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DIVERSITY OF FEATHER MITES (ACARI: ASTIGMATA) ON DARWIN'S FINCHES

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ABSTRACT: Feather mites are a diverse group of ectosymbionts that occur on most species of birds. Although Darwin's finches are a well-studied group of birds, relatively little is known about their feather mites. Nearly 200 birds across 9 finch species, and from 2 locations on Santa Cruz Island, Galápagos, were dust-ruffled during the 2009 breeding season. We found 8 genera of feather mites; the most prevalent genus was *Mesalgoides* (53–55%), followed by *Trouessartia* (40–45%), *Amerodectes* and *Proctophyllodes* (26–33%), *Xolalgoides* (21–27%), *Analges* and *Strelkoviacarus* (0–6%), and *Dermoglyphus* (2–4%). There was no evidence for microclimatic effects (ambient temperature and relative humidity) on mite diversity. Host body mass was significantly correlated with mean feather mite abundance across 7 of 8 well-sampled species of finches. *Certhidea olivacea*, the smallest species, did not fit this pattern and had a disproportionately high number of mites for its body mass.

Feather mites (Acari: Astigmata: Analgoidea, Pterolichoidea) are the most diverse groups of arthropods found on birds (Gaud and Atyeo, 1996; Janovy, 1997; Proctor, 2003; Clayton et al., 2010), with about 2,500 described species representing more than 30 families (Mironov and Proctor, 2011). Feather mites are obligatory associates of birds that live on or in the skin, inside the quills, or on the surface of feathers. Depending on the taxon, they feed on uropygial oil, skin flakes, fungus, bacteria, and, to a lesser extent, on the feathers themselves. Feather mites are highly specialized for life on their hosts (Dabert and Mironov, 1999) and they occur on almost all species of birds, with the likely exception of penguins (Mironov and Proctor, 2008).

Darwin's finches are a well-studied group of birds endemic to the Galápagos Islands (Grant, 1986). They are a monophyletic group with 14 recognized species belonging to 5 genera (Grant and Grant, 2008); however, very little is known about the feather mites that inhabit Darwin's finches. Previous knowledge of these mites comes from studies that concentrated on ground finches (*Geospiza* spp.). Mironov and Perez (2002) conducted a survey that documented 2 species of mites associated with 4 species of ground finches. Surveys by Lindström et al. (2004, 2009) and OConnor et al. (2005) found that small ground finches (*Geospiza fuliginosa*) harbor 7 species of feather mites from 6 genera, but they included only 6 of 14 species of Darwin's finches.

One important factor often overlooked when examining ectosymbiont diversity is the impact of the host's abiotic environment (Malenke et al., 2011). In particular, bird-associated arthropod diversity can be influenced by many climatic factors (Merino and Potti, 1996; Møller, 2010). Unlike endosymbionts, which inhabit more stable environments regulated by host physiology, ectosymbionts, like feather mites, can be influenced by variation in ambient temperature and humidity (McClure, 1989; Davidson et al., 1994; Janovy, 1997; Moyer et al., 2002; Møller, 2010). For instance, Moyer et al. (2002), Bush et al. (2009), and Malenke et al. (2011) found that ambient humidity influences the community structure of feather lice on different groups of birds. Wiles et al. (2000) found that feather mites shift their microhabitats on blue tits (*Parus caeruleus*) in response to seasonal changes in temperature.

Despite their small geographic extent, the Galápagos Islands have a highly variable climate. Annual rainfall can vary by an order of magnitude, and seasonal differences in rainfall strongly influence finch evolution (Grant and Grant, 2008). Large climatic differences are often present between microhabitats on the same island. Santa Cruz Island, in particular, provides good examples of changes in climate and vegetation that occur with increasing elevation (Grant and Grant, 2008). For example, climate between lowland arid zones and highland scalesia zones differ significantly in relative temperature and humidity (Grant and Grant, 2008). These contrasting climatic zones harbor a diversity of Darwin's finches, some of which are found in both microhabitats. The major goal of this paper was to test whether variation in abiotic factors such as temperature and humidity shape feather mite communities of Darwin's finches.

Host body mass can also influence feather mite diversity. Larger-bodied hosts provide more resources and therefore support larger populations of ectosymbionts (Poulin and Rohde, 1997; Poulin, 2007). For instance, Rózsa (1997) examined wing-dwelling feather mites on 17 species of Portuguese passerines and found that mite abundance was positively correlated with host body mass. Similarly, Clayton and Walther (2001) found that feather louse abundance was positively correlated with host body mass across 52 species of Peruvian birds. Previous studies examining the effect of host body mass on feather mite abundance examined individuals within a single finch species (Lindström et al., 2009). The body mass of Darwin's finches varies 4-fold among species. The smallest of Darwin's finches, the warbler finch (*Certhidea olivacea*), weighs about 8 g. The largest of the finches, the large ground finch (*Geospiza magnirostris*), weighs about 35 g (Grant and Grant, 2008).

We set out to test 2 hypotheses concerning the potential impact of (1) climate and (2) host body size on aspects of feather mite diversity among Darwin's finches. The first hypothesis was that, within host species, feather mite prevalence and abundance are higher in more humid environments. The second hypothesis was that, across host species, feather mite abundance is correlated with body size; larger-bodied finch species have more mites per individual. To test our predications, we quantified components of the diversity (prevalence and abundance) of feather mites infesting 9 species of Darwin's finches from 2 different locations on Santa Cruz.

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MATERIALS AND METHODS

Study sites and birds

Our study was conducted between January and April 2009 on Santa Cruz Island in the Galápagos Archipelago, Ecuador. Nine species of Darwin's finches from 4 genera were sampled for feather mites: *G. magnirostris*, *G. fortis*, *G. scandens*, *G. fuliginosa*, *Platyspiza crassirostris*, *Camarhynchus psittacula*, *C. parvulus*, *Cactospiza pallidus*, and *Certhidea olivacea*.

Birds were sampled at 2 locations: a highland site near Los Gemelos (LG; 0°37′50.95″S, 90°23′26.54″W), and a lowland site at the Charles Darwin Research Station (CDRS) on Academy Bay, Puerto Ayora (0°44′27.55″S, 90°18′10.10″W). The LG field site, which is located at an altitude of 450 m, is a patchwork of humid nondeciduous forest consisting mainly of Tree scalesia (*Scalesia pedunculata*). Environmental descriptors (ambient temperature and humidity) of the highlands were collected by a weather station (Climate DataZone) near the town of Bellavista, which is somewhat lower in elevation than LG, but with a comparable microclimate (Dudaniec et al., 2007). The coastal CDRS field site, which is at sea level, is hotter and drier than the highlands. The CDRS field site is characterized by arid adapted plants, such as *Opuntia* cacti, *Croton scouleri*, and the trees *Bursera graveolens*, *Pisonia floribunda*, and *Piscidia carthagenensis*. Environmental descriptors of the lowlands (same as above) were collected by a weather station at CDRS (Climate DataZone).

Feather mite collection

Identical methods for capturing birds and collecting feather mites were used at both field sites. Birds were captured with mist nets between 0600 and 1100 hr or 1600 and 1800 hr, and placed individually in single-use paper bags to avoid mixing parasites among birds. Feather mites were collected using the dust-ruffling method (Walther and Clayton, 1997; Clayton and Drown, 2001). Birds were held in 1 hand over a cafeteria tray lined with clean, white paper. Over the course of about 1 min, 1 hand was used to work ca. 1 tsp. of dusting powder into the plumage of the wings, tail, keel, vent, back, head, and neck. Care was taken to avoid getting dust in the bird's nostrils or eyes. The dust was a pyrethin-based powder containing 0.1% pyrethrins and 1.0% piperonyl butoxide (Zodiac Flea and Tick Powder®). Birds were held for 2 min to allow the powder to take effect. The feather tracts were then ruffled for a combined total of 1 min. Each bird was banded with a metal band, which allowed us to avoid resampling birds for mites. Dust and mites from the paper were funneled into a labeled vial of 70% ethanol.

Feather mite processing

Upon return to the United States, contents of the vials were transferred directly to white 110-mm filter paper using distilled water. Papers were then sprayed gently with 95% ethanol before being folded and stored in individual plastic Ziploc® bags. For quantification and identification of mites, the filter papers were placed over a plastic grid (1.3 cm) and examined using a microscope under ×100 magnification. Observers (C.L.B. and J.A.H.K.) examined the grid systematically to quantify and identify feather mites. Early in the study a subset of mite samples (exemplars of all observed morphotaxa) were sent to H.C.P. for identification, and the resulting guide was used by C.L.B. and J.A.H.K. for identification of mites. Slide-mounted exemplars of adults within each of these genera were used to represent a single morphospecies; however, because some taxa may have been present only as juveniles, it is possible that more than 1 species per genus was actually present. Since we could not be sure that there were no other species represented among the juvenile stages, we conservatively refer to all taxa at the genus rather than the species level. Mites were subsequently removed from the paper and stored in vials of 95% ethanol.

Statistics

Mean monthly temperature and relative humidity at the 2 field sites were both compared using Student's *t*-tests. Mite prevalence was compared between host species and sites using Fisher's exact tests. Mite abundance was first log transformed (log [n + 1]) to achieve normality, and values were compared between sites using Student's *t*-tests. The abundance of mites among finch species was compared using a 1-way analysis of variance with Tukey post hoc tests and sequential Bonferroni corrections.

Mite diversity was compared between host species and sites using rank abundance plots and Kolmogorov–Smirnov 2-sample tests. This allowed us to compare patterns of mite communities with respect to both richness and relative evenness of mite genera (Magurran, 2004). Rank abundance patterns of mite communities are thought to be more sensitive measures than species richness alone, and are less influenced by sampling bias than diversity indices (Tokeshi, 1993). Statistical analyses were conducted in JMP® v.9.0.

RESULTS

Microclimatic differences between sites

Mean monthly temperature across the year differed significantly between the 2 sites (Fig. 1A; Student's *t*-test, $t = 2.28$, $P = 0.03$). Mean monthly temperature (± SE) in the highlands (LG) was 23.32 ± 0.48 C compared with 24.78 ± 0.43 C in the lowlands (CDRS). Mean monthly relative humidity (RH) across the year also differed significantly between the 2 sites (Fig. 1B; $t = 3.84$, $P < 0.001$). Mean monthly RH in the highlands was 84.75 ± 1.74% compared with 80.06 ± 1.37% in the lowlands.

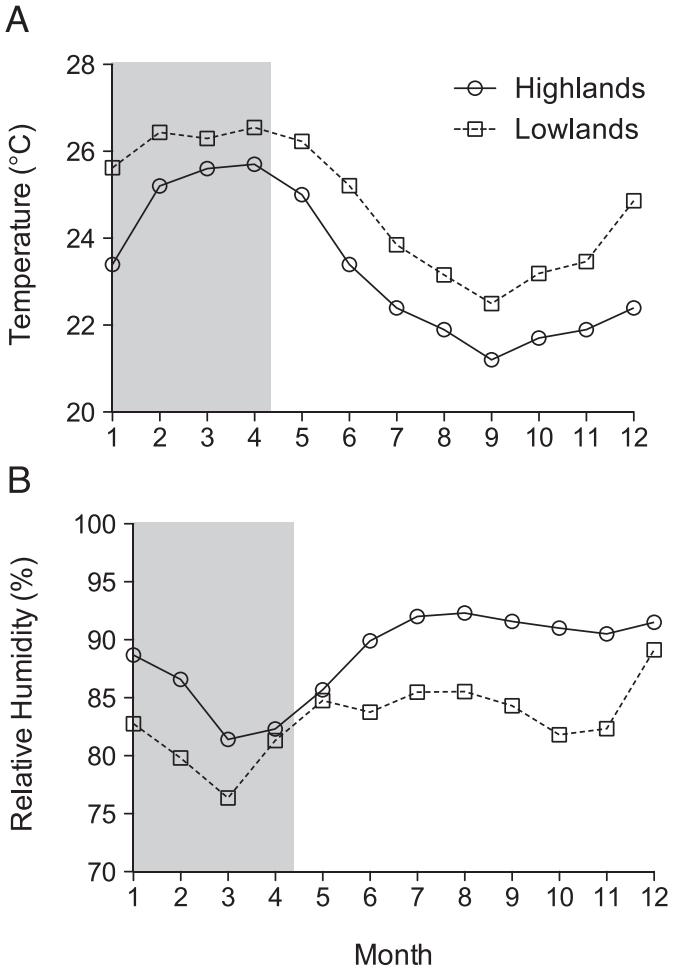

FIGURE 1. (**A**) Mean monthly temperature and (**B**) humidity at the highlands (Los Gemelos: LG) and lowlands (Charles Darwin Research Station: CDRS) in 2009. The main breeding season (January–April) for finches, i.e., when all birds were dust-ruffled, is highlighted in gray.

TABLE I. Prevalence of feather mites (%) on Darwin's finches (OLI [*Certhidea olivacea*], PAR [*Camarhynchus parvulus*], FUL [*Geospiza fuliginosa*], PSI [*C. psittacula*], SCA [*G. scandens*], FOR [*G. fortis*], PAL [*Cactospiza pallidus*], CRA [*Platyspiza crassirostris*], MAG [*G. magnirostris*]) according to the habitat (A. highlands [Los Gemelos, LG] vs. B. lowlands [Charles Darwin Research Station, CDRS]). Feather mites are organized by family (Dermo = Dermoglyphidae; Psoro = Psoroptoididae; Troues = Trouessartiidae; Xolal = Xolalgidae) and genus (*Analg* = *Analges*; *Strelk* = *Strelkoviacarus*; *Derm* = *Dermoglyphus*; *Amero* = *Amerodectes*; *Procto* = *Proctophyllodes*; *Unkn* = *Unknown*; *Mesal* = *Mesalgoides*; *Trou* = *Trouessartia*; *Xola* = *Xolalgoides*). *Unknown* indicates early instar juvenile feather mites that could only be identified to family and were either *Amerodectes* or *Proctophyllodes*.

	Analgidae		Dermo	Proctophyllodidae			Psoro	Troues	Xolal
Host (n)	*Analg*	*Strelk*	*Derm*	*Amero*	*Procto*	*Unkn*	*Mesal*	*Trou*	*Xola*
A. Highlands (LG)									
PAL (11)	0.0	0.0	9.1*	36.4*	45.5*	0.0	72.7*	36.4*	0.0
PAR (21)	0.0	4.8*	0.0*	28.6*	33.3*	4.8*	38.1*	23.8*	38.1*
PSI (4)	0.0	0.0	0.0	25.0*	50.0*	0.0	75.0*	50.0*	25.0*
OLI (20)	30.0*	10.0*	0.0	70.0*	15.0*	25.0*	60.0*	75.0*	50.0*
FOR (16)	0.0	6.3*	0.0	18.8	25.0*	0.0	50.0	31.3	18.8
FUL (26)	0.0	0.0	3.8	15.4	30.8	3.8	50.0	50.0	15.4
Overall (98)	6.1	4.1	2.0	32.7	29.6	7.1	53.1	44.9	26.5
B. Lowlands (CDRS)									
PAL (1)	0.0	0.0	0.0	100.0*	0.0	0.0	100.0*	0.0	0.0
PAR (8)	0.0	12.5*	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FOR (23)	0.0	0.0	4.3*	30.4	43.5*	8.7	60.9	56.5	30.4
FUL (15)	0.0	0.0	0.0	13.3	40.0	6.7	60.0	53.3	46.7
MAG (10)	0.0	0.0	0.0	50.0	30.0	10.0	70.0*	70.0	30.0*
SCA (21)	0.0	0.0	9.5*	23.8	19.0*	4.8	52.4	38.1	14.3
CRA (23)	0.0	0.0	4.3*	30.4*	43.5*	4.3*	60.9*	21.7*	8.7*
Overall (101)	0.0	1.0	4.0	26.7	32.7	5.9	55.4	40.6	21.8

* Indicates new host record.

Host species captured at each site

At the highland site (LG) we sampled 98 individuals representing 6 species of Darwin's finches: *G. fortis*, *G. fuliginosa*, *Camarhynchus psittacula*, *C. parvulus*, *Cactospiza pallidus*, and *Certhidea olivacea*. At the lowland site (CDRS) we sampled 101 individuals representing 7 species of finches: *G. magnirostris*, *G. fortis*, *G. scandens*, *G. fuliginosa*, *Platyspiza crassirostris*, *Camarhynchus parvulus*, and *Cactospiza pallidus*.

Description of mite taxa found on Darwin's finches

Eight genera of analgoid feather mites (Acari: Astigmata), representing 6 families, were collected (Tables I, II). Five of the 8 observed morphospecies are described species already known from Darwin's finches: *Amerodectes* (previously *Pterodectes*) *atyeoi* (OConnor et al., 2005), *Mesalgoides geospizae* Mironov and Perez, 2002, *Proctophyllodes darwini* OConnor et al., 2005, *Trouessartia geospiza* OConnor et al., 2005, and *Xolalgoides palmai* Mironov and Perez, 2002. Adults of the *Analges*, *Strelkoviacarus*, and *Dermoglyphus* specimens appear to belong to as-yet-undescribed species.

Representatives of 4 mite genera—*Mesalgoides*, *Trouessartia*, *Proctophyllodes*, and *Amerodectes*—were found on all nine sampled Darwin's finch species. Although most feather mite genera infested multiple host species, members of 1 genus, *Analges*, were found exclusively on *Certhidea olivacea*.

Because of the dust-ruffling method of collecting we were not able to record microhabitats of the mite taxa, but typically members of the Proctophyllodidae and Trouessartiidae inhabit the vanes of flight feathers. *Analges*, *Mesalgoides*, and *Xolalgoides* are associated with the downy parts of feathers. Species of *Dermoglyphus* spend most of their life cycle inside quills, and their relative rarity in the dust-ruffling samples may be due to their living in this protected microhabitat (Proctor, 2003). *Strelkoviacarus* has the body shape typically associated with skin-dwelling feather mites (Gaud and Atyeo, 1996; Dabert and Mironov, 1999). Very small numbers of other mite taxa were collected, but were not included in our analyses; these mites included a blood-feeding *Pellonyssus* sp. (Mesostigmata: Macronyssidae) and detritus-feeding nest mites from the families Acaridae and Winterschmidtiidae (Astigmata).

Comparison of mite diversity between sites

From the highland finch species, we collected 8 genera of feather mites (Tables IA, IIA). Across all highland birds, 70.4% (69/98) of finches were infested with at least 1 feather mite. Mite richness ranged between 0 and 5 genera per individual host; overall mite abundance (mean ± SE) was 44.0 ± 10.3 mites per individual host. Overall mite abundance is the average number of mites per host individual regardless of mite genera or host species. Five mite taxa were relatively common (prevalence >25%; Table IA); *Mesalgoides* was the most prevalent feather mite genus, being found on 53.1% (52/98) of sampled finches.

From the lowland finches, we collected seven genera of mites (Tables IB, IIB). Across all lowland birds, 62.4% (63/101) of finches were infested with at least 1 feather mite. Mite richness ranged between 0 and 5 genera per individual host; overall mite abundance was 33.0 ± 6.1 mites per individual host. Four mite taxa were relatively common (prevalence >25%; Table IB); *Mesalgoides* was also the most prevalent feather mite genus, being found on 55.4% (56/101) of sampled finches.

TABLE II. Abundance (mean ± SE) of feather mites on Darwin's finches (OLI [*Certhidea olivacea*], PAR [*Camarhynchus parvulus*], FUL [*Geospiza fuliginosa*], PSI [*C. psittacula*], SCA [*G. scandens*], FOR [*G. fortis*], PAL [*Cactospiza pallidus*], CRA [*Platyspiza crassirostris*], MAG [*G. magnirostris*]) according to the habitat (A. highlands [Los Gemelos, LG] vs. B. lowlands [Charles Darwin Research Station, CDRS]). Feather mites are organized by family (Dermo = Dermoglyphidae; Psoro = Psoroptoididae; Troues = Trouessartiidae; Xolal = Xolalgidae) and genus (*Analg = Analges*; *Strelk = Strelkoviacarus*; *Derm = Dermoglyphus*; *Amero = Amerodectes*; *Procto = Proctophyllodes*; *Unkn = Unknown*; *Mesal = Mesalgoides*; *Trou = Trouessartia*; *Xola = Xolalgoides*). *Unknown* indicates early instar juvenile feather mites that could only be identified to family and were either *Amerodectes* or *Proctophyllodes*.

	Analgidae		Dermo	Proctophyllodidae			Psoro	Troues	Xolal
Host (n)	*Analg*	*Strelk*	*Derm*	*Amero*	*Procto*	*Unkn*	*Mesal*	*Trou*	*Xola*
A. Highlands (LG)									
PAL (11)	0.0	0.0	0.1 (0.1)*	44.1 (30.1)*	2.8 (1.2)*	0.0	11.9 (4.8)*	2.5 (1.6)*	0.0
PAR (21)	0.0	0.1 (0.1)*	0.0	0.4 (0.1)*	11.0 (6.2)*	0.1 (0.1)*	2.8 (1.3)*	0.8 (0.4)*	2.2 (1.1)*
PSI (4)	0.0	0.0	0.0	6.8 (6.8)*	8.3 (7.0)*	0.0	82.3 (71.1)*	1.0 (0.7)*	1.8 (1.8)*
OLI (20)	3.0 (1.4)*	0.5 (0.4)*	0.0	24.2 (12.1)*	0.3 (0.2)*	1.6 (0.8)*	5.9 (2.7)*	53.2 (21.6)*	10.5 (3.8)*
FOR (16)	0.0	0.1 (0.1)*	0.0	0.6 (0.4)	5.1 (3.3)*	0.0	25.5 (15.3)	9.9 (6.4)	0.6 (0.4)
FUL (26)	0.0	0.0	0.04 (0.04)	0.2 (0.1)	1.6 (0.8)	0.1 (0.1)	3.3 (1.1)	2.5 (1.0)	0.8 (0.5)
Overall (98)	0.6 (0.3)	0.1 (0.1)	0.02 (0.01)	10.4 (4.3)	4.3 (1.5)	0.4 (0.2)	11.5 (4.0)	13.6 (4.9)	3.0 (0.9)
B. Lowlands (CDRS)									
PAL (1)	0.0	0.0	0.0	17.0*	0.0	0.0	9.0*	0.0	0.0
PAR (8)	0.0	0.1 (0.1)*	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FOR (23)	0.0	0.0	0.3 (0.3)*	3.5 (2.3)	16.2 (7.4)*	0.5 (0.4)	8.7 (2.4)	4.2 (1.6)	0.7 (0.3)
FUL (15)	0.0	0.0	0.0	0.3 (0.2)	3.9 (2.6)	0.9 (0.9)	4.8 (2.2)	7.3 (5.9)	1.8 (0.8)
MAG (10)	0.0	0.0	0.0	26.9 (15.3)	23.7 (23.3)	2.4 (2.4)	43.8 (15.5)*	9.3 (3.9)	1.4 (1.1)*
SCA (21)	0.0	0.0	0.4 (0.3)*	0.7 (0.4)	1.7 (1.0)*	0.1 (0.1)	7.8 (3.7)	1.0 (0.3)	0.3 (0.2)
CRA (23)	0.0	0.0	0.2 (0.2)*	17.4 (12.6)*	6.4 (2.6)*	0.4 (0.4)*	13.6 (6.4)*	1.3 (0.9)*	0.2 (0.1)*
Overall (101)	0.0	0.01 (0.01)	0.2 (0.1)	7.8 (3.3)	8.4 (2.9)	0.6 (0.3)	11.9 (2.5)	3.4 (1.1)	0.7 (0.2)

* Indicates new host record.

To compare the prevalence, abundance, and diversity of mites on conspecific hosts at the highland (LG) and lowland (CDRS) sites, we used host species for which at least 10 individuals were sampled per site (Tables IA, B, IIA, B). Two species met this criterion: *G. fortis* and *G. fuliginosa*. We found no significant difference in mite prevalence (Fisher's exact $P = 0.80$) or abundance ($t = 0.94$, $P = 0.35$) between sites for *G. fortis* or *G. fuliginosa* (Fisher's exact $P = 1.00$; $t = 1.10$, $P = 0.28$). We found no significant difference in mite diversity between the 2 sites (Fig. 2A, B) for *G. fortis* (Kolmogorov–Smirnov two-sample, $D = 4.63$, $P > 0.10$) or *G. fuliginosa* ($D = 0.60$, $P > 0.10$).

We also compared feather mite prevalence, abundance, and diversity between the overall highland and lowland finch assemblages (Tables IA, B, IIA, B). There were no significant differences between the 2 sites in overall prevalence (Fisher's exact $P = 0.65$) or abundance (*t*-test, $t = 0.28$, $P = 0.78$). Similarly, there was no significant difference in mite diversity between the 2 sites (Fig 2C; $D = 3.28$, $P > 0.10$). Since neither prevalence nor diversity differed significantly between sites, we combined sites within each host species for the analysis of mite abundance vs. host body mass reported below.

Relation of host body mass to mite abundance

The overall prevalence and abundance of mites collected from each of our 9 Darwin's finch species are given in Table III. First, we compared the abundance of mites among 8 of the 9 finch species (Fig. 3), *Camarhynchus psittacula* being excluded from the comparison because of the low sample size (n = 4 sampled individuals). There was no significant relationship between host body mass and mite abundance across these 8 host species (n = 194; $r = 0.08$, $P = 0.29$). However, we found a highly significant correlation between mite abundance and host body mass (n = 174; $r = 0.25$, $P = 0.0009$) when *Certhidea olivacea* was removed from the analysis. Indeed, *C. olivacea* showed significantly more feather mites than *Camarhynchus parvulus* ($P < 0.001$), *G. fuliginosa* ($P < 0.001$), and *G. scandens* ($P = 0.01$) (Fig. 3).

DISCUSSION

Our study is the most comprehensive survey of feather mites from Darwin's finches to date. To our knowledge, this is the first time feather mites have been recorded from *Platyspiza crassirostris*, *Camarhynchus psittacula, C. parvulus*, *Cactospiza pallidus*, or *Certhidea olivacea*. From our 9 study species of finches, we identified a total of 8 genera of feather mites, representing 6 mite families (Tables IA, B, IIA, B). All of these genera have been previously recorded from Darwin's finches (Mironov and Perez, 2002; OConnor et al., 2005), with the exception of *Analges* (found on *C. olivacea*), which has only been recorded from Galápagos mockingbirds (Stefka et al., 2011).

Before our study, OConnor et al. (2005) used dust-ruffling to quantify feather mites on 24 individuals of a single species of Darwin's finch, *G. fuliginosa*, from the Santa Cruz lowlands (Puerto Ayora). Our lowland (CDRS) results are consistent with OConnor et al. (2005) in that we found the same 5 genera of feather mites. They noted that *G. fuliginosa* was commonly infested (prevalence >25%) with 4 of the 5 genera. The prevalence of these genera on our birds (Table IB) was similar to those reported by OConnor et al. (2005): *Proctophyllodes* = 29.2% (Fisher's exact $P = 0.75$), *Trouessartia* = 83.3% ($P = 0.44$),

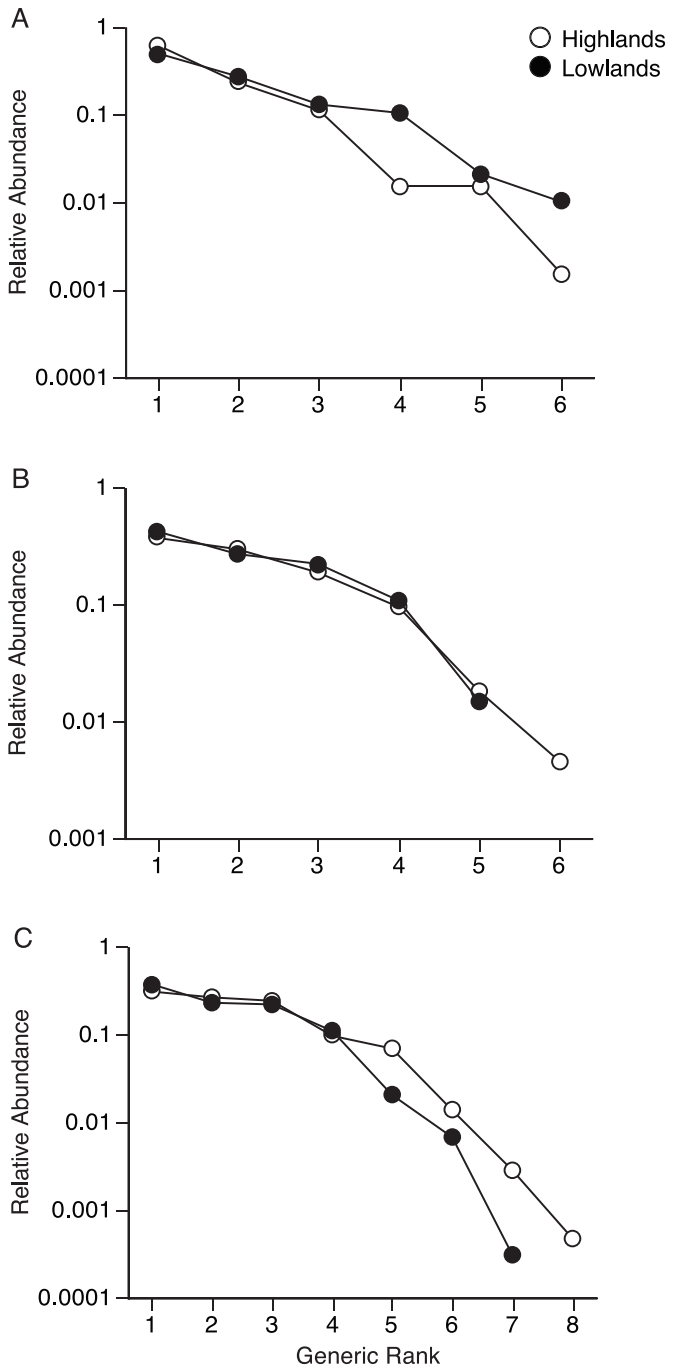

FIGURE 2. Rank abundance plots of feather mite communities from highlands and lowlands, (**A**) *Geospiza fortis*, (**B**) *Geopsiza fuliginosa*, and (**C**) overall finch assemblages. y-Axes are log transformed.

Mesalgoides = 45.8% ($P = 0.78$), and *Xolalgoides* = 33.3% ($P = 0.76$).

We compared the diversity of Darwin's finch feather mites at highland and lowland sites on Santa Cruz Island. The 2 sites differed significantly in relative temperature and humidity. Despite these differences, we found no significant difference in mite prevalence, abundance, or diversity between the sites. This lack of difference might be explained by the fact that the microclimatic differences between the sites were not of sufficient magnitude to influence the feather mites. For example, Gaede and Knülle (1987) experimentally determined that nonfeeding *P. troncatus* could not withstand a RH below 55%, causing them to desiccate and die. Since neither highland nor lowland sites reached a RH below 75%, it is unlikely that mite diversity is affected by this abiotic factor. Moreover, if feather mites are affected by microclimatic differences, we can expect that they might shift microhabitats on the body of the host (Wiles et al., 2000) to counteract these effects. It would be interesting to compare the distributions of feather mites on highland and lowland Darwin's finch species in the future. Unfortunately, the dust-ruffling technique we used did not allow us to compare mite microhabitat distributions. Finally, the lack of difference in mite diversity may be explained by finch dispersal. Galligan et al. (2012) found that during the rainy season when resources are plentiful, *G. fuliginosa* regularly fly between highland and lowland habitat, resulting in a breakdown of any genetic or ecological barriers that would otherwise separate finch populations. A panmictic population of highland and lowland finches would promote feather mite transmission between host populations and homogenize the mite diversity between the 2 sites.

TABLE III. Prevalence and abundance (mean ± SE) of feather mites in Darwin's finches (OLI [*Certhidea olivacea*], PAR [*Camarhynchus parvulus*], FUL [*Geospiza fuliginosa*], PSI [*C. psittacula*], SCA [*G. scandens*], FOR [*G. fortis*], PAL [*Cactospiza pallidus*], CRA [*Platyspiza crassirostris*], MAG [*G. magnirostris*]). Data for highland (Los Gemelos, LG) and lowland (Charles Darwin Research Station, CDRS) sites are combined.

		Feather mite	
Host (n)	Host body mass (mean ± SE)*	Prevalence (%)	Abundance (mean ± SE)
OLI (20)	9.1 (0.1)	95.0	98.9 (38.0)
PAR (29)	12.8 (0.1)	45.0	12.6 (5.8)
FUL (41)	13.8 (0.2)	68.3	12.4 (3.6)
PSI (4)	18.0 (0.5)	75.0	100.0 (77.1)
SCA (21)	21.3 (0.3)	61.9	12.0 (4.1)
FOR (39)	21.5 (0.5)	64.1	37.3 (10.9)
PAL (12)	22.5 (0.4)	75.0	58.5 (29.4)
CRA (23)	31.3 (0.4)	65.2	40.0 (15.0)
MAG (10)	32.2 (0.5)	70.0	107.5 (36.2)

* Host body mass in grams.

Host body mass is known to have a fundamental influence on the diversity of parasites and other associates (Poulin, 1997; Poulin and Rohde, 1997; Clayton and Walther, 2001; Schmid-Hempel, 2011). We did find a significant relationship between host body mass and feather mite abundance across the 7 of our 8 well-sampled ($n \geq 10$) species of Darwin's finches. The exception to this pattern, *C. olivacea*, was the only species of finch with significantly more mites than any other species (Fig. 3), despite the fact that it is the smallest-bodied species of finch sampled.

The surprisingly high abundance of feather mites on *C. olivacea* may be related to the fact that this species is in severe decline on Santa Cruz Island. A recent study by Dvorak et al. (2012) estimates that, over the past century, Santa Cruz populations of *C. olivacea* have declined from more than 1 million males to about 55,000 males, which is a steeper decline

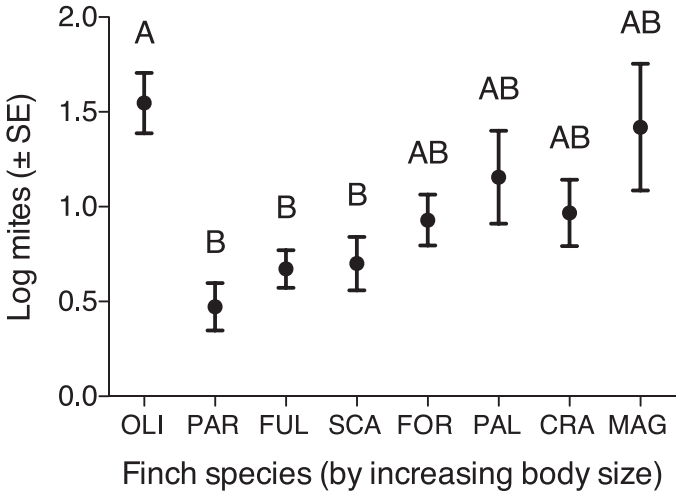

FIGURE 3. Mean abundance of feather mites (log [n + 1] ± SE) for 8 species of Darwin's finches, arranged in order of increasing body mass: OLI (*Certhidea olivacea*), PAR (*Camarhynchus parvulus*), FUL (*Geospiza fuliginosa*), SCA (*G. scandens*), FOR (*G. fortis*), PAL (*Cactospiza pallidus*), CRA (*Platyspiza crassirostris*), MAG (*G. magnirostris*). Different letters indicate significant differences for $P < 0.05$. See Table III for sample sizes and mean body masses.

than any other species of finch on the island. The authors suggest that habitat destruction and herbicides have reduced the abundance of insects upon which *C. olivacea* feeds (Dvorak et al., 2012), implying that birds may devote more time to foraging. A reduction in insects may affect stenotopic species like *C. olivacea* that are exclusively insectivores much more than eurytopic species that have mixed or seed diets.

In addition, invasive parasites may also increase the amount of time birds need to devote to anti-parasite behavior (O'Connor et al., 2010). Since evidence suggests that feather mites are not parasites, but rather commensals (Galván et al., 2012), mite populations may be collaterally influenced by preening (Clayton, 1991), which is an important defense against ectoparasites, such as feather lice (Clayton et al., 2010). If *C. olivacea* populations are indeed stressed, they may not be able to devote the normal amount of time and energy to preening, which is energetically costly (Viblanc et al., 2011). In other words, the abundance of feather mites on Darwin's finches may be indicative of the poor "health" of the host population. Although this hypothesis is speculative, it could explain the surprising abundance of feather mites on such a small-bodied species of finch.

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