Nest mites (*Pellonyssus reedi*) and the reproductive biology of the house finch (*Carpodacus mexicanus*)

Andrew M. Stoehr, Paul M. Nolan, Geoffrey E. Hill, and Kevin J. McGraw

Abstract: We investigated the effects of a hematophagous nestling mite (*Pellonyssus reedi*, Acari: Macronyssidae) on the reproductive biology of the house finch (*Carpodacus mexicanus*) in east-central Alabama, U.S.A. Mites were absent from nests for the first half of the breeding season, but after their initial appearance they increased in number and were present in almost all nests. High nest-mite levels were associated with decreased nestling mass and hematocrit, but not with decreased nestling tarsus length. Experimental elimination of mites from some nests confirmed that the effects observed were mite-induced, not seasonal. The plumage colour of breeding adult male house finches was not correlated with nest-mite levels, nor did it appear that redder males' offspring suffered less from the effects of mites. Adult house finches fed nestlings from highly parasitized nests less often than those from nests with few or no mites. It appears unlikely that mites are directly involved in the sexual selection of bright male plumage coloration in this population of house finches. However, it is known that early-nesting females preferentially pair with redder males, therefore the benefit of nesting early and avoiding mite infestations is greater for redder male house finches.

Résumé : Nous avons étudié les effets de la présence au nid d'acariens hématophages (*Pellonyssus reedi*, Acari : Macronyssidae) sur la biologie de la reproduction du Roselin familier (C*arpodacus mexicanus*) dans le centre-est de l'Alabama, É.-U. Il n'y avait pas d'acariens dans les nids durant la première moitié de la saison de la reproduction, mais après leur apparition initiale, les acariens sont devenus de plus en plus nombreux et ont envahi presque tous les nids. La densité des acariens était en corrélation avec la masse diminuée des oisillons et l'hématocrite, mais pas avec la longueur du tarse des oisillons. L'élimination expérimentale des acariens dans certains nids a confirmé que les effets observés étaient effectivement dus aux acariens et n'étaient pas des effets saisonniers. La couleur du plumage chez les adultes reproducteurs n'était pas en corrélation avec le nombre d'acariens, et il ne semble pas que les rejetons issus des oiseaux plus rouges aient moins souffert de la présence des acariens. Les roselins adultes nourrissaient moins souvent leurs petits lorsque ceux-ci étaient dans des nids parasités que ceux dont les nids ne comptaient que quelques acariens, voire aucun. Il semble peu probable que les acariens soient directement responsables de la sélection sexuelle d'un plumage très coloré chez les mâles de cette population de roselins. On sait cependant que les femelles qui nichent tôt s'accouplent de préférence à des mâles plus rouges; les bénéfices de la nidation hâtive et de l'absence des acariens sont plus importants chez les mâles plus rouges.

[Traduit par la Rédaction]

Introduction

While it has long been known that such factors as predation, resource availability, and competition play a role in determining fitness among animals, the effects of parasites on host reproductive success have been relatively neglected until recently (Price 1980; Loye and Zuk 1991; Clayton and Moore 1997). Because birds are host to a multitude of parasites, they provide model systems for understanding the influence of parasites on host fitness (Crompton 1997). Nest ectoparasites can have particularly important effects on fitness in birds because such parasites may affect not only nestling growth, health, and survival (Oppliger et al. 1994; Darolova et al. 1997; Pacejka et al. 1998) but also the breeding and parental behaviours of adults (Moss and Camin 1970; Johnson and Albrecht 1993; Tripet and Richner 1997).

In this study we investigated the effects of an ectoparasitic nestling mite, *Pellonyssus reedi*, on the breeding biology of the house finch (*Carpodacus mexicanus*). *Pellonyssus reedi* (syn. *Pellonyssus passeri*, Acari: Macronyssidae) is a hematophagous nest-dwelling mite originally described from specimens taken from a nestling house sparrow (*Passer domesticus*) (Clark and Yunker 1956) but since reported from a variety of avian hosts worldwide (Burley et al. 1991; Payne 1997; Lindholm et al. 1998). Although little is known about the life history of this mite, it appears that, like many related macronyssids, it does not live on its avian host but rather lives and breeds

Received February 11, 2000. Accepted August 30, 2000.

A.M. Stoehr,[1] P.M. Nolan, G.E. Hill, and K.J. McGraw.[2] Department of Biological Sciences, Auburn University, Auburn, AL 36849, U.S.A.

[1]Author to whom all correspondence should be sent at the following address: Department of Biology, University of California, Riverside, CA 92521, U.S.A. (e-mail: amstoehr@citrus.ucr.edu).

[2]Present address: Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, U.S.A.

in the nest material, emerging periodically to feed on the nestlings (Clark and Yunker 1956; authors' personal observation).

The specific purposes of this study were several. First, we sought to document the seasonal pattern of appearance and abundance of *P. reedi* in house finch nests. Nest-parasite abundance has been shown to vary seasonally in a variety of avian hosts (Burtt et al. 1991) and such variation may have important effects on various aspects of host breeding biology, such as the timing of breeding or clutch size (Møller 1991; Richner and Heeb 1995). Second, we investigated the effects of the mites on nestlings because such effects should be particularly likely to influence host fitness (Loye and Zuk 1991; Clayton and Moore 1997).

We also examined the possibility that *P. reedi* might play a role in the breeding biology of adult house finches. The house finch has become a model organism for studies of sexual selection and plumage colour (Andersson 1994; Olson and Owens 1998). Several hypotheses that attempt to explain the evolution of bright male plumage colour invoke some form of parasite-mediated sexual selection, suggesting, for example, that plumage colour serves as an honest indicator of parasite load (Borgia and Collis 1989) and (or) resistance (Hamilton and Zuk 1982). The relationship between plumage colour and parasite level in male house finches has been investigated (Brawner et al. 2000; Thompson et al. 1997) but to date no studies have examined the relationship between male plumage colour and nestling parasite levels in the house finch. Thus, we tested the prediction that redder male house finches would have fewer mites in their nests and (or) that their nestlings would suffer less from mites (as indicated by hematocrit values). Finally, we examined whether mite levels were correlated with levels of parental care because research has suggested that in some cases adult birds may reduce the effects of nestling parasites by increasing their parental investment (Johnson and Albrecht 1993), whereas in other cases adults do not increase parental investment and nestlings clearly suffer from the effects of parasites (Moreno et al. 1999).

Methods

We conducted this study on the campus of Auburn University in east-central Alabama, U.S.A., during the breeding seasons of 1997, 1998, and 1999. To insure that we could monitor as many nests as possible we placed nest boxes on the study site. The nest boxes were wooden, three-sided with an open front and top, and 12 cm long on each side and 7.5 cm high. We placed inside the box a cup consisting of the bottom 7.5 cm cut from a 1.89-L plastic milk container. House finches are open-cup nesters and therefore readily nested in these boxes. House finches will frequently reuse their own nests as well as nests of other house finches, which could influence nest parasite loads (Møller 1989); however, we replaced nest cups after each nesting attempt, for several reasons. First, replacing nest cups between nesting attempts insured that the mite levels we observed were associated with the particular pair of house finches nesting in that box at that time and were not a particularly heavy mite load from a previous pair. Second, as part of other ongoing studies we placed a small electronic scale under the nest cup of some nests, and cups with multiple nests interfered with the proper functioning of these scales. Thus, to maintain consistency throughout the study we replaced the cups in all nest boxes after use. About 80% of nests built by house finches in our study population were built in nest boxes (McGraw et al. 2000) and we excluded from this study all nests not built in boxes. We observed mite-free and mite-infested nests both inside and outside of boxes, so the presence of mites in the nests we studied seems not to have been an artifact of using nest boxes.

We captured adult birds in traps and gave each bird one numbered aluminum U.S. Fish and Wildlife Service leg band and a unique combination of three plastic coloured leg bands. We quantified plumage colour (hue) of males using a Colortron™ hand-held reflectance spectrophotometer (Light Source, San Rafael, Calif.). We made three colour measurements from each of the three body regions that are brightly pigmented: crown, breast, and rump. The measurements from each region were averaged to obtain an overall plumage colour score for each male. Colour measurements obtained with the Colortron™ device are represented as points on a 360° colour wheel, with lower numbers corresponding to redder hues (for details see Hill 1998).

When nestlings were 11 days old, we estimated mite loads for each nest by visually inspecting the first nestling pulled randomly from the nest. We chose to examine nestlings on day 11 because this was the latest day on which we felt we could safely handle nestlings without forcing them to fledge prematurely. We pulled the nestling from the nest, immediately lifted its left wing, and counted the mites on the underside of the wing. We scored mite loads according to the following scale: 0 = no mites observed, 1 = 1–10 mites, 2 = 11–20 mites, 3 = over 20 mites. We used the first nestling pulled from the nest to estimate mite loads because disturbing the nest caused the mites to retreat farther into the nest material. Although the nests themselves often contained hundreds to thousands of mites, we assumed that our method of scoring mite loads was appropriate for the relative level of mite infestations in the nests. A similar visual technique has been used to estimate loads of a related macronyssid mite, *Ornithonyssus bursa*, in barn swallows (*Hirundo rustica*) and found to give an accurate estimate of the relative mite loads in nests (Møller 1990*a*, 1990*b*).

Following the estimation of mite loads, we weighed each nestling to the nearest 0.1 g with an electronic balance and measured the length of its right tarsus to the nearest 0.1 mm with calipers. Because hematophagous arthropods may cause detrimental or lethal hyperanemia (Olson 1965), we collected a small blood sample (approximately 50 μL) in a heparinized microhematocrit capillary tube by puncturing the brachial vein of each nestling's left wing. We then centrifuged the tubes for 5 min and used the ratio of the volume of packed red blood cells to total blood volume, hereafter referred to as the hematocrit, as a measure of anemia. We replaced the nestlings in the nest following processing and then monitored the nest twice weekly to determine if they fledged or died. All of the above described procedures were conducted between 14:00 and 17:00 CST.

In 1999 we eliminated mites from a subset of nests (n = 10) to determine if the effects we observed were truly mite-induced or were seasonal correlates of some other factor that we had failed to consider. We manipulated mite loads in late-season nests (after the seasonal appearance of mites) by placing three 0.1-g pieces of commercially available "No-Pest Strip" (Prozap Insect Guard, Loveland Industries, Inc.; active ingredient dichlorvos, 2,2-dichlorovinyl dimethyl phosphate) in the cup below the nest material. Treatment was carried out when the nestlings were 6 days old. At this time, mites are absent or very rare in nests (even late-season nests) and thus have not yet had time to affect the nestlings.

We videotaped parental behaviour by placing video cameras 0.5–1.0 m from nests, which did not appear to alarm the birds as indicated by their willingness to resume normal behaviours shortly after our departure. We started each taping shortly after dawn and taped nests for 2 h in 1997 and 8 h in 1998 and 1999. Nests were

taped on the same day that measurements were taken and taping was completed before handling the nestlings. From the videotapes we calculated parental feeding rates as the number of feeding trips per nestling per hour made by the adults. We determined the sex of the adults unambiguously from plumage colour and unique colour-band combinations.

