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Repeatable length and mass but not growth rate of individual feathers between moults in a passerine bird

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Abstract. Plumage is regularly replaced over the lifetime of birds, and, consequently, variable conditions experienced during plumage development can affect feather growth rate or the expression of feather characteristics. We assessed intra-individual constancy in the length, mass, and growth rate of tail feathers between complete moults of 13 free-living individual Blackcaps *Sylvia atricapilla*. Between-moult repeatability was high for the length and mass, but not for growth rate of individual tail feathers. The feathers produced in the later moult grew at a slower rate, which shows that the time to produce similar feathers increases with age.

Key words: developmental plasticity, feather traits, ptilochronology, Blackcap, *Sylvia atricapilla*, within-individual repeatability

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Phenotypic traits that are repeatedly developed over the lifetime of individuals (such as flowers, antlers, clutches, etc.) usually vary in their expression each time they are produced (Bartos et al. 2007, Brown & Shine 2007). Within-individual variation may either have an extrinsic origin (changes in resource availability, social context, etc.; Pigliucci 2001, Nussey et al. 2007) or be associated with intrinsic individual changes (such as increasing experience, senescence, etc.; Partridge 2001). In principle, both sources of variation may affect the final expression of characters, a circumstance which has been observed for reproductive output or secondary sexual characters, among other kinds of traits (Nussey et al. 2007). However, there is less evidence of variability in developmental rates of the same traits, which could counteract the aforementioned sources of variation and maintain a similar expression of the character during lifetime.

Phenotypic variation of repeatedly produced traits has long been studied in birds, mostly in relation to life-history traits (such as laying date, egg size and clutch size; e.g. Bennett & Owens 2002), but also regarding plumage, which is periodically produced during moults. The analysis of repeatability of plumage characters (i.e. size of colour patches or the extent of moult) has revealed high degrees of within-individual constancy between moults (Battley 2006, Hegyi et al. 2006), but the contribution of developmental plasticity (i.e. plasticity in moult rate) to lifetime variation in feather traits has seldom been investigated. Such a lack of knowledge is surprising because feathers are essential for birds, as they play critical roles in flight performance, thermoregulation and social interactions (Jenni & Winkler 1994).

Phenotypic plasticity in feather growth and structure may be high if individuals experience variable environmental conditions in different moult periods (Grubb 2006) or aging impairs developmental processes (Partridge 2001). Besides, such plasticity may be constrained by strong selection for plumage functionality (Jenni & Winkler 1994), or be buffered by individuals' experiences, which may adjust their moulting effort to maintain a constant feather structure. In order to explore these questions, we studied between-moult repeatability of feather length, mass and growth rate in Blackcaps *Sylvia atricapilla*.

We studied Blackcaps in a Mediterranean forest located at the southern edge of the Iberian Peninsula (Sierra de Ojén, 36°10′N 5°36′W). Local sedentary Blackcaps share this area with migratory Blackcaps from further to the North during winter and migration periods (Pérez-Tris & Tellería 2002), but individuals of either population type can be readily distinguished by distinct morphology and recapture rate at different times of year (Pérez-Tris et al. 1999, De la Hera et al. 2007).

In Blackcaps, the first set of flight feathers is retained during the first year of life (young birds undergo a partial moult that rarely affects flight feathers; Jenni & Winkler 1994). During the second year and annually from that moment, the whole plumage is replaced in a complete moult that takes place in autumn. It is important to note that nestling feather growth and complete moult are fundamentally different developmental processes, which are affected by different environmental challenges and genetic influences. Such differences make the phenotypic traits of the first set of flight feathers not comparable to the traits of subsequent plumages. Therefore, we did not consider juvenile flight feathers in our study, which was based on repeated measures of adult feather characters. Blackcaps carrying such juvenile feathers were identified using plumage characteristics, skull pneumatization and iris colour (Jenni & Winkler 1994).

We captured Blackcaps using mist-nets, from February 2001 to March 2007 (80 sampling days in total). We collected one or the two fifth tail feathers (rectrices) to Blackcaps that had fully grown, undamaged feathers, and stored them in dry envelopes until laboratory analyses. Out of 901 different Blackcaps captured in total, 180 birds had already undergone at least one complete moult when they were first sampled feathers, and of these, 14 were recaptured and sampled again after a subsequent complete moult, so that they were sampled feathers twice, each time with a different set of adult feathers. One of these Blackcaps was identified as migratory and consequently it was excluded from the analyses (to prevent confounding effects due to mixing populations in the analysis), which rendered a final sample size of 13 individuals with repeated measures of adult feather characters. Repeated sampling involved two consecutive plumages (10 cases) or plumages separated by two (one case) or three moult events (two cases).

