DIFFERENT SCALES OF SPATIAL SEGREGATION OF TWO SPECIES OF FEATHER MITES ON THE WINGS OF A PASSERINE BIRD

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ABSTRACT: The "condition-specific competition hypothesis" proposes that coexistence of 2 species is possible when spatial or temporal variations in environmental conditions exist and each species responds differently to those conditions. The distribution of different species of feather mites on their hosts is known to be affected by intrinsic host factors such as structure of feathers and friction among feathers during flight, but there is also evidence that external factors such as humidity and temperature can affect mite distribution. Some feather mites have the capacity to move through the plumage rather rapidly, and within-host variation in intensity of sunlight could be one of the cues involved in these active displacements. We analyzed both the within- and between-feather spatial distribution of 2 mite species, *Trouessartia bifurcata* and *Dolichodectes edwardsi*, that coexist in flight feathers of the moustached warbler *Acrocephalus melanopogon.* A complex spatial segregation between the 2 species was observed at 3 spatial levels, i.e., "feather surfaces," "between feathers," and "within feathers." Despite certain overlapping distribution among feathers, *T. bifurcata* dominated proximal and medial regions on dorsal faces, while *D. edwardsi* preferred disto-ventral feather areas. An experiment to check the behavioral response of *T. bifurcata* to sunlight showed that mites responded to light exposure by approaching the feather bases and even leaving its dorsal face. Spatial heterogeneity across the 3 analyzed levels, together with response to light and other particular species adaptations, may have played a role in the coexistence and segregation of feather mites competing for space and food in passerine birds.

Knowing the patterns of spatial distribution and the processes that generate them are essential to understanding the ecology of populations and communities (Amarasekare et al., 2004). These patterns can provide important clues about coexistence mechanisms of interacting individuals and species within communities (Dammhahn and Kappeler, 2008).

Observed spatial segregation between 2 species of the same ecological guild is often explained by competition (Pianka, 2000). Ecological theory and empirical data indicate that competition should lead to exclusion of one of the interacting species when resources are limited (Gause, 1932; Tilman, 1982). Nevertheless, competitive exclusion can be avoided through various mechanisms (Tilman, 1982; Chesson, 2000; Calcagno et al., 2006; Leisnham and Juliano, 2009). One hypothesis that can explain coexistence of 2 competitors is "condition-specific competition" (Chesson, 2000), which proposes that coexistence is possible when spatial or temporal variations in environmental conditions exist and each species responds differently to those conditions. For a given species in a heterogeneous environment, intraspecific competition must be stronger than interspecific competition in favorable areas and, in contrast, interspecific competition is expected to be stronger in areas with non-optimal conditions for that species. As a result, the competing species are restricted to species-specific favorable parts of the habitat and are excluded from the unfavorable parts. This leads to spatial segregation, allowing local stable coexistence at the larger scale.

Spatial heterogeneity is considered one of the most important elements that favor species coexistence (Segurado and Fiqueiredo, 2007), and it can also be a factor generator of spatial segregation itself, even without the reinforcement of competition. In this case, each species displays adaptations that allow it to inhabit the

regions that the other species does not tolerate, without previous competitive exclusion.

"Habitat" is not always easy to define for organisms free to roam a wide area, e.g., forest-dwelling birds. However, it is easier to demarcate for obligatory symbionts of animals, i.e., "habitat" = the host. An individual host has clear edges. Much research on endosymbionts, e.g., intestinal helminthes, has demonstrated that spatial distribution of symbionts is affected by both competition and by adaptation to particular microhabitats (Poulin, 2006). Less research has been aimed at ectosymbionts, although a recent study on feather lice has shown that species inhabiting body feathers can exclude wing lice from this preferred feeding area (Bush and Malenke, 2008); however, body lice do not have the morphological adaptations to venture out on the wings, where wing lice are able to maintain a firm hold.

Feather mites (Arachnida: Acari) are obligatory epibionts of birds and are represented by approximately 2,500 named species belonging to 2 superfamilies of the cohort Astigmatina: Analgoidea, and Pterolichoidea. A previously named third superfamily, Freyanoidea, is considered to be nested within the Pterolichoidea (OConnor, 1982, 2009). The large majority of known species of feather mites live permanently on the surface of feathers. For the most part, these plumicolous mites feed on preen oil produced by the uropygial gland and detritus associated with the surface of the barbules (Blanco and Tella, 2001; Galván et al. 2008).

Many groups of feather mites are specialized for living on the surfaces of flight feathers. These are very stressful microenvironments, with low humidity and strong aerodynamic and frictional forces (Dubinin, 1951). To withstand these adverse conditions, mites that live on the vanes of flight feathers (hereafter "vane-dwelling mites") have acquired a number of adaptations, including reduction of dorsal setae, extensively sclerotized dorsal plates, flattened bodies, and strong legs laterally inserted into the body (Dabert and Mironov, 1999; Proctor, 2003).

