference between groups.

adults old enough to breed); during breeding period there were no seasonal changes in abundance of either *M. alaudae* or *R. microcephalus* ($F = 1.14$ and 0.03 correspondingly, both P's > 0.1). Breeding birds of both sexes had greater abundance of nest mites *P. reedi* than did non-breeding birds (breeding vs. non-breeding: males, $\chi^2 = 8.8$; females, $\chi^2 = 13.29$, both P's < 0.05; breeding status × sex: $F = 0.06$, NS; Fig. 3a and b). During breeding season, older males had more *P. reedi* than young males ($\chi^2 = 4.32$, $P < 0.05$), and older females tended to have more nest mites than older

males ($\chi^2 = 2.62$, $P = 0.05$; Fig. 3e and f). Abundance of *M. alaudae* and *R. microcephalus* did not differ between the sexes or breeding and non-breeding birds (all F's < 1.4, P's > 0.1; Fig. 3a and b).

Molt season

During molt season, louse *R. microcephalus* was not detected and only six birds had nest mite *P. reedi*. Abundance of *Strelkoviacarus* and *Dermoglyphus* feather mites differed between the sexes (F's = 6.13 and 7.35 correspondingly, both P's < 0.05, $n = 455$), increased with sampling date within molt season (F's = 10.75 and 8.08, both P's < 0.01) and differed between molting and non-molting males (*Strelkoviacarus*: $\chi^2 = 10.31$, $P < 0.01$; *Dermoglyphus*: $\chi^2 = 4.59$, $P < 0.05$; Fig. 3c and d), but not between molting and non-molting females (*Strelkoviacarus*: $\chi^2 = 0.17$, NS; *Dermoglyphus*: $\chi^2 = 1.38$, NS). During molt season, young males had higher abundance of feather mites compared with older males (*Strelkoviacarus*: $\chi^2 = 2.72$, $P < 0.05$; *Dermoglyphus*: $\chi^2 = 3.78$, $P < 0.05$). *Dermoglyphus* abundance was greater in older males compared with older females ($\chi^2 = 3.02$, $P < 0.05$) and in young males compared with young females ($\chi^2 = 3.32$, $P < 0.05$; Fig. 3e and f). In males, abundance of *M. alaudae* similarly increased with sampling date within molt season ($F = 5.57$, $P < 0.05$). Feather mite and louse M. alaudae abundance were greater in molting males compared to molting females (*Strelkoviacarus*: $\chi^2 = 8.36$, $P < 0.01$; *Dermoglyphus*: $\chi^2 = 7.87$, $P < 0.01$, *M. alaudae* $x^2 = 4.06$, $P < 0.05$, $n = 100$ males and 84 females).

Discussion

Study of ectoparasite diversity and distribution provides a starting point for elucidating mechanisms of parasite-mediated natural selection. We documented a previously unknown diversity of ectoparasites in a resident host population of house finches across continuous 12-month monitoring and present evidence that some ectoparasites might synchronize their life cycles with those of their host (Table 1; Fig. 3). As predicted, breeding birds had more nest mites than non-breeders, molting males had more feather mites than non-molting males, older birds had more nest mites than young birds, and young males had more feather mites than older males. We found no age differences in lice infestation. In addition, the difference in parasite infestation between the sexes was most pronounced during molt – molting males had higher abundance of three species of ectoparasites compared with molting females, the result consistent with the hypothesis that molting males experience additional energetic costs during annual post-breeding molt of sexual ornamentation.

Ectoparasites vary in host specificity, from those that parasitize more than one order of birds, as *Strelkoviacarus* and *Dermoglyphus*, to family-specific – *P. reedi* and *M. alaudae*, to species-specific – *R. microcephalus*. In this study we report feather mites of genera *Strelkoviacarus* and *Dermoglyphus* for the first time in house finches despite several prior studies. Our results suggest that these mites might have been difficult to detect because they are present on birds during only a particular season, are small and unpigmented, so that microscopic examination of fumigation jar contents is necessary for their visualization and identification.

Our results support the hypothesis that ectoparasites' life cycles generally coincide with annual cycles of their avian hosts. The mechanisms underlying the apparent synchronization of ectoparasite and host life cycles are not well understood. For some ectoparasites, there is evidence that ingestion of host's reproductive hormones from plasma triggers ectoparasites' breeding (Rothschild & Ford, 1964, 1972). Because abundance of *P. reedi* and both louse species peaked during host reproductive season, and these species incorporate blood in their diets, similar mechanisms may operate in these species. For *P. reedi* overwintering in nests or litter, mite egg hatching can be temperature-induced, producing pronounced seasonal pattern of infestation (Stoehr *et al.*, 2000; Badyaev *et al.*, 2006). Lice, however, are permanent ectoparasites, and thus might increase in abundance during host reproduction and molt because during these costly annual events hosts might have less energy to devote to defensive physiology or preening behaviors (Møller & Rózsa, 2005). Alternatively, the variation in abundance could represent differential reproduction or dispersal of parasites or their effects on host survival. However, the sampling protocol of this study minimizes the potentially confounding association between capture probability and ectoparasite presence.

As expected, breeding birds had higher numbers of *P. reedi* than non-breeders. Because *P. reedi* infests nests, breeders are at higher risk for nest mites through contact transmission associated with time spent at the nest. This mite species generates a non-specific immune response in other bird species (Szabó *et al.*, 2002). Thus, greater infestation of breeding birds may reflect both greater opportunity for contact with the ectoparasites and higher energetic trade-offs between mounting an immune response to nest mites and reproduction (Gustafsson *et al.*, 1994; Richner & Heeb, 1995).

Little is known about the basic biology of most feather mites (Proctor & Owens, 2000). We found that prevalence and abundance of *Strelkoviacarus* and *Dermoglyphus* increased during host molt and was also higher in young birds and in males. Feather mites may prefer new feathers to old; we found several *Strelkoviacarus* attached to the outside of the calamus on growing pinfeathers (Fig. 1d). Interestingly, in canary *Serinus canaria*, only pinfeathers had *Dermoglyphus* mites (Wehr, 1952). Increase in abundance and preference for new feathers suggest that feather mites may synchronize either their reproduction or dispersal with host molting season. Parasite dispersal strategies might include preference for new feathers as a mechanism for avoiding being shed with molting feathers (Jovani *et al.*, 2006; Pap *et al.*, 2006; Galván *et al.*, 2008).

Young males had more feather mites than older males and this may reflect age- and sex-related physiological,

immunological or behavioral differences (Marshall, 1981; Duckworth *et al*., 2001). Young age bias has been reported for lice, louse flies and feather mites in several avian host species (Blanco *et al*., 2001; Dowling *et al*., 2001). Ectoparasites may spread more easily among young birds than older birds because the former, in some species, spend less time preening (e.g. Alonso & Alonso, 1993) and more time in large flocks with greater potential for contact transmission. It was also suggested that feather mites might attack young birds more than old birds because young birds may produce more uropygial gland oil, the probable diet of *Strelkoviacarus* (Dowling *et al*., 2001; Proctor, 2003; Galván *et al*., 2008).

Lice and feather mites typically do not directly affect host fitness (Clayton, 1991). However, their prevalence during molt and greater abundance on male hosts might lead to alteration of male plumage coloration and structure and thus increase cost of production of sexual ornamentation and displays (Hamilton & Zuk, 1982; Møller, 1990*a*, 1991; Thompson *et al*., 1997). In contrast, the nest mite *P. reedi* exerts high fitness costs (Stoehr *et al*., 2000; Weddle, 2000; Szabó *et al*., 2002) and can favor evolution of maternal strategies of sex-biased ovulation order and associated rapid growth of nestlings in infested nests (Hart, 1997; Badyaev *et al*., 2006; Badyaev & Oh, 2008). In summary, the presence of *P. reedi* nest mites during breeding season and in breeding birds, *Strelkoviacarus* and *Dermoglyphus* feather mites during molting season, and *M. alaudae* and *R. microcephalus* lice during both energetically demanding annual activities, suggest an association between ectoparasites' and hosts' life cycles, providing great opportunity to examine co-evolution of host and ectoparasites in this system.

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References

Alonso, J.A. & Alonso, J.C. (1993). Age-related differences in time budgets and parental care in wintering common cranes. *Auk* **110**, 78–88.

Altizer, S., Davis, A.K., Cook, K.C. & Cherry, J.J. (2004). Age, sex, and season affect the risk of mycoplasmal conjunctivitis in a southeastern house finch population. *Can. J. Zool.* **82**, 755–763.

Atyeo, W.T. & Gaud, J. (1979). Ptyssalgidae, a new family of Analgoid feather mites (Acarina: Acaridida). *J. Med. Entomol.* **16**, 306–308.

Badyaev, A.V., Hamstra, T.L., Oh, K.P. & Acevedo Seaman, D. (2006). Sex-biased maternal effects reduce ectoparasite-induced mortality in a passerine bird. *Proc. Natl. Acad. Sci. USA* **103**, 14406–14411.

Badyaev, A.V. & Oh, K.P. (2008). Environmental induction and phenotypic retention of adaptive maternal effects. *BMC Evol. Biol.* **8**, 3.

Badyaev, A.V. & Vleck, C.M. (2007). Context-dependent ontogeny of sexual ornamentation: implications for a trade-off between current and future breeding efforts. *J. Evol. Biol.* **20**, 1277–1287.

Blanco, G. & Frías, O. (2001). Symbiotic feather mites synchronize dispersal and population growth with host sociality and migratory disposition. *Ecography* **24**, 113–120.

Blanco, G., de la Puente, J., Corroto, M., Baz, A. & Colás, J. (2001). Condition-dependent immune defence in the magpie: how important is ectoparasitism? *Biol. J. Linn. Soc.* **72**, 279–286.

Brown, C.R., Brown, M.B. & Rannala, B. (1995). Ectoparasites reduce long-term survival of their avian host. *Proc. Roy. Soc. Lond. Ser. B* **262**, 313–319.

Burley, N., Tidemann, S.C. & Halupka, K. (1991). Bill colour and parasite levels of zebra finches. In *Bird–parasite interactions: ecology, evolution, and behaviour*: 359–376. Loye, J.E. & Zuk, M. (Eds). New York: Oxford University Press.

Clayton, D.H. (1991). Coevolution of avian grooming and ectoparasite avoidance. In *Bird–parasite interactions: ecology, evolution, and behaviour*: 258–289. Loye, J.E. & Zuk, M. (Eds). Oxford: Oxford University Press.

Clayton, D.H. & Moore, J. (1997). *Host–parasite evolution: general principles and avian models*. Oxford: Oxford University Press.

Cook, E.F. & Beer, J.R. (1958). A study of louse populations of the meadow vole and deer mouse. *Ecology* **39**, 645–659.

Dietsch, T.V. (2005). Seasonal variation of infestation by ectoparasitic chigger mite larvae (Acarina: Trombiculidae) on resident and migratory birds in coffee agroecosystems of Chiapas, Mexico. *J. Parasitol.* **91**, 1294–1303.

Dowling, D.K., Richardson, D.S., Blaakmeer, K. & Komdeur, J. (2001). Feather mite loads influenced by salt exposure, age and reproductive stage in the Seychelles Warbler *Acrocephalus sechellensis*. *J. Avian Biol.* **32**, 364–369.

Duckworth, R.A., Mendonça, M.T. & Hill, G.E. (2001). A condition-dependent link between testosterone and disease resistance in the house finch. *Proc. Roy. Soc. Lond. Ser. B* **268**, 2467–2472.

Fitze, P.S., Clobert, J. & Richner, H. (2004). Long-term life-history consequences of ecoparasite-modulated growth and development. *Ecology* **85**, 2018–2026.

Foster, M.S. (1969). Synchronized life cycles in the orange-crowned warbler and its mallophagan parasites. *Ecology* **50**, 315–323.

Fowler, J.A. & Cohen, S. (1983). A method for the quantitative collection of ectoparasites from birds. *Ringing Migr*. **4**, 185–189.

Galván, I., Barba, E., Piculo, R., Cantó, J.L., Cortés, J.L., Monrós, J.S., Atiénzar, F. & Proctor, H. (2008). Feather mites and birds: an interaction mediated by uropygial gland size? *J. Evol. Biol*. **21**, 133–144.