The methods described here were approved by the Auburn University Institutional Animal Care and Use Committee (PRN No. 0206-R-2166) and used in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Data analysis

Treatment of data

Because some breeding pairs of finches raised more than one brood per season, and bred in more than one season, certain birds were represented more than once in our initial data set. Thus, to insure that each bird was represented only once in the data that were ultimately analyzed, we grouped all nests by mite level and, with no knowledge of the variables to be analyzed, eliminated from the data set all but one nest from each breeding pair. We did this in such a way as to preserve the largest possible sample sizes within each mite-level category. For example, if one pair had two nests during the season, one with a mite level of 1 and the other with a mite level of 3, we excluded the nest that fell into the category with the larger sample size. Because data were missing in some cases, sample sizes were not identical for each variable examined. In all cases, body masses, tarsus lengths, and hematocrit values for each nest were expressed as the mean for the entire brood. Mite levels were not related to brood size ($r_s = -0.12$, $n = 56$, $P = 0.40$), therefore brood size was not considered further in this study.

We pooled data across years for analysis, but prior to pooling we standardized hematocrit values and tarsus lengths to a mean of 0 and a standard deviation of 1. We did this for hematocrit values because we used a different centrifuge in the first year (1997) of the study, which resulted in different hematocrit values for that year. By spinning two capillary tubes of blood from each of 11 birds in each centrifuge, we determined that hematocrits for a given bird were consistently lower (4.36 ± 0.39%, $n = 11$) when spun in one centrifuge than when they had they been spun in the other. Furthermore, hematocrit values were very similar ($t_{35} = -0.531$, $P = 0.60$) in 1998 and 1999, when the same centrifuge was used, so we assumed that differences between hematocrit values from the first year and later years were due to differences in centrifuges rather than true biological factors. Finally, mite levels were similar in all 3 years of this study (Kruskal–Wallis test, $\chi^2 = 2.48$, $P = 0.30$). We standardized tarsus lengths because again there was a difference in mean tarsus lengths across years (1997 vs. 1998: $t_{29} = 4.33$, $P < 0.001$; 1997 vs. 1999: $t_{40} = 6.02$, $P < 0.001$; 1998 vs. 1999: $t_{36} = -1.44$, $P = 0.14$). We assumed that these differences in tarsus length between 1997 and later years were also methodological, not biological, for two reasons. As stated above, mite levels were similar in all 3 years. In addition, in 1997 tarsus lengths were measured by different people and using a slightly different technique.

Effect of pesticide treatment and date

We used one-way ANOVA to compare nestling masses, tarsus lengths, and hematocrit values for early-season, untreated late-season, and treated late-season nests. Early season was defined as the period before mites appeared in any nest at the study site; late season was defined as the period 19 days or more after the initial appearance of mites in any nest at the study site because the treated nests were from 19 days or later. Thus, late-season nests were matched for date as closely as possible. Although dividing the breeding season into early- and late-season components may appear somewhat artificial, the pattern of mite infestation in our house finch population (see Results) suggests that this is a reasonable categorization. If the one-way ANOVA was significant we used Tukey–Kramer HSD tests to determine which means among the groups were significantly different at or below the 5% level. Data from nests treated with pesticide were used only for the comparisons designed to test the hypothesis that mites were the agent responsible for the effects observed; these data were not used in any other analyses.

Other analyses

We used Spearman's rank correlations to examine relationships between mite level and other variables because mite level was measured on an ordinal scale (Siegel and Castellan 1988). In all cases, statistical tests are two-tailed and corrected for ties in ranks if they occurred.

Results

Seasonal patterns of mite infestation

Mites were absent from all nests until May (well over 50 days into the breeding season), but after the initial appearance of mites (day 0) there was an increase in the level of mite infestation ($r_s = 0.56$, $n = 25$, $P = 0.004$) as well as a rapid increase in the percentage of nests infested with mites (Fig. 1). Within 10 days of the initial appearance of mites, 58% (7 of 12) of all nests were infested. Within 20 days and for the duration of the breeding seasons, virtually all nests had mites. We first observed mites in nests (day 0) on 10 May in 1997, 23 May in 1998, and 2 May in 1999. The mites appeared shortly after the peak of the breeding season (Fig. 1).

Nest treatment and season

Treatment with pieces of "No-Pest Strip" successfully prevented mite infestation in all nests (0 mites; $n = 10$) treated. Nestlings from early-season, untreated late-season, and treated late-season nests differed significantly in body mass ($F_{[2,52]} = 3.40$, $P = 0.04$; Fig. 2*a*), with a significant difference between early-season and untreated late-season nests (Tukey–Kramer HSD test, $P < 0.05$). Nestlings also had significantly different hematocrit values among the three treatments ($F_{[2,45]} = 10.59$, $P < 0.001$; Fig. 2*b*), with significant differences between early- and untreated late-season nests and between treated and untreated late-season nests (Tukey–Kramer HSD test, $P < 0.05$) but not between early-season and treated late-season nests ($P > 0.05$). Tarsus lengths did not differ significantly among the three treatments ($F_{[2,52]} = 2.27$, $P = 0.11$; Fig. 2*c*).

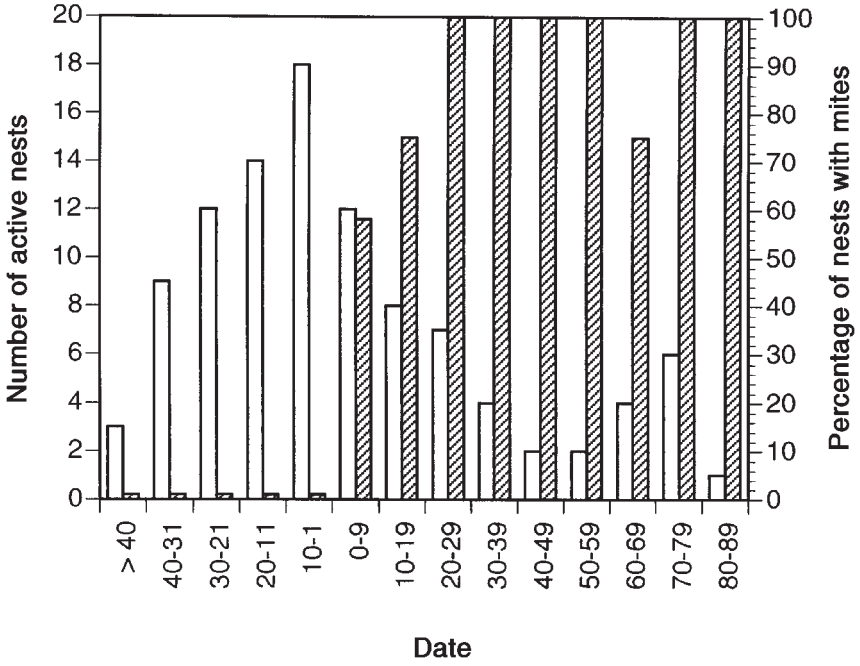
Mite levels and nestling mass, tarsus length, hematocrit value, and survival

Nestling mass was significantly negatively related to mite level ($r_s = -0.45$, $n = 55$, $P < 0.001$; Fig. 3*a*) as was nestling hematocrit value ($r_s = -0.55$, $n = 47$, $P < 0.001$; Fig. 3*b*). However, nestling tarsus length was not significantly related to mite level ($r_s = -0.08$, $n = 55$, $P = 0.55$; Fig. 3*c*). We found dead nestlings older than 11 days in eight nests, and in all of these cases the nestlings were covered with thousands of mites.

Male plumage colour and parental feeding rates

Male plumage colour was unrelated to mite level ($r_s = -0.09$, $n = 38$, $P = 0.59$). In addition, among nests with mites, mean nestling hematocrit value was not significantly

Fig. 1. Seasonal pattern of mite (*Pellonyssus reedi*) infestation of house finch (*Carpodacus mexicanus*) nests. Data are from 1997, 1998, and 1999. Dates are shown in 10-day periods and as the number of days relative to the appearance of mites, day 0 being the first day mites on which were observed in any nest in each year (10 May, 23 May, and 2 May in 1997, 1998, and 1999, respectively). Thus, data including and to the right of period 0–9 refer to nests after the initial appearance of mites and data to the left refer to nests prior to the initial appearance of mites. Open bars denote the number of active nests on the study site during that 10-day period and hatched bars the percentage of nests infested with mites during that 10-day period.



related to the plumage colour of the father (r_s = –0.19, n = 18, P = 0.28). The feeding rate of males was significantly negatively related to mite level (r_s = –0.30, n = 44, P = 0.05). The feeding rate of females was also negatively related to mite level but the result was not significant (r_s = –0.25, n = 44, P = 0.10). Similarly, as pairs (i.e., the summed feeding rates of the male and female of each pair), house finches fed offspring significantly less often if the nestlings harboured more mites (r_s = –0.44, n = 40; P < 0.01; Fig. 4).

Discussion

Our study describes an interaction between parasite infestation, time of year, and the breeding biology of a passerine bird. In house finch nests on our Alabama study site, *P. reedi* infestation increased dramatically midway through the breeding season. Mites appeared to be absent from nests until May, after which time most nests were infested. The level of infestation increased as the breeding season progressed, but the initial appearance of mites was most striking in that the percentage of house finch nests infested went from 0 to almost 100% in a short period of time. It is possible that mites were present but inactive or dormant in nests throughout the breeding season and we simply failed to detect them. If this is so, however, they are unlikely to have been present in numbers capable of substantially harming nestlings; during 3 years of observations we handled over 600 nestlings and mites were never observed before May of each year. Thus, it appears that for house finches on our study site, infestation by nest mites was predictable and unavoidable: the mites appeared in nests at the same time each year and after this time virtually every breeding pair's nest harboured mites.

The close correspondence between mite prevalence and season, however, complicates the assessment of causal relationships between mite level and nestling health and survival. Indeed, our comparisons of early- and untreated late-season nests revealed a significant seasonal decline in nestling hematocrit value and body mass. If these seasonal effects were due to some other correlate we failed to measure, we would have expected to observe a similar seasonal decline in nestling hematocrit value and mass when comparing early-season nests with late-season nests treated to eliminate mites. The hematocrit values and masses of nestlings from early-season and treated late-season nests, however, did not differ significantly. Furthermore, our comparison of treated and untreated late-season nests revealed that hematocrit value and mass were higher (although not significantly so in the case of mass) for nestlings from treated nests, a result that also supports the notion that mites were responsible for the observed effects on nestlings. Thus, although we were unable to increase mite loads in nests, we believe that the evidence presented here makes a convincing case that the mites themselves had negative effects on nestlings.

Although in a few studies no negative effects of ectoparasites on the health or growth of nestling birds have been detected (Johnson and Albrecht 1993; Tripet and Richner 1997; Pacejka et al. 1998), the results of our study are consistent with those of the majority of studies, which have usually shown a decrease in nestling health in association with nest-parasite infestation (see Møller et al. 1990). Indeed, we observed what appeared to be mite-induced mortality. Except

Fig. 2. Seasonal effects of mites and the results of treating nests with pesticide. Values are shown as the mean ± standard error of nestling body mass (*a*), hematocrit (*b*), and tarsus length (*c*) from early-season nests, untreated late-season nests, and late-season nests treated with pesticide to prevent mite infestation. Means with the same letter are not significantly different; those with different letters are significantly different.

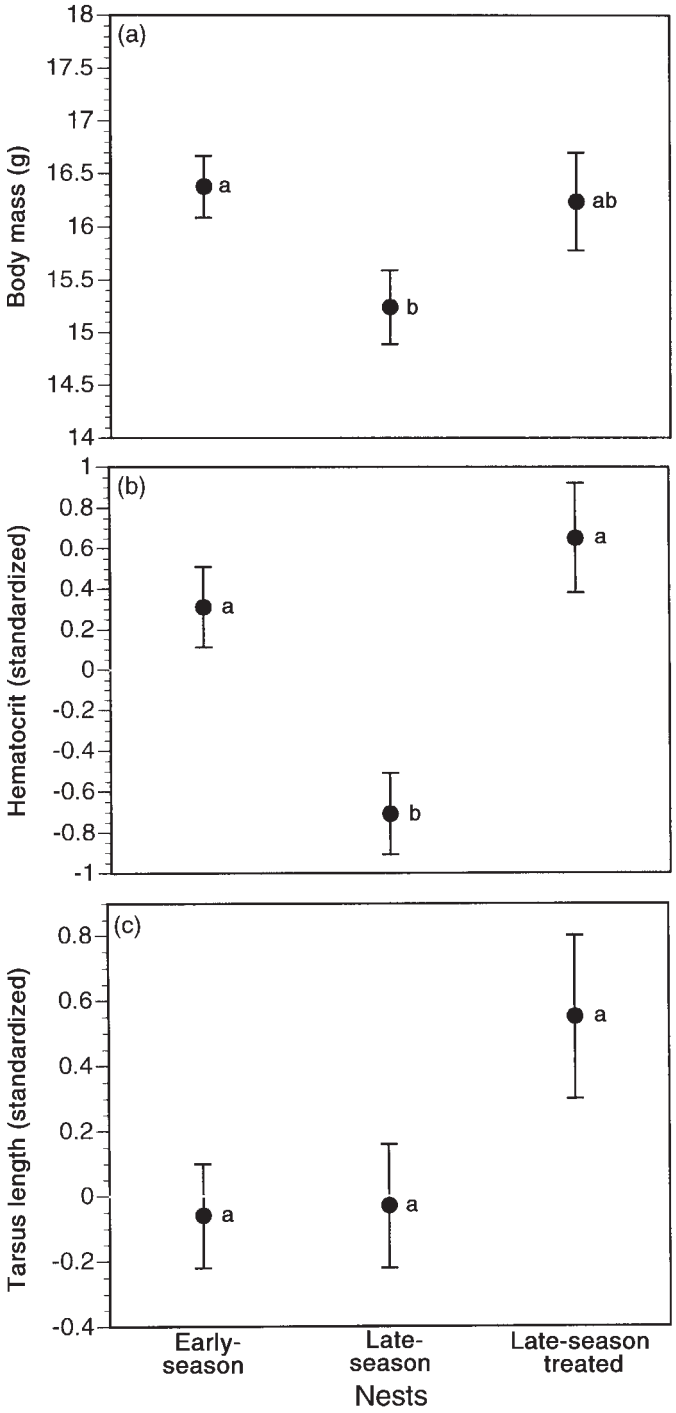
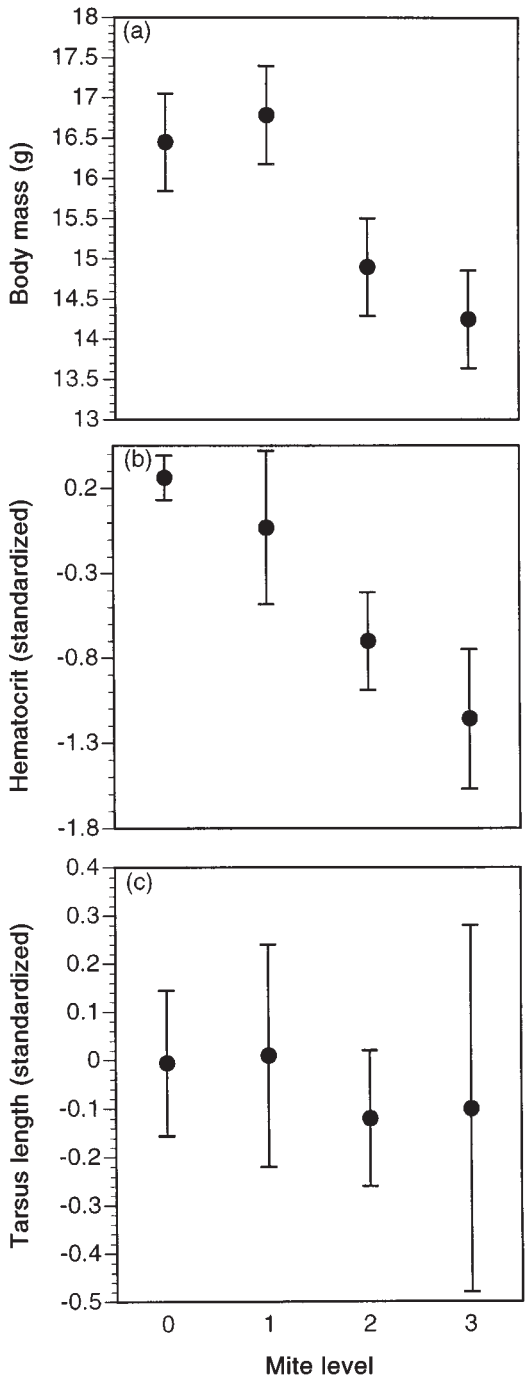
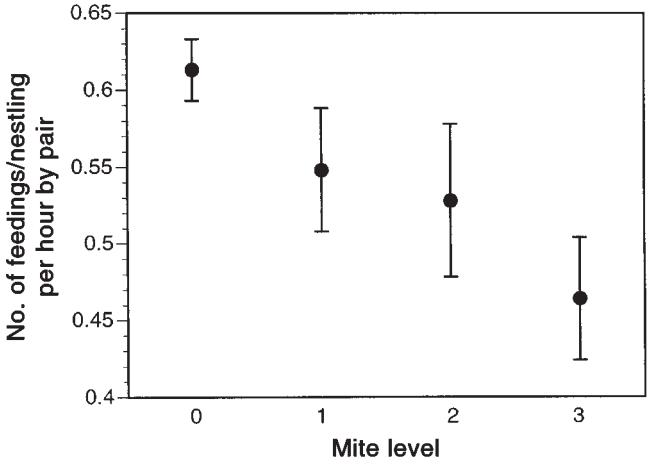