There are some studies on the patterns of distribution of vane-dwelling mites, but almost all deal with the distribution at the "between feathers" spatial level (e.g., Dubinin, 1951; Wiles et al., 2000; Mironov and Malyshev, 2002; Bridge, 2003; Jovani and Serrano, 2004). Only a few works examine the mite distribution within feathers, and all of them focus on non-passerine birds

(Choe and Kim, 1989, 1991). The distribution of mites between, and within, feathers can be affected by microhabitat factors such as turbulences, humidity, or temperature (Dubinin, 1951; Wiles et al., 2000). Some studies have revealed an effect of host molting status on the distribution of mites among flight feathers (Jovani and Serrano, 2001; Jovani et al., 2006; Pap et al., 2006). The transmission of feather mites between host birds occurs, in most cases, from parents to nestlings, and some studies have focused on the feather mite distribution in nestlings (Mironov and Malyshev, 2002). Many species of vane-dwelling feather mites are capable of crawling through the plumage rather rapidly, and so changes in mite distribution on a host can take place within a few minutes (Jovani and Serrano, 2004). Little research has been done to determine what stimuli induce mites to move to a different area. Light is one stimulus. Dubinin (1951) observed in sunning cormorants that vane-dwelling mites responded to light by moving to feather bases. McClure (1989) noted that birds caught at dusk and held until dark experienced a "crepuscular rush 'of mites' from the protection of the rachis out onto the vanes." Temperature also affects mite location on the host. Dubinin (1951) placed starlings in an icehouse and observed that mites moved off the wings and toward the host's body. Likewise, Wiles et al. (2000) found that mites on the wings of blue tits moved in response to changes in ambient temperature. Mechanical cues may also play a role. Mites on molting barn swallows apparently sense the vibrations or changes in airflow of wing feathers about to drop out and move to a more stable feather (Pap et al., 2006).

Most species of flight feather mites live on the ventral surface of feathers (Dubinin, 1951; Proctor, 2003). The dorsal surface of flight feathers is a very adverse environment for many feather mite species because it is much smoother than the ventral surface and, therefore, environmental disturbances, such as wind, friction between feathers, sunlight, or preening by the host bird (Dubinin, 1951; Choe and Kim, 1989), are difficult to stand. However, as an exception among the feather mites, almost all members of the analgoid trouessartiids (which currently includes 11 genera) are adapted to living on the upper surface of the vanes of flight feathers (Mironov, 1987). Species of *Trouessartia* have some features that appear to allow them to inhabit the dorsal smooth and strongly airflow disturbed surfaces of flight feathers, such as dark pigmentation, strongly sclerotized dorsal shields, lateral insertion of strong legs, opisthosomal lobes in both sexes, and large ambulacra (Dubinin, 1951; Proctor, 2003).

The present work analyzes both the within- and between-feather spatial distribution of 2 vane-dwelling feather mite species that coexist in the small ($\sim$220 mm^2) flight feathers of the moustached warbler, *Acrocephalus melanopogon*, Temmick 1823 (Passeriformes: Sylviidae). The mites are *Trouessartia bifurcata*, Troessart 1885 (Trouessartiidae) and *Dolichodectes edwardsi*, Troessart 1885 (Proctophyllodidae). In addition to analyzing the spatial distribution of these 2 species, we tested experimentally whether *T. bifurcata* individuals responded to direct sunlight in the same way as the mites observed by Dubinin (1951), i.e., moving to the feather bases.

MATERIALS AND METHODS

Our study focused on a population of *A. melanopogon* living in the Pego-Oliva's Natural Park (Valencia, Spain). Urios et al. (1993) provide a general description to this protected wetland. The moustached warbler is a passerine bird associated with coastal lagoons and marshes with a Turkestan–Mediterranean distribution (Castany, 2004). The Pego-Oliva wetland contains the larger breeding population of this species in the Iberian Peninsula (Castany and López, 2006). Birds were captured by means of mist nets and were all ringed. Numerous samples of each different morphotaxon of feather mites were sent to the Proctor laboratory for identification. Mites were cleared in lactic acid for 24 hr and mounted on slides in commercially available PVA medium (BioQuip Products, Rancho Dominguez, California, http://www.bioquip.com). The slides were cured for 4 days on slidewarmers at 40–45 C and then examined using a Leica DMLB compound microscope with differential interference contrast lighting. Mites were identified using Gaud and Atyeo (1996) and Santana (1976). All but 1 of the several hundred specimens examined were either *T. bifurcata* or *D. edwardsi*. The single exception was a male *Proctophyllodes* cf. *clavatus* Fritsch (Proctophyllodidae). Since we only found 1 individual of this species after the examination of more feather samples from more bird individuals, we did not consider it likely to affect the results of our study. Slide-mounted exemplars are deposited in the E.H. Strickland Entomological Museum, University of Alberta, Edmonton, Alberta, Canada. Some mites and feathers preserved in ethanol were critical-point dried prior to observation using a Philips XL 30 scanning electron microscope, at the University of Valencia, Valencia, Spain. Field and statistic work was divided in 2 parts (see below): (1) obtaining and analyzing data related to feather mite distribution on the host and (2) obtaining and analyzing behavioral data from an experiment testing effects of sunlight on the distribution of *T. bifurcata*.

Acquisition and analysis of data on feather mite distribution

Fieldwork to obtain data on feather mite distribution was carried out between December 2008 and early April 2009, coinciding with the moustached warbler pre-mating period (Castany, 2004). The study period was chosen in order to avoid possible effects of feather mite transmissions between birds during the breeding session (Mironov and Malyshev, 2002) and bird molting (Jovani et al., 2006) on feather mite distribution. Birds were captured between 0700 and 1200 hr. We caught 37 birds, and for each bird we counted the number of feather mites (including both adults and nymphal stages) present on the right wing flight feathers (10 primary, 6 secondary, and 3 tertiary feathers), always distinguishing between the 2 feather mite species, *T. bifurcata* and *D. edwardsi*. For each of the 2 species, we obtained 3 separate measures of abundance from each individual feather, corresponding to proximal, medial, and distal regions. A ruler was used to divide the feathers into 3 equal regions; mites were counted using a hand magnifier. The nomenclature used to designate feathers is based on bird molting processes (Jenni and Winkler, 1994).

The analysis of feather mite distribution was focused on 2 different spatial levels, i.e., between, and within, feathers. For the analysis of between-feather spatial distribution, the number of each mite species per feather was weighted dividing by feather's area in order to work with densities. For each mite species, we constructed a feather dendrogram using the Ward clustering method and Euclidean distance (Fielding, 2007) calculated with the *hclust* package for *R-cran v. 2.9.2* (R Development Core Team, 2009) in order to obtain groups of flight feathers based on average feather mite density per feather type (feathers of a particular group, e.g., primaries, and position within the group, e.g., third primary). Then, we tested the differences between the resulting groups with a generalized linear mixed model (GLMM), testing a fixed effects factor (group of feathers) and a random effects factor (individual bird) (Brew and Maddy, 1995). The model family was Poisson and the link function was logarithmic. Since our data did not show overdispersion (for *T. bifurcata*, $D = 128.71$, $P > 0.05$; for *D. edwardsi*, $D = 127.67$, $P > 0.05$; overdispersion test by the *qcc* package from *R-cran*), we used a Z-Wald test, appropriate for GLMMs with no overdispersed data (Bolker et al., 2009). GLMM was performed using the *lme4* package for *R-cran*.

To analyze the distribution "within feathers," we applied a GLMM to data on feather mite number per feather region, with a fixed factor (feather region) and a randomized factor (individual bird). For this analysis, we did not consider feather P10 because there were no mites in any of the P10 feathers studied. Data on feather mites number per feather were overdispersed (for *T. bifurcata*, $D = 63767.37$, $P < 0.01$; for *D. edwardsi*, $D = 60714.50$, $P < 0.01$, *R-cran qcc* overdispersion test). Therefore, we chose a quasi-Poisson model family, which adds a correction parameter for the overdispersion (Zuur et al., 2007), and logarithmic link function.

To test for the effects of the fixed factor "feather region" we used a t-Wald test, appropriate for overdispersed data (Bolker et al., 2009).

Acquisition and analysis of experimental data for the response to sunlight in *T. bifurcata*

Experiments were performed in the field during June 2009, a suitable period with regard to brightness of the day. We captured 29 birds during 4 sessions between 0700 and 1200 hr on sunny days. From each bird, we took 2 flight feathers (of similar type) containing individuals of *T. bifurcata*, 1 from each wing. These 2 feathers were immediately placed on a cardboard sheet with a background of graph paper with a 1-mm^2 grid, and a high-resolution digital picture of their dorsal face was taken. One of the feathers was fully covered immediately with an opaque plastic cap ("dark feather") and the other was exposed to direct solar radiation on its dorsal face for 5 min ("light feather"), after which we took another photo of the 2 feathers. Photos were taken using a Nikon D80 SLR camera with a Sigma 105 mm objective. The camera was situated on a tripod in the same position during the experiment, to facilitate the subsequent calculations. Photos were later analyzed with a digital picture treatment software: *Gimp v. 2.6* (GIMP Documentation Team, 2009). In *Gimp*, for all photos, we calculated distances from all *T. bifurcata* mites to the feather base, d_i (the basal point of the feather raquis where barbs start to appear). Then, we calculated the mean distance of mites to the feather base for each photo, d_m. Finally, for each feather, we obtained the change in mean distance from mites to feather base, from the beginning, d_{mi}, to the end of the experiment after 5 min, d_{mf} : $\Delta d_m = d_{mf} - d_{mi}$.

To compare the differences in Δd_m between illuminated and dark feathers, we applied a Student's t-test for paired data. Additionally, we used a t-test for paired data to compare the differences between the standard deviation of d_i at the beginning and the end of the experiment to check for mite clumping or dispersion. We also calculated the proportion of mites that remained in the dorsal face of the feather during the experiment with respect to the initial mites. To do this, we applied a t-test for paired data to compare the number of mites that disappeared from the dorsal surface of illuminated versus dark feathers. Finally, to check for potential effects of time of day on the average change in mite distances, we applied a linear regression analysis using *R-cran*.

RESULTS

All captured birds for the analysis of feather mite distribution ($n = 37$) had mites belonging to the 2 species considered (mites are illustrated in Fig. 1). Birds presented an average number of 322 ± 175 feather mites of *T. bifurcata* and 117 ± 41 of *D. edwardsi* on the 19 right wing flight feathers analyzed. All individuals of *T. bifurcata* were found in the dorsal faces, while all the individuals of *D. edwardsi* were in the ventral surfaces of feathers.

The 2 mite species presented a similar bimodal between-feather distribution, with 2 high density peaks separated by a depression in the wing center, which coincides with the transition between primary and secondary feathers and minimum densities on the 2 extremes of the wings (Fig. 2). In both species, we can see an absence of, or very low, mite densities in the most external wing feathers, e.g., P7–P10 in *T. bifurcata*, that affect a greater number of feathers for *D. edwardsi* (P4–P10), which shows a more restricted distribution and lower maximum densities. There is a partial overlapping between the distributions of both species; however, density peaks of *D. edwardsi* are slightly displaced toward the base of the wing in comparison with peaks of *T. bifurcata* (Fig. 2).

Based on the cluster results for *T. bifurcata*, we classified feathers into 3 groups, according to mite density, i.e., low density group G_l, intermediate density group G_m, and high density group G_h. The application of a GLMM gave significant differences between these 3 groups (G_m, $Z = 2.26$, $P < 0.05$; G_h, $Z = 2.90$, P

< 0.05; Fig. 3; Table I). The dendrogram for *D. edwardsi* allows separation of 2 feather groups with low and high mite densities, respectively, i.e., g_l and g_h with significant differences according to GLMM results (g_l, $Z = -3.55$, $P < 0.05$; Fig. 3; Table I).

The GLMM analysis of mite distribution "within feathers" for *T. bifurcata* showed that there were significantly fewer mites in distal than in proximal ($Z = 43.20$, $P < 0.01$) and medial ($Z = 50.20$, $P < 0.01$) regions of individual feathers. In contrast, the number of *D. edwardsi* individuals was lower in medial ($Z = -26.31$, $P < 0.01$) and proximal ($Z = -17.98$, $P < 0.01$) regions than distal ones (Table II).

Results from the experiment on direct sunlight effect on *T. bifurcata* distribution showed that the absolute variation in average distance to the feather base Δd_m was higher in feather mites subjected to solar radiation than mites in darkness ($t = -4.69$, $P < 0.01$), that is, in the dark treatment, mites did not move far from their initial position ($\Delta d_m = 0$, $t = -0.66$, $P = 0.51$), while "light" mites, on average, moved large distances toward the feather bases ($\Delta d_m < 0$, $t = -4.65$, $P < 0.01$; Fig. 4). We did not detect significant trends toward grouping or dispersion either for "light" mites ($t = -0.93$, $P = 0.36$) or for "dark" mites ($t = -1.27$, $P = 0.21$). The proportion of mites that left the dorsal face of the feather during the 5 min of the experiment was higher in "light" mites (for "light" mites, $\mu = 0.24 \pm 0.31$; for "dark" mites, $\mu = 0.02 \pm 0.11$; $t = -4.55$, $P < 0.01$). Some of the mites that left the dorsal face escaped from the feather, while others sought refuge from the ventral surface of the feather. There were no effects of the initial number of mites on Δd_m, either in "light" mites ($F = 0.01$, $P = 0.91$) or in "dark" mites ($F = 0.40$, $P = 0.53$). There was also no significant effect of the time of the day on Δd_m ($F = 0.58$, $P = 0.45$).

DISCUSSION

Mite distribution on dorsal and ventral feather surfaces

The dorsal and ventral surfaces of flight feathers have very different microstructural and environmental features that are reflected in the different morphological adaptations of the 2 mite species under consideration. The distal barbule rows of flight feather barbs tend to bend in their distal part toward the ventral face of feathers. Moreover, the 2 barbule rows of a barb are inserted on the barb axis (ramus), so that the ramus is also projected, in height, toward the ventral surface of feathers. As a result, ventral surfaces of flight feathers are not smooth, and they offer protected space between the ramus of a barb and the barbule margins of the distal barbule row of the contiguous barb. This space is used by *D. edwardsi*, which have a very narrow, elongate (adults length around 450 μm and width around 90 μm) and torpedo-shaped body with slightly flattened ventral side (Fig. 1A–C). This allows them to rest adjacent to one side of the ramus, well protected against wind disturbances, friction within feathers, solar radiation, and preening by the host, but it also limits their mobility (Fig. 1D). In contrast, dorsal flight feather surfaces are completely smooth and without protection against aerodynamic and frictional stresses or solar radiation, but they offer a greater potential for rapid movement over the feather. *Trouessartia bifurcata* individuals also have a flattened, but much larger and more heavily sclerotized, body (520 μm of length and 160 μm of width [approximate]), with strong pigmentation (Proctor 2003)
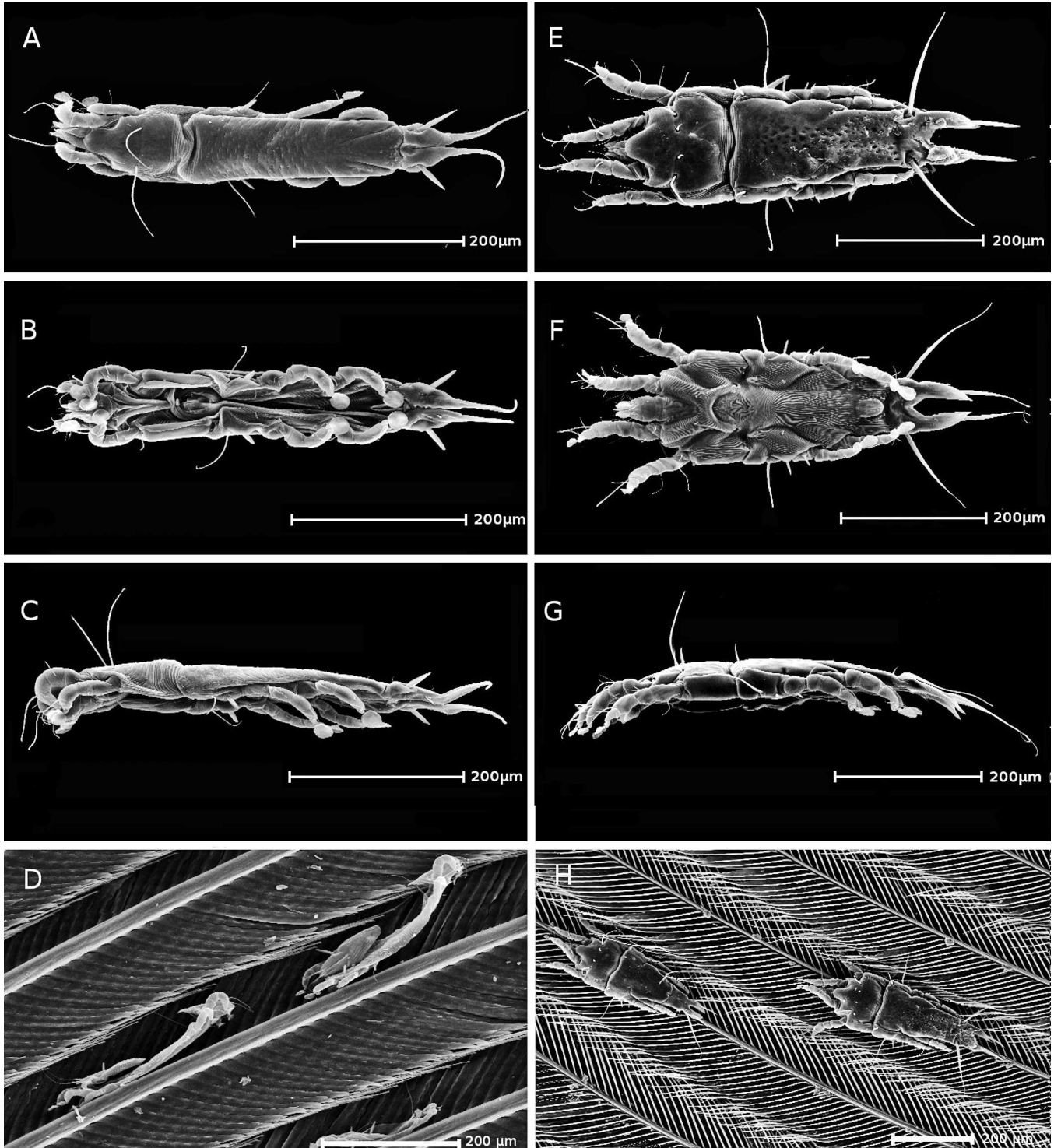
FIGURE 1. Scanning electron microscope pictures of *Dolichodectes edwardsi* (**A–D**) and *Trouessartia bifurcata* (**E–H**). Dorsal (A, E), ventral (B, F) and lateral (C, G) views are shown. Different microhabitats (D, H) are also presented. Exuviae of *D. edwardsi* on the ventral surface of feathers (D) and adults of *T. bifurcata* (H) on the dorsal surface of feathers from moustached warbler.

(Fig. 1E–G) that allow them to accommodate themselves longitudinally over the barb ramus and, therefore, better resist the physical stresses of dorsal surfaces (Fig. 1H). Moreover, they have more separated and prolongated forelegs, which likely provide them with greater mobility (Fig. 1E, F).

Mite distribution between feathers

Feather mite distribution among flight feathers showed a similar pattern in the 2 species studied, with some small differences. The low density or absence of mites at the external
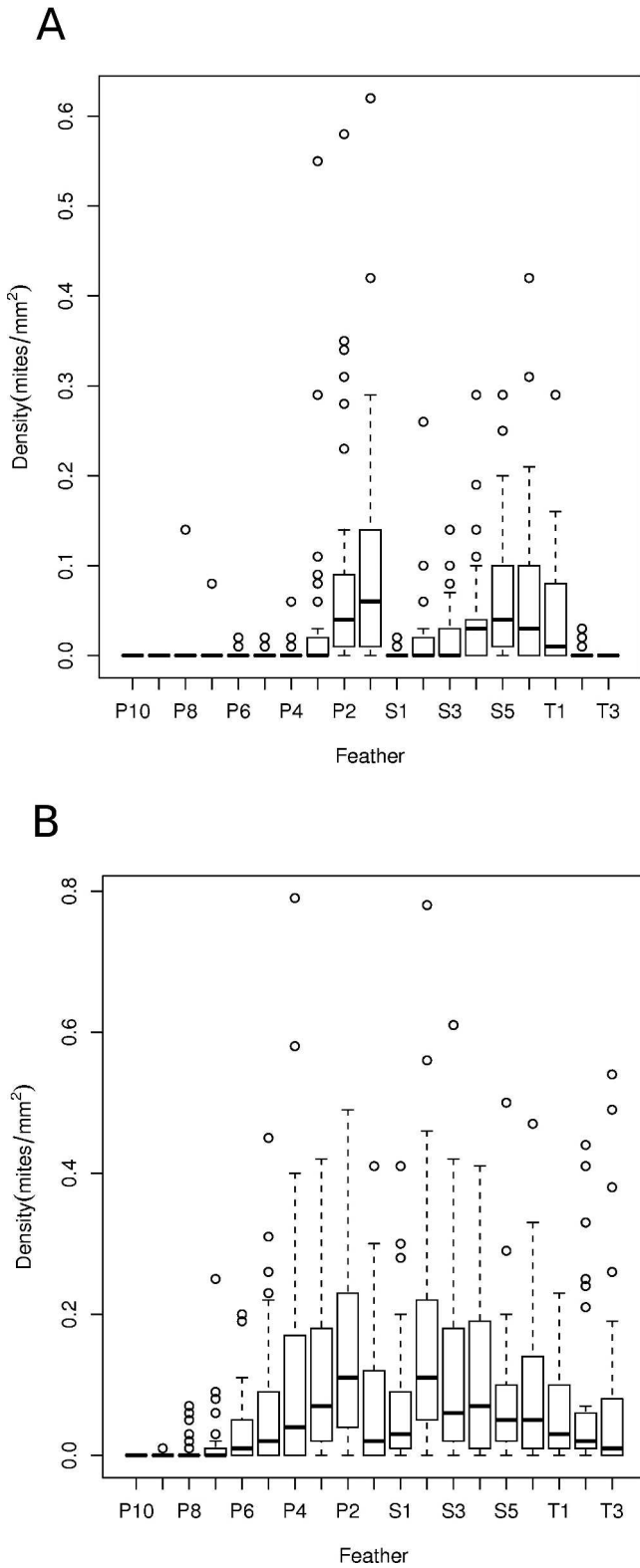
A

B

FIGURE 2. Densities boxplots of *Dolichodectes edwardsi* (**A**) and *Trouessartia bifurcata* (**B**) in the different flight feather types of moustached warbler right wings. Feathers are ordered following their position in the wing from external (P10) to internal (T3) feathers.
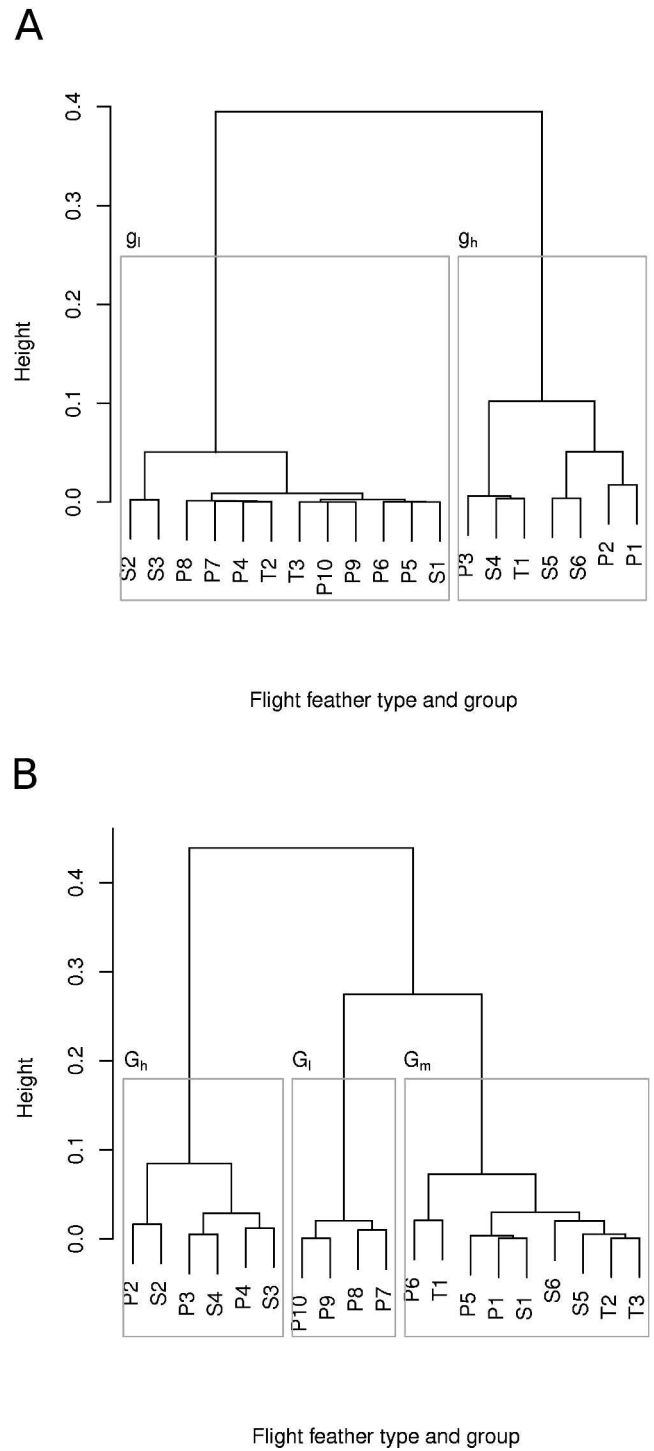
A

Flight feather type and group

B

Flight feather type and group

FIGURE 3. Cluster analysis of moustached warbler wing feathers based on densities (mites/mm^2) of *Dolichodectes edwardsi* (**A**) and *Trouessartia bifurcata* (**B**) using the Ward method and the Euclidean distance.

wing feathers, the concentration of mites to the central wing feathers, and the scarcity of mites in the first secondary feather (S1) are shared features that have been described also in other vane-dwelling mite species (Choe and Kim, 1989; Jovani and Serrano, 2004). Although flight feathers of passerine birds do not present great variations in their structure compared with those of non-passerines (Dubinin, 1951), they can differ in their environ-

TABLE I. GLMM results on the distribution of *Dolichodectes edwardsi* and *Trouessartia bifurcata* between wing flight feathers of moustached warbler comparing different groups generated by the cluster analysis (Fig. 3).

Species	Feather group effect	Estimate	SE	Density (mites/mm^2)
D. edwardsi	g_l	−2.73	0.77	0.004
	g_h	0.00	—	0.065
	Intercept	−2.73	0.24	—
T. bifurcata	G_l	0.00	—	0.007
	G_m	2.36	1.05	0.068
	G_h	3.03	1.04	0.133
	Intercept	−5.05	1.03	—

mental conditions as a result of their different position in the wing. The strong stress generated by aerodynamic forces over the most external wing feathers could be one of the explanations for the absence of mites in this region. Furthermore, the scarcity of mites in feather S1, situated at the center of distribution, could result from the special aerodynamic features of this feather or the additional mechanical stress related to the friction between feathers resulting from the location of this feather at the wing articulation (Jovani and Serrano, 2004). However, inner density peaks of both species show a partial segregation, i.e., an overlapping, but discordant, spatial distribution (e.g., regarding feather types P6, S1, or T3), possibly because of the displacement of the internal distribution peak of *D. edwardsi* as a consequence of competitive processes (see discussion below). Dabert (1992) proposed the existence of competitive mechanisms that generate spatial segregation patterns at the level "between feathers" for 3 feather mite species, *Bychovskiata charadrii*, *Dichobrephosceles actitidis*, and *Avenzoaria totani*, that coexist in the ventral surfaces of flight feathers of the common sandpiper *Actitis hypoleucos*. In that study, Dabert explains that *B. charadrii*, from the little ringed plover *Charadrius dubius*, invaded the wings of *A. hypoleucos*, already inhabited by the 2 native species, *D. actitidis* and *A. totani*, and became established in the primary feathers. The author suggested the possibility of displacement of both native species to new microhabitats. In *A. totani,* the hypothetical displacement may have resulted in a strong reduction in population size. In the same way, the more restricted distribution

TABLE II. GLMM results on the distribution of *Dolichodectes edwardsi* and *Trouessartia bifurcata* between the longitudinal regions of moustached warbler flight feathers.

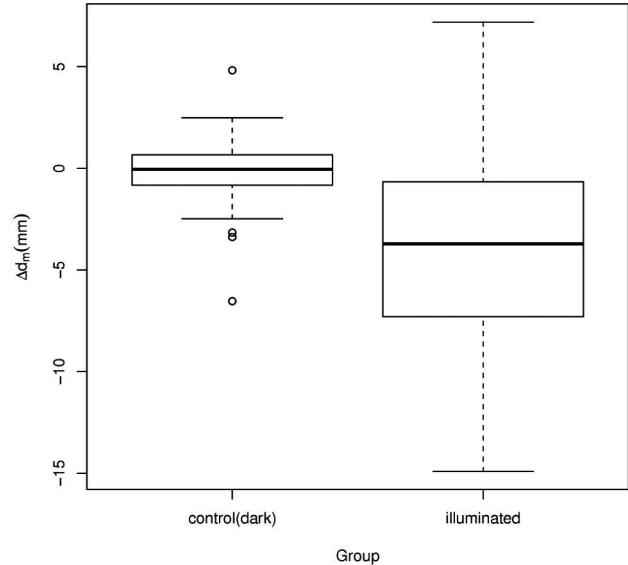| Species	Feather group effect	Estimate	SE	Density (mites/mm^2)
D. edwardsi	Intercept	0.90	0.21	—
	Proximal region	−5.70	0.03	0.0002
	Medial region	−0.90	0.32	0.0248
	Distal region	0.00	—	0.0607
T. bifurcata	Intercept	0.28	0.11	—
	Proximal region	1.52	0.04	0.0919
	Medial region	1.74	0.03	0.1140
	Distal region	0.00	—	0.0201

FIGURE 4. Boxplots showing variation in average change on *Trouessartia bifurcata* distance to feather basis Δd_m for the 2 experimental treatments: control (feathers in the dark) and illuminated feathers.

and the lower densities of *D. edwardsi* (Fig. 2; Table I), together with the apparent displacement of the inner density peak of *D. edwardsi* on *T. bifurcata*, could be a result of competitive processes between both species.

Mite distribution within feathers

With the present survey, we have shown how feather mites segregate spatially not only in different faces of feathers or between feathers, but also across longitudinal regions of individual feathers. A similar type of segregation, i.e., within feathers, was found by Dabert (1992) between the 2 native mite species living in the secondary feathers of *A. hypoleucos*, as cited above. While *A. totani* occurred on dark parts of feathers, *D. actitidis* appeared on white ones. Along their longitudinal axes, flight feathers present environmental differences derived from external factors (aerodynamic and frictional disturbances, solar irradiation, etc.) and also inherent microstructural differences (Pettingill, 1985; Choe and Kim, 1989). As a consequence, individual feathers present spatial heterogeneity that seem to differentially affect the 2 mite species we studied.

Distal regions of flight feathers are subject to higher airflow speeds and, in addition, aerodynamic perturbations are greater here due to the vortex effect (Pettingill, 1985). Furthermore, frictional forces between feathers are stronger toward distal regions because feather displacements in these zones are greater during feather activities, e.g., during flight (Proctor, 2003). Consequently, physical and mechanical stresses more strongly affect distal feather parts and *T. bifurcata*, which is more exposed because of smooth structure of dorsal feather surfaces and could, therefore, experience limited distribution toward medial and proximal feather regions. These regions in the passerine flight feathers are more protected, first because proximal regions are partially protected by wing cover feathers, and second because overlapping of resting wing feathers is usually higher in proximal and medial than distal regions (Choe and Kim, 1989).

In contrast, *D. edwardsi* has a distribution apparently determined by other factors, some of which could be related to feather structure. Medial and distal feather regions have higher barb heights, i.e., the distance from the insertion of the barbules to the distal limit of the ventral part of the barb axis or ramus (Choe and Kim, 1989). This higher barb height may favor *D. edwardsi* because it contributes to a greater amount of protected space, while *T. bifurcata*, living mainly over the dorsal face, is not affected by this feature. This could explain the strong negative effect of proximal region on *D. edwardsi* density (Table II). However, this may not be the only factor involved in the distribution of *D. edwardsi* because barbs are even higher in medial than distal feather regions in *A. melanopogon* (data not shown), as in other species (Choe and Kim, 1989); this conflicts with the greater presence of *D. edwardsi* in distal regions. Therefore, other factors must be involved. One possible explanatory hypothesis could be the competitive exclusion of *D. edwardsi* by *T. bifurcata* in medial regions.

The effect of sunlight on the distribution of *T. bifurcata*

Experimental results on sunlight effects on the distribution of *T. bifurcata* demonstrate that this species has a clear behavioral response to direct sunlight. They respond with non-random, directional movement toward the base of the flight feather. This suggests that these mites have the ability to orient themselves on the feather in the absence of clues that would normally be provided by the host's body. This ability could be based on sensing changes in feather microstructure, e.g., orientation of barbs and barbules, allowing them to find the way toward the highest protection under the wing cover feathers. Thus, light intensity may be one of the factors that limit the distribution of *T. bifurcata* toward more basal regions of flight feathers. This could result from an adaptive response so that sunlight avoidance may benefit *T. bifurcata* individuals that, with this behavior, avoid humidity reduction, increase of temperature, and dangerous radiation, or even a greater airflow risk or detection and elimination by the host with the beak during preening. In the last 2 suggestions, sunlight could act as a cue that the host is opening its wings, with increasing risk to mites, e.g., to start flying or for feather preening by the host.

Is there competition between *T. bifurcata* and *D. edwardsi*?

We have suggested competition processes as possible explanations of some aspects of the spatial segregation found in the 2 mite species studied. A priori, there are 2 resources that are interrelated and could provoke competition between the 2 mite species, i.e., food and space. First, based on observations of gut contents of these and related species of feather mites, both species consume the oil that covers the feathers, together with trapped particles (Blanco and Tella, 2001; Galván et al., 2008). Second, flight feather space on moustached warblers is very small (240 mm² for the largest primary feathers), and it can contain a high density of mites. The feathers with the largest populations of both species in our study (P2, P3, and S4) presented an average number of 44 mites per feather but, in some cases, possessed more than 150 individuals. *Trouessartia bifurcata* mites are larger than *D. edwardsi* and appear to have greater ability to move over the entire feather, dorsally and ventrally; therefore, they may be able to access and consume resources faster than *D. edwardsi*, i.e., act

as the stronger competitor. However, we must bear in mind that unlike the 3 cited feather mite species studied by Dabert (1992), the 2 species in our study occupy, usually, different surfaces. Nevertheless, if *T. bifurcata* can easily access the food on the ventral side of the feather surface, either via crawling there as we observed in our experiment or by reaching through the dorsal surface (barbules are very fine) with its chelicerae, it could provoke competition between the 2 mite species.

Although spatial segregation can be one of the consequences of interspecific competition, empirical evidence shows that spatial segregation between 2 species taxonomically, or ecologically, related does not necessarily indicate the occurrence of competition between them. It would be necessary to analyze in more detail the spatial patterns of coexistence between the 2 mite species considered, in order to elicit more direct evidence of competition. Some evidence could derive from changes in habitat selection comparing sympatric and allopatric populations, or by performing experiments to test the effects of the coexistence on each species distribution (e.g., Connell, 1961; Segurado and Fiqueiredo, 2007).

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