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Plumage colour is related to ectosymbiont load during moult in the serin, *Serinus serinus*: an experimental study

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Various hypotheses propose that plumage ornamentation is a reliable indicator of the health or resistance to parasites and illness of individuals. The impact of endoparasites on plumage brightness has only recently been demonstrated experimentally. We tested the impact of ectosymbionts, in particular feather mites, on plumage brightness, using 2 years of observational data and experiments in the field. The abundance of feather mites during moult was negatively correlated with brightness and saturation of plumage coloration developed by male serins. The application of an insecticide before moult resulted in experimental males developing a brighter plumage than control individuals. Experimental adult males, but not juveniles, also developed more saturated plumages in one of the years, but did not differ from controls in the other year. This is the first experimental demonstration that ectosymbionts (including mites) have a negative impact on the characteristics of the plumage developed and consequently can signal the healthiness of their hosts.

In many species, individuals choose mates with well-developed ornaments (Andersson 1994). From this choice they can obtain 'good genes' if such characters signal some heritable component of viability (Møller & Alatalo 1999). Alternatively, the benefits can be direct if more ornamented individuals are more able to defend or provide resources for their mates or offspring (Møller & Thornhill 1998). Parasites can potentially affect both types of characters. According to Hamilton & Zuk (1982), bright coloration in birds could function as a reliable indicator of genetic resistance to parasites. Parasites can also reduce the quantity of resources allocated to reproduction and increase the risk of infestation of the mate (Milinski & Bakker 1990; Hillgarth 1996).

In the great tit, *Parus major*, and the cirl bunting, *Emberiza cirlus*, brightly coloured males are healthier than drab males (Dufva & Allander 1995; Figuerola et al. 1999a), a necessary condition for parasite-regulated sexual selection to work. Studies investigating the relations between parasite burdens and the expression of sexually selected traits at the intraspecific level have produced contradictory results, however, with positive, negative and nonsignificant relations between parasite abundance and ornament size or brightness (reviewed in Møller 1990). Experiments seem to provide a more consistent approach, but few have been done (Clayton 1991; Hill & Brawner 1998; McGraw & Hill 2000).

The contradictory results of observational studies could be caused by ignorance of the effects of most parasites on the condition of wild hosts or by the different pathogenicity of different parasite species (Atkinson & Van Riper 1991). Another common problem found in studies testing the relation between plumage brightness and parasite burdens is that parasite burden is usually measured well after the development of the plumage characteristics studied. Owing to seasonal variation in the intensity of infestation, measures obtained from random sampling may not be representative of the period of plumage development (e.g. Allander & Sundberg 1997), and obscure the real patterns of covariation between parasites and plumage.

Only Thompson et al. (1997) and Harper (1999) have examined the relation between parasite load during moult and the brightness of the plumage developed. Thompson et al. (1997) reported that both feather mites, *Proctophyllodes* sp., and endoparasitic avian pox viral infections were negatively correlated with body condition and plumage brightness in male house finches, *Carpodacus mexicanus*. Harper (1999) expanded these analyses by reporting a negative relation between feather

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mite burdens during moult and the brightness of the plumage developed in five species of European passerines. However, both plumage brightness and parasite load can be related to individual condition. Consequently, this correlation necessitates experimental manipulation to evaluate whether there is a life history tradeoff between parasites and coloration in the present case (Grafen 1988).

Despite the results of such observational studies with feather mites, no evidence indicates that these organisms have negative effects on host condition and fitness (e.g. Price 1980; Anderson & May 1982; Lehman 1993 for authors considering feather mites as parasites; e.g. Peterson 1975; O'Connor 1982; Blanco et al. 1997, 2001; Jovani & Blanco 2000 for authors considering feather mites as nonparasites or even mutualists). The apparent effect of feather mites on coloration can be explained, for example, by a correlation between ecto- and endoparasite load (Hill 1999). The lack of knowledge about the real nature of the interactions between most symbiotic organisms and their hosts (Bronstein 1994; Proctor & Owens 2000) can produce misleading results, and makes necessary experiments to assess the relevance of the ectosymbiont community for the development of bright plumage.

In this study, we tested the hypothesis that feather mite, *Proctophyllodes serini*, load affects the relative brightness of the plumage developed by male serins, using both observational and experimental approaches. We first examined the relation between mite load during the moult and the brightness of the plumage developed, as did Thompson et al. (1997) on the house finch. However, we expanded their study by using fine colorimetry to determine the characteristics of the plumage and providing quantitative measures of mite load rather than using semiquantitative approaches. We then experimentally removed ectosymbionts just before the moult and measured the characteristics of the plumage developed.

METHODS

The serin is a small, sexually dichromatic finch. Males display patches of carotenoid-based yellow coloration on the breast and crown. The size and coloration of patches of carotenoid pigment are important for sexual selection in several other cardueline finches (reviewed in Hill 1999).

We trapped serins in baited traps in the suburbs of Barcelona, northeast Spain, in a habitat characterized by intermixed forests, shrubs, gardens and orchards. Weekly trapping sessions were done from sunrise to midday (usually 1500 hours local time). We monitored traps with binoculars, and birds were removed from traps a few minutes after capture. Data were collected from July 1998 to June 2000. Only males that were captured before the moult and recaptured after the moult session were included in this study (N=29). Serins were aged (first postjuvenile plumage or adult birds) and sexed by plumage characteristics (Svensson 1996). The birds were individually ringed and wing length and body mass were recorded.

A Minolta DR200 colorimeter was used to measure colours; this machine sends a standard light flash on the area and analyses the characteristics of the reflected light (Minolta Company 1994). Measurements of colour were taken at the crown, breast and belly (repeatability for the serin 0.88–0.99; Figuerola et al. 1999b), and only from individuals with no active moult replacement in these areas of the body. Colour in the visible human spectra was characterized by hue, brightness and chroma values. Hue corresponds to wavelength and is expressed as degrees of a circle starting with red, continuing through yellow, green and blue and completing the circle again with red. Brightness corresponds to the physical light intensity on a scale from 0 for black to 100 for white. Chroma corresponds to the colour purity on a scale of 0 for white to 100 for pure colour. Three principal components analyses were done, one for each of the colour components, to summarize the measurements obtained in the three body areas studied. The first component of each of these analyses was used as an index of coloration. The brightness component summarized 51% of the variance in the three body areas studied (factor loading for crown=0.51, breast=0.63, belly=0.54). The chroma component summarized 84% of the variance (factor loadings of 0.56, 0.60, 0.57, respectively) and the hue component 72% (0.58, 0.63, 0.52, respectively).

We scored mite infestation by counting with an eyescope (10 ×) the number of individuals on the primary, secondary and tertiary feathers of the right wing, which we extended against a brightly lit background.

Experimental Manipulation of Mite Load

During the summers of 1998 and 1999 we did a mite reduction experiment to test the effects of mite loads on the characteristics of the plumage developed after the moult. Thirty-five randomly chosen males trapped before the moult were dusted with Drione, an insecticide that effectively eliminates feather mites (reinfestation time 15 to more than 60 days), reducing the levels of feather mites on the birds we recaptured during the 50 days following the treatment (Table 1). We manipulated control males (N=45) in the same way, but without applying the insecticide. Coloration developed after the moult could be measured in the 17 experimental and 13 control birds recaptured after the moult period.

Drione is a nontoxic insecticide for birds that is commonly used by chicken breeders. It kills the arthropods by scratching the surface of the cuticle, causing rapid desiccation, and removes oil from feathers. This can be dangerous for birds caught in rain within a few days of dusting. Consequently, no dusting was done in rainy weather, which was infrequent during the study period (precipitation in June 1998: 6.8 mm; July: 1.6 mm; June 1999: 9.8 mm; July: 9.4 mm).

The birds were captured with the permission of the Subdirecció General de Conservació de la Natura, Generalitat de Catalunya. Experimental procedures used by the Zoology Museum in behavioural research were approved by the Ethical Committee of Generalitat de Catalunya.

