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No effects of a feather mite on body condition, survivorship, or grooming behavior in the Seychelles warbler, *Acrocephalus sechellensis*

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Abstract A common assumption of studies examining host-symbiont interactions is that all symbiotic organisms are parasitic. Feather mites are widespread symbionts of birds that do not appear to deplete the host of any vital resources. Instead they feed on the oily secretions that cover the feathers and the detritus caught in these secretions. Therefore, a more logical assumption might be that feather mites are non-parasitic. We investigated whether infestation by a feather mite, Trouessartia sp. (Trouessartiidae), has any detrimental effects on the Seychelles warbler, Acrocephalus sechellensis. Feather mite load was not correlated with body condition. Survivorship of birds per territory was lower for birds with lower mite loads, but this result is explained by these birds also living in low-quality territories with low food availability. The amount of time birds spent grooming was not related to feather mite load and grooming did not decrease following the experimental removal of mites. Additionally, although males groom more than females, they do not have larger mite loads than females. Although this study is largely non-experimental, the combined results indicate that the relationship between these feather mites and the Seychelles warbler is probably benign.

Keywords Parasites · Seychelles warbler · Feather mites · Grooming

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Introduction

According to parasitologists, a parasite is defined as an organism that either lives on or in a host from which it acquires biological necessities such as food. However, evolutionary biologists make the further assumption that a parasite has debilitating effects on its host (Clayton and Moore 1997).

Symbiotic organisms (parasitic, commensal, or mutualistic) outnumber free-living organisms (Thompson 1996) and many have the potential to adversely affect their hosts. Thus, not surprisingly, host-parasite interactions have become the focus of many studies. Some have demonstrated detrimental effects of parasites (hematozoan, gut, and ectoparasites) on host growth, fitness, and survival (e.g., Moss and Camin 1970; Brown and Brown 1986; Rätti et al. 1993; Alves 1997) and some have shown that parasites may even play a role in the sexual selection of their hosts (e.g., Clayton 1990; Hillgarth 1990; Møller 1990a). Others have found no effects of symbionts on host ecology or sexual selection (e.g., Gibson 1990; Hausfater et al. 1990; Pacejka et al. 1998).

Feather mites are common symbionts of birds and recent attention has focused on their impacts. Although their role is poorly understood, they are usually assumed to be parasitic (Fowler and Williams 1985; Choe and Kim 1987, 1989; McClure 1989). This is controversial, because feather mites do not appear to deplete the host of any vital resources, such as blood or feather material, feeding instead almost exclusively on the oily secretions that cover the feathers and the detritus in these secretions (OConnor 1982). Currently, there is limited evidence supporting both parasitic (Rosen et al. 1988; Gaud and Atyeo 1996; Thompson et al. 1997; Harper 1999) and non-parasitic (Blanco et al. 1997, 1999) roles of feather mites.

Approximately 320 Seychelles warblers, *Acrocephalus sechellensis*, occupy Cousin Island (29 ha), Republic of the Seychelles, and all of its suitable habitat is covered with breeding territories (Komdeur 1996). The cooperatively breeding Seychelles warbler is host to three

potential ectoparasites: two feather mites, Trouessartia sp. and Analges sp., and a chewing louse, Myrsidea sp. We examined *Trouessartia* sp. feather mites because most birds were uninfested or hosted very small infestations of Analges sp. mites. Additionally, Trouessartia sp. mite loads were not correlated with Myrsidea sp. loads (D.K. Dowling, unpublished data). Cousin is characterized by two seasons, determined by changes in wind direction. A strong (force 5), constant southeast trade wind blows between May and November. The lighter (force 3), less persistent northwest monsoon prevails between December and March (Komdeur 1991). Salt-spray, blown onto the island by the prevailing winds, is a major factor influencing the feather mite loads of birds, with birds in territories exposed to high degrees of salt-spray carrying significantly smaller infestations than birds in territories unaffected by salt-spray. Additionally, juvenile birds have larger feather mite infestations than adults, while incubating birds have smaller infestations than birds in other stages of reproduction (Dowling et al. 2001).

In this study, we investigated whether infestation by a feather mite, *Trouessartia* sp. (Trouessartiidae), affects body condition or survivorship in the Seychelles warbler. Additionally, we determined through both a correlative study and experimental manipulation whether time spent grooming by individuals is an indication of their mite load, and whether grooming times are influenced by other factors such as host sex or exposure to sea-salt.

Methods

Study population

The study was conducted between June and September 1998. The population of Seychelles warblers on Cousin is individually colorbanded and the complete life history is known for each marked bird.

Breeding activity for birds of each territory was determined by following territorial females for 15 continuous minutes. This observation period was long enough to determine whether birds had begun nesting. Reproduction was divided into four categories: not nesting, nest building, incubation, and feeding of the nestling.

Bird capture and biometric measurements

Birds were caught in mist-nets and, if they had not been caught previously, banded with a unique combination of color rings. The lengths of both tarsi were measured and averaged, and the weight of each bird recorded. An index of body condition was calculated as the residuals from the linear regression of weight on tarsus length. Ages were determined by examining eye color. Juvenile birds (<1 year old) have gray eyes whereas eye color in adults (>1 year) is chestnut brown (Komdeur 1991). Blood samples were collected and the DNA extracted from them was subsequently used to determine the sex of each individual using a molecular technique (Griffiths et al. 1998).

Quantification of feather mites

The *Trouessartia* sp. mites are present on the primary and secondary wing feathers and are individually visible without magnifica-

tion. After capturing a bird, the absolute number of *Trouessartia* sp. mites on all primary and secondary feathers was immediately scored. Although distinguishing between live mites and skin casts is difficult using this method (Proctor and Owens 2000), we subsequently verified the efficacy of this method for this host-symbiont system by comparing counts obtained using this technique with those obtained from the same birds using a 'dust-ruffling' technique described below, where it is possible to distinguish between live mites and skin casts.

Although time of day is a factor that can potentially affect feather mite loads and hence confound analyses relating mite load to other parameters, it is unrelated to feather mite load in this host-symbiont system ($F_{3,47}$ =0.672, P=0.573; Dowling et al. 2001). Thus, we did not need to control for this factor in subsequent analyses.

Feather mites from 13 individuals were removed by dust-ruffling (Walther and Clayton 1997). Birds were held over a collecting plate and a small dose of Exelpet flea control powder for dogs (0.25% pyrethrins and 2% piperonyl butoxide) was applied in puffs onto the body plumage and under the wings. This was dusted throughout the plumage for 1 min. Pyrethrin is a natural biodegradable insecticide that is completely safe for use on birds (Walther and Clayton 1997). The plumage was then ruffled for a short period until all ectosymbionts had fallen onto the collecting plate.

The ectosymbionts collected using the dust-ruffling technique were classified and counted using a binocular microscope. They were then sent to the Veterinary Faculty, University of Utrecht, where all ectosymbionts were identified to genus level.

Quantification of salt levels

20×15 cm cloth strips were hung from branches (chest height) to accumulate salt in territories where birds were caught. Cloth strips were exposed at the same time in each territory for 17 days during the season characterized by southeast tradewinds that expose coastal territories on the southeast side of the island to salt-spray. Samples were collected and sealed in separate plastic bags. Then, 200 ml of demineralized water were added to each bag and the samples analyzed using an ion electrode (Chlorocounter) that measures the number of chloride ions. This was converted into a relative measure of NaCl concentration (mg/l).

Analysis of survivorship

We analyzed survivorship of birds from September 1997 to September 1998 by monitoring all territories on a regular basis for the presence of color-ringed birds. Once a bird disappeared from its territory, we checked all other territories to assess dispersal. We assumed that missing birds had died because Seychelles warblers have never colonized other islands naturally (Komdeur et al. 1998). By monitoring territories in this way, a complete list of birds alive on Cousin to September 1998 was created and compared to a list created using the same method the previous year to assess bird survival. The proportion of birds surviving per territory was compared for birds that had occupied salt-affected territories (birds with small feather mite loads, mean=44, SE=11, n=10; Dowling et al. 2001) to birds that had occupied territories unaffected by salt (birds with large feather mite loads, mean=149, SE=18, n=42; Dowling et al. 2001). We used this analysis of survivorship per territory (and assumed that all birds from salt-affected territories had low mite loads) rather than comparing the survivorship of birds with known mite loads to increase the power of the statistical test. Additionally, because salt levels vary according to territories and not individuals, territories were the appropriate independent unit of analysis. Territories affected by sea-salt are salt-affected every year between May and November, the period of persistent southeast tradewinds (personal observation).

Grooming behavior

Grooming in birds includes preening with the bill or scratching with the feet (Hart 1997). Grooming observations were obtained from two samples of birds. Each time a bird was followed, the total time it was followed and the time it spent grooming was recorded. The proportion of time each bird spent grooming was then calculated. The first sample consisted of birds not caught between June–September 1998 (\hat{n} =51). Grooming data were retained if a bird had been followed for 20 continuous minutes. Possible effects of age, sex, time, reproductive stage, and date on grooming were investigated using analysis of variance and linear regression. Grooming observations were also obtained from a smaller sample of birds that had been caught (n=12) and for which data on feather mite load, exposure to salt-spray, and body condition were available. For this sample, grooming observations were retained if a bird had been followed for 15 continuous minutes. Stepwise regression analysis was applied to this data set.

An experiment was conducted to examine the effects of feather mite infestation on grooming times, using a sample of six birds that were dust-ruffled. Grooming times were collected from these birds prior to dust-ruffling and compared with those following the removal of all potential ectoparasites from their plumage. Grooming times were collected 48–72 h following the dust-ruffling treatment, from continuous observations of at least 20 min.

Power analyses

Power was determined for non-significant results. The power of a statistical test is the probability that it will yield statistically significant results given that there is a biologically real effect in the population being studied (Thomas and Krebs 1997). The desirable level of power suggested by Cohen (1988) is 80%. For regression analyses, we present power for three β_1 values that indicate three effect sizes (small, medium, and large). Effect size is the difference between the null and alternative hypotheses. The three effect sizes represent three different slopes in the regression analyses linking the variables. The power of detecting a large effect size is the probability of detecting a significant result if the relationship between the variables being tested is characterized by a steep slope (large gradient) and the power of detecting a small effect size is the probability of detecting a relationship characterized by a gentle slope. Power increases with effect size.

Results

Comparison of techniques for quantifying feather mites

The number of *Trouessartia* sp. feather mites per bird counted by visual examination of both wings was positively correlated with that obtained using dust-ruffling (r^2 =0.85, n=13, P<0.001).

Effects of mites on body condition and survivorship

Feather mite load was not correlated with body condition (r^2 =0.003, n=47, P=0.709, β_1 =-0.002, -0.005, and -0.01; power=53%, 99%, and 100% for small, medium, and large effect size, respectively).

Survivorship per territory was significantly lower in territories that were salt-affected (birds with small feather mite loads) than territories unaffected by salt (birds with large mite loads; Mann-Whitney test: U=82.5, n=34, P=0.03, Fig. 1).

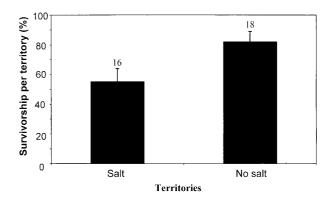


Fig. 1 Mean (+SE) percentage survivorship per territory for territories exposed to salt and those not exposed to salt. *Values above bars* indicate sample size

Table 1 Relationships between independent variables and proportion of time spent grooming for the larger sample (n=51) and the smaller sample (n=12). Statistically significant values are italicized. With date as an independent variable, r²=0.55, P=0.157 (n=38)

Independent variable/Interaction	$F_{numerator\textit{df},denominator\textit{df}}$	P
Large data set		
Age Time Age×time Sex Sex×time Reproductive stage	$\begin{array}{c} 0.012_{1,49} \\ 1.619_{1,42} \\ 0.864_{1,42} \\ 5.652_{1,45} \\ 0.581_{1,38} \\ 0.822_{3,47} \end{array}$	0.914 0.210 0.358 0.022 0.451 0.488
Small data set Sex Body condition Feather mite load Sodium chloride (NaCl)	$\begin{array}{c} 5.133_{1,11} \\ 0.097_{1,11} \\ 0.040_{1,11} \\ 0.000_{1,11} \end{array}$	0.047 0.762 0.846 0.989

Grooming

On average, birds spent 3.4% of their time grooming (SE=0.06%, n=53). Analysis of both data sets revealed that grooming was influenced only by sex (Table 1), with males preening more frequently than females (Fig. 2). All other variables, including feather mite load, were unrelated to grooming; however, the power of the tests was low in most cases. For example, the power of the regression between feather mite load and grooming was only sufficient for a large effect size (β_1 =-1.12×10⁻⁴, -2.08×10⁻⁴, and -4.17×10⁻⁴, power=16%, 35% and 83%, for small, medium, and large effect size, respectively). Although males groomed more than females, feather mite infestations did not differ with sex (F=2.539, df=1,33, P=0.121, power=100%).

There was no difference in the time that birds devoted to grooming prior to and following the removal of all potential ectoparasites by dust-ruffling (Wilcoxon paired-sample test: z=-1.572, n=6, P=0.116, power=76%).

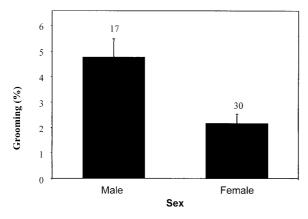


Fig. 2 Mean (+SE) percentage of time spent grooming by males and females. *Values above bars* indicate sample size

Discussion

We found no effects of Trouessartia sp. feather mite infestations on body condition, survivorship, or grooming in the Seychelles warbler. These data contrast with previous studies that have found detrimental effects of feather mites on various indices of individual quality. The feather mite Megninia hologastra apparently induces scratching and a 10% reduction in egg-laying rate in commercial chickens (Rosen et al. 1988). Similarly, a feather mite, *Dubininia melopsittaci*, of budgerigars, Melopsittacus undulatus, induces depluming (Gaud and Atyeo 1996). However, these domesticated birds are restricted in their normal flight activities and this may induce irritation. Evidence from natural populations is more equivocal. Thompson et al. (1997) determined that house finches, Carpodacus mexicanus, with large infestations of feather mites, *Proctophyl*lodes sp., grow shorter wing feathers and duller plumage than less-infested individuals. However, feather mite loads were also correlated with avian pox viral infections that are probably pathogenic and more likely to be the cause of poor feather quality. Although Harper (1999) also found that feather mites were correlated with poor feather quality in house finches, he did not control for avian pox lesions. However, he did show that feather mites generally appeared to have similar effects on wing length and plumage brightness in eight other species.

Yet, similar to this study, others have not found detrimental effects of feather mites on host ecology. Blanco et al. (1999) found no effects of the feather mite, *Proctophyllodes pinnatus*, on host nutritional condition or male sexually selected traits in the linnet, *Carduelis cannabina*. Interestingly, the feather mite in that study is congeneric to the species that Thompson et al. (1997) and Harper (1999) suggest is parasitic on house finches. Blanco et al. (1997) determined that feather mite, *Gabucinia delibata*, loads on red-billed choughs, *Pyrrhocorax pyrrhocorax*, were positively correlated with body condition, thus suggesting the feather mite is

non-parasitic and possibly mutualistic if the mites actually improve feather cleaning or protect the host from infestations with more pathogenic organisms.

However, these studies have drawbacks. They are correlative studies and interpreting correlations is difficult: they can only reveal patterns, not causation. Confounding factors may either generate a relationship when no causal relationship exists or possibly mask a relationship (Kempenaers and Sheldon 1998). The problems of interpreting correlations are particularly difficult for studies showing significant effects. For example, both Thompson et al. (1997) and Harper (1999) suggest feather mites are parasitic. However, feather mites may covary with the abundance of other pathogenic parasites, as appears to be the case in house finches (Thompson et al. 1997). Additionally, concluding whether poor physiological condition is a cause or consequence of high feather mite loads is not possible. Nevertheless, these recent studies of feather mite-host relationships have provided the impetus required for future experimental manipulations, in which feather mite loads are either experimentally increased or decreased and subsequent changes in individual condition, reproduction, and behavior monitored. Similar manipulations have provided definitive evidence that other avian ectosymbionts, such as hematophagous mites (Møller 1990b), lice (Clayton 1990), and fleas (Richner et al. 1993), are parasitic.

Feather mites and survivorship

Birds occupying salt-affected territories have lower feather mite loads (Dowling et al. 2001). All territories that are salt-affected between May and November are also low-quality territories and, during this time, the birds in these territories harbor lower mite infestations than birds in territories that remain unaffected by salt. However, these salt-affected territories not only contain a lower number of feather mites, but also a lower density of insect prey items. Therefore, the birds present in these territories are poorly nourished (Komdeur 1992). Survivorship per territory for birds in salt-affected territories was significantly lower than for birds in territories unaffected by salt. Thus, food availability, rather than mite loads, is affecting survivorship. Interestingly, individuals with low feather mite loads have a reduced chance of surviving between seasons, which is not expected if the mites negatively affect host fitness.

Grooming

Grooming is one of the most frequently performed antiparasite behaviors, although it also serves other important functions such as conditioning the plumage by removing dirt and stale preen oil (Hart 1997). Feather mite load was not correlated with grooming, and birds did not groom less once their feather mites were experimentally removed. Sex was the only factor that was correlated with grooming, with males grooming more often than females. Yet, feather mite loads do not differ between sexes. Thus, males are not grooming more because they have larger mite infestations. Instead, male plumage may function in female mate choice and males may groom more to keep their plumage neat and convey an honest indication of health to females. Alternatively, males may groom more than females because they are involved in a greater number of aggressive interactions (Veen et al. 2000) and consequently their plumage is displaced more often.

In the only other study investigating feather mites and grooming behavior, Blanco et al. (1997) determined that mite loads did not differ for red-billed choughs with normal bills (capable of grooming) or with crossed bills (a deformity preventing efficient grooming), thus suggesting that birds were not grooming to remove mites.

Conclusion

Our finding that *Trouessartia* sp. feather mites are benign has implications for studies that seek to examine the role of symbiotic organisms in sexual selection. It is necessary to confirm, rather than assume, that a symbiont is parasitic. Further studies are needed to determine whether parasitism is a normal or rare occurrence in feather mites, and whether studies documenting their detrimental effects are confounded by the effects of other variables. Definitive answers will be obtained through monitoring changes following experimental manipulations of feather mite infestations on birds.

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References

- Alves MAS (1997) Effects of ectoparasites on the sand martin *Riparia riparia* nestlings. Ibis 139:494–496
- Blanco G, Tella JL, Potti J (1997) Feather mites on group-living red-billed choughs: a non-parasitic interaction? J Avian Biol 28:197–206
- Blanco G, Javier S, Javier de la P (1999) Showiness, non-parasitic symbionts, and nutritional condition in a passerine bird. Ann Zool Fen 36:83–91
- Brown CR, Brown MB (1986) Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonata*). Ecology 67: 1206–1218

- Choe JC, Kim KC (1987) Community structure of arthropod ectoparasites on Alaskan seabirds. Can J Zool 65:2998–3005
- Choe JC, Kim KC (1989) Microhabitat selection and coexistence in feather mites (Acari: Analgoidea) on Alaskan seabirds. Oecologia 79:10–14
- Clayton DH (1990) Mate choice in experimentally parasitized rock doves: lousy males lose. Am Zool 30:251–262
- Clayton DH, Moore J (1997) Introduction. In: Clayton DH, Moore J (eds) Host-parasite evolution: general principles and avian models. Oxford University Press, Oxford, pp 1–6
- Cohen J (1988) Statistical power analysis for the behavioral sciences, 2nd edn. Erlbaum, Hillsdale, NJ
- Dowling DK, Richardson DS, 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
- Fowler JA, Williams LR (1985) Population dynamics of Mallophaga and Acari on reed buntings occupying a communal winter roost. Ecol Entomol 10:377–383
- Gaud J, Atyeo WT (1996) Feather mites of the world (Acarina: Astigmata): the supraspecific taxa. Ann Zool Wetenschappen 277:1–193
- Gibson RM (1990) Relationships between blood parasites, mating success and phenotypic cues in male sage grouse *Centrocercus urophasianus*. Am Zool 30:271–278
- Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. Mol Ecol 7:1071–1075
- Harper DGC (1999) Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. Anim Behav 58:553–562
- Hart BL (1997) Behavioural defence. In: Clayton DH, Moore J (eds) Host-parasite evolution: general principles and avian models. Oxford University Press, Oxford, pp 59–77
- Hausfater G, Gerhardt C, Klump GM (1990) Parasites and mate choice in gray treefrogs, Hyla versicolor. Am Zool 30: 299–311
- Hillgarth N (1990) Parasites and female choice in the ring-necked pheasant. Am Zool 30:227–233
- Kempenaers B, Sheldon BC (1998) Confounded correlations: a reply to Lifjeld et al. and Wagner et al. Anim Behav 55:241–244
- Komdeur J (1991) Cooperative breeding in the Seychelles warbler. PhD thesis, University of Cambridge
- Komdeur J (1992) Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. Nature 358:493–495
- Komdeur J (1996) Seasonal timing of reproduction in a tropical bird, the Seychelles warbler: a field experiment using translocation. J Biol Rhythms 11:333–346
- Komdeur J, Kappe Å, Zande L van de (1998) Influence of population isolation on genetic variation and demography in Seychelles warblers: a field experiment. Anim Conserv 1:203–212
- McClure HE (1989) Occurrence of feather mites (Proctophyllodidae) among birds of Ventura County lowlands, California. J Field Ornithol 60:431–450
- Møller AP (1990a) Effects of a haematophagous mite on the barn swallow (*Hirundo rustica*): a test of the Hamilton and Zuk hypothesis. Evolution 44:771–784
- Møller AP (1990b) Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. Ecology 71: 2345–2357
- Moss WW, Camin JH (1970) Nest parasitism, productivity, and clutch size in purple martins. Science 168:1000–1003
- OConnor BM (1982) Evolutionary ecology of astigmatid mites. Ann Rev Entomol 27:385–409
- Pacejka AJ, Gratton CM, Thompson CF (1998) Do potentially virulent mites affect house wren (*Troglodytes aedon*) reproductive success? Ecology 79:1797–1806
- Proctor H, Owens I (2000) Mites and birds: diversity, parasitism and coevolution. Trends Ecol Evol 15:358–364
- Rätti O, Dufva R, Alatalo RV (1993) Blood parasites and male fitness in the pied flycatcher. Oecologia 96:410–414

- Richner H, Oppliger A, Christe P (1993) Effect of an ectoparasite on reproduction in great tits. J Anim Ecol 62:703–710
- Rosen S, Hadani A, Perlstein Z (1988) The occurrence of *Megninia hologastra* (Analgidae Gaud, 1974) on poultry in Israel. Avian Pathol 17:921–924
- Thomas L, Krebs CJ (1997) A review of statistical power analysis software. Bull Ecol Soc Am 78:126–139
- Thompson JN (1996) Evolutionary ecology and the conservation of biodiversity. Trends Ecol Evol 11:300–303
- Thompson CW, Hillgarth N, Leu M, McClure HE (1997) High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. Am Nat 149:270–294
- Veen T, Richardson DS, Blaakmeer K, Komdeur J (2000) Experimental evidence for innate predator recognition in the Seychelles warbler. Proc R Soc Lond B 267:2253–2258
- Walther BA, Clayton DH (1997) Dust-ruffling: a simple method for quantifying ectoparasite loads of live birds. J Field Ornithol 68:509–518