Fig. 3. Relationships (mean ± standard error) between mite level and nestling body mass (*a*), hematocrit (*b*), and tarsus length (*c*). In *a* and *c*, samples sizes are 31, 6, 10, and 8 for mite levels 0, 1, 2, and 3, respectively. In *b*, sample sizes are 23, 7, 10, and 7 for all mite levels.



in cases of depredation, house finch nestlings on our study site rarely die during the period between 11 days of age and fledging. However, in all eight nests in which nestlings died after day 11, the nests were so heavily infested that the dead nestlings were covered with hundreds of mites. Nestlings that survived heavy infestations may still have incurred an increase in mortality after they left the nest. In our study, nestlings from highly parasitized nests had both lower mass and lower hematocrit than nestlings from nests with few or no mites, a finding similar to observations in pied flycatchers (*Ficedula hypoleuca*) (Merino and Potti 1995; Moreno

Fig. 4. Relationship (mean ± standard error) between parental feeding rate and mite level. The feeding rate is the sum of the feeding rates of the male and female of each pair of birds. Sample sizes are 19, 5, 9, and 7 pairs of birds for mite levels 0, 1, 2, and 3.



et al. 1999; Potti et al. 1999). Lower mass at fledging may be associated with increased mortality, especially later in the breeding season, because birds of lower mass may not be able to obtain the resources necessary to sustain them through their fall moult and into winter (Magrath 1991). Furthermore, low hematocrit levels are likely to affect the ability of fledglings to repay oxygen debt and sustain flight, resulting in poor foraging and an increased risk of predation (Phillips et al. 1985; Clark 1991).

Despite the effects of mites on nestling mass and hematocrit, nestlings from parasitized nests did not suffer a reduction in tarsus length, an index of skeletal body size. Ectoparasites reduced mass but not tarsus length in barn swallows (Møller 1990*b*) and cliff swallows (*Hirundo pyrrhonota*) (Chapman and George 1991) as well. These observations suggest that tarsus length is relatively insensitive to environmental variation in some avian species, an idea supported by Alatalo et al. (1990), who found that phenotypic variation in tarsus length of collared flycatchers (*Ficedula albicollis*) was largely heritable, but variation in nestling mass was largely due to environmental factors. Similarly, variation in hematocrit in pied flycatchers has low heritability (Potti et al. 1999).

The negative effects of mites on house finches suggest that the mites have the potential to affect reproductive success in these birds, and thus we might expect the finches to respond in some way to the presence of the mites. Birds may respond to parasites immunologically (Møller 1990*a*; Brinkhof et al. 1999) or behaviourally (Hart 1997). Because house finches have been studied extensively in the context of sexual selection, an obvious question is whether the mites play a role in the sexual selection of bright male plumage in this species. Hill (1990, 1991) has shown that female house finches prefer to mate with redder males. Hamilton and Zuk (1982) argued that male plumage colour may be an indicator to females of male parasite resistance, but parasite-mediated sexual selection might also operate through other mechanisms, such as female choice to avoid direct transmission of parasites (Borgia and Collis 1989) or female choice of males that provide superior parental care (Hoelzer 1989), that might compensate for the detrimental effects of parasites. Because we rarely observed mites on adults and because virtually all adults breeding after mid-May could expect to have their nests parasitized, the parasite-avoidance hypothesis is unlikely to apply in this case.

Although a negative relationship between plumage colour and parasite level in male house finches has been observed (Thompson et al. 1997; Brawner et al. 2000), we found no evidence that redder males provide their offspring with greater resistance to nestling ectoparasites. Redder males' nests were likely to harbour as many mites as the nests of more drably plumaged males, and among nests with mites, the offspring of redder males did not have significantly higher hematocrit values as we might expect if these nestlings were somehow able to reduce the ability of the mites to feed on them. We may have failed to detect a relationship between nestling mite level and male plumage colour because there was relatively little variation among males in plumage coloration in this population during the years of this study; an earlier epidemic of mycoplasmal conjunctivitis selectively killed drably plumaged males, changing the mean plumage redness of males in the population (Nolan et al. 1998) and significantly decreasing variation in plumage redness (authors' unpublished data).

As a behavioural response to nestling parasitism, adult birds may alter their parental investment. Johnson and Albrecht (1993) argued that an increase in parental care to compensate for the detrimental effects of parasites might explain why some studies have failed to show any effects of nest ectoparasites on nestling quality, a hypothesis supported by Tripet and Richner's (1997) study of blue tits (*Parus caeruleus*). In our population of house finches, however, adults fed nestlings less often with increasing parasite loads, a result consistent with those observed in some other species (Møller 1994; Darolova et al. 1997). Theory predicts that at low levels of parasitism, adults should increase parental effort if it offsets the effects of parasites but should reduce effort at higher levels of parasitism, when increasing effort is futile and may affect future reproductive success (Forbes 1993; Perrin et al. 1996). Our observations suggest that even at the lowest mite levels we observed, adult house finches do not increase their parental effort. The sudden seasonal onset of mite infestation coupled with the rapid increase in mite levels within nests between days 6 and 11 of the nestling period might mean that the period of low infestation, when nestlings might benefit from increased parental effort, is simply too brief for adults to respond; however, more detailed observations of the patterns of parental effort within the nestling period might determine if this is the case.

Although studies have shown that female house finches prefer to pair with redder males (Hill 1990, 1991; Hill et al. 1999), our study has failed to show that by doing so these females are gaining superior parasite-resistance genes for their offspring, nor does it appear that they are choosing better fathers for their parasitized young. The best, and indeed perhaps the only, way for house finches to avoid nest mites in this population is to begin nesting before they appear. From earlier studies we know that early-nesting females pair with redder males (Hill 1991; Hill et al. 1999) and these

pairs have higher reproductive success in a season than do later nesters (McGraw et al. 2000). Thus, these birds are able to fledge more offspring by fledging one brood of young before the mites appear or reach levels high enough to impact the nestlings. Although many factors may contribute to the advantages of early breeding, it is likely that avoidance of a nest parasite is one of the more important factors in the case of house finches in Alabama. Furthermore, the benefits of early nesting, and thus mite avoidance, appear to be greater for redder males. Whether this is a form of parasite-mediated sexual selection is unclear, and this may be a case where the already blurry line between natural and sexual selection is blurred even further.

Acknowledgments

We thank Dr. G.R. Mullen of Auburn University's Entomology Department for identifying the mites. Numerous assistants helped with all aspects of fieldwork and to them we are grateful. For criticism and comments that improved the quality of the manuscript, we thank B. Ballentine, A. Dervan, R. Duckworth, L. Siefferman, and two anonymous reviewers. This research was supported by the Department of Biological Sciences and the College of Science and Mathematics at Auburn University, the Alabama Agricultural Experiment Station, and the National Science Foundation (grant No. IBN9722171 to G.E.H.). LightSource, Inc., kindly provided a spectrophotometer.

References

Alatalo, R.V., Gustafsson, L., and Lundberg, A. 1990. Phenotypic selection on heritable size traits: environmental variance and genetic response. Am. Nat. **135**: 464–471.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Borgia, G., and Collis, K. 1989. Female choice for parasite-free male satin bowerbirds and the evolution of bright male plumage. Behav. Ecol. Sociobiol. **25**: 445–454.

Brawner, W.R., Hill, G.E., and Sundermann, C.R. 2000. Effects of coccidial and mycoplasmal infections on carotenoid-based plumage ornamentation. Auk, **117**: 956–967.

Brinkhof, M.W.G., Heeb, P., Kölliker, M., and Richner, H. 1999. Immunocompetence of nestling great tits in relation to rearing environment and parentage. Proc. R. Soc. Lond. B Biol. Sci. **266**: 2315–2322.

Burley, N., Tideman, S.C., and Halupka, K. 1991. Bill colour and parasite levels of zebra finches. *In* Bird–parasite interactions: ecology, evolution, and behaviour. *Edited by* J.E. Loye and M. Zuk. Oxford University Press, New York. pp. 359–376.

Burtt, E.H., Chow, W., and Babbitt, G.A. 1991. Occurrence and demography of mites of tree swallow, house wren, and eastern bluebird nests. *In* Bird–parasite interactions: ecology, evolution, and behaviour. *Edited by* J.E. Loye and M. Zuk. Oxford University Press, New York. pp. 104–122.

Chapman, B.R., and George, J.E. 1991. The effects of ectoparasites on cliff swallow growth and survival. *In* Bird–parasite interactions: ecology, evolution, and behaviour. *Edited by* J.E. Loye and M. Zuk. Oxford University Press, New York. pp. 69–92.

Clark, G.M., and Yunker, C.E. 1956. A new genus and species of Dermanyssidae (Acarina: Mesostigmata) from the English sparrow, with observations on its life cycle. Proc. Helminthol. Soc. Wash. **23**: 93–101.

Clark, L. 1991. The nest protection hypothesis: the adaptive use of plant secondary compounds by European starlings. *In* Bird–parasite interactions: ecology, evolution, and behaviour. *Edited by* J.E. Loye and M. Zuk. Oxford University Press, New York. pp. 205–221.

Clayton, D.H., and Moore, J. 1997. Host–parasite evolution: general principles and avian models. Oxford University Press, New York.

Crompton, D.W.T. 1997. Birds as habitat for parasites. *In* Host–parasite evolution: general principles and avian models. *Edited by* D.H. Clayton and J. Moore. Oxford University Press, New York. pp. 253–270.

Darolova, A., Hoi, H., and Schleicher, B. 1997. The effect of ectoparasite nest load on the breeding biology of the Penduline Tit *Remiz pendulinus*. Ibis, **139**: 115–120.

Forbes, M.R.L. 1993. Parasitism and host reproductive effort. Oikos, **67**: 444–450.

Hamilton, W.D., and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? Science (Washington, D.C.), **218**: 384–387.

Hart, B.L. 1997. Behavioural defence. *In* Host–parasite evolution: general principles and avian models. *Edited by* D.H. Clayton and J. Moore. Oxford University Press, New York. pp. 59–77.

