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Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird

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Migratory birds have less time for moulting than sedentary birds, which may force them to produce their feathers faster at the expense of reducing feather quality. However, the effects of migration on the trade-off between moult speed and plumage quality remain to be studied in natural populations. We analysed the relationship between growth rate and quality of individual feathers, taking advantage of natural variation between migratory and sedentary populations of blackcaps *Sylvia atricapilla*. As predicted by life-history theory, individual blackcaps showed variable individual quality, which was revealed by positive correlations between feather growth rate and feather mass within populations. However, migrants grew up their feathers faster, producing lighter feathers than sedentary blackcaps. These results support the idea that feather growth rate and feather quality are traded against each other in blackcaps. Such a trade-off is apparently caused by different selection associated to migratory and sedentary life styles, which opens new insights into the diversification of moult patterns in birds. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **97**, 98–105.

ADDITIONAL KEYWORDS: bird migration – individual quality – moult – ptilochronology – *Sylvia atricapilla*.

INTRODUCTION

Trade-offs between costly traits contribute to explain phenotypic variation in natural populations (Roff, 1992; Stearns, 1992). Such trade-offs have been studied in a wide variety of organisms, but birds have been favourite research models. For example, avian studies have greatly contributed to understand trade-offs involving survival, reproduction, and development (Bennett & Owens, 2002). However, there are major events in the life cycle of birds whose evolution remains poorly investigated. One such event is moulting, the process through which birds replace old feathers by new ones, which is essential for maintaining plumage functions, such as body insulation, flight ability or social communication (Ginn & Melville, 1983). This process requires a substantial amount of energy and time, which could otherwise be used for other functions (Jenni & Winkler, 1994). Accordingly, moulting seldom overlaps with other costly activities in the life cycle of birds, such as reproduction or migration (Jenni & Winkler, 1994; Hemborg & Lundberg, 1998; Norris *et al.*, 2004).

Most passerine species replace the whole plumage annually after reproduction, moulting in their breeding territories before migration in migratory species or populations. Therefore, the time available for moulting depends on the timing of migration, which might force early-migrating birds to moult faster than late-migrating ones (Jenni & Winkler, 1994; Kjellén, 1994). Although time constraints on moult duration could have contributed to the diversification of moult patterns in birds (Svensson & Hedenström, 1999; Hall & Tullberg, 2004), the consequences of such constraints have rarely been investigated in natural populations.

To date, time constraints on moulting have been investigated mainly by manipulating the photoperiod

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*Corresponding author. E-mail: idelahera@bio.ucm.es in the laboratory. Birds subjected to a shortened moult period grow up their feathers faster, but produce feathers of lower quality than normally-timed birds (Dawson *et al.*, 2000; Hall & Fransson, 2000; Serra *et al.*, 2007). According to these experiments, rapid moulting is probably possible only at the expense of reducing plumage quality, which may impair feather function (Dawson *et al.*, 2000; Serra, 2001). However, photoperiod manipulations cannot incorporate other costs of migration that can greatly affect the moult process, such as fattening and flight costs (Lindström, Dann & Visser, 1994; Bonier *et al.*, 2007). In turn, our knowledge of natural variation in feather traits in relation to migratory behaviour is limited, which seriously hampers our understanding of the consequences of migration on the trade-off between moult speed and plumage quality.

Unfortunately, trade-offs are difficult to detect in natural conditions because territory quality, social status or endogenous differences in the efficiency with which resources are stored and mobilized all differ between individuals, which can mask negative relationships between conflicting traits (Stearns, 1992; Cuthill & Houston, 1997). As a consequence of variation in individual quality, counterintuitive positive correlations are often observed between traits expected to trade against each other (Van Noordwijk & De Jong, 1986). An alternative to experiments in the study of trade-offs in unmanipulated populations may comprise the analysis of populations in which conflicting traits are subjected to disruptive natural selection (Roff, 1992). In such cases, life-history theory allows predictions to be made about the variation of such traits, both among individuals within populations in relation to differences in phenotypic quality, and among populations in relation to trade-offs between traits.

We used migratory and sedentary populations of blackcaps *Sylvia atricapilla* to investigate natural variation in moult performance in relation to migratory behaviour. Migratory blackcaps need to complete their moulting soon after reproduction to avoid the cost of overlapping moulting with migration, whereas sedentary blackcaps are less time-constrained because they do not migrate (Kjellén, 1994; Bonier *et al.*, 2007). As a consequence, migratory blackcaps may be selected for an increased moult speed, whereas sedentary blackcaps may be selected for increased feather quality instead, which they can afford because they can moult at a slower pace (Serra, 2001).

The question remains as to whether increasing feather growth rate comes at the expense of low feather quality in migratory blackcaps, and whether such a trade-off can be observed in natural populations. According to Van Noordwijk & De Jong (1986), we predict that variation in individual quality will cause positive correlations between feather growth rate and feather quality in both migratory and sedentary blackcap populations (Fig. 1). However, if blackcaps trade feather growth rate against feather quality, we predict that migratory blackcaps will develop their feathers more rapidly, but will produce feathers of lower quality than sedentary blackcaps (Fig. 1).

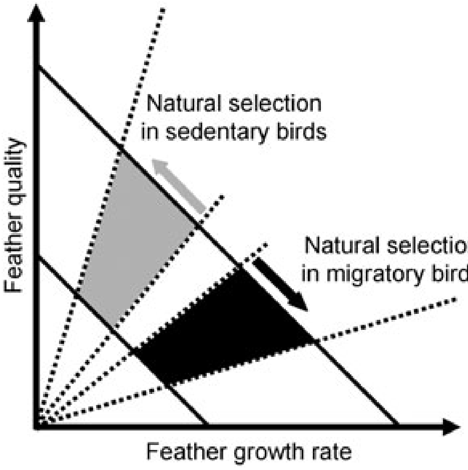

Figure 1. Predicted relationships between feather growth rate and feather quality in migratory and sedentary birds. The possible outcomes of such relationship are bounded by the range of individual phenotypic qualities indicated by solid lines (which reflect variable amounts of resources available to individuals for feather production) and the range of resource allocation rules along the trade-off between feather growth rate and feather quality, indicated by broken lines. In migratory populations, natural selection favours faster feather production, which constrains feather quality within low levels (black area). However, in sedentary populations natural selection favours high feather quality (grey area), which should be associated to slow feather growth. Although feather growth rate and feather quality are traded against each other by migratory and sedentary populations, both traits are positively correlated within populations, revealing variation in phenotypic quality among individuals (note that both black and grey areas point upwards in the graph; for details, see Van Noordwijk & De Jong, 1986).

MATERIAL AND METHODS

STUDY AREA AND GENERAL METHODS

We studied blackcaps wintering in the Campo de Gibraltar region, southern Spain (36°01′N, 5°36′W), where local sedentary blackcaps share the habitat with migratory blackcaps that breed in northern and central Europe (Pérez-Tris & Tellería, 2002). We mist-netted birds in different habitat types to secure a broad representation of the different populations wintering in the area (Pérez-Tris & Tellería, 2002).

We captured 456 blackcaps during five consecutive seasons, between January and February from 2001 to 2005. We distinguished first-year birds from older birds (hereafter termed adults) because blackcaps have two generations of feathers during their first year of life, resulting from a partial moult of the juvenile plumage (Svensson, 1992; Jenni & Winkler, 1994). Given that first-year birds have never-moulted flight feathers but keep the juvenile set of feathers, we did not consider them in our analyses of feather growth rate and quality.

We measured blackcaps to distinguish between sedentary and migratory individuals, for which we took advantage of the great morphological variation associated with migratory behaviour in this species (Tellería & Carbonell, 1999). We combined the length of the eighth primary feather, the length of the tail, and the difference between the primary distances 1 and 9 (distances from the tip of each primary feather to the wing tip) in a discriminant function analysis, which has been shown previously to correctly classify approximately 90% of Iberian breeding blackcaps as either migratory or sedentary (Pérez-Tris, Carbonell & Tellería, 1999). Conveniently, the discriminant function greatly improves its ability to correctly classify individuals when northern migrants, which have exaggerated migratory-like morphology, are included in the sample. Increased discriminating power in sympatrically wintering populations is revealed by higher posterior classification probabilities of birds classified as migratory (De la Hera, Pérez-Tris & Tellería, 2007). Thus, although we assume that approximately 10% of sedentary birds have been incorrectly classified as migratory in the present study (four out of 40 cases), we can safely assume that less than 1% of birds classified as migratory were misclassified (De la Hera *et al.*, 2007). It is also important to note that incorrectly classified birds lower the statistical power of our comparisons, meaning that the possibility that some birds were misclassified actually makes the study conservative.