In the laboratory, we weighed feathers with a digital balance (Mettler Toledo AG-245, resolution 0.01 mg), and measured the total length (from the calamus base to the feather tip) and feather growth rate with a digital calliper (Mitutoyo ® 500, resolution 0.01 mm). Feathers show a pattern of alternating dark and light bands perpendicular to the feather shaft, where light bands are produced during night and dark bands during day. Therefore, one light band plus one dark band (which is known as a daily growth bar) correspond to a 24-hour period of feather growth (Brodin 1993). Growth bars are directly observable under certain light conditions and they allow for estimating feather growth rate (a technique called ptilochronology; Grubb 2006). For that purpose, one of us (IH) placed feathers on a black card and marked the length occupied by 10 growth bars on the attack border of the feather employing two pins. Measurements were taken always in the same part of the feather (i.e. 10 growth bars centred at the point two-thirds of the distance towards the tip of the feather, see Grubb 2006). After removing the feather from the card, the distance between both pins was measured using the digital calliper.

In our analyses we used the average value for samples which had both tail feathers. Each sample was blindly measured twice to estimate methodological repeatabilities, which were high for all traits (the lowest value was obtained for feather growth rate: $r_i = 0.75$, $F_{25,26} = 7.1$, $p < 0.001$). To quantify the variability of feather traits over time, we calculated within-individual repeatabilities between moults. Within-individual variation between moults could be due to fluctuating deviations from an average individual pattern, or be associated to directional changes systematically expressed during life. To distinguish between these two alternatives, we conducted repeated measures ANOVA to compare feather traits produced during an earlier moult (the first moult sampled) to traits produced during a later moult (the second moult sampled). We also conducted regression analyses to obtain the residuals of the association between feather trait values realised during both moult periods. We used such residuals to evaluate whether changes in feather growth rate between moults are associated to corresponding changes in feather structure, which could show the existence of a trade-off between both characteristics (see Dawson et al. 2000).

Between-moult repeatability was high and significant for feather length ($r_i = 0.87$, $F_{12,13} = 13.98$, $p < 0.001$) and feather mass ($r_i = 0.79$, $F_{12,13} = 8.35$,

$p < 0.001$). None of these two traits showed significant variation between moults, as shown by repeated measures ANOVA (feather length: $F_{1,12} = 1.55$, $p = 0.24$; feather mass: $F_{1,12} = 2.03$, $p = 0.18$). These results were also supported by regression analyses, with both feather traits being strongly correlated between moults (feather length: $r = 0.87$, $p < 0.001$; feather mass: $r = 0.8$, $p < 0.001$) and showing slopes of the regression lines not statistically different from 1 (feather length: $t_{11} = -0.96$, $p = 0.36$; feather mass: $t_{11} = -1.1$, $p = 0.3$, Fig. 1a and 1b).

However, between-moult repeatability of feather growth rate was low and statistically not significant ($r_i = 0.29$, $F_{12,13} = 1.81$, $p = 0.15$). Feather growth rate showed directional variation between moults ($F_{1,12} = 12.84$, $p < 0.01$), with the early-produced feathers growing faster than the late-produced ones (mean and standard deviation: first sample = 31.05 ± 1.1 mm; second sample = 30.03 ± 1.08 mm). Nevertheless, a regression analysis of feather growth rates showed a moderate and nearly significant positive association between moults ($r = 0.55$, $p = 0.05$, Fig. 1c), whose slope was not significantly different from 1 ($t_{11} = -1.84$, $p = 0.09$).

When we analysed the relationships between the residuals obtained in the regression analyses reported above, we found that individuals with relatively accelerated growth from the early to late-produced feathers also produced relatively longer and heavier feathers (Multivariate test: Wilk's Lambda = 0.52, $F_{2,10} = 4.69$, $p = 0.04$). A posterior test of univariate effects showed that, although both feather length and feather mass contributed to the overall effect, such contributions were statistically significant for feather length ($r = 0.67$, $p = 0.01$, Fig. 2) but not for feather mass ($r = 0.48$, $p = 0.1$, Fig. 2).

Individual Blackcaps produced similar feathers in two different complete moults, as shown by highly repeatable length and mass of their tail feathers (Fig. 1a and 1b). Repeatable feather length and mass could result from selection favouring essential functionality of flight feathers (Jenni & Winkler 1994), reduced phenotypic plasticity associated to strict genetic control (Berthold & Querner 1982), or the effects of a common environment experienced during life (Grubb 2006). Whatever the reason why feather traits remain similar between moults, it was striking to observe that such consistency resulted from a growth process which was virtually unrepeatable between moults. Interestingly, low between-moult repeatability of feather growth rate was not the outcome of stochastic variation in developmental conditions (as it would happen if a variable

