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Showiness, non-parasitic symbionts, and nutritional condition in a passerine bird

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The study of host-symbiont interactions has mainly focused on how parasites influence the fitness and behaviour of their host. Two common assumptions of such studies are that all symbiontic organisms are parasites, and that they are directly or indirectly related to host traits which act as signals of quality in mate choice. We assessed the prevalence and abundance of feather mites (*Proctophyllodes pinnatus*; Astigmata; Protocphyllodidae) on Linnets (*Carduelis cannabina*; Aves; Carduelinae) and examined how the abundance of mites may be related to the condition and plumage colour of Linnets. Mite prevalence was so high (near 100%) that no variation could be found between age classes or sexes. However, mite abundance was significantly higher in males than in females. No significant relationship was found between mite abundance and host nutritional condition, except for yearling females. Nutritional condition and showiness of secondary sexual traits (carotenoid-based plumage patches) were not correlated in male linnets. Size and brightness of red patches in the plumage of males varied with age, but were unrelated to mite abundance when age was taken into account. The absence of effects of mites is in agreement with the long held, neglected view that feather mites form non-parasitic associations with birds. Higher mite abundance on males may be attributed to more secretions of the uropygial gland, on which mites feed. Gender variation in plumage colour and abundance of feather mites suggests a common hormonal-mediated mechanism regulating both traits.

1. Introduction

Mutualism and comensalism are well documented symbiotic associations (Thompson 1994) but, contrary to parasitism, little is known about their occurrence or frequency among birds. Studies of avian host-parasite interactions have mainly focused on how parasites influence host fitness and behaviour (Møller *et al*. 1990, Loye & Zuk 1991). Although these studies have made a considerable contribution to our understanding of the roles some symbionts may have in sexual selection, much less attention has been paid to proximate mechanisms regulating host-parasite interactions. Many studies frequently rely on two common assumptions which are still a matter of controversy: (i) many symbiotic organisms are parasitic and cause detrimental effects to host fitness, and (ii) the resulting reduction in host fitness is directly or indirectly related to the expression or size of some trait(s) acting as signals of quality in mate choice. However, a number of studies have not found support for these assumptions (Borgia & Collis 1990, Seutin 1994, Potti & Merino 1995, Tella *et al*. 1995, Tompkins *et al*. 1997, Dawson & Bortolotti 1998). Therefore, doubts have arisen as to the generality of the view that all symbiont organisms should be thought of as being parasitic (Blanco *et al*. 1997), and that the presence of these organisms is related to variation in host colour (Bortolotti *et al*. 1996).

The prediction that bird showiness is negatively correlated with parasite abundance has been tested in numerous studies which have produced contrasting results (Møller 1990, Weatherhead 1990, Andersson 1994, Seutin 1994, Dufva & Allander 1995, John 1995, Sundberg 1995, Potti & Merino 1996), but it has never been assessed by considering the case of symbionts whose nature is probably non-parasitic. We studied the interaction between Linnets (*Carduelis cannabina*; Aves; Carduelinae) and particular symbionts (*Proctophyllodes pinnatus*; Astigmata Protocphyllodidae; order Acariformes; hereafter feather mites). The Linnet is a gregarious (in winter), sexually dichromatic passerine in which adult males are noticeably red while females and juveniles are duller. Males display patches of carotenoid-based pigmentation in the breast and crown, whose size and brightness may play a role in sexual interactions if similar to other reddish cardueline finches (Hill 1990, Seutin 1994). Courtship includes a conspicuous visual display with the males ruffling their breast and crown feathers in front of the females, suggesting an important role for plumage traits in mate choice (Cramp & Perrins 1994).

Feather mites are common symbionts of birds (Peterson 1975) and are usually assumed to act as parasites (Fowler & Williams 1985, Choe & Kim 1989, 1991, McClure 1989, Poulin 1991, Poiani 1992, Rózsa 1997, Thompson *et al*. 1997), although the functional significance of the interactions between feather mites and their avian hosts has not been well documented (OConnor 1982). Among astigmatid mites associated with birds there are taxa in the lineages Pterolichoidea and Analgoidea, collectively known as feather mites, that live in comensalistic associations on the feather surface of their hosts (Fain 1965, Peterson 1975, OConnor 1982). The existence of comensalistic and mutualistic associations between Astigmatic mites and both their invertebrate and vertebrate hosts are long known (OConnor 1982), but it has been ignored in studies concerning feather mites on birds.

In this paper we assessed the relationship between abundance of mites and the nutritional condition of linnets. Contrary to other studies dealing with feather mites and birds, we chose commensalism as our null hypothesis because feather mites feed on feather oil secreted by the uropygial gland and other material trapped in this oil (OConnor 1982, Phillips 1990). Mites do not impair host plumage quality as no damage (holes, feather debris, structural alteration) is visible externally on the wing or tail feathers of linnets or the other bird species examined (Blanco *et al*. 1997, authors' unpubl. data). Further, the only study in which the functional nature of the interaction between feather mites and the nutritional condition of their avian host has been documented suggests that a commensalistic or possibly a mutualistic, rather than a parasitic relationship exists (Blanco *et al*. 1997). Therefore, commensalism is considered the most parsimonious interaction according to the available information on this particular system. We focused on the possibility that the plumage colour of male Linnets could reflect the abundance of non-parasitic symbionts living on their feathers. We also assessed whether the red colour of male linnets reflects their nutritional condition at sampling time.

2. Methods

The study took place at San Martín de la Vega (40°13´N, 3°35´W), Madrid, Spain, an agricultural area devoted to irrigated crops, mainly maize (*Zea mays*). Linnets were caught in mistnets about one hour before sunset, when they arrived at a communal roost in a large reed bed traditionally occupied between October to April. The roost contained varying numbers of birds, with peaks in mid-winter when several thousands joined the roost. The period of capture (March–April 1997) coincided with the period when linnets were departing from their wintering areas towards breeding areas.

We distinguished birds in their first year of life from adults using the criteria described in Jenni and Winkler (1994) and Svensson (1996). All birds were banded, sexed and weighed (to the nearest 0.1 g). Wings (maximum chord to the nearest 1 mm) and tarsus (distances between bending points, precision 0.01 mm) were also measured for each bird. We captured and sexed 421 linnets (196 males and 225 females), 344 of which were aged (233 yearlings and 111 adults). Therefore, sample sizes varied among analyses.

Mite abundance was estimated by scoring the number of mites attached to the wing (primary and secondary feathers) and tail feathers when they were extended and exposed against a lamp. Feather mites exclusively occurred in the slots between the pennaceous barbs of flight feathers, on the ventral surface. Mite abundance was assessed for each feather and the mean number of mites per feather was scored as 0 (no mites), 1 (1–10 mites per feather), 2 (11–20), 3 (21–30), 4 (31–40) and so on. Since we searched for mites in the entire left wing (15 feathers) and tail (12 feathers), and mite abundances usually differed somewhat among feathers of the same bird, we also used intermediate scores (0.5, 1.5, etc) when a similar number of feathers were assigned to two different, consecutive, scores (Blanco *et al.* 1997).

Male linnets were scored for plumage colour of the breast by using a colour scale increasing in brightness as the amount of reddish colour of the feathers increased. Redness was scored as 1 = pale orange to 10 = bright red. Redness of the crown patch was scored on a similar scale with only six categories (1 = dull, 6 = bright) because we previously ascertained that brightness was less variable in the crown than in the breast. The extent of the red breast patch was measured by placing a grid (4 × 4 cm, square size = 5 mm^2) over it and then counting the number of squares containing detectable carotenoid pigmentation (*see* Hill 1990). Breast patch area scores were proportional to the breast surface, with carotenoid coloration varying from 6 to 50 ($N = 164$). Although the brightness of the breast and crown and the extent of the breast patch were intercorrelated (Spearman rank correlations: breast patch area–breast brightness $r_s = 0.56$, $P < 0.0001$, $N = 161$; breast brightness–crown brightness $r_s = 0.38$, $P < 0.0001$, $N = 164$; breast patch area–crown brightness $r_s = 0.43$, $P < 0.0001$, $N = 162$), we also defined an overall index of redness by combining brightness and extent of the carotenoid pigmentation as follows: redness index = breast patch extent + [(breast + crown brightness scores) × 3]; the sum of brightness and extent of the breast patch were multiplied by a factor of 3 to equalize scoring ranks. We pooled brightness and patch area because the potential signalling value for females of the sexual coloration of males may be assessed in a more realistic fashion by considering multiple rather than single traits (Hill 1990, 1994, Bortolotti *et al.* 1996). That is, if carotenoid-based colouration reflects genetic quality in terms of resistance to parasites and diseases or the nutritional condition of males, females may rely on a combination of traits rather than single traits when selecting mates (Andersson 1994, Moller 1994). Redness scores varied from 15 (a small pale orange breast patch) to 86 (a large bright red breast patch). Because linnets were not recaptured across the study period, we assessed the repeatability of plumage scores by using museum skins of male linnets ($N = 30$) from the Museo de Ciencias Naturales, Madrid; museum skins were examined twice with an interval of 2 hours. There was a strong positive correlation between scores for breast brightness ($r_s = 0.64$, $P < 0.001$), crown brightness ($r_s = 0.92$, $P < 0.0001$) and breast patch area ($r_s = 0.93$, $P < 0.0001$). To reduce possible biases, only one of us measured the birds (JP), scored mite abundance (GB) and plumage colour (JS).

To investigate the variation in mite prevalence, i.e. the proportion of hosts infected, by age and sex of bird, we conducted log-linear analysis (Sokal & Rohlf 1981). This procedure resembles the analysis of variance in that total variance of frequency data is partitioned into different factors, making it possible to test the interactions between them. The test was run hierarchically, beginning with the highest order (3) interaction and proceeding backwards until all terms/interactions retained by the model reached significance ($P < 0.05$). We tested whether the dropping of an interaction would impair the model significantly. The same procedure was used to investigate the variation of feather mite abundance (wing and tail pooled) with host plumage colour (redness index) controlling for the effect of age. To this aim, we considered three equal-length categories of increasing redness and four categories of feather mite abundance (0 = no mites, plus three categories of increasing mite abundance).

An index of nutritional condition was calculated as the residuals from the multiple regression of body mass on wing^3 and date of capture ($F_{2,397} = 46.05$, $P < 0.0001$, $R^2 = 0.18$; wing^3: t-value = 8.35, $P < 0.001$; date: t-value = 5.83, $P < 0.001$). We used wing^3 rather than tarsus^3 as a measure of structural size because the first explained more variance in body mass ($r = 0.34$, $P < 0.0001$, $R^2 = 11.92$) than tarsus ($r = 0.18$, $P = 0.0006$, $R^2 = 3.19$). When appropriate, we also used separate nutritional condition indices for each sex (males: $F_{2,185} = 14.24$, $P < 0.0001$, $R^2 = 0.12$; females: $F_{2,210} = 19.72$, $P < 0.0001$, $R^2 = 0.15$). The use of the residuals of mass on a size factor is a well-established method to estimate the nutritional condition of birds (Kirk & Gosler 1994, Moller *et al.* 1996, Tella *et al.* 1997). We then looked for relationships among host colour and body condition and mite abundance using Spearman rank correlation coefficients. Since we used ranked variables, age and sex variation in mite abundance and plumage colour were analysed using non-parametric Mann-Whitney U-tests.

3. Results

3.1. Mite prevalence and abundance

Mite prevalence varied from 97.2% to 100% on the wing of first-year females and adult males respectively, and between 92.6% and 98.2% on the tail of adult females and males, respectively (Table 1). A log-linear analysis taking into account the variation in mite prevalence on wing and tail with age and sex of the birds showed no 3-way or 2-way interactions ($P > 0.25$ in all casses), the fit of the model being adequate for wing (goodness-of-fit, $G = 1.45$, $P = 0.23$) and tail (goodness-of-fit, $G = 1.10$, $P = 0.29$). This means that mite prevalence was so high (almost 100%) that no variation was found between ages or sexes (Table 1).

No differences in wing and tail mite abundance were detected between the age of either sex (Table 1). There were also no significant age differences when mite abundances on wing and tail were pooled (Mann-Whitney *U*-test, males: $U = 1.66$, $P = 0.09$, $N = 107$ yearlings, $N = 57$ adults; females: $U = 1.41$, $P = 0.16$, $N = 126$ yearlings, $N = 54$ adults). When ages were pooled, mite abundance was significantly higher in males than in females (Mann-Whitney *U*-test, $U = 4.30$, $P = 0.00001$, $N = 196$ males, $N = 225$ females), both in the wing (Mann-Whitney *U*-test, $U = 13.21$, $P = 0.0003$, $N = 164$ males, $N = 180$ females) and tail (Mann-Whitney *U*-test, $U = 11.35$, $P = 0.0007$, $N = 164$ males, $N = 180$ females). The same trend was found for the two age classes when analysed separately (wing and tail mites pooled, yearlings: $U = 2.84$, $P = 0.004$, $N = 107$ males, $N = 126$ females; adults: $U = 2.26$, $P = 0.02$, $N = 57$ males, $N = 54$ females).

The abundance of mites varied among flight feathers. Mite abundance on the wing correlated positively with that on the tail of males (ages pooled, $r_s = 0.83$, $P < 0.0001$, $N = 196$) and females ($r_s = 0.80$, $P < 0.0001$, $N = 225$), and mites were always more abundant on the wing than on the tail within individual linnets (Wilcoxon test for matched-pairs, males: $Z = 10.94$, $P < 0.0001$, $N = 164$; females: $Z = 11.41$, $P < 0.0001$, $N = 180$).

3.2. Mite abundance and hosts' nutritional condition

A two-way ANOVA showed that nutritional condition did not vary between sexes ($F_{1,396} = 0.59$, $P = 0.45$) and ages ($F_{1,396} = 2.11$, $P = 0.15$; in-

Table 1. Prevalence and abundance of feather mites on wings and tails of linnets of different age-sex classes. Between-age differences in mite abundance within each sex was assessed by Mann-Whitney *U*-tests.

	Prevalence (%)	Abundance mean (S.E.)	*n*	Mann-Whitney *U*-test	
				U	*P*
Wing					
First-year male	97.2	3.4 (0.2)	107	1.94	0.14
Adult male	100	4.1 (0.3)	57		
First-year female	97.6	2.8 (0.2)	126	1.31	0.19
Adult female	98.1	3.0 (0.3)	54		
Tail					
First-year male	94.4	1.5 (0.1)	107	1.85	0.06
Adult male	98.2	2.0 (0.2)	57		
First-year female	92.9	1.2 (0.1)	126	1.39	0.16
Adult female	92.6	1.4 (0.1)	54		

teraction: $F_{1,396} = 0.009$, $P = 0.92$) so we pooled all birds to look for the relationships between nutritional condition and mite abundance. No significant relationship was found between nutritional condition and mite abundance, either considering wing and tail mites separately (wing: $r_s = -0.07$, $P = 0.17$, $N = 342$; tail: $r_s = -0.05$, $P = 0.32$, $N = 342$) or pooled ($r_s = -0.07$, $P = 0.20$, $N = 342$). Since mite abundance varied between sexes and because there seems to be a tendency for age differences in nutritional condition, we also looked for relationships between mite abundance and condition for each age and sex class. We computed nutritional condition separately for each sex and failed to find any significant relationships with mite abundance scorings, except for yearling females which showed a negative relationship between condition and mite load (Table 2).

3.3. Relationships between male colour and nutritional condition

No significant relationship was found between nutritional condition of male linnets and breast patch area ($r_s = -0.005$, $P = 0.95$, $N = 135$), breast brightnesss ($r_s = 0.02$, $P = 0.76$, $N = 136$), crown brightness ($r_s = 0.07$, $P = 0.42$, $N = 137$) and, consequently, redness index ($r_s = 0.02$, $P = 0.78$, $N = 134$). Similar results were obtained for the two age classes analysed independently (yearlings: redness index $r_s = 0.058$, $P = 0.58$, $N = 89$, all other measurements $P > 0.37$; adults: redness index $r_s = 0.065$, $P = 0.67$, $N = 45$, all other measurements $P > 0.15$).

3.4. Male colour and mite abundance

Adult males had significantly higher scores for breast brightness, crown brightness, patch area, and redness index than yearling males (Table 3). The relationship between overall mite abundance and male plumage characteristics was positive but not significant when patch area and brightness were considered separately (Spearman rank correlation, all $P > 0.05$), but reached significance when pooled in the redness index ($r_s = 0.17$, $P = 0.03$, $N = 156$). Also, the redness index of male linnets correlated significatively with the abundance of both wing mites ($r_s = 0.17$, $P = 0.03$, $N = 156$) and tail mites ($r_s = 0.16$, $P = 0.046$, $N = 156$). However, this trend was confounded by the covariation of redness with male age as no significant relationship was found between mite abundance and redness for the two age classes taken independently (Spearman rank correlation, all $P > 0.05$). In addition, a log-linear analysis showed that mite abundance was not linked to redness or age, but increasing redness was associated with age (Table 4).

The hypothesis that larger hosts may have larger breast patch areas and offer more space for mites can be rejected because of the absence of relationships between wing and tarsus length (as a measure of bird size) and breast patch size (wing: $r_s = 0.12$, $P = 0.11$, $N = 162$; tarsus: $r_s = 0.018$, $P = 0.82$, $N = 161$) and mite abundance (wing: $r_s = -0.28$, $P = 0.69$, $N = 196$; tarsus: $r_s = -0.058$, $P = 0.42$, $N = 194$). Further, the condition index used is independent from the size of the birds.

4. Discussion

Our results show that the nutritional condition of linnets was unrelated to mite abundance except

Table 2. Relationships between nutritional condition and feather mite abundance on wings, tails and pooled wings and tails of linnets of different age and sex classes. Spearman rank correlation coefficients were used.

	r_s	*P*	*n*
First-year male			
Wing	–0.06	0.51	107
Tail	–0.03	0.70	107
Pooled	–0.06	0.54	107
Adult male			
Wing	0.02	0.86	57
Tail	0.09	0.48	57
Pooled	0.04	0.73	57
First-year female			
Wing	–0.19	0.03	124
Tail	–0.22	0.01	124
Pooled	–0.20	0.02	124
Adult female			
Wing	0.04	0.75	54
Tail	0.07	0.60	54
Pooled	0.03	0.81	54

in yearling females. Yearling females were lighter but they were not in a condition worse than other classes, and they showed the lowest abundance of feather mites. Therefore, it seems unlikely that mite load was the cause of their lower body condition. Mites may increase in numbers when their hosts are unable to preen efficiently or when they do not devote sufficient time to this activity (Clayton 1991, McClure 1989, Brawner 1997), because old feather oil and detritus accumulate on feathers. Feather mites feed upon the secretion of the uropygial gland covering the feathers, removing the old oil and the microorganisms contained therein (OConnor 1982, Phillips 1990). A relationship between food resources for mites and host body condition may explain the results obtained for yearling females. For example, yearling females may be subordinates in foraging flocks and may devote more time to food searching to the detriment of the time devoted to preening (Clayton 1991, Moller 1991). On the other hand, yearling females may provide less food resources for mites than other age-sex class independently of their preening activities, because of a smaller secretion by the uropygial gland due to lower levels of circulating androgens (Jacob & Zwisler 1982). This may explain both the low abundance of mites on yearling females and the negative relationship between body condition and mite abundance in this age-sex class. Therefore, our results are contrary to the contention that feather mites are parasitic in nature (Price 1980, Anderson & May 1982, Lehman 1993), but they are in agreement with the view that feather mites form non-parasitic associations on flight feathers (Peterson 1975, OConnor 1982, Blanco *et al.* 1997). Considering feather mites lived on nearly all linnets examined, and their tiny size and food requirements (*see* references above), the interaction is better defined as commensalistic than parasitic. These results highlight the need to assess mechanisms regulating the interaction between host and symbionts, e.g., the assessment of how and what the symbionts feed on, and how the interaction may impair or benefit host fitness.

Our results clearly show higher mite abundance on males than on females. This might be attributed to the more abundant secretion of the uropygial gland, on which mites feed, that may be stimulated by the higher androgen levels in males (Jacobs & Ziswiler 1982). Therefore, male flight feathers may offer a habitat with more abundant food resources. The same trend was found in a study of the interaction between feather mites (*Gabucinia delibata*; Gabuciniidae) and group-living Choughs *Pyrrhocorax pyrrhocorax* (Blanco *et al.* 1997). It could be argued that a sex difference in mite abundance might be due to testosterone-mediated immunosuppression (Folstad & Karter 1992, Zuk 1996), which in turn would be indirect evidence favouring the view that feather mites were parasites. However, this alternative hypothesis is inconsistent with our finding that there was no sex-biased detrimental effect of mites on the nutritional condition of linnets. Another explanation, that sexual differences result from differences in behaviour or sociality influencing the rate of encounter with mites (Blanco *et al.* 1997), is not likely because male and female linnets join in mixed foraging flocks and roost together. Nevertheless, dominance relationships within flocks and access to food may influence both nutritional condition and preening activity thus affecting the availability of food for mites.

The red colour of males is more extensive and intense in adult than in juvenile linnets after post-

Table 3. Plumage characteristics of male linnets as a function of age. Data are means ± S.E., sample size in brackets. Between-age differences were assessed by Mann-Whitney *U*-tests.

	Male age		Mann-Whitney *U*-test	
	First-year	Adult	*U*	*P*
Breast redness	5.75 ± 0.20 (90)	7.13 ± 0.29 (46)	3.85	< 0.0001
Breast patch extent	19.5 ± 0.72 (90)	27.49 ± 1.00 (45)	5.87	< 0.0001
Crown redness	2.75 ± 0.14 (91)	3.33 ± 0.18 (46)	2.56	= 0.01
Redness index	48.4 ± 0.20 (87)	63.15 ± 1.92 (45)	5.14	< 0.0001

juvenile moult, but it is not related to nutritional condition or mite abundance. Parasites may directly or indirectly affect plumage colour only during moult except in the case of arthropods such as louse lice (Mallophaga) which feed exclusively on feathers. Therefore, host colour at times other than moult may reflect past rather than present levels of symbiont abundance, although this has only been tested by considering external parasitic arthropods (Weatherhead *et al.* 1993, Saino & Moller 1994). In addition to the temporal gap between moult and colour scoring, the potential influence of different hormone levels influencing secondary sexual characters during moult and the quantity of uropygial gland's waxes as food for mites at other times may explain the absence of a correlation between host colour and mite abundance. The plumage brightness of birds is usually estimated in totality (including this study) and its components (hue, tone and intensity) are rarely taken into account as independent variables. In this sense, feather brightness might be related to the quantity and composition (mostly monoester waxes) of the uropygial gland secretion (Jacob & Ziswiler 1982), a neglected potential factor influencing variation in plumage brightness both within and between species.

There is evidence that bright colour is linked to condition in wild birds (Burley 1986, Hill 1991, Hill & Montgomerie 1994, Dufva & Allander 1995, Johnstone 1995, Bortolotti *et al.* 1996). However, if we consider feather mites as being parasitic, our results do not support the current hypothesis of colour as an honest signal advertising male quality, i.e. nutritional condition or parasite resistance. On the contrary, colour variability might not be totally functional (Bortolotti *et al.* 1996) and mites may not have detrimental effects on their hosts (Blanco *et al.* 1997). In this way, age-specific differences in colour among males might be due to physiological limitations in the processing of carotenoids by juvenile birds during moult (Bortolotti *et al.* 1996). Gender effects on plumage colour and on feather mite abundance may suggest common hormone-mediated mechanisms. Although endocrine effects on oil secretion and the abundance of feather mites might be consistent with the immunocompetence theory, feather mites would have act as true parasites. We suggest that non-parasitic symbionts should be added as a further factor in the intrincate system of interactions between a host' secondary sexual characters, hormones, immune system and parasites (Folstad and Karter 1992). If future studies demonstrate the existence of mutualistic relationships with their hosts, feather mites could play a particular relevant role in this interaction system by indirectly enhancing the host' immune system through fighting or competing with parasites.

Table 4. Log-linear analysis of carotenoid-based plumage (redness index) of male linnets in relation to age and mite abundance. Goodness-of-fit test statistic for model adequacy: $G = 4.24$, d.f. = 6, $P = 0.64$. Non-significant three- and two-way interactions which were removed without any lack of fit of the model are also showed.

Effect	d.f	*G*	*P*
Redness × age × abundance	6	4.24	0.64
Redness × age	2	18.46	0.0001
Mite abundance × age	3	4.29	0.23
Mite abundance × redness	6	6.90	0.33

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