ANALYSIS OF FEATHER TRAITS

Information on individual moult performance can only be obtained by directly monitoring birds in active moult, which is impractical (Ginn & Melville, 1983; Bensch & Grahn, 1993). However, feather growth rate and feather quality can easily be measured on individual feathers plucked to birds. Although using traits of individual feathers as proxies of the characteristics of the whole plumage remains to be validated, such a method greatly facilitates the analysis of moulting in natural populations.

In the field, we collected the fifth pair of tail feathers (rectrices) from each individual, counting from the innermost to the outermost feather. Feathers were stored in dry paper envelopes until laboratory analyses. To avoid any source of bias, all feather measurements were taken by the same person (I.H.). We measured the total length of the feathers (the distance from the calamus base to the distal feather tip) using a Mitutoyo 500 digital calliper (0.01 mm resolution). We also measured the width of ten growth bars, counting five bars on either side of the point located at two thirds of the total feather length (Grubb, 2006). Feather growth bars are formed by one light band and one dark band, corresponding to feather material produced during the night and day, respectively (Brodin, 1993). Therefore, ten growth bars represent the amount of feather material produced during 10 days of feather growth; the wider the growth bars, the faster the growth of feathers (such a direct estimation of individual feather growth rate based on feather growth bars is technically known as ptilochronology; Grubb, 2006). Obviously, moult speed not only depends on individual feather growth rate, but also is determined by the number of simultaneously growing feathers. Because the present study was based on individual feathers, we could only investigate one of these two components of moult speed, which somewhat limits the reach of our conclusions. However, birds that moult many feathers at once also grow their feathers faster (Bensch & Grahn, 1993), supporting the idea that our measures of feather growth rate are suitable correlates of moult speed.

We used feather mass as a proxy to feather quality (Carbonell & Tellería, 1999). Direct measures of feather quality are difficult to obtain and may be less reliably measured than feather mass (which may be unambiguously measured with a high-resolution balance). However, feather mass can only be used as a measure of feather quality if variation in feather mass is correlated with the development of structural elements that determine feather quality. For example, both the durability and the aerodynamic properties of feathers depend on structural features, such as the density of barbs on the feather vane or the width of the feather rachis, which in turn determine variation in feather mass. Such relationship has been demonstrated in European starlings, *Sturnus vulgaris*, that were experimentally forced to produce either high-quality or low-quality feathers (Dawson *et al.*, 2000). In this species, both feather stiffness and hardness (i.e. two important determinants of feather aerodynamic properties; Bonser & Purslow, 1995; Bonser, 1996; Corning & Biewener, 1998) were positively correlated with the width of the feather rachis, which was in turn positively correlated with feather mass (Dawson *et al.*, 2000).

We weighed feathers using a Mettler Toledo AG-245 digital balance (instrumental repeatability: 0.01 ± 0.02 mg). We also measured the maximum dorsiventral width of the rachis at the base of the feather vane, the density of feather barbs (i.e. number of barbs counted on a 10-mm section located at the centre of the feather; Aparicio, Bonal & Cordero, 2003), and the length of the inner feather barbs (i.e. maximum barb length in the same section of the feather). Barb density and barb length were measured with the aid of a microscope (×10 magnification). Feather mass primarily depended on feather length, but it was also positively correlated with all structural traits analysed (Table 1), thereby confirming the relationship between mass and structural complexity of feathers in blackcaps.

STATISTICAL ANALYSIS

We estimated the repeatability of feather traits by blindly measuring twice 15 randomly selected feathers, with an elapsed time between measurements of 1–12 months. The repeatability of all feather traits was high and statistically significant (feather length: $r_i = 0.99$; feather mass: $r_i = 0.99$; feather growth rate: $r_i = 0.91$; rachis width: $r_i = 0.85$; barb density: $r_i = 0.93$; barb length: $r_i = 0.97$; all $P < 0.0001$).