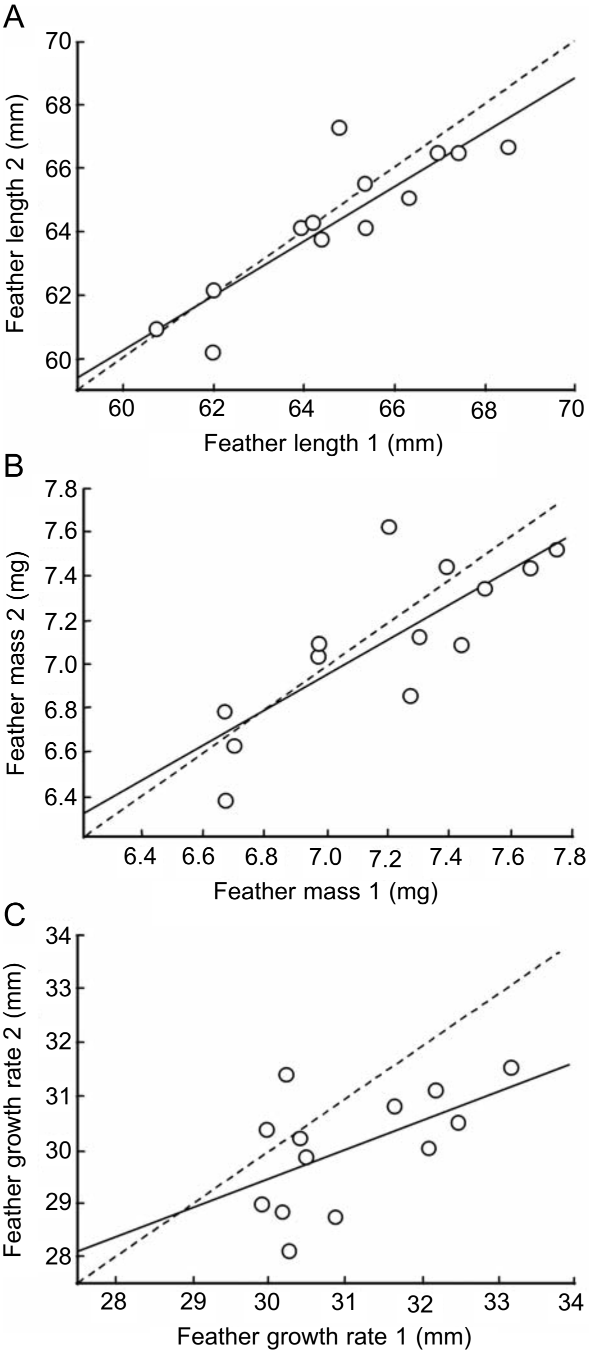

Fig. 1. Relationship between length (A), mass (B) and growth rate (measured by the width of 10 growth bars) (C) of feathers produced in the early moult (X axis) and the later moult (Y axis). Each graph shows the observed regression line (solid line) and the line corresponding to a slope of b = 1 (broken line).

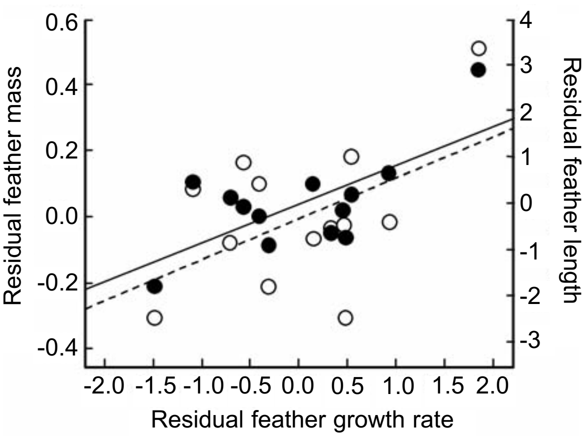

Fig. 2. Association between residuals of feather growth rate and, in each axis, residuals of feather mass (open dots and broken line) and residuals feather length (black dots and solid line).

environment strongly influenced feather growth; Grubb 2006), but resulted from directional changes in feather growth rate with age, with the feathers produced in the early moult growing faster than feathers produced in the later moult.

Given that tail feather length and mass did not change between moults, we conclude that Blackcaps take longer to produce a functionally similar plumage as they age. Such result might reveal an effect of senescence (Partridge 2001), which may impair the ability of older birds to synthesize the plumage, for example if metabolism slows down with age (Broggi et al. 2007). In addition, older birds may allocate more resources to activities such as reproduction or social interactions than to self maintenance, including plumage growth (Bennett & Owens 2002). Finally, individuals may adaptively adjust individual feather growth rates to realised environmental conditions, to avoid the cost of growing fast where an equally functional plumage could be produced at a reduced pace (Metcalfe & Monaghan 2001). The latter strategy could be particularly adaptive in a sedentary population — like the one studied — in which moult duration is not constrained by migration (Battley 2006).

Several studies have shown a negative correlation between feather growth rate and feather mass and length (Dawson et al. 2000, Hall & Fransson 2000), and a trade-off between feather growth and structure has been hypothesized, so that fast-growing feathers would incorporate less material than slow-growing feathers. By repeatedly measuring feathers of the same individuals produced under natural conditions, we found that individual over-investments in feather growth (measured by positive residuals of between-moult regression of growth rates) were associated to parallel increases in feather length and mass (Fig. 2). We do not believe that such result contradicts the existence of a trade-off between feather growth and feather quality. Instead, we interpret our results as a direct consequence of the fact that individuals of variable phenotypic quality (or living in territories of different quality) repeatedly produce feathers under variable environmental conditions, and perform better when environmental conditions allow a larger investment in both feather growth and feather structure (Van Noordwