Short communications

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Feather mite loads influenced by salt exposure, age and reproductive stage in the Seychelles Warbler Acrocephalus sechellensis

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Many factors may affect symbiont distributions within host populations. Intrinsic factors, such as genotype, body condition and age may account for variations in symbiont loads between individuals. However, abiotic factors may also contribute to variations. We investigated correlates of variation in the number of feather mites, *Trouessartia* sp. (Trouessartiidae), per individual in the Seychelles Warbler *Acrocephalus sechellensis* on Cousin Island. Warblers from territories exposed to high levels of salt spray had lower feather mite loads than warblers from territories unaffected by salt spray, and juveniles had higher mite loads than adults. When the effects of salt spray were controlled for statistically, incubating birds had lower mite loads than birds in other stages of reproduction. Thus, an extrinsic and two intrinsic factors contribute to predicting feather mite loads.

Symbiotic organisms (parasitic, commensal or mutualistic) are probably present on every free-living organism (Price 1980), but host individuals often vary considerably in their symbiont loads (Hudson and Dobson 1997). Although theoretical studies have modelled the factors that can generate observed patterns of parasite distributions within host populations (e.g. Crofton 1971a, b, Anderson and May 1978, May and Anderson 1978, Anderson and Gordon 1982), fewer studies have described non-parasitic symbiont distributions (e.g. Fowler and Miller 1984, Fowler and Williams 1985). Furthermore, until recently, few empirical studies have examined these factors within natural populations.

A host provides a symbiont with an environment for population growth. Therefore, differences in host behaviour or susceptibility to symbiont infestation may determine symbiont distributions among individuals (Anderson and Gordon 1982). Variation in symbiont loads between individuals may be due to differences in factors such as host genotype (Hamilton and Zuk 1982), age (Hudson and Dobson 1997), reproductive effort (Siikamäki et al. 1997), sex (Poulin 1996) or size (Rozsa 1997). However, these distributions may also be affected by environmental or abiotic factors extrinsic to hosts, such as climate (Eeva et al. 1994), geographical region (Greiner et al. 1975), season (Fowler et al. 1983) and time of day (Gore et al. 1982). Although it is acknowledged that abiotic sources of variation in symbiont distributions may complicate interpretations of studies examining host-symbiont interactions (Kirkpatrick et al. 1991), relatively few studies have actively examined their impact.

The incidence of infection with haematozoan blood parasites is markedly reduced in birds that breed in coastal and arctic environments (Greiner et al. 1975, Bennett et al. 1992, Figuerola 1999). It has been suggested that these patterns are due to microhabitat. That is, coastal- and arctic-breeding birds escape infection with haematozoa because the insect vectors required to transmit the parasites cannot survive in coastal areas exposed to salt spray or in extremely cold arctic environments (Bennett et al. 1992). If insects struggle to exist in saline environments (Cheng 1976), it is possible that all arthropod ecto-symbionts, be they insects or not, may struggle to exist in these habitats. Interestingly, this hypothesis has been tested in just one empirical study. Dubinin (1951) examined the effects of salt load on feather mites (Acari), common ecto-symbionts of birds, in 12 species of birds captured on lakes with high salt concentrations (albeit with very low sample sizes in each bird species). With the exception of ducks, gulls and terns, whose feather mites are protected from contact with salt by ventrally expanded tufts on the primary wing feathers, feather mites of other bird species were killed by salt loading on wing feathers. Furthermore, Dubinin determined experimentally that spraying the wings of birds with salt solutions eradicated three different species of feather mites (*Gabucinia delibata*, *Ardeacarus ardeae* and *Michaelichus heteropus*).

In this study, we investigated the causes of variation in the intensity of infestation by a feather mite, *Trouessartia* sp. (Trouessartiidae), on the Seychelles Warbler *Acrocephalus sechellensis*. We examined whether factors intrinsic to the warbler may account for variation in feather mite loads, or whether an extrinsic factor, salt exposure, regulates mite distributions.

Materials and methods

Study area and data collection

The study was conducted between June and September 1998 on Cousin Island (29 ha), Republic of the Seychelles. The island is covered with Seychelles Warbler breeding territories, with approximately 320 birds occupying these (Komdeur 1992). Most of these birds are individually colour-banded and the complete life-history is known for each marked bird. Cousin Island is dominated by *Pisonia grandis* (Nyctaginaceae) and *Morinda citrifolia* (Rubiaceae) woodland. The climate is characterised by two seasons, determined by changes in wind direction. A strong (force 5), constant southeast trade wind blows from May/June to October/November. The lighter (force 3), less persistent northwest monsoon prevails between December and March. The periods between these two seasons are characterised by lighter winds (Komdeur 1991).

The breeding activity of birds in each territory was determined by following territorial females continuously for 15 min. 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.

Birds were caught in mist-nets and, if they had not been caught previously, banded with a unique combination of colour rings. *Trouessartia* sp. feather mites infesting the Seychelles Warbler occupy the primary and secondary wing feathers and are individually visible without magnification. After capturing a bird, the absolute number of mites on all primary and secondary feathers was immediately scored. Although it is difficult to distinguish between live mites and skin casts using this method (Proctor and Owens 2000), we verified its efficacy 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 in Walther and Clayton 1997), where it is possible to distinguish between live mites and skin casts ($r^2 = 0.85$, $n = 13$, $p < 0.001$, Dowling et al. 2001). 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. Birds were aged as less or more than 1 year old based on eye colour (Komdeur 1991). Blood samples were collected and the DNA extracted from them subsequently used to determine the sex of each individual using a molecular technique (Griffiths et al. 1998).

Quantification of salt

Salt spray is blown onto the island by the prevailing winds. Vegetation growing in salt affected areas develops thick, waxy leaves. Exposure to salt burns the leaves and they subsequently fall off (pers. obs.). To quantify salt levels during the southeast trade winds in August 1998, 20 cm × 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. Samples were collected and sealed in separate plastic bags. 200 ml of demineralised water were added to each bag and the samples were analysed using an ion electrode (Chlorocounter®) that measures the number of chloride ions in each sample. This was converted into a relative measure of sodium chloride (NaCl) concentration (mg/l).

Seasonality

Between December and March, the region is subjected to lighter, less persistent northwest winds that expose the opposite side of the island to salt spray. To determine whether there is a seasonal effect on feather mite loads, nine birds were caught in January 1999 from territories that had been salt affected between June and September to examine feather mite loads in this alternative season. Salt levels were quantified in the same territories as the previous season using the method described above.

Statistical analysis

Analysis was conducted on a sample of 52 birds. Feather mite loads were $\log_{10}$ transformed. Although a small number of birds used in the analyses were captured from the same territories, individual birds, rather than territories, were used as the main level of statistical analysis. We were interested in testing effects of age, sex and time of capture on mite loads, variables that are inherent to individuals. To confirm that any effect of salt exposure was not confounded by perceived pseudoreplication, given that salt exposure varies by territory, we also present this main effect using territory as the main level of analysis. Main effects and possible interactions between independent variables (age, body condition, date of capture, NaCl, reproductive stage, sex, time of day) on mite loads were tested. Additionally, the effects of age and reproductive stage on mite load were tested once the effect of the abiotic factor, NaCl, had been controlled for using analysis of covariance.

Results

Correlates of feather mite loads

NaCl ($r^2 = 0.135$, $n = 52$, $p = 0.017$) and age ($F = 4.871_{1,50}$, $p = 0.032$) correlated significantly with feather mite loads. Feather mite loads decreased with increases in NaCl (mg/l) and juvenile birds possessed larger mite loads than adults. When mite loads of birds caught within the same territories were averaged, NaCl still correlated significantly with mite loads ($r^2 = 0.180$, $n = 38$, $p = 0.017$). The relationship between feather mite loads and reproductive stage approached significance ($F = 2.342_{3,48}$, $p = 0.085$). Other variables and interactions were not related to mite loads.

When the effects of NaCl on mite load were controlled, age was still related to mite loads (age: $F = 5.215_{1,49}$, $p = 0.027$; NaCl: $F = 7.016_{1,49}$, $p = 0.011$, Fig. 1). Furthermore, the effects of reproductive stage on mite load became significant (reproductive stage: F: $8.064_{3,47}$, $p < 0.001$; NaCl: $F = 23.416_{1,47}$, $p < 0.001$, Fig. 2). Incubating birds had the lowest feather mite loads and birds that were not nesting or that were nest building the highest. Individuals that were feeding nestlings tended to have larger mite loads than incubating birds, but lower mite loads than birds that were not nesting or nest building. The effects of age on mite load were not controlled when examining reproductive stage, because only a small number of birds ($n = 8$) were juveniles. However, if juveniles are excluded from the analysis, the relationship remains significant (reproductive stage: $F = 6.929_{3,39}$, $p < 0.001$; NaCl: $F = 17.465_{1,39}$, $p < 0.001$).

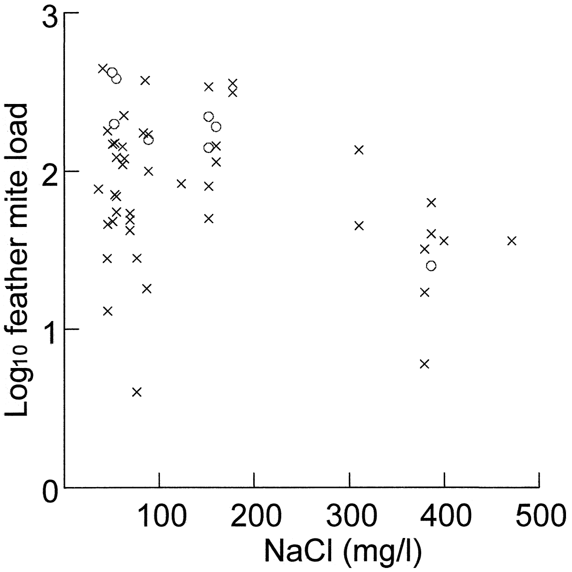

Fig. 1. Relationship between $\log_{10}$ feather mite loads and NaCl (mg/l). Open circles represent juvenile birds and crosses represent adults.

Seasonality

Between December and March, when light northwest winds prevail, the vegetation in the southeast coastal territories, which becomes highly salt affected between June and September, recovers to a level typical of territories unaffected by salt. Additionally, territories on the northwest edge of the island are exposed to moderate amounts of salt spray (pers. obs). NaCl (mg/l) concentrations were significantly higher in territories that were classified visually as salt affected during Janu-

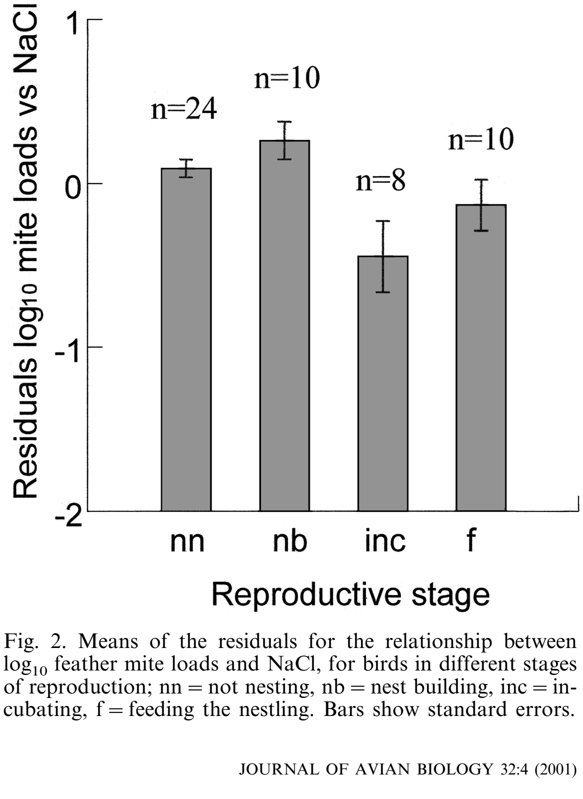

Fig. 2. Means of the residuals for the relationship between $\log_{10}$ feather mite loads and NaCl, for birds in different stages of reproduction; nn = not nesting, nb = nest building, inc = incubating, f = feeding the nestling. Bars show standard errors.

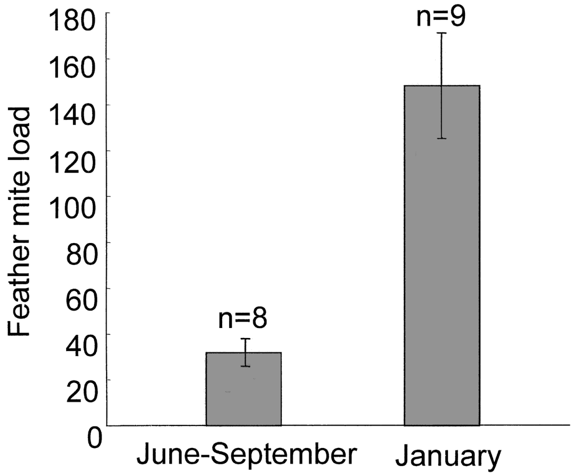

Fig. 3. Mean feather mite loads of birds caught between June and September and those caught in January in territories that had been strongly salt affected between June and September. Bars show standard errors.

ary (the northwest coastal territories) than those classified as unaffected by salt (Mann-Whitney test: $U = 7.0$, $n = 21$, $p < 0.0001$).

Feather mite loads on birds caught during January in territories that had been strongly salt affected during the June–September breeding season (but were no longer salt affected) were significantly higher than those of birds caught in salt affected territories between June and September (Mann-Whitney test: $U = 0.5$, $n = 17$, $p < 0.0001$, Fig. 3).

Discussion

Correlates of feather mite loads

Previous studies investigating host-symbiont systems have not examined the effects of both biotic and abiotic factors on symbiont loads. In this study, infestation by an ecto-symbiotic feather mite, *Trouessartia* sp., decreased with increased exposure to salt and with host age. Additionally, incubating birds had lower mite loads than birds in other stages of reproduction.

Sodium chloride

Although this is a correlative study, and therefore cannot prove per se that salinity is a major causal factor influencing mite loads, we find strong support for Dubinin's (1951) experimental findings that salt can have a major effect on feather mites. The functional nature of feather mites is controversial, with limited correlative evidence supporting their commensal (Blanco et al. 1999), parasitic (Rosen et al. 1988, Thompson et al. 1997, Harper 1999) and even mutualistic (Blanco et al. 1997) roles. The *Trouessartia* sp. mites in this study are probably non-parasitic (Dowling et al. 2001). Although it appears that feather mite distributions are affected by salinity, there is currently no evidence that this may apply to other ecto-symbionts. Interestingly, if salt similarly affects other ecto-symbionts that are parasitic, then hosts may choose to live in saline environments to escape the effects of parasitism (Piersma 1997).

Vegetation exposed to regular salt spray on Cousin wilts and dies (pers. obs.). In the same way that only salt tolerant vegetation is able to survive in areas characterised by high salinity (Larcher 1991), it is probable that only salt tolerant ecto-symbionts are able to survive in highly saline areas. Selection pressures for the evolution of salt tolerance in this feather mite may be weak because most of the island is not salt affected and the direction of the winds changes twice a year (Komdeur 1991). Therefore, the areas in which vegetation is salt affected change between seasons. Additionally, the feather mite species might have a wide range of host species in different habitats, and this would decrease the possibility the species would evolve salt tolerance.