Hill, G.E. 1990. Female house finches prefer colourful males: sexual selection for a condition-dependent trait. Anim. Behav. **40**: 563–572.

Hill, G.E. 1991. Plumage colouration is a sexually selected indicator of male quality. Nature (Lond.), **350**: 337–339.

Hill, G.E. 1998. An easy, inexpensive means to mechanically quantify plumage coloration. J. Field Ornithol. **69**: 353–363.

Hill, G.E., Nolan, P.M., and Stoehr, A.M. 1999. Pairing success relative to male plumage redness and pigment symmetry in the house finch: temporal and geographic constancy. Behav. Ecol. **10**: 48–53.

Hoelzer, G.A. 1989. The good parent process of sexual selection. Anim. Behav. **38**: 1067–1078.

Johnson, L.S., and Albrecht, D.J. 1993. Effects of haematophagous ectoparasites on nestling house wrens, *Troglodytes aedon*: who pays the cost of parasitism? Oikos, **66**: 255–262.

Lindholm, A.K., Venter, G.J., and Ueckermann, E.A. 1998. Persistence of passerine ectoparasites on the diederik cuckoo *Chrysococcyx caprius*. J. Zool. (Lond.), **244**: 145–153.

Loye, J.E., and Zuk, M. 1991. Bird–parasite interactions: ecology, evolution, and behaviour. Oxford University Press, New York.

Magrath, R.D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. J. Anim. Ecol. **60**: 335–351.

McGraw, K.J., Stoehr, A.M., Nolan, P.M., and Hill, G.E. 2000. Plumage redness predicts breeding onset and reproductive success in the house finch: a validation of Darwin's theory. J. Avian Biol. In press.

Merino, S., and Potti, S. 1995. Mites and blowflies decrease growth and survival in nestling pied flycatchers. Oikos, **73**: 95–103.

Møller, A.P. 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? Oikos, **56**: 421–423.

Møller, A.P. 1990*a*. Effects of a haematophagous mite on the barn swallow (*Hirundo rustica*): a test of the Hamilton and Zuk hypothesis. Evolution, **44**: 771–784.

Møller, A.P. 1990*b*. Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. Ecology, **71**: 2345–2357.

Møller, A.P. 1991. Ectoparasite loads affect optimal clutch size in swallows. Funct. Ecol. **5**: 351–359.

Møller, A.P. 1994. Parasite infestation and parental care in the barn swallow *Hirundo rustica*: a test of the resource-provisioning model of parasite mediated sexual selection. Ethology, **97**: 215–225.

Møller, A.P., Allander, K., and Dufva, R. 1990. Fitness effects of parasites on passerine birds: a review. *In* Population biology of passerine birds: an integrated approach. *Edited by* J. Blondel, A. Gosler, J. Lebreton, and R. McCleery. Springer-Verlag, Berlin. pp. 269–280.

Moreno, J., Merino, S., Potti, S., de León, A., and Rodríguez, R. 1999. Maternal energy expenditure does not change with flight costs or food availability in the pied flycatcher (*Ficedula hypoleuca*): costs and benefits for nestlings. Behav. Ecol. Sociobiol. **46**: 244–251.

Moss, W.W., and Camin, J.H. 1970. Nest parasitism, productivity, and clutch size in Purple Martins. Science (Washington, D.C.), **168**: 1000–1003.

Nolan, P.M., Hill, G.E., and Stoehr, A.M. 1998. Sex, size, and plumage redness predict house finch survival in an epidemic. Proc. R. Soc. Lond. B Biol. Sci. **265**: 961–965.

Olson, C. 1965. Avian hematology. *In* Diseases of poultry. *Edited by* H.E. Biester and L.H. Schwarte. Iowa State University Press, Ames. pp. 100–119

Olson, V.A., and Owens, I.P.F. 1998. Costly sexual signals: are carotenoids rare, risky or required? Trends Ecol. Evol. **13**: 510–514.

Oppliger, A., Richner H., and Christe, P. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the great tit (*Parus major*). Behav. Ecol. **5**: 130–134.

Pacejka, A.J., Gratton, C.M., and Thompson, C.F. 1998. Do potentially virulent mites affect house wren (*Troglodytes aedon*) reproductive success? Ecology, **79**: 1797–1806.

Payne, R.B. 1997. Avian brood parasitism. *In* Host–parasite evolution: general principles and avian models. *Edited by* D.H. Clayton and J. Moore. Oxford University Press, New York. pp. 338–369.

Perrin, N., Christe, P., and Richner, H. 1996. On host life-history response to parasitism. Oikos, **75**: 317–320.

Phillips, J.G., Butler, P.J., and Sharp, P.J. 1985. Physiological strategies in avian biology. Blackie, London.

Potti, J., Moreno, J., Merino, S., Frías, O., and Rodríguez, R. 1999. Environmental and genetic variation in the haematocrit of fledgling pied flycatchers *Ficedula hypoleuca*. Oecologia, **120**: 1–8.

Price, P.W. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, N.J.

Richner, H., and Heeb, P. 1995. Are clutch and brood size patterns in birds shaped by ectoparasites? Oikos, **73**: 435–441.

Siegel, S., and Castellan, N.J. 1988. Nonparametric statistics for the behavioral sciences. McGraw–Hill, New York.

Thompson, C.W., Hillgarth, N., Leu, M., and McClure, H.E. 1997. High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. Am. Nat. **149**: 270–294.

Tripet, F., and Richner, H. 1997. Host responses to ectoparasites: food compensation by parent blue tits. Oikos, **78**: 557–561.