Table 1. Number of feather mites (mean±SE) on the right wing of control and experimental males on capture and on first recapture in the 50 days after initial manipulation (dusting with insecticide or control manipulation)

		Number of mites				
	N	First capture	Recapture	Paired t_{10}	*P*	Time interval (days)
Control	11	95.36±18.32	162.91±43.07	0.53	0.61	24±4
Experimental	11	78.81±30.88	9.36±3.73	2.46	0.03	29±5

Differences in feather mite load were tested with a paired *t* test. No differences in the time interval (days) between first and second capture were detected between the control and experimental group (Mann–Whitney *U* test: $U=475$, $N_1=N_2=11$, $P=0.39$).

Table 2. Relation between coloration developed after the moult by males and feather mite load ($N=29$)

	PCA brightness			PCA chroma			PCA hue		
Factor	Estimate	$F_{1,39}$	*P*	Estimate	$F_{1,20}$	*P*	Estimate	$F_{1,24}$	*P*
Year	−0.881	3.05	0.10	−0.731	6.66	0.02	−0.525	6.45	0.02
Age	−0.977	11.47	0.003	−1.059	9.76	0.005	0.516	1.68	0.21
Year*age	—	0.37	0.55	—	0.28	0.60	—	0.03	0.88
Feather mites	−6.650	12.16	0.003	−7.248	10.48	0.004	—	0.88	0.36
Year*feather mites	0.611	5.09	0.04	—	0.39	0.54	—	0.42	0.66
Age*feather mites	—	0.06	0.81	—	0.49	0.49	—	0.48	0.62
Months since moult	0.624	1.13	0.30	0.584	0.73	0.40	0.257	6.00	0.02
Year*months since moult	—	1.02	0.33	—	0.82	0.38	—	0.01	0.95
Age*months since moult	—	0.78	0.39	—	0.25	0.62	−0.223	4.68	0.04
Mites*months since moult	0.523	7.38	0.01	0.561	6.10	0.02	—	0.60	0.56
Hour of capture	−0.895	3.75	0.07	−0.890	2.76	0.11	—	0.29	0.60
Year*hour	—	0.28	0.61	—	0.00	0.97	—	1.49	0.25
Age*hour	—	0.05	0.83	—	2.13	0.16	1.12	0.35	
Mites*hour	0.697	11.85	0.003	0.736	9.66	0.006	—	0.31	0.82
Months since moult*hour	−0.204	5.93	0.02	−0.209	4.41	0.05	—	0.57	0.57
R^2	0.59			0.85			0.62		

Estimates correspond to the regression parameters of each factor included in the final model obtained by backwards regression.

Statistical Analyses

We analysed the relation between feather mite load during moult and the coloration developed by males by backwards regression including the two-way interactions between the variables considered. The factor contributing least to the model was removed at each step. Variables were retained in the model until all the interactions including the variable had been excluded from the model, using a lower probability limit of 0.10 to retain a factor in the model. Year and age (first-year or adult birds) were included as factors in the analyses. Hour of capture on the day the feather mites were counted was included as a continuous variable, because birds were measured at different times (0700–1600 hours, $\bar{X} \pm \mathrm{SE}=0900 \pm 0.3$ hours) and the number of feather mites present in the wing varies during the day (Dubinin 1951), probably in response to changes in ambient air temperature (Wiles et al. 2000). The coloration of the plumage was measured over a long period (September–May, $\bar{X} \pm \mathrm{SE}=$ November $\pm$ 0.4 months). For this reason, the last variables considered were the number of months elapsed between the completion of moult (assuming that all individuals had completed the moult in September) and the measurement of plumage colour to account for seasonal changes in plumage coloration caused by feather abrasion or fading (J. Figuerola, J. Domènech & J. C. Senar, unpublished data). In the analysis of observational data, we included data from birds captured before the experiment and from birds included in the experiment as controls, but not data from individuals dusted with insecticide.

In the analyses of the experimental data, we included three variables and their two-way interactions: experimental treatment, age and year. Three-way interactions could not be included because of the few individuals that we recaptured after moult completion. Months since moult (September–May, $\bar{X} \pm \mathrm{SE}=$November $\pm$ 0.4 months) were also considered in a first run of these analyses, but were not included in the results presented here, because this variable did not enter significantly in any of the final models. All the analyses were done in JMP v.3, using log-transformed mite numbers, and we report mean ± SE for the untransformed data. All probabilities correspond to two-tailed tests.

RESULTS

Most of the variation in plumage hue was explained by three variables not related to mite load (Table 2). Hue varied both between and within years, increasing with

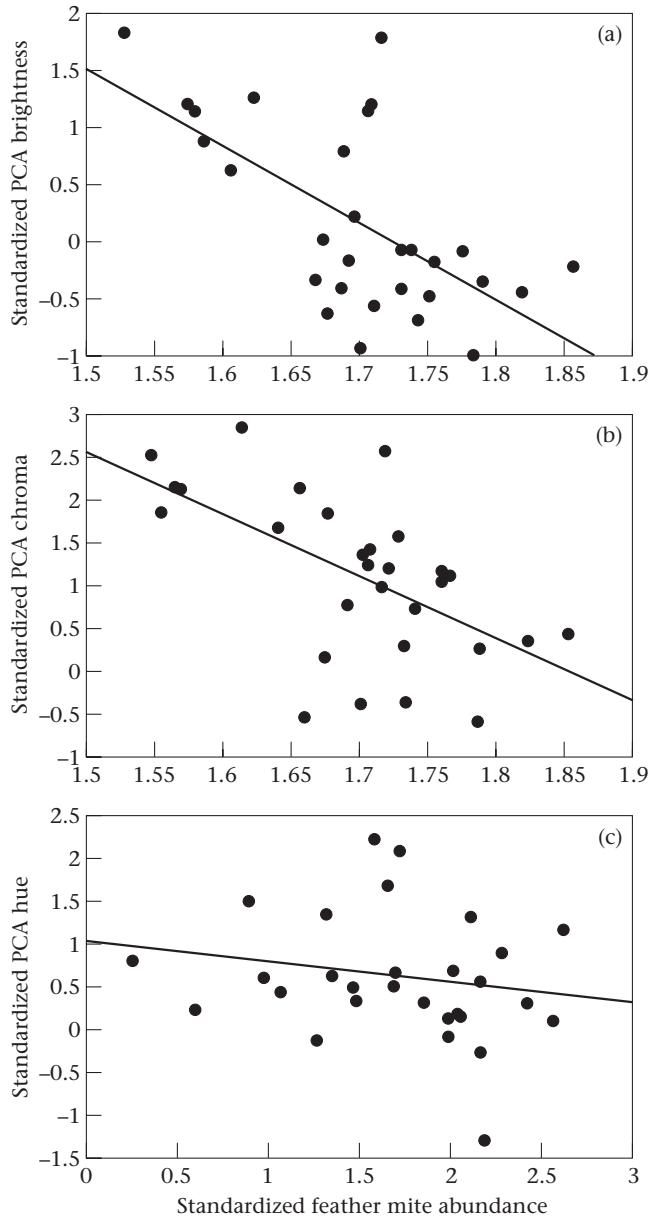

Figure 1. Relation between plumage coloration (standardized by regression of the other variables in the final models in Table 2, but excluding feather mites) and feather mite abundance (also standardized by regression of the other independent variables in the models of Table 2). (a) Brightness, (b) chroma and (c) hue.

the number of months since moult. The significant interaction between age and months since moult suggests that the slope of this regression is lower for adult birds.

Brightness and chroma also varied according to study year and age. No significant direct effect of months since moult on coloration was detected, but this variable interacted significantly with feather mites for both brightness and chroma, as we discuss below.

Feather Mites and Coloration

We found a negative relation between feather mite load during the moult and brightness and chroma of the plumage coloration developed afterwards (Table 2, Fig. 1) and no significant relation between mite load and hue. The slope of the regression for brightness was higher in 1999 than in 1998 ($F_{1,19}$=5.09, P=0.04), but no such difference was found for chroma ($F_{1,20}$=0.39, P=0.54). A significant interaction existed between mite abundance and months since moult for both brightness and chroma. The positive estimate for this interaction (Table 2) indicates that the slope of the relation between mites and coloration was steeper for birds measured longer after moult. The positive interaction between mites and hour of capture also indicates that the slope of the relation between mites and plumage coloration was more positive for birds measured at midday compared with birds measured in the morning (Table 2). These interactions were due to a higher abundance of feather mites in summer 1999 than in 1998 (least square mean for log-transformed mite abundance, controlling for months since moult and hour of capture: 1998: 1.15 ± 0.19; 1999: 2.12 ± 0.15; $F_{1,26}$=13.96, P=0.0009), changes in the abundance of feather mites during the year (Fig. 2), and an increase in feather mites in the wing flight feathers from early morning towards midday ($F_{1,26}$=8.55, P=0.007).

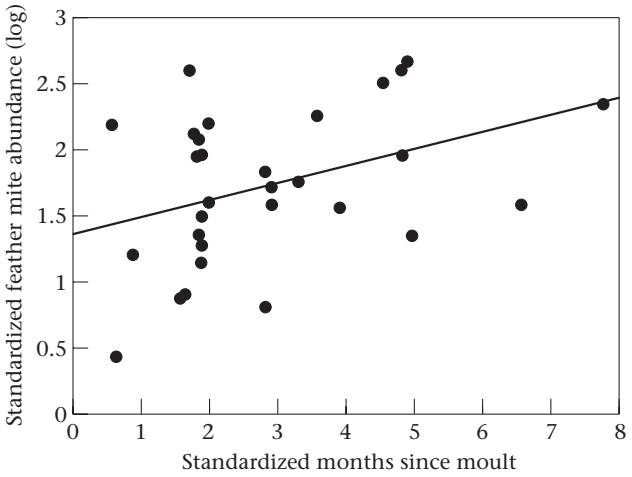

Figure 2. Relation between feather mite abundance (standardized by regression on hour of capture and study year) and months since completion of moult ($F_{1,26}$=4.66, P=0.04).

Mite Removal Experiment

We recaptured 30 control and experimental males after they had finished moulting (Table 3). The effects of the insecticide treatment were significant for brightness (Fig. 3a) but not for chroma. In the case of chroma, a significant interaction between year and experiment was detected owing to a significant effect of the experiment in 1999 (control: 0.946 ± 0.345, N=7; experimental: 1.352 ± 0.264, N=12; t_{23}=2.68, P=0.01), but not in 1998, when all the birds showed lower chroma (control: 0.713 ± 0.557, N=6; experimental: 0.668 ± 0.610, N=5; t_{23}=0.72, P=0.48; Fig. 3b). A significant interaction between age and experiment was detected because the experiment affected the chroma of adult birds (control:

Table 3. Comparison of colour characteristics of control and experimental (insecticide-treated) males controlling for age and year of the experiment (N=30)

	PCA brightness			PCA chroma			PCA hue		
	Estimate	$F_{1,27}$	P	Estimate	$F_{1,23}$	P	Estimate	$F_{1,28}$	P
Experiment	−0.439	5.79	0.02	−0.385	3.49	0.07	—	0.02	0.89
Year	—	0.01	0.92	0.016	0.00	0.95	−0.393	5.99	0.02
Experiment*year	—	0.01	0.99	0.588	5.44	0.03	—	0.42	0.66
Age	−0.477	6.20	0.02	−0.073	0.09	0.77	—	0.10	0.72
Experiment*age	—	0.01	0.95	0.847	8.93	0.007	—	0.08	0.97
Year*age	—	1.04	0.37	-0.612	5.78	0.02	—	0.07	0.93

A backwards selection procedure was followed to obtain the final model.

0.605 ± 0.416, N=4; experimental: 1.853 ± 0.340, N=6; t_{23}=2.89, P=0.008; Table 3) but not juveniles (control: 0.942 ± 0.371, N=9; experimental: 0.768 ± 0.336, N=11; t_{23}=1.83, P=0.08). No effect of the experimental manipulation on the hue of the plumage developed was detected (Fig. 3c).

DISCUSSION

The brightness of carotenoid-derived coloration seems to be important for mate choice in cardueline finches (Hill 1999), although no information is available for the serin. A larger ectosymbiont load during the previous moult can reduce the brightness of the plumage developed, as well as the mating possibilities and expected fitness of males in the next breeding season.

Our results support the importance of ectosymbionts in the regulation of the expression of bright coloration. First, at the correlational level, our results agree with those of previous studies in the house finch (Thompson et al. 1997) and five European species of passerines (Harper 1999), because coloration was related to feather mite load. Altogether, present evidence indicates that individuals with greater infestations of proctophyllodid mites during moult grow duller plumage. We also found an important effect of hour and months since moult on the relation between coloration and mites. Feather mite distribution changes during the day (Dubinin 1951; this study) and during the winter (J. Figuerola, J. Domènech & J. C. Senar, unpublished data; this study), and coloration changes during the winter because of abrasion (J. Figuerola, J. Domènech & J. C. Senar, unpublished data). These sources of variation could explain why some studies have failed to detect a relation between feather mites and coloration (e.g. Blanco et al. 1999).

The manipulation of mite loads using a dust insecticide was consistent with the correlation between mites and coloration, because treated individuals grew brighter plumage. We found the correlational relation between coloration and mites for both brightness and chroma colour characteristics, the same two variables for which an effect of experimental manipulation was detected.

The results of the insecticide experiment should be interpreted cautiously, because the treatment is not specific for feather mites. Consequently, we have shown experimentally that the ectosymbiont community affects coloration, but not the identity of the specimen or species causing such a relation. For example, in addition to killing arthropods, the insecticide might indirectly affect the microbial community that can also affect the quality of the bird's plumage (Burtt & Ichida 1999). Hence, the relation between insecticide and coloration could be explained by factors unrelated to mite abundance, such as if mite abundance covaried with the abundance of damaging parasites (Thompson et al. 1997) or bacteria. This could be the case if ill individuals preen less, resulting in an accumulation of old oil and detritus on feathers, and thus an increase in the feeding resources available to feather mites. However, given the design and characteristics of our study, such an illness should be produced by an ectoparasite rather than an endoparasite, because the application of the insecticide also affected the characteristics of the coloration developed.

Of the different arthropods potentially able to affect plumage coloration, mites are by far the most abundant observed in our serin population, with the other groups occurring at low prevalences (two ticks observed in several thousand individuals examined, 1.3% of louse fly prevalence: Senar et al. 1994; <2% of lice prevalence: J. Figuerola, J. Domènech & J. C. Senar, personal observations). Nevertheless, although mites are the most probable arthropods causing the detected change in plumage coloration, we lack information on the abundance of other less easily detected species owing to either their small size (e.g. skin mites) or their sporadic presence in the birds (e.g. parasites living in the nests, such as soft ticks; Clayton & Walther 1997). Given that feather mites seem to consume oil and fungi that adhere to the feather surface (Dubinin 1951; Walter & Proctor 1999), the way feather mites, at least the ones living on the feather surface, could reduce host condition is unknown (Proctor & Owens 2000). However, the alternative possibility that individuals with poor foraging abilities had both drab plumage and larger feather mite loads is ruled out by the results of our experiment.

The three components of plumage coloration were affected differently by feather mite abundance. Brightness improved in experimentally defaunated individuals, but changes in chroma were statistically significant only in 1999 (otherwise the year with higher feather mite abundance). However, the hue component was unrelated to mite abundance and also to bird age.

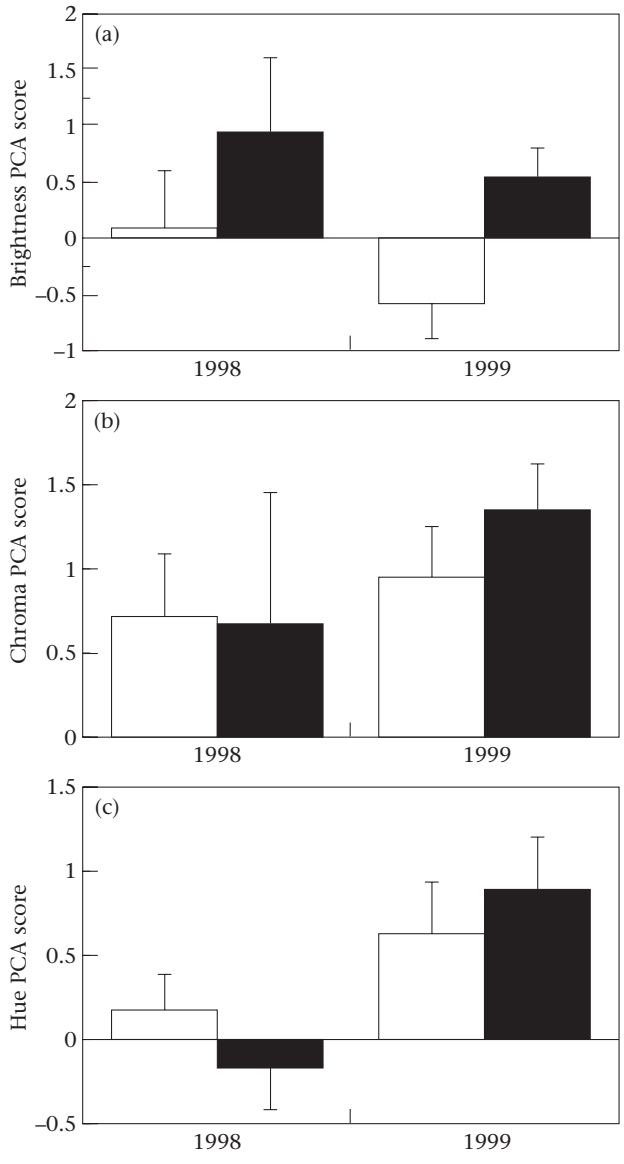

Figure 3. (a) Brightness, (b) chroma and (c) hue of the plumage developed after moult of control (□, *N*=13) and experimental (■, *N*=17) serins.

Only study year, months since moult and the interaction of this factor with age were related to variation in coloration hue. We lack information on the potential role of each of these colour components in serin biology.

In conclusion, this study provides the first experimental evidence under field conditions that ectosymbionts limit the development of bright plumage in birds. Further work specifically manipulating the loads of different ectosymbionts is necessary to identify the species responsible for such a negative effect on hosts.

Acknowledgments

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References

Allander, K. & Sundberg, J. 1997. Temporal variation and reliability of blood parasite levels in captive yellowhammer males *Emberiza citrinella*. *Journal of Avian Biology*, **28,** 325–330.

Anderson, R. M. & May, R. M. 1982. *The Population Biology of Infectious Disease*. Berlin: Springer-Verlag.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Atkinson, C. T. & Van Riper III, C. 1991. Pathogenicity and epizootiology of avian haematozoa: *Plasmodium*, *Leucocytozoon* and *Haemoproteus*. In: *Bird–Parasite Interactions* (Ed. by J. E. Loye & M. Zuk), pp. 19–48. Oxford: Oxford University Press.

Blanco, G., Tella, J. L. & Potti, J. 1997. Feather mites on group-living red-billed choughs: a non-parasitic interaction? *Journal of Avian Biology*, **28,** 197–206.

Blanco, G., Seoane, J. & de la Puente, J. 1999. Showiness, non-parasitic symbionts, and nutritional condition in a passerine bird. *Annales Zoologici Fennici*, **36,** 83–91.

Blanco, G., Tella, J. L., Potti, J. & Baz, A. 2001. Feather mites on birds: costs of parasitism or conditional outcomes? *Journal of Avian Biology*, **32,** 271–274.

Bronstein, J. L. 1994. Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution*, **9,** 214–217.

Burtt, E. H. & Ichida, J. M. 1999. Occurrence of feather-degrading bacilli in the plumage of birds. *Auk*, **116,** 364–372.

Clayton, D. H. 1991. The influence of parasites on host sexual selection. *Parasitology Today*, **7,** 329–334.

Clayton, D. H. & Walther, B. A. 1997. Appendix C: Collection and quantification of arthropod parasites of birds. In: *Host–Parasite Evolution: General Principles and Avian Models* (Ed. by D. H. Clayton & J. Moore), pp. 419–440. Oxford: Oxford University Press.

Dubinin, V. B. 1951. Feather mites (Analgesoidea) Part I. Introduction to their study. *Fauna SSSR Paukoobraznye*, **6,** 1–363.

Dufva, R. & Allander, K. 1995. Intraspecific variation in plumage coloration reflects immune response in great tit (*Parus major*) males. *Functional Ecology*, **9,** 785–789.

Figuerola, J., Muñoz, E., Gutiérrez, R. & Ferrer, D. 1999a. Blood parasites, leucocytes and plumage brigthness in the cirl bunting *Emberiza cirlus*. *Functional Ecology*, **13,** 594–601.

Figuerola, J., Senar, J. C. & Pascual, J. 1999b. The use of colorimeters on free-living birds: sex, age and locality differences in blue tit (*Parus caeruleus*) coloration. *Ardea*, **87,** 269–275.

Grafen, A. 1988. On the uses of data on lifetime reproductive success. In: *Reproductive Success* (Ed. by T. H. Clutton-Brock), pp. 454–471. Chicago: University of Chicago Press.

Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science*, **218,** 384–386.

Harper, D. G. C. 1999. Feather mites (Acari, Procophyllodidae), pectoral muscle condition, wing length and plumage coloration of passerines. *Animal Behaviour*, **58,** 553–562.

Hill, G. E. 1999. Mate choice, male quality, and carotenoid-based plumage coloration. In: *Proceedings of the 22nd International Ornithology Congress, Durban* (Ed. by N. Adams & R. Slotow), pp. 1654–1668. Johannesburg: Birdlife South Africa (CD-ROM).

Hill, G. E. & Brawner, W. R. I. 1998. Melanin-based plumage coloration in the house finch is unaffected by coccidial infection. *Proceedings of the Royal Society of London, Series B*, **265,** 1105–1109.

Hillgarth, N. 1996. Ectoparasite transfer during mating in ring-necked pheasants *Phasianus colchicus*. *Journal of Avian Biology*, **27,** 260–262.

Jovani, R. & Blanco, G. 2000. Resemblance within flocks and individual differences in feather mite abundance on long-tailed tits, *Aegithalos caudatus* (L.). *Ecoscience*, **7,** 428–432.

Lehman, T. 1993. Ectoparasites: direct impact on host fitness. *Parasitology Today*, **9,** 8–13.

McGraw, K. J. & Hill, G. E. 2000. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London, Series B*, **267,** 1525–1532.

Milinski, M. & Bakker, T. C. M. 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitised males. *Nature*, **344,** 330–333.

Minolta Company 1994. *Precise Color Communication: Color Control from Feeling to Instrumentation*. Ramsey, New Jersey: Minolta.

Møller, A. P. 1990. Parasites and sexual selection: current status of the Hamilton and Zuk hypothesis. *Journal of Evolutionary Biology*, **3,** 319–328.

Møller, A. P. & Alatalo, R. V. 1999. Good-genes effects in sexual selection. *Proceedings of the Royal Society of London, Series B*, **266,** 85–91.

Møller, A. P. & Thornhill, R. 1998. Male parental care, differential parental investment by females and sexual selection. *Animal Behaviour*, **55,** 1507–1515.

O'Connor, B. M. 1982. Evolutionary ecology of astigmatid mites. *Annual Review in Entomology*, **27,** 385–409.

Peterson, P. C. 1975. An analysis of host–parasite associations among feather mites (Acari: Analgoidea). *Miscellaneous Publications of the Entomological Society of America*, **9,** 237–242.

Price, P. 1980. *Evolutionary Biology of Parasites*. Princeton, New Jersey: Princeton University Press.

Proctor, H. & Owens, I. 2000. Mites and birds: diversity, parasitism and coevolution. *Trends in Ecology and Evolution*, **15,** 358–364.

Senar, J. C., Copete, J. L., Domenech, J. & von Walter, G. 1994. Prevalence of louse-flies Diptera, Hippoboscidae parasitising a cardueline finch and its effect on body condition. *Ardea*, **82,** 157–160.

Svensson, L. 1996. *Guía Para la Identificación de los Passeriformes Europeos*. Madrid: Sociedad Española Ornitología.

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

Walter, D. E. & Proctor, H. C. 1999. *Mites: Ecology, Evolution and Behaviour*. New York: CAB International.

Wiles, P. R., Cameron, J., Behnke, J. M., Hartley, I. R., Gilbert, F. S. & McGregor, P. K. 2000. Season and ambient air temperature influence the distribution of mites (*Proctophyllodes stylifer*) across the wings of blue tits (*Parus caeruleus*). *Canadian Journal of Zoology*, **78,** 1397–1407.