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Feather mites at night: an exploration of their feeding, reproduction, and spatial ecology

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Birds host a vast diversity of feather symbionts of different kingdoms, including animals (e.g., lice, mites), fungi, and bacteria. Feather mites (Acariformes: Astigmata: Analgoidea and Pterolichoidea), the most abundant animal ectosymbionts of birds, are permanent inhabitants of the pterosphere (*ptero* feather in Greek; Labrador et al. 2020), and the ones studied here are easily spotted as small (ca. 0.5 mm) dots on the surface of flight feathers. They are highly host specific symbionts (Doña et al. 2018), and they seem to be commensals or even mutualists of birds by taking detritus and microorganisms such as fungi and bacteria from feathers, some of which are keratinophilic and therefore can damage the feathers (Blanco and Tella 1997, Galván 2012, Doña et al. 2019). However, many basic questions remain to be answered, such as the moments and the places where feather mites eat. Indeed, we wondered whether this might be partly because feather mites have been studied mainly during the day, when (most) birds fly, rather than during the night when mites seem to move more freely on the wings, according to two old anecdotal reports (Dubinin 1951, McClure 1989). To investigate the night ecology of feather mites, we initially spent a whole night observing them on two individual birds. At that point, we were unaware of how it would change our understanding of the pterosphere.

On February 13, 2020, we captured two blackcaps *Sylvia atricapilla* (Linnaeus, 1758) (Sylviidae), with mist nets at 17 h (still in daylight). To quantify the mites and study their spatial ecology, we held the extended wings and tail of the birds in front of a white paper with a light source behind, and took photographs of each primary (10 feathers), secondary (6), and tertial (3) feather of the two wings, and the 12 tail feathers, placing a ruler close to the feathers for subsequent measurements. Then, we kept the birds outdoors overnight (minimum night temperature 4°C) in profusely perforated paperboard boxes, repeating the photographs at 20 h (night already), 23 h, 2 h, 5 h, and 9 h (daylight again) (see Appendix S1: Section S1 for methodological details). When we saw the abundance and unusual (for us) distribution of mites on the first blackcap at 20 h, we guessed that many findings were ahead, and not merely about their nocturnal occurrence on the wings.

By studying the abundance of mites, we found that (Fig. 1a): (1) The total number of mites increased on the wings and tail until midnight and then decreased toward dawn to reach abundances on the wings that were even lower than those recorded at dusk. (2) Different mite species and developmental stages showed different abundance dynamics: adult *Proctophyllodes sylviae* Gaud, 1957 (Proctophyllodidae) initially slightly increased in numbers, decreasing afterward. Similarly, juvenile *P. sylviae* suddenly appeared at night on the wings and tail and almost disappeared again at dawn. Lastly, *Trouessartia* sp. (likely *T. bifurcata* (Trouessart, 1885) (Trouessartiidae) based on host records in Doña et al. 2016) did not show the initial increase found in *P. sylviae*, but instead gradually decreased during the night. These results supported the previous non-quantitative records of mites increasing at dusk and moving along the wings overnight (Dubinin 1951, McClure 1989), and show that different species and stages behave differently during the nighttime.

To further analyze the nocturnal activity of feather mites, we digitized their position on the feathers from the photographs (totaling 4,643 mite coordinates). We