The seasonal changes in salt exposure, which occur as a result of the change in prevailing winds, provide an opportunity to further test the hypothesis that exposure to NaCl is a major causal factor determining the feather mite loads of individuals. We expected a seasonal change in feather mite loads on birds from coastal territories. In support of this, during December and March, feather mite loads on birds that occupied territories that were salt affected between May and November, increased to numbers typical of individuals that occupy territories unaffected by salt. It is unlikely this change is due to a general seasonal decline in feather mites because the birds caught in territories that remain unaffected by salt throughout the year had characteristically high mite loads during both periods (June–September: $n = 42$, January: $n = 3$).

Age

Host age may also be important in determining feather mite loads in the Seychelles Warbler. Juveniles had higher mite loads than adults. A possible process behind this difference in mite loads may be that the two age classes have differential exposures to the mites. Increased exposure occurs only through increased contact with other individuals because feather mites spend their entire life-cycle on their hosts (Clayton and Walther 1997). However, in this instance, differential exposure to mites is unlikely. Although juveniles spend more time outside their natal territories than adults (J. Komdeur and P. Edelaar unpubl.), and thus probably interact with a greater number of individuals, any accumulation of mites should then be passed on to adults within their natal territories.

Alternatively, differences in anti-parasite behaviours, such as grooming, may be responsible for age-related differences in ectoparasite loads (Burley et al. 1991). This is unlikely in the Seychelles Warbler because grooming does not appear to be related to feather mite removal in this species and it is unlikely that the mites are parasitic (Dowling et al. 2001). Perhaps the most plausible explanation behind this age-related difference is that juveniles may produce larger amounts of uropygial-gland oil, the food source of feather mites (Dubinin 1951, Walter and Proctor 1999), and thus harbour larger mite loads. This is untested.

Reproductive stage

Once the effects of NaCl on mite loads were controlled, feather mite loads differed according to the reproductive stage of the birds. Individuals that were not nesting, were nest building or feeding progeny had larger mite loads than individuals that were incubating. Given that the feather mites in this study are probably benign, differences in mite loads of birds according to their reproductive stage may be due to decreases in exposure to feather mites during incubation, perhaps because incubating birds have fewer interactions with others since they need to attend the nest.

Conclusions

This study, together with a number of others (see Forbes et al. 1994), provides a clear demonstration that many factors may influence symbiont distributions. It is the first study to support Dubinin's finding that salt exposure affects feather mite loads. Mite loads were also associated with two intrinsic factors: host age and reproductive stage. Thus, both biotic and abiotic factors may jointly influence symbiont loads. This has implications for studies that examine parasitic symbionts. In addition to examining factors that are intrinsic to the host, future studies of host-parasite interactions should investigate the potential role of a variety of abiotic factors in the regulation of parasite distributions within host populations.

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Foraging trip duration increases for Humboldt Penguins tagged with recording devices

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Marine animals equipped with data recording devices sometimes show changes in their foraging behaviour, which can indicate an adverse effect of the instrument. We attached time-depth recorders (TDRs) and radio-transmitters to study foraging behaviour in Humboldt Penguins *Spheniscus humboldti* and observed an increase in the duration of foraging trips. We suggest that further tagging of this endangered species be approached with caution since this increase in trip duration may negatively affect reproductive and foraging success.

Foraging behaviour in penguins is difficult to observe directly because individuals typically travel large distances at sea or spend considerable time below the surface (Wilson et al. 1986). Consequently, instruments such as satellite tags, radio-transmitters, and time-depth recorders are increasingly used to study aspects of foraging behaviour including foraging trip duration, foraging location, and dive characteristics. Despite the valuable information that these instruments collect, their deployment on some species can have negative effects on foraging behaviour and reproductive success (Wilson et al. 1986, Davis and Miller 1992, Watanuki et al. 1992, Hull 1997).

Research on the impact of instruments on behaviour and reproductive success of penguins has produced equivocal results. Several researchers have found no significant effect of instrument deployment on trip duration (Croxall et al. 1988, Williams et al. 1992, Watanuki et al. 1992, Wienecke and Robertson 1997)