Goater, C.P. & Holmes, J.C. (1997). Parasite-mediated natural selection. In *Host–parasite evolution: general principles and avian models*: 9–29. Clayton, D.H. & Moore, J. (Eds). Oxford: Oxford University Press.

Gustafsson, L., Nordling, D., Andersson, M., Sheldon, B.C. & Qvarnström, A. (1994). Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philos. Trans. Biol. Sci*. **346**, 323–331.

Hamilton, W.D. & Zuk, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

Hart, B.L. (1997). Behavioural defence. In *Host–parasite evolution: general principles and avian models*: 59–77.Clayton, D.H. & Moore, J. (Eds). Oxford: Oxford University Press.

Hartup, B.K., Stott-Messick, B., Guzy, M. & Ley, D.H. (2004). Health survey of house finches (*Carpodacus mexicanus*) from Wisconsin. *Avian Dis*. **48**, 84–90.

Jovani, R., Serrano, D., Frías, Ó. & Blanco, G. (2006). Shift in feather mite distribution during the molt of passerines: the case of the barn swallows (*Hirundo rustica*). *Can. J. Zool*. **84**, 729–735.

Lindholm, A.K., Venter, G.J. & Ueckermann, E.A. (1998). Persistence of passerine ectoparasites on the diederik cuckoo *Chrysococcyx caprius*. *J. Zool*. **244**, 145–153.

Lindström, A., Visser, G.H. & Daan, S. (1993). The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiol. Zool*. **66**, 490–510.

Loye, J. & Carroll, S. (1995). Birds, bugs and blood: avian parasitism and conservation. *Trends Ecol. Evol*. **10**, 232–235.

Marshall, A.G. (1971). The ecology of *Basilia hispida* (Diptera; Nycteribiidae) in Malaysia. *J. Anim. Ecol*. **40**, 141–154.

Marshall, A.G. (1981). *The ecology of ectoparasitic insects*. London: Academic Press.

Merino, S. & Potti, J. (1995). Mites and blowflies decrease growth and survival in nestling pied flycatchers. *Oikos* **73**, 95–103.

Mohr, C.O. (1947). Table of equivalent populations of North American small mammals. *Am. Midl. Nat*. **37**, 223–249.

Møller, A.P. (1990*a*). Effects of a haematophagous mite on the barn swallow (*Hirundo rustica*): a test of the Hamilton and Zuk hypothesis. *Evolution* **44**, 771–784.

Møller, A.P. (1990*b*). Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. *Ecology* **71**, 2345–2357.

Møller, A.P. (1991). Parasites, sexual ornaments, and mate choice in the barn swallow. In *Bird–parasite interactions: ecology, evolution, and behaviour*: 328–348. Loye, J.E. & Zuk, M. (Eds). New York, NY: Oxford University Press.

Møller, A.P. (1993). Ectoparasites increase the cost of reproduction in their hosts. *J. Anim. Ecol*. **62**, 309–322.

Møller, A.P. (1994). *Sexual selection and the barn swallow*. New York, NY: Oxford University Press.

Møller, A.P. & Rózsa, L. (2005). Parasite biodiversity and host defenses: chewing lice and immune response of their avian hosts. *Oecologia* **142**, 169–176.

Morales-Montor, J., Chavarria, A., De León, M.A., Del Castillo, L.I., Escobedo, E.G., Sánchez, E.N., Vargas, J.A., Hernández-Flores, M., Romo-González, T. & Larralde, C. (2004). Host gender in parasitic infections of mammals: an evaluation of the female host supremacy paradigm. *J. Parasitol*. **90**, 531–546.

Nelson, B.C. (1972). *A revision of the new world species of Ricinus (Mallophaga) occurring on Passeriformes (Aves), 68*. University of California Publications in Entomology, 1–175.

OConnor, B.M., Foufopoulos, J., Lipton, D. & Lindström, K. (2005). Mites associated with the small ground finch, *Geospiza fuliginosa* (Passeriformes: Emberizidae), from the Galápagos Islands. *J. Parasitol*. **91**, 1304–1313.

Oh, K.P. & Badyaev, A.V. (2008). Evolution of adaptation and mate choice: parental relatedness affects expression of additive genetic variance in a natural population. *Evol. Biol*. **35**, 111–124.