Table 1. Results of a general linear model analysing variation in feather mass in relation to structural features (feather size, rachis width, barb density, and barb length). The analysis includes the sex and migratory behavior of birds as potential confounding variables ($N = 175$)

	Beta	d.f.	*F*	*P*
Migration		1,167	2.12	0.147
Sex		1,167	6.22	0.014
Migration × Sex		1,167	0.13	0.717
Feather length	0.610	1,167	113.41	< 0.0001
Rachis width	0.327	1,167	35.59	< 0.0001
Barb density	0.161	1,167	5.63	0.019
Barb length	0.185	1,167	7.74	0.006

We used general linear models (GLM) to analyse variation in feather growth rate and feather mass between migratory and sedentary blackcaps. Such models included sex and year as fixed effects, and feather length as a covariate to control for possible effects of feather size on growth rate or mass. We specifically tested for differences between migratory and sedentary blackcaps in the slope of the relationship between feather growth rate and feather quality (estimated by the interaction between migratory behaviour and the covariate in the models). To increase statistical power to detect such interaction, we reduced the number of parameters in the model by means of the best subsets method for model selection implemented in the GRM module of STATISTICA, version 6.1, which selects the best model based on effect sizes (Statsoft, 2002).

We used the average trait values of both feathers in our analyses. A few feathers were dirty and therefore could not be accurately weighed, and others did not have visible growth bars. All these feathers were excluded from the corresponding analyses, which caused variation in sample size among analyses.

RESULTS

FEATHER GROWTH RATE AND QUALITY

A GLM of feather growth rate revealed a significant effect of feather length on feather growth rate, with longer feathers growing up faster than shorter feathers. Controlling for such effect, migratory blackcaps grew up feathers faster than sedentary blackcaps (Fig. 2A, Table 2).

Table 2. Results of a general linear model analysing variation in feather growth rate and feather mass, in relation to migratory behavior, sex and year of capture of blackcaps, and including feather length as a covariate

	Feather growth rate ($N = 175$)				Feather mass ($N = 176$)			
	Beta	d.f.	*F*	*P*	Beta	d.f.	*F*	*P*
Migration		1,154	23.62	< 0.0001		1,155	8.90	0.003
Sex		1,154	2.19	0.141		1,155	5.98	0.016
Year		4,154	0.30	0.878		4,155	0.56	0.693
Migration × Sex		1,154	1.86	0.174		1,155	1.92	0.168
Sex × Year		4,154	0.51	0.729		4,155	0.92	0.453
Migration × Year		4,154	0.67	0.612		4,155	2.00	0.097
Three-way interaction		4,154	0.82	0.515		4,155	1.21	0.310
Feather length	0.517	1,154	64.54	< 0.0001	0.637	1,155	107.05	< 0.0001

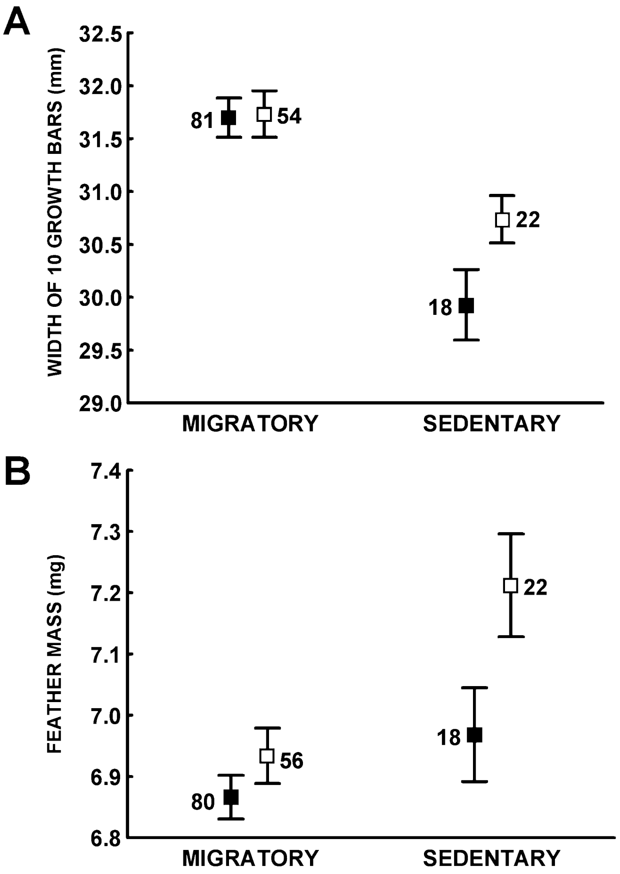

Figure 2. Variation in feather growth rate (A) and feather mass (B) between migratory and sedentary blackcaps. Variation between males (black squares) and females (open squares) is also shown. The graphs show means (adjusted by other effects included in the models shown in Table 2), standard errors and sample sizes.

Feather mass was also positively correlated with feather size, and also varied in relation to sex, with females producing heavier feathers than males. Controlling for these effects, migratory blackcaps produced lighter feathers than sedentary blackcaps (Fig. 2B, Table 2).

FEATHER GROWTH RATE AND FEATHER QUALITY OF INDIVIDUAL BLACKCAPS

We found a positive relationship between feather growth rate and feather mass in blackcaps, which did not reach statistical significance (Table 3), probably because such relationship changed between population types (i.e. the interaction between migratory behaviour and feather growth rate was significant; Table 3). The increase in feather mass with increasing feather growth rate was steeper in sedentary blackcaps (beta = 0.29) than in migratory blackcaps (beta = 0.09; Fig. 3). When estimated separately, these effects did not reach statistical significance due to the loss of statistical power associated to smaller sample sizes (sedentary blackcaps $P = 0.12$, $N = 40$, power = 0.28; migratory blackcaps $P = 0.22$, $N = 130$, power = 0.15; power of the interaction between migratory behaviour and feather growth rate in the model = 0.74).

DISCUSSION

The results obtained in the present study reveal a negative correlation between feather growth rate and feather quality between migratory and sedentary populations, which is expected if moulting birds trade these two traits against each other. Such result, which has seldom been observed in natural populations, was revealed in blackcaps by using ptilochro-

Table 3. Reduced general linear model (best subsets solution) analysing variation in feather mass in relation to feather growth rate in migratory and sedentary blackcaps. All variables used in the analysis are shown, but the statistics have been computed only for variables included in the final model ($N = 170$).

	d.f.	Beta	*F*	*P*
Migration				
Sex				
Year	4,158		0.57	0.684
Feather length	1,158	0.551	57.50	< 0.0001
Feather growth rate	1,158	0.146	3.56	0.061
Sex × Migration				
Sex × Year				
Migration × Feather growth rate	1,158		11.27	0.001
Migration × Year	4,158		2.31	0.060
Sex × Migration × Year				

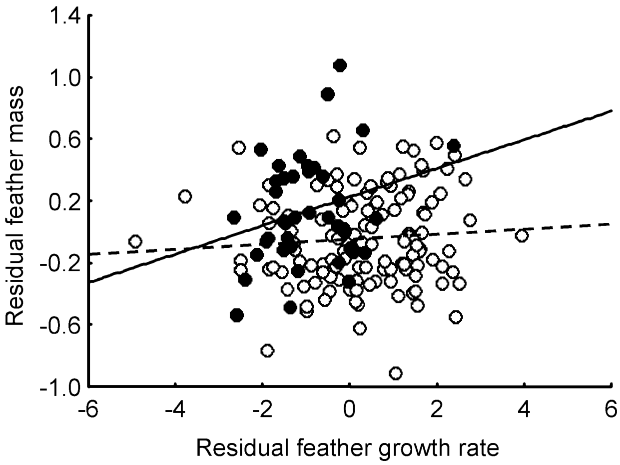

Figure 3. Relationship between feather growth rate and feather mass in migratory (open circles and broken line) and sedentary blackcaps (filled dots and solid line). Because of the great dependence of feather growth rate and feather mass on feather size, the graph was drawn with the residuals of both variables on feather length.

nology to estimate moult rate, and feather mass as an index of feather quality. The existence of a trade-off between feather growth rate and feather quality was supported by the negative correlation between the two traits, which we uncovered by comparing feather traits of migratory and sedentary blackcaps. Simultaneously, our analysis revealed natural variation in phenotypic quality among individual blackcaps, in the form of positive associations between feather growth rate and feather quality within populations.

We found significantly different slopes of the associations between feather growth rate and feather mass in migratory and sedentary populations (Fig. 3), an interaction which was expected according to life-history theory (Van Noordwijk & De Jong, 1986), at least if the span of variation in individual quality does not differ between migratory and sedentary populations, although the advantages of rapid moulting versus high-quality feathers differ between populations. Our results support the idea that resource allocation during the moult of migrants is more constrained by the need to moult fast than by the need to produce high-quality feathers. Thus, migrants would favour rapid moulting over slow moulting, even if the latter allows them to produce better feathers with a given amount of resources available for moulting. By contrast, sedentary blackcaps are less time-constrained because they do not need to migrate and, consequently, they may benefit from producing feathers of the highest possible quality with a given amount of resources available for moulting. In turn, divergent allocation rules in migratory and sedentary blackcaps would produce a steeper association between feather growth rate and feather quality in sedentary blackcaps and a shallower association in migratory blackcaps (Fig. 1), an interaction which we observed in the present study (Fig. 3).

The present study shows that comparing natural populations subjected to divergent selection pressures can improve our knowledge of trade-offs, particularly when devising appropriate experiments is difficult. The trade-off between feather growth rate and feather quality has only been investigated experimentally with photoperiod manipulations that mimic time constraints during moulting. Such experiments have shown that rapid moulting is associated with reduced plumage quality (Dawson *et al.*, 2000; Serra *et al.*, 2007). The present study bridges laboratory research with field observations, by illustrating the extent to which the trade-off between feather growth rate and feather quality can constrain natural phenotypic variation. Other studies have tried to illustrate such effects in unmanipulated bird populations (Serra, 2001), but could only indirectly estimate moult speed (i.e. by looking at the average size of moult gaps in different populations) and feather quality (i.e. by measuring seasonal differences in wing length due to wear in each population). Importantly, we could estimate the growth rate and the quality of the same individual feathers, which allowed us to test relevant predictions derived from the existence of a trade-off between these two traits.

Arguably, phenotypic variation among blackcap populations might not be adaptive but be caused by genetic drift occurred during long periods of population isolation. However, differences in migratory behaviour are not associated with population ancestry in blackcaps (Pérez-Tris *et al.*, 2004). In this species, migratory behaviour is highly heritable (Berthold, 1996) and can evolve very rapidly, both historically and in ecological time (Berthold *et al.*, 1992; Pérez-Tris *et al.*, 2004; Bearhop *et al.*, 2005). Rapid evolution of migration in blackcaps has involved parallel changes in other phenotypic traits associated with migratory or sedentary life styles, such as fat metabolism or wing morphology (Pérez-Tris *et al.*, 2004; Fiedler, 2005). Interestingly, both the duration and the timing of moulting in relation to migration are genetically controlled in the blackcap (Pulido & Coppack, 2004; Pulido & Widmer, 2005). Therefore, variation in feather traits observed in blackcaps is better interpreted as the outcome of natural selection associated with different migratory behaviours, as predicted by life-history theory.

The results obtained in the present study may contribute to understand the evolutionary relationships between moulting and migration, an important conflict in birds' life (Kjellén, 1994). Time constraints associated with the need to migrate might explain the diversification of moult patterns among bird species (Svensson & Hedenström, 1999; Hall & Tullberg, 2004). According to our results, rapid moulting comes at the expense of reduced feather quality, which may explain why some long-distance migrant species have postponed their moulting until reaching nonbreeding quarters. Delayed moulting would evolve in time-constrained migratory species when the cost of reduced feather quality overrides the benefits of moulting fast before migration. Therefore, considering constraints related to the need of producing high-quality feathers may prove essential in future research on the evolution of moulting strategies.

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