Parasites and the blackcap's tail: implications for the evolution of feather ornaments

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Although parasites may impair the expression of tail ornaments in birds, the importance of parasitism in driving the evolution of the initial stages of tail ornamentation is not well understood. Parasites could have negatively affected the expression of nonexaggerated, functional traits before these evolved ornaments, or they could have played a relevant role only after tails became ornamental and hence too costly to produce. To shed light on this issue, we studied the correlation between the abundance of feather mites (Acari, Proctophyllodidae) and the size, quality, growth rate and symmetry of tail feathers of blackcaps (*Sylvia atricapilla*), a non-ornamented passerine. Tail length was not correlated with mite load, yet blackcaps holding many mites at the moment of feather growth (fledglings) had lighter and more asymmetric feathers that grew at relatively lower rates. In blackcaps whose mite load was measured one year after feather growth (adults), only the negative correlation between mite intensity and feather symmetry remained significant. Changes in mite load since the moult season could have erased the correlation between condition-dependent feather traits and current parasite load in adults. Our results support the idea that different traits of non-ornamental feathers can signal parasite resistance. Therefore, parasitism could have played a central role in the evolution of tail ornamentation ever since its initial stages.   © 2002 The Linnean Society of London. *Biological Journal of the Linnean Society*, 2002, **76**, 481–492.

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INTRODUCTION

Since Hamilton & Zuk (1982) introduced the idea that parasites may affect mate choice, parasitism has become an important issue for understanding the evolution of ornaments (Clayton, 1991a; Zuk, 1992; Andersson, 1994; Møller, 1994). Central to this hypothesis is that an intense parasite infection may impair the host body condition (Lehman, 1993; Lochmiller *et al.*, 1993; Møller *et al.*, 1998), reducing the expression of ornaments that are costly to produce (Zuk, 1992; Hill & Montgomerie, 1994; Veiga & Puerta, 1996). In turn, ornaments may indicate the ability of individuals to overcome parasite challenges, thereby acting as honest signals relevant to mate choice and other social contests (Borgia & Collis, 1989; Clayton, 1990; Houde & Torio, 1992; Zuk *et al.*, 1993; Mateos & Carranza, 1997; Senar & Camerino, 1998).

Ornamental tails of birds may be particularly adequate to test the role of parasites in the expression of condition-dependent characters. Tail ornaments combine large amounts of variation in size and pattern with extraordinary measurement facilities (Fitzpatrick, 1998a; Cuervo & Møller, 2000). In addition, tail ornamentation is costly not only because of the abundant energy and structural resources required for feather production (Lindström *et al.*, 1993; Murphy, 1996), but also because of its negative effect on flight performance (Balmford *et al.*, 1993; Norberg, 1995; Fitzpatrick, 1999). Tail ornamentation commonly involves feather elongation, as well as the emergence of shapes, structures and markings that amplify honest signalling (Andersson, 1994; Møller,

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1994; Fitzpatrick, 1998a). For example, ornamental tails usually show pin feathers, lyres or graduated forks as amplifiers of the signalling value of tail length and symmetry, or special colour schemes as amplifiers of the signalling value of feather resistance to abrasion (Fitzpatrick, 1998a, 1998b). A negative effect of parasites on the expression of these characteristics of feather ornaments has been supported by several studies (Thompson *et al.*, 1997; Harper, 1999).

Although the study of tail ornamentation has produced a good picture of the diversity of extant feather ornaments (e.g. Fitzpatrick, 1998a; Cuervo & Møller, 2000), very little is known about how ornamental tails could have evolved from nonextravagant, fully functional tails. In particular, the role that parasites could have played in the early evolutionary stages of tail ornamentation remains obscure. Although mounting an immune response may be costly (Møller *et al.*, 1998), this might not affect the expression of traits which are not too costly to produce. In this case, parasites should not have affected feather characteristics before tails were exaggerated into costly ornaments. Thus, the study of nonexaggerated traits could shed light on the possible role of parasites in the early evolution of ornaments (Fisher, 1930; Zahavi, 1975; Hamilton & Zuk, 1982). However, while true ornaments have received much attention, the relationship between parasitism and the expression of less eye-catching feather characters has never been explicitly tested. For example, it would be important to determine whether length, symmetry and quality of tail feathers can signal parasite resistance before the tail becomes a true ornament. The study of non-ornamented species would give a critical support for the importance of parasites in the initial evolutionary stages of tail ornamentation if, for example, highly parasitized individuals faced more problems to grow their tails, thereby producing shorter, more asymmetric and less finely built feathers than healthy individuals.

We studied the correlation between the intensity of infection by feather mites (Acari, Proctophyllodidae) and the capacity to produce a well-constructed tail in blackcaps (*Sylvia atricapilla* [L.]). The blackcap has a dusky brown plumage without distinctive characters, apart from the crown feathers which differentiate between the sexes (black cap in males and brownish cap in females; Cramp, 1992). The blackcap's tail is homogeneously dark, shows no extravagant adornment or sexual dimorphism, and cannot be considered to be ornamental (see a definition of ornamental tails in Cuervo & Møller, 1999). If the basic features of feathers were affected by parasite load, highly parasitized blackcaps should face additional problems for growing their tails, which could be related to different aspects of the growth process:

FEATHER GROWTH RATE

We studied the rate of feather growth in blackcaps using ptilochronology, a method that relies on growth bars as exact markers of daily feather production, and on the sensitivity of the moult process to slight changes in the body condition of birds (Grubb, 1995). Growth bars are visible as alternate dark and light bands perpendicular to the rachis, each couple of bands corresponding to a 24 h period of feather growth. It has been demonstrated experimentally that the worse the nutritional conditions experienced by a moulting bird, the narrower the growth bars on its feathers (Grubb, 1995). Because parasites remove body resources from their hosts, highly infected blackcaps should face more difficulties for producing feathers and should show lower growth rates.

FEATHER SIZE AND QUALITY

Because feather growth is such a costly activity, the difficulties faced by birds during that process could translate into a reduced length and/or quality of feathers (Murphy *et al.*, 1988; Murphy, 1996). We studied the correlation between the intensity of parasite infection and the length and quality of feathers. We used the ratio between feather mass and feather length as an index of feather quality, since it depends on the density of structural elements, and hence indicates feather durability (Murphy *et al.*, 1988; Carbonell & Tellería, 1999).

FLUCTUATING ASYMMETRY

Fluctuating asymmetry (FA) is the small, random deviation from perfect symmetry in an otherwise bilaterally symmetric trait (Palmer & Strobeck, 1986). Many studies support that FA measures developmental instability reflecting the adverse effects of both genetic and environmental factors on development (Møller & Swaddle, 1997). Symmetry is thought to be an important feature of tail ornaments (Fitzpatrick, 1998a; Cuervo & Møller, 1999). For example, in barn swallows (*Hirundo rustica*) FA of tail length increases with parasite load, and females prefer to mate with more symmetric males (Møller, 1994). If parasites also affect the shape of non-ornamental tails, blackcaps holding many parasites should have more asymmetric tails than less parasitized individuals.

METHODS

SPECIES AND FIELD METHODS

The blackcap is a small (16 g) passerine widely distributed across Europe, where it shows considerable variation in morphology and migratory behaviour

(Shirihai *et al.*, 2001). This could affect the functional relationship between parasites and condition-dependent traits, due to possible covariation between migratory behaviour and parasite resistance (Møller & Erritzøe, 1998), changes in host morphology (Rózsa, 1997) or exposure to parasite infections in different habitats (Bennett *et al.*, 1995). Because of this, we conducted our study in two structurally similar localities (Álava, 42°55′N 2°29′W and Guadarrama, 40°54′N 3°53′W, two oak forests in the northern half of Spain), where previous data have shown that blackcaps have the same migratory behaviour, morphology and habitat preferences (Carbonell & Tellería, 1998; Tellería & Carbonell, 1999).

From mid-June to mid-July 1997, we mist-netted blackcaps coinciding with the peak of the fledging period in each locality. We measured birds to control for variations in morphology or body mass that could bias parasite abundance (Table 1). Blackcaps were classified as adults (individuals in their second year or older) or fledglings (individuals with juvenile plumage). At the time of capture, fledgling blackcaps had just produced their tail, which they conserve until the first complete moult one year later: over 90% individuals retain all tail feathers after postjuvenile moult in north-European blackcaps (Shirihai *et al.*, 2001), as did all the individuals we studied (pers. obs.). On the other hand, birds classified as adults had grown their tail one year before their capture, regardless they were

second-year or older birds. This difference is particularly important to our study because it means that parasite load was measured immediately after feather growth in juveniles, but one year later in adults. We ringed all birds to avoid repetition. We plucked their fifth rectrices after confirming that they were fully grown by observing the absence of sheaths at the feather base. Feathers were stored in dry paper envelopes to avoid distortion or damage, and birds were released.

In the laboratory, we measured the feather length and the width of 10 growth bars in the centre of the feather vane with a digital calliper, both to the nearest 0.01 mm. We also weighed feathers with a Mettler Toledo® AG-245 balance (0.01 ± 0.02 mg resolution). All measurements were highly repeatable between left and right side feathers (intraclass correlation coefficients: feather length $r_i = 0.98$, $F_{66,67} = 92.45$; feather mass $r_i = 0.95$, $F_{65,66} = 39.03$; width of growth bars $r_i = 0.93$, $F_{67,68} = 29.62$; all $P < 0.0001$), so we used the average value of both sides in our analyses. We measured twice the feathers of 10 randomly selected individuals to estimate repeatability of asymmetry, which was very high too ($r_i = 0.90$, $F_{9,10} = 18.85$, $P < 0.0001$). In some cases, we could measure one feather only, because the other one was lost or strongly abraded, or showed too light bands that were hardly measurable. To avoid personal bias, all measurements were taken by RC, who did so blindly with respect to the hypoth-