Pap, P.L., Szép, T., Tökölyi, J. & Piper, S. (2006). Habitat preference, escape behavior, and cues used by feather mites to avoid molting wing feathers. *Behav. Ecol*. **17**, 277–284.

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. (2002). Parasites and the blackcap's tail: implications for the evolution of feather ornaments. *Biol. J. Linn. Soc*. **76**, 481–492.

Poiani, A. (1992). Ectoparasitism as a possible cost of social life: a comparative analysis using Australian passerines (Passeriformes). *Oecologia* **92**, 429–441.

Poulin, R. (1996). Sexual inequalities in helminth infections: a cost of being a male? *Am. Nat*. **147**, 287–295.

Price, R.D. (1977). The *Menacanthus* (Mallophaga: Menoponidae) of the Passeriformes (Aves). *J. Med. Entomol*. **14**, 207–220.

Proctor, H. & Owens, I. (2000). Mites and birds: diversity, parasitism and coevolution. *Trends Ecol. Evol*. **15**, 358–364.

Proctor, H.C. (2003). Feather mites (Acari: Astigmata): ecology, behavior, and evolution. *Annu. Rev. Entomol*. **48**, 185–209.

Richner, H. & Heeb, P. (1995). Are clutch and brood size patterns in birds shaped by ectoparasites? *Oikos* **73**, 435–441.

Richner, H., Oppliger, A. & Christe, P. (1993). Effect of an ectoparasite on reproduction in great tits. *J. Anim. Ecol*. **62**, 703–710.

Rothschild, M. & Clay, T. (1952). *Fleas, flukes and cuckoos: a study of bird parasites*. London: Collins.

Rothschild, M. & Ford, B. (1964). Breeding of the rabbit flea (*Spilopsyllus cuniculi* (Dale) controlled by the reproductive hormones of the host. *Nature* **201**, 103–104.

Rothschild, M. & Ford, B. (1972). Breeding cycle of the flea *Cediopsylla simplex* is controlled by breeding cycle of host. *Science* **178**, 625–626.

SAS Institute (1989) SAS/STAT User's Guide, Version 6 edn. Cary, North Carolina, US.

Stearns, S.C. (1989). The evolutionary significance of phenotypic plasticity. *BioScience* **39**, 437–445.

Stoehr, A.M., Nolan, P.M., Hill, G.E. & McGraw, K.J. (2000). Nest mites (*Pellonyssus reedi*) and the reproductive biology of the house finch (*Carpodacus mexicanus*). *Can. J. Zool.* **78**, 2126–2133.

Szabó, K., Szalmás, A., Liker, A. & Barta, Z. (2002). Effects of haematophagous mites on nestling house sparrows (*Passer domesticus*). *Acta Parasitol.* **47**, 318–322.

Thompson, C.W., Hillgarth, N., Leu, M. & McClure, H.E. (1997). High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. *Am. Nat.* **149**, 270–294.

Thompson, W.L. (1960*a*). Agonistic behavior in the house finch. Part I: annual cycle and display patterns. *Condor* **62**, 245–271.

Thompson, W.L. (1960*b*). Agonistic behavior in the house finch. Part II: factors in aggressiveness and sociality. *Condor* **62**, 378–402.

Visnak, R.M. & Dumbacher, J.P. (1999). Comparison of four fumigants for removing avian lice. *J. Field Ornithol.* **70**, 42–48.

Weatherhead, P.J. & Bennett, G.F. (1991). Ecology of red-winged blackbird parasitism by haematozoa. *Can. J. Zool.* **69**, 2352–2359.

Weddle, C.B. (2000). Effects of ectoparasites on nestling body mass in the house sparrow. *Condor* **102**, 684–687.

Wehr, E.E. (1952). D*ermoglyphus elongatus* (Mégnin, 1877), a quill mite of the house canary in the United States. *J. Parasitol.* **38**, 548–549.

Wheeler, T.A. & Threlfall, W. (1986). Observations on the ectoparasites of some Newfoundland passerines (Aves: Passeriformes). *Can. J. Zool.* **64**, 630–636.