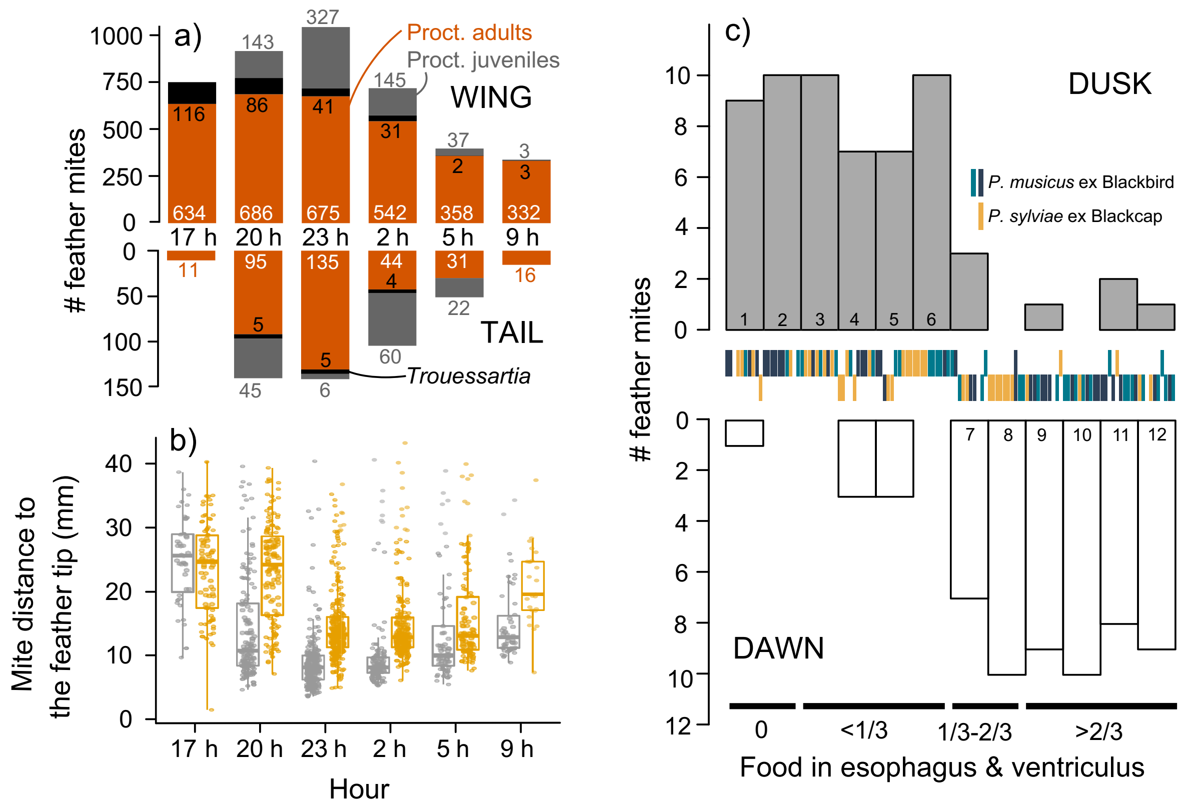

FIG. 1. (a) Total abundance of different species and stages of feather mites on the wings and tail of two blackcaps (*Sylvia atricapilla*) observed from dusk to dawn. Numbers indicate the quantity of mites of each species and stage. Additionally, two feather mites of a third morphotype were recorded on a tail at 23 h and one at 2 h, likely *Analges* sp. (they were not collected for identification). (b) Box-plot of the distance of each feather mite (points) to the tip of its feather. Colors indicate the two blackcap individuals. Only primary feathers of the right wing are shown (see also Appendix S1: Fig. S1). (c) Vertical colored lines (top row: dusk; bottom row: dawn) show the 120 *Proctophyllodes* spp. mites ranked according to the amount of food ingested, from mites without food items (left) to the ones with the esophagus and ventriculus full of food (right). Corresponding rough estimates of the amount of filling of the ventriculus and esophagus are shown in the bottom *x*-axis. Top panel indicates mites collected at dusk (i.e., showing daytime feeding) and the bottom panel indicates mites collected at dawn (i.e., showing night feeding) from the same birds. Numbers from 1 to 12 link to example photographs in Fig. 2a.

discovered: (1) Mites migrated toward the feather tips (which were seldom occupied at 17 h, and are not usually occupied by blackcap feather mites during the day; ML, JD, DS, RJ, *personal observation*). This pattern was mainly observed in primaries (but also in secondaries) and was followed by a progressive return to more proximal positions toward dawn (Fig. 1b; Appendix S1: Fig. S1). (2) Mites tightly aggregated by developmental stage and species among and within feathers (Appendix S1: Fig. S1). This distribution was especially apparent in *P. sylviae* juveniles, which were clustered in certain feathers and particular locations within feathers (Appendix S1: Fig. S1). (3) Mites at night occupied central tail feathers, which are rarely occupied during the day (ML, JD, DS, RJ, *personal observation*, Appendix S1: Fig. S1). (4) During the night, *P. sylviae* occurred on the ventral surface of feathers and *Trouessartia* sp. occurred on the dorsal one, as they did during the daytime and as previously found (Dabert and Mironov 1999, Proctor 2003, Mestre et al. 2011, Fernández-González et al. 2013; ML, JD, DS, RJ, *personal observation*).