Table 1. Morphological traits of adult and fledgling blackcaps in the populations studied. Means, standard errors and sample sizes are shown. None of these measurements varied between sites nor age classes (two-way ANCOVA with minimum $P = 0.14$ for effects and interactions), except wing length which significantly changed between populations ($P = 0.001$). Variation in mite prevalence (percentage of individuals infected) and mite abundance (mean intensity of infection measured as the number of mites counted on one wing, with standard error) is also shown

	Álava		Guadarrama	
	Adults	Fledglings	Adults	Fledglings
Tarsus length (mm)	20.12 ± 0.12 (16)	20.14 ± 0.11 (35)	20.22 ± 0.22 (13)	20.30 ± 0.19 (11)
Wing length (mm)	72.44 ± 0.41 (16)	71.93 ± 0.21 (36)	70.62 ± 0.48 (13)	71.16 ± 0.32 (11)
Tail length (mm)	61.06 ± 0.56 (16)	60.06 ± 0.36 (36)	60.21 ± 0.26 (12)	60.09 ± 0.98 (11)
Body mass (g)	16.79 ± 0.23 (16)	16.19 ± 0.22 (36)	16.23 ± 0.36 (12)	15.69 ± 0.37 (11)
Mite prevalence	75% (16)	75% (36)	84.6% (13)	90.9% (11)
Mite abundance	44.94 ± 12.04 (16)	29.67 ± 5.39 (36)	30.31 ± 6.97 (13)	29.45 ± 8.21 (11)

esis being tested during a study of the morphology and body condition of several populations of Iberian blackcaps (Carbonell & Tellería, 1999; Tellería & Carbonell, 1999).

FEATHER MITES AS INDICATORS OF PARASITE LOAD

Proctophyllodid feather mites (genus *Proctophyllodes* Robin 1868, probably *P. sylviae* on Iberian blackcaps, see Behnke *et al.*, 1999) are attached to the flight feathers of blackcaps. They are contagious ectosymbionts, whose transmission depends on the body-to-body contact between hosts (Dabert & Mironov, 1999). During the late breeding season, blackcaps do not get in close contact with other conspecifics, for instance by using communal roosts or crowded feeding sites (Cramp, 1992), which precludes horizontal transmission of mites (Poulin, 1991; Blanco *et al.*, 1997). This means that young blackcaps must acquire their mites in the nest through contagion from their parents.

 Compared to other avian symbionts, proctophyllodid mites have the advantage that their prevalence and abundance can be easily and accurately measured in many birds by simple visual inspection (Blanco *et al.*, 1997, 1999; Behnke *et al.*, 1999). Blackcaps only held mites on the vanes of flight feathers. We counted all mites present on one wing by searching on the whole vane of primaries, secondaries and tertials, holding the bird with the wing extended and exposed against sunlight. Individuals with lost or growing feathers were discarded. The amount of mites on wings is fairly correlated with their abundance on other feather tracts, so mite abundance on a single wing can be used as a proper estimate of total mite load (Behnke *et al.*, 1999).

 However, the effect that feather mites could play on their hosts is still a matter of controversy. Some authors consider that holding many mites may be detrimental to the bird fitness (Choe & Kim, 1991; Poulin, 1991; Poiani, 1992; Thompson *et al.*, 1997; Harper, 1999), but recent studies support that mites could be commensalistic or mutualistic symbionts, which seems more realistic (Proctor & Owens, 2000; Blanco *et al.*, 2001). Because the small or null pathogenicity of proctophyllodid mites is unlikely to affect body condition of their hosts, the 'negative effects' of mites found in some studies are likely to be explained by correlations between mite abundance and the abundance of true parasites (Blanco *et al.*, 2001). This association between true parasites and non-parasitic feather mites may be mediated by behavioural changes in parasitized birds, which usually devote less time to preening than healthy individuals and hence may be less capable to get rid of feather-dwelling ectosymbionts (Blanco *et al.*, 2001). Whatever the case, the abundance of proctophyllodid mites can be used as

an indicator of overall parasite infections (Thompson *et al.*, 1997; Harper, 1999), which is a realistic assumption because (1) birds infected by pathogenic parasites – like pox-viruses or some endoparasites – have been found to hold more mites than parasite-free birds (Marshall, 1981; Thompson *et al.*, 1997), and (2) chickens whose immunoresponsiveness was experimentally increased showed a lower intensity of infection by mites (as well as by pathogenic parasites like *Mycoplasma*, *Eimeria* and splenomegalia viruses) than others whose immune defence was lowered (Boa-Amponsem *et al.*, 1997).

 During 1997 and 1998, we searched for true ectoparasites on 83 adult and 96 fledgling blackcaps, on which we also counted feather mites. A detailed visual inspection of feathers and skin was carried out on head, neck, back, breast and belly of blackcaps. We found lice (Mallophaga, infecting seven adults and 10 fledglings), ticks (Ixodidae, on one adult and one fledgling) and louse flies (Hippoboscidae, on five fledglings), which have all been proved to be detrimental to their hosts (e.g. Lehman, 1993; Clayton & Moore, 1997). We used these data to evaluate whether mite load may actually indicate infection by true parasites in blackcaps, as it has been found in other species (Boa-Amponsem *et al.*, 1997; Thompson *et al.*, 1997).

 We evaluated possible variation between localities in mite prevalence (the proportion of individuals that were infected) and mite abundance (the number of mites counted per host), which could confound the relationship between mite abundance and feather traits if the latter also varied between populations (Bennett *et al.*, 1995). We also analysed whether mite load varied in relation to other possible confounding factors, such as date and time of capture or body mass of birds (Blanco *et al.*, 1997; Jovani & Blanco, 2000; Blanco & Frías, 2001).

STATISTICAL ANALYSES

We did not consider gender in our analyses, because fledgling blackcaps are sexually monomorphic and hence only adults could be sexed. Condition-dependent traits may be exhibited by both males and females due to genetic correlation between sexes (Falconer, 1989). In this case, the expression of such characters may be negatively related to parasite load in both sexes (Potti & Merino, 1996). The tail of blackcaps shows no ornament or sexual dimorphism in size, shape or colour (Tellería & Carbonell, 1999; Shirihai *et al.*, 2001), so its expression is unlikely to depend on different selection pressures on males and females (Amundsen, 2000). On the other hand, we did not find differences between adult males and females in mite prevalence (Fisher exact test: $P = 0.65$) or abundance ($F_{1,27} = 0.34$, $P = 0.57$). Similar results (not shown) were found when

locality was controlled for, although within-cell sample size was much smaller in these analyses.

We assessed variation between populations and age classes in mite prevalence by means of log-linear analysis (StatSoft, 1999). We also evaluated to what extent individual variation in wing length—a measure of the size of the habitat potentially available to mites—is associated to variations in mite load in our sample (Rózsa, 1997). The distribution of parasites is usually aggregated, with many hosts lacking parasites and a few suffering strong infections (Margolis *et al.*, 1982). However, the majority of blackcaps held mites in our study, which buffered aggregation and allowed mite abundance to adjust to a normal distribution after log-transformation (Filliben's correlation between observed and expected probit-transformed frequencies: $r = 0.95$, test for deviation from $r = 1$: $F_{1,72} = 1.98$, $P = 0.16$, see StatSoft, 1999). Because of this, we used parametric statistics to test for interactions, estimate effect sizes and partition out the variation accounted for by each variable.

We analysed whether parasite load was correlated with the different traits measured on blackcaps' feathers, and also if such correlations were common to adults and juveniles. All the feather traits measured in our study are different components of the same process: feather growth. This may be viewed as a non-measurable variable defined by the covariation between growth rate, length, mass and symmetry of feathers (these traits correlated to each other more than expected by random, as shown by a Bartlett's test for sphericity with $P < 0.0001$). Because of this, we first conducted a multivariate general linear model testing for variation in all four variables together in relation to age and mite abundance. This model included population and age as categorical predictors, and mite abundance as a continuous predictor (resembling a multivariate two-way ANCOVA), but also included the interaction between age and mite abundance, thus testing for changes between age classes in the effect of mite load on feather traits. Once the relationship between mite abundance and the feather growth process was examined, we conducted separated analyses for each trait (that is, protected models) to estimate their particular contribution to overall variation in tail characteristics. When interactions between age and mite load were obtained, we evaluated a posteriori the effect of mite abundance on feather traits of adults and fledglings, considering in this analyses all the terms that were significant in the initial models.

Missing values for some of the variables utilized led to different sample sizes in our analyses. We transformed variables when it was necessary to meet the assumptions of parametric statistics. All analyses involving general linear models were done with the Visual GLM module implemented in STATISTICA ® 5.5 (StatSoft, 1999).

RESULTS

MITE PREVALENCE AND ABUNDANCE

The prevalence of mite infections was high and homogeneous between localities and age classes (Table 1). The log-linear analysis with the frequency of adults and fledgling that held mites in each site found no association between mite prevalence and age ($\chi^2_1 = 0.06$, $P = 0.80$), nor between mite prevalence and locality ($\chi^2_1 = 1.24$, $P = 0.27$). This caused a lack of fit of any model including interactions (Chi-square of goodness-of-fit to the lack of two–way interactions: $\chi^2_3 = 4.89$, $P = 0.17$). The intensity of infection (Table 1) was similar to that obtained in other Iberian blackcap populations (cf. Behnke *et al.*, 1999), it did not vary either between localities or age classes, and it was not influenced by wing size of blackcaps (Two-way ANCOVA, Locality: $F_{1,71} = 0.38$ $P = 0.54$, Age: $F_{1,71} = 0.14$ $P = 0.71$, locality × age: $F_{1,71} = 0.10$ $P = 0.75$, Covariate wing length: $F_{1,71} = 0.10$ $P = 0.75$, all test of parallelism with $P > 0.07$).

Date and time of capture had no influence on mite load (date $F_{1,73} = 0.27$, $P = 0.60$, time $F_{1,73} = 0.21$, $P = 0.65$, non-significant population and age effects not estimated), and neither mite abundance was associated with the body condition of their hosts measured as body mass relative to body size (ANCOVA with body mass as the dependent variable, age and population as factors, and mite abundance and tarsus length—a measure of body size—as covariates, variables Log_{10}-transformed to linearize relationships: age $F_{1,68} = 4.93$, $P = 0.030$, population $F_{1,68} = 4.78$, $P = 0.032$, body size $F_{1,68} = 16.85$, $P < 0.001$, mite abundance $F_{1,68} = 0.001$, $P = 0.98$, all interactions between independent variables with $P > 0.25$).

MITE ABUNDANCE AND INFECTION BY DELETERIOUS PARASITES

Among fledglings, individuals infected by ectoparasites (lice, ticks or louse flies) held more mites than non-infected birds ($F_{1,94} = 6.03$ $P = 0.016$; Fig. 1). However, this effect was not significant in adults ($F_{1,82} = 1.12$ $P = 0.29$), although the small prevalence of ectoparasites (n = 8 adults) combined with a troublesome statistical distribution of mite abundance (which led to a standard error in this group five times larger than in-non-parasitized birds) made this result hardly reliable. Notwithstanding the analytical caveats associated to the very small number of blackcaps infected by ectoparasites, our results with fledglings support the assumption that the abundance of
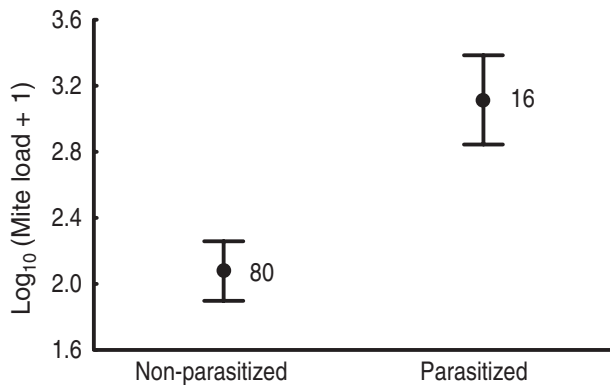
Figure 1. Variation in abundance of proctophyllodid feather mites of fledgling blackcaps in relation to infection by deleterious ectoparasites (lice $n = 10$, ticks $n = 1$, and louse flies $n = 5$). Means, standard errors and sample sizes are shown.

feather mites is correlated with infections by true parasites. We could not assess whether these parasites may affect feather growth, because only five parasitized birds were sampled for feathers.

MITE LOAD AND THE FEATHER GROWTH PROCESS

As a first step in our analyses, we checked for potential confounding factors affecting each feather trait measured. We studied whether feather length influenced feather growth rates (Grubb, 1995) by using a model including feather length as a covariate together with mite load. This showed that feather growth rate did not depend on final feather length (effect of feather length: $r^2 = 0.005$, $F_{1,61} = 0.60$, $P = 0.44$), this relationship being common to both populations (interaction between feather length and population: $r^2 = 0.014$, $F_{1,61} = 1.83$, $P = 0.18$) and age classes (interaction between feather length and age: $r^2 = 0.006$, $F_{1,61} = 0.82$, $P = 0.37$). Given that the final size of feathers did not influence the relationship between mite load and feather growth rates, we did not consider feather size in further analyses.

We also checked the methodological assumptions of the analysis of fluctuating asymmetry (reviewed by Swaddle *et al.*, 1994). Signed right minus left values of feather length were normally distributed (Kolmogorov-Smirnov test: d = 0.93, $n = 67$, Lilliefors' $P = 0.20$) and averaged zero (one-sample *t*-test: $t = 0.59$, d.f. = 66, $P = 0.55$). We derived normally distributed absolute values of asymmetry by using the Box-Cox transformation FA′ = $(FA + 0.01)^{0.009}$, where 0.01 is the smallest value in the distribution and 0.009 is a coefficient that allows the best fit to the normal distribution (Swaddle *et al.*, 1994). Results of Filliben's correlation showed a suitable fit to normality ($r = 0.92$, test for deviation from $r = 1$: $F_{1,65} = 2.69$, $P = 0.11$).

Controlling for variation in the feather growth process in relation to age and locality, the multivariate model including all feather traits as dependent variables showed a slight but significant effect of mite abundance on feather characteristics (Wilks' lambda = 0.84, $F_{4,57} = 2.62$, F obtained by Rao's approximation, $P = 0.044$). However, the weakness of the effect of mite abundance was due to the existence of marked difference between age classes (interaction between mite load and age: Wilks' lambda = 0.79, $F_{4,57} = 3.74$, $P = 0.0090$). Thus, controlling for site effects we found no effect of mite load on overall variation in feather traits of adults (Wilks' lambda = 0.83, $F_{4,17} = 0.90$, $P = 0.48$, although the small sample size could have caused a lack of statistical power). However, there was a strong correlation between mite load and feather characters in fledglings (Wilks' lambda = 0.50, $F_{4,37} = 9.39$, $P < 0.0001$). These results show that there is an effect of mite abundance on feather growth, and that this effect changes between age classes. Therefore, we conducted protected analyses with each particular feather trait to evaluate their particular contributions to overall variation in feather characters in relation to age and mite abundance.

MITE LOAD AND FEATHER GROWTH RATE

Controlling for mite abundance, blackcaps showed higher feather growth rates in Álava than in Guadarrama, and adults grew their feathers faster than juveniles in Álava but not in Guadarrama, which led to a significant interaction between population and age (Table 2). Feather growth rate was correlated with mite load in fledgling but not in adult blackcaps, which masked the effect of mite load in the model but led to a significant interaction between age and mite abundance (Table 2). A posterior evaluation of this effect within age classes, controlling for variation between populations, showed that mite abundance explained 16% of variation in feather growth rate of fledgling blackcaps ($r^2 = 0.160$, $F_{1,43} = 9.41$, $P = 0.0037$), but was not correlated with feather growth rate of adults ($r^2 = 0.031$, $F_{1,24} = 1.66$, $P = 0.21$; Fig. 2).

MITE LOAD AND FEATHER SIZE AND QUALITY

Controlling for wing length, both adult and fledgling blackcaps had a similar feather size, although they reached a slightly longer tail in Guadarrama than in Álava (Table 2). No correlation could be found between mite load and feather size in juveniles or in adults (Table 2, Fig. 2). However, like growth rate, feather quality showed different associations with mite load depending on age, leading to an interaction between age and mite abundance (Table 2). A posterior evaluation of the effect of mite load within age classes

Table 2. Results of general linear models analysing the variation in feather length (controlling for wing length), feather quality (measured as the ratio feather mass/feather length), feather growth rates (measured as the width of 10 growth bars) and fluctuating asymmetry of feather length in relation to locality, age and mite abundance. The size of effects (r^2) is also shown

	Feather length			Feather quality			Feather growth rate			Feather asymmetry		
	$F_{1,65}$	P	r^2	$F_{1,61}$	P	r^2	$F_{1,67}$	P	r^2	$F_{1,61}$	P	r^2
Locality	4.51	0.038	0.035	0.71	0.402	0.009	38.30	<0.0001	0.307	0.08	0.783	0.001
Age	0.48	0.490	0.004	12.75	0.0007	0.165	4.63	0.035	0.037	0.03	0.874	0.0004
Locality × age	0.18	0.674	0.001	1.70	0.197	0.022	13.43	<0.0001	0.108	0.45	0.506	0.006
Mite load	0.20	0.653	0.002	0.10	0.756	0.001	0.10	0.749	0.001	6.30	0.015	0.091
Wing length	52.77	<0.0001	0.412	–	–	–	–	–	–	–	–	–
Age × mite load	0.95	0.334	0.007	8.82	0.0043	0.114	8.09	0.006	0.065	0.01	0.930	0.0001
Test of parallelism	0.90	0.178	*	1.31	0.258	†	0.001	0.982	†	0.23	0.637	†

* The most significant of all interaction terms is shown (d.f. = 1,61).

† Locality × mite load interaction, not included in the model.

showed that feather quality was not correlated with mite load in adults ($r^2 = 0.094$, $F_{1,22} = 2.28$, $P = 0.15$), but significantly decreased with intensity of infection in fledgling blackcaps ($r^2 = 0.171$, $F_{1,41} = 8.43$, $P = 0.0059$; Fig. 2).

MITE LOAD AND FLUCTUATING ASYMMETRY

Fluctuating asymmetry of feather length was homogeneous between populations and age classes. However, asymmetry was positively correlated with mite load (Fig. 2), this effect being common to adult and fledgling blackcaps as shown by the lack of interaction between age and mite load in the model (Table 2).

DISCUSSION

The health status of blackcaps at the moment of feather development was apparently related to the expression of their feather characters, as shown by the negative correlations found between mite load (an indicator of parasite infection) and feather growth rate, quality and symmetry in fledglings. However, contrasting with other work (Thompson *et al.*, 1997; Harper, 1999) the final feather size was not correlated with intensity of infection in our study. Small sample size alone cannot account for this negative result: mite load explained only 0.1% of variance in feather size, which is a very small effect compared with that found in other species for feather length (Thompson *et al.*, 1997; Harper, 1999) or for other traits in our study. In blackcaps, this lack of correlation between mite infections and feather size could be due to different factors, other than body condition, that could also affect

feather dimensions. Although feathers may achieve a smaller size due to nutritional restrictions (Murphy *et al.*, 1988), in general their dimensions are highly heritable, particularly when they are important for flight performance (Berthold & Querner, 1982; Boag & van Noordwijk, 1987; Potti, 1999). In blackcaps, an experimental manipulation of the quality of diet supplied to nestlings produced a similar feather length in both the control and the undernourished groups, although the latter took longer to achieve the final feather size (Berthold, 1976). That final feather size does not depend on nutritional condition in blackcaps is also shown in our study by an absence of correlation between feather length and growth rate (which measures the competence of individuals to produce feather material). However, although feather size did not vary with intensity of infection, growth rates, feather quality and symmetry were negatively related to mite load in young individuals. This is consistent with the view that different traits differentially respond to deprivation imposed by parasite challenges (Møller *et al.*, 1998). Indeed, mite abundance showed highest correlations with feather quality and growth rate, which are closely dependent on body condition during feather growth (Murphy *et al.*, 1988; Grubb, 1995).

Previous analyses of the relationship between proctophyllodid mite load and condition-dependent feather traits of birds have shown a reduced ornamentation (shorter and duller feathers) with increasing infection, but also a lack of correlation outside the moult period. Thus, in several passerine species in which mites were counted during the active moult, mite abundance was negatively correlated with the final size and brightness of feathers (Harper, 1999). However, no such effect of mite abundance could be found in a study of male linnets *Carduelis cannabina* whose mite load
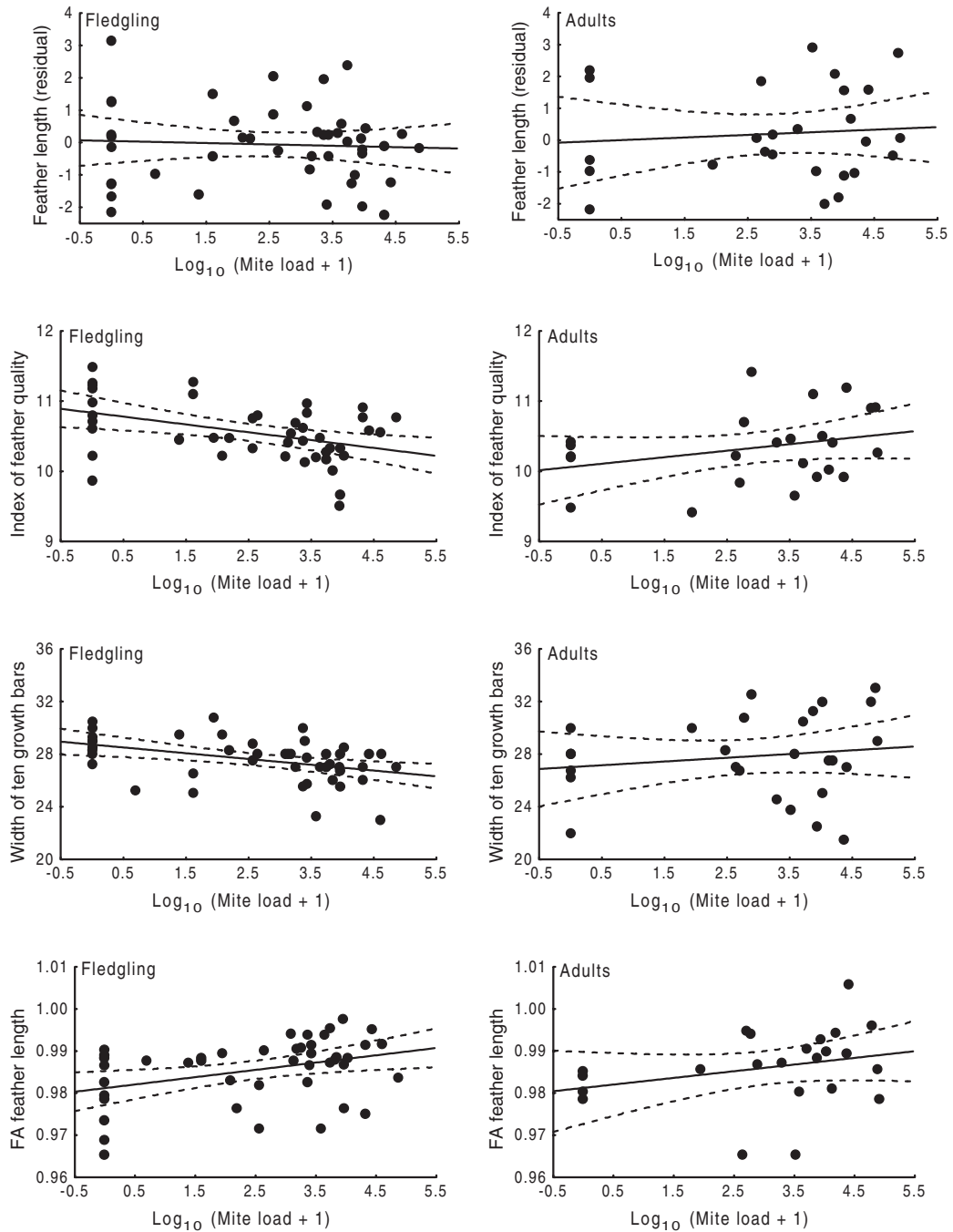
Figure 2. The correlation between mite load and size (controlling for wing length), quality (feather density measured as the ratio feather mass/feather length), growth rate (measured as width of 10 growth bars) and fluctuating asymmetry (FA) of feathers in fledgling and adult blackcaps. Regression lines and 95% confidence bands are shown.

was measured several months after moult (Blanco *et al.*, 1999). Finally, Thompson *et al.* (1997) tested for year-round variation in the relationship between mite load and plumage brightness in house finches *Carpodacus mexicanus*. They found a negative correlation between intensity of infection and feather ornamenta-

tion in freshly moulted individuals, but not in birds studied several months after moult. Our results are consistent with others in showing negative correlations between condition-dependent traits (feather quality and growth rates) and parasite load during feather development, which were no longer found

several months after feather growth. Nonetheless, our results also indicate that different traits may have a different value as indicators of health status of their bearers at different times of year, as shown by the negative correlation between mite load and feather symmetry in both juvenile and adult blackcaps.

The studies so far conducted to test for parasite-mediated expression of morphological traits in wild animals have produced mixed results (for a review see Møller & Saino, 1999). Some of them have found a negative correlation between parasite load and trait expression (e.g. Milinski & Bakker, 1990; for feather mites see Thompson *et al.*, 1997), but others have failed to detect such an effect (e.g. Seutin, 1994; for feather mites see Blanco *et al.*, 1999). This inconsistency could be partially explained because most studies have dealt with only one or two characters. For example, little attention has been paid to the possible differences among traits in the degree to which they are condition-dependent, or in their suitability for reflecting the phenotypic quality of their bearers. In turn, whether a negative association between the expression of morphological traits and parasitism is detectable at different times of year could largely depend on the traits considered.

Correlational studies have the drawback that they cannot overcome important caveats on the functional relationship between feather traits and parasites. One problem is that natural variation in feather traits that is not mediated by body condition could confound the relationship between final feather characters and parasite load (Thomas *et al.*, 1995). For example, the relation between parasites and feather traits may be confounded by concomitant relations, on the one hand between age and feather size and/or brightness (Savalli, 1995; Pérez-Tris & Tellería, 2001), and on the other hand between age and parasite load (Potti & Merino, 1995; Thomas *et al.*, 1995). In addition, plumage characters may be to a large extent inherited, especially feather dimensions (Berthold & Querner, 1982; Boag & van Noordwijk, 1987; Potti, 1999). Individuals with inherited, condition-independent shorter wings and duller feathers may hold more ectoparasites because they are subordinates in foraging flocks or territorial contests (size and colouration are good correlates of dominance, Mateos & Carranza, 1997; Senar & Camerino, 1998) and hence devote less time to preening (Clayton, 1991b; Møller, 1991). In these hypothetical cases, condition-dependence would not have been involved in the expression of traits. The study of multiple characters with different degrees of condition-dependence may help overcome these problems. For example, traits such as feather quality and feather growth rates have been proved to be more dependent on body condition than feather size (Murphy *et al.*, 1988; Grubb, 1995; Carbonell &

Tellería, 1999), and consistent with this fact they were better related to parasite load in blackcaps. In our view, to combine genuine ornaments (such as size, quality, symmetry and colour) with features of these traits that fairly signal condition-dependence (like growth rates in the case of feather ornaments) could allow a more satisfactory interpretation of how parasites affect the expression of ornaments in correlational studies.

PARASITES AND THE EVOLUTION OF TAIL ORNAMENTATION

Because immunocompetence does not demand as much energy as does growth (Møller *et al.*, 1998), parasites might affect less intensely the expression of a nonexaggerated tail than the production of a costly ornament. In that case, the early evolution of tail ornamentation would have been driven by processes independent of parasite resistance, of the type of runaway sexual selection due to genetic correlation between female preferences and male ornamentation (Fisher, 1930). However, our results support the idea that parasites may impair the expression of non-ornamental feather traits, and hence might have affected tail ornamentation ever since its initial evolutionary stages.

We found no correlation between parasitism and the size of blackcap's tails, hence our results fail to support the view that feather elongation might have been affected by parasitism before the tail became a true ornament. As discussed above, both mechanical and production costs of a long tail may not be counterbalanced by signalling benefits in a non-ornamented species (Balmford *et al.*, 1993). However, the tails of highly parasitized blackcaps were lighter and less symmetrical, and moreover they grew at lower rates. Both feather consistency and symmetry are important components of tail ornamentation, whose signalling value has been amplified in many ornamented species (Fitzpatrick & Price, 1997). For example, ornamented tails are characterized by shapes which increase the difficulty of producing a symmetric tail (such as the presence of tail streamers or tail graduation; Møller, 1994; Fitzpatrick, 1998a). Ornamented tails may also show special colour schemes, such as non-pigmented areas. Because melanin confers durability to feathers, birds that are able to maintain fresh white patches on tail are demonstrating a high feather consistency (Bonser, 1995; Fitzpatrick, 1998a, 1998b). Recent studies even suggest that white spots could be ornaments designed to reveal infection by feather-dwelling ectoparasites (Kose & Møller, 1999).

Within the genus *Sylvia*, tail ornamentation has evolved in the form of tail graduation (an amplifier of the signalling value of tail symmetry) and the appear-

ance of white patches symmetrically positioned on the rectrices (an amplifier of the signalling value of both tail symmetry and feather consistency), which are exhibited by all species in the genus except the ancient species pair formed by blackcaps and garden warblers, *Sylvia borin* (Shirihai *et al.*, 2001). Remarkably, tail symmetry and feather density were negatively affected by mite load in one of these ancient species, supporting the idea that the association between parasites and condition-dependent tail features could have played a role in the evolution of tail ornamentation in these warblers.

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