The nocturnal presence and activity of feather mites on wing and tail feathers made us wonder whether mites could be feeding during the night. To test this, on February 20, 2020, we sampled feather mites at dusk and then at dawn from two blackbirds *Turdus merula* Linnaeus, 1758 (Turdidae) and another blackcap, and investigated mite gut contents under the microscope (see Appendix S1: Section S2 for methodological details). Many mites had no visible food items in their esophagus and ventriculus (first gut compartments where food arrives when ingested; Alberti and Dabert 2012), but many other mites had their esophagus and ventriculus fully packed with food (Fig. 2a). To test whether mites taken at dawn were those full of food (i.e., which would show night feeding), we took pictures from 120 randomly selected adult female *Proctophyllodes* mites (*P. musicus* Vitzthum, 1992 from blackbirds; *P. sylviae* from blackcaps), 20 from each of the three birds and the two sampling times. Then, we coded the slides so that three of us could blindly sort the pictures according to the amount of food found in the esophagus and ventriculus. Afterward, we discussed our minor discrepancies to achieve a consensus rank among mites and counted the number of food boluses and fecal pellets as a measure of previous feeding events (Alberti and Dabert 2012).

We found an almost perfect division between the mites sampled at dusk and those at dawn (Fig. 1c vertical colored lines, Fig. 2a). At dusk, mites had either no food items (31.7%) or <1/3 of the ventriculus with food items (56.7%). In contrast, at dawn, most mites had 1/3–2/3 (28.3%) or >2/3 (60.0%) of the ventriculus full of food items (Figs. 1c, 2a). Moreover, this pattern was consistent across the three individual birds studied (Fig. 1c vertical colored lines). Conversely, most mites sampled at dusk (76.7%) and dawn (91.7%) had one food bolus and one fecal pellet (Fig. 2a; Appendix S1: Fig. S2).

Later, when working on Fig. 2a, we noticed a large but tenuous and transparent egg inside one of the

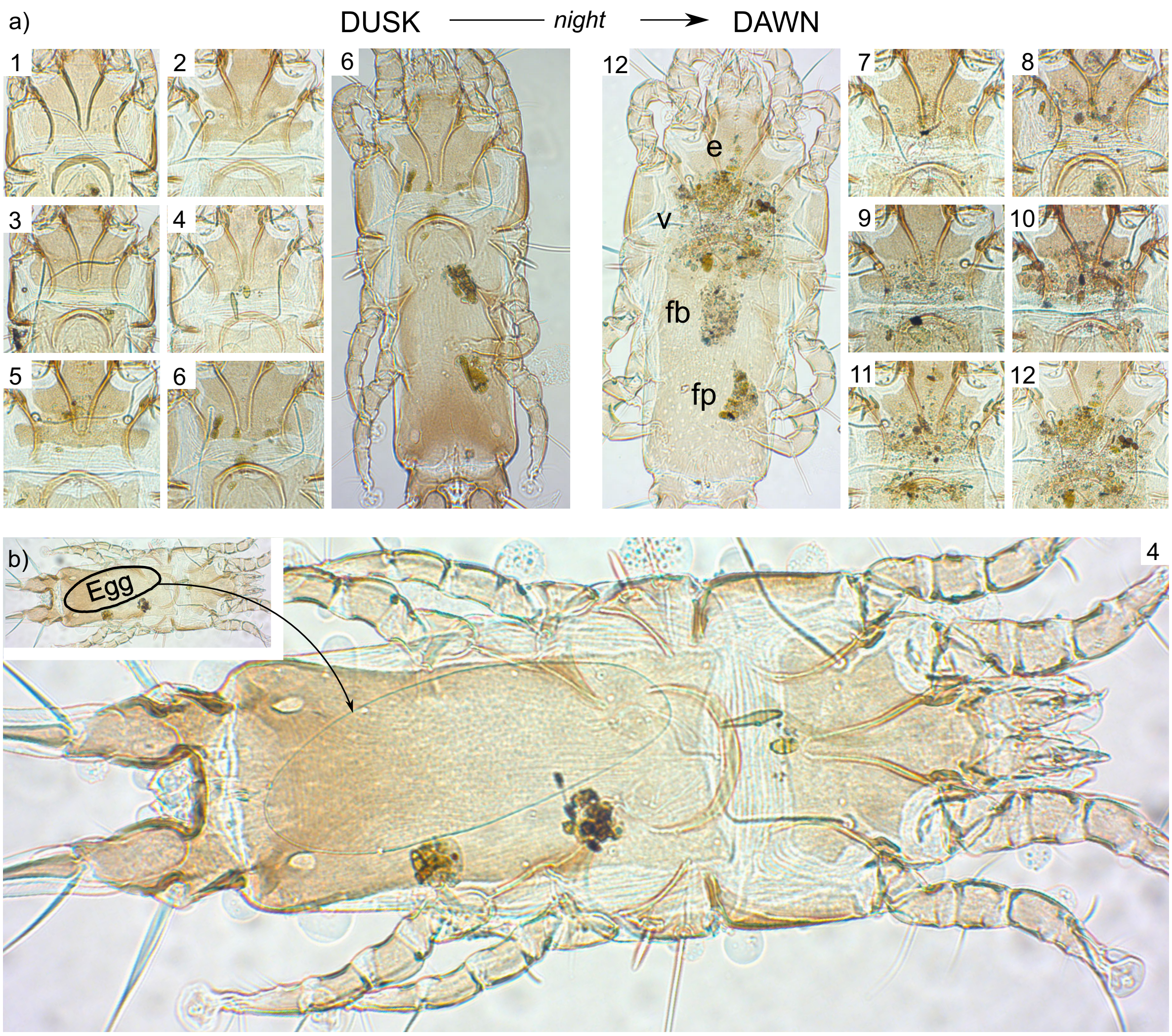

Fig. 2. (a) Example photographs showing that feather mites sampled at dusk (left) had many fewer food items in the esophagus (e) and ventriculus (v) than those sampled the next dawn (right) from the same individual birds. However, most feather mites sampled either at dusk or dawn had one food bolus (fb) and one fecal pellet (fp). Numbers indicate the mites' positions in Fig. 1c bins. Note that small photographs only show the esophagus and ventriculus. Individuals are *Proctophyllodes musicus* from *Turdus merula* (mites 2, 5, 7, 9, 10, 11, and 12) and *P. sylviae* from *Sylvia atricapilla* (mites 1, 3, 4, 6, and 8). (b) *P. sylviae* female sampled at dusk with an egg, only a few food items in the ventriculus, one food bolus, and one fecal pellet.

females (Fig. 2b). We went through the 120 pictures again and then discovered 21 females with an egg inside. Perhaps more interestingly, while as many as 20 out of the 60 (33.3%) females collected at dusk carried an egg, only one out of 60 (1.7%) did so at dawn. Again, this pattern was consistent in the three birds sampled: the blackcap (dusk: 5 females with egg/15 without egg, dawn: 1/19), the first blackbird (dusk: 7/13, dawn: 0/20), and the second blackbird (dusk: 8/12, dawn: 0/20).

The results presented here are based on a large sample of feather mites but a low number of individual birds and of mite and bird species, and will therefore need further exploration in dedicated studies that include a larger sample of birds (and therefore also of mites) of different species. However, the nocturnal patterns of abundance, spatial distribution, feeding behavior, and egg-laying that we have reported here suggest that feather mites are nocturnal organisms. This has several implications:

First, it could be that survey of feather mite abundance on individual birds are systematically underestimated because the most common method of assessment consists of counting mites on wing and tail feathers during the daytime. This underestimation may potentially differ between mite species and stages, as Fig. 1a suggests. Importantly, further studies are needed to ascertain whether this day/night difference in feather mite counts varies among bird species. If so, current data on feather mite abundances across bird species may be potentially biased (e.g., Galván et al. 2012, Diaz-Real et al. 2014).

Second, we have found that mites were able to move from the center of primary feathers to more distal positions in three hours (Appendix S1: Fig. S1), confirming that they have the potential to change their position rapidly (e.g., in response to changes in environmental conditions, Dubinin 1951, McClure 1989, Wiles et al. 2000). Furthermore, feather mites presented a non-random nocturnal spatial distribution among and within feathers (Appendix S1: Fig. S1) and showed clear location preferences (as they do during the day, e.g., Pérez and Atyeo 1984), which also differed between mite species and stages. Thermo-orientation could potentially be a driver of these location changes, as has been found in wing feather lice. Specifically, some lice have been seen to rapidly change position in search of specific feather regions with more suitable temperatures (that vary depending on lice life stage) (Harbison and Boughton 2014).

The migration of mites toward the tip of the primary feathers in the first half of the night is intriguing. A potential explanation would be that feather tips accumulate more organic particles to feed upon. Another possibility is that mites would take up water by moving to feather tips (dangerous during the day in a flying bird), as these feather regions are more exposed to air humidity when the wing is folded in a roosting bird. Indeed, Gaede and Knülle (1987) found atmospheric water vapor to be the most important water source for *Proctophyllodes troncatus* Robin, 1877 (the only feather mite species in which this aspect has been studied), as also occurs in bird lice (Rudolph 1983).

Our observations of food items in mites under the microscope also have important implications (Figs. 1c, 2a; Appendix S1: Fig. S2). In short, feather mites collected at dusk had empty esophagus–ventriculus, one food bolus, and a fecal pellet. The mites sampled at dawn had full esophagus–ventriculus and (again) one food bolus and one fecal pellet. Therefore, it is reasonable to suggest that feather mites feed at night, and during the day the food in the esophagus–ventriculus becomes a food bolus, the food bolus becomes a fecal pellet, and one fecal pellet is egested. If this proposed process was correct, it would have several implications:

First, most mites feed every night, given that almost all mites had a medium–high abundance of food items in the esophagus–ventriculus at dawn (Fig. 1c), and one food bolus and a fecal pellet (see above; Appendix S1: Fig. S2). This potential need for filling the ventriculus every night poses the scenario of feather mites being sensitive to food shortages, and therefore population dynamics of feather mites being (at least partly) bottom-up regulated by food resources found on feathers.

Second, by taking advantage of our data, we can make a very rough estimation of the amount of organic material that feather mites could clean from feathers' surface (see Appendix S1: Section S3 for the calculus details). Every night, feather mites could eliminate an average of ca. 0.17 mm^2 of compacted (as found in a vacuum cleaner filter) fungi, bacteria, and other organic particles from the wing flight feathers of a single blackbird. This would lead to ca. 0.62 cm^2 every year on a blackbird and a rough yearly estimate of ca. 80,000 m^2 in just European passerines. Most importantly, these back-of-the-envelope calculations showed that while bacteria, fungi, and feather mites are microscopic, feather mites can daily clean feathers at a macroscopic scale. This result reinforces the idea that feather mites play a role in cleaning bird feathers (Doña et al. 2019), and that they may top-down regulate pterosphere's microorganisms.

While preliminary, our findings suggest that a major adaptation for living on bird flight feathers is to undertake important biological functions such as feeding or egg-laying during the night (i.e., when it is safer to move along flight feathers). This should encourage nocturnal studies on feather mites and other bird ectosymbionts, which often show convergent adaptations (Jovani 2003). Indeed, pigeon wing lice also seem to change their abundance on wing feathers at night (Sarah E. Bush, *personal communication*), encouraging further studies on the selective value of this behavior. Overall, our exploration of the nocturnal natural history of these few species of feather mites may trigger a major shift in our understanding of the pterosphere.

Acknowledgments

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3550/suppinfo

Open Research

Data (Labrador et al. 2021) are available from the Figshare repository: https://doi.org/10.6084/m9.figshare.14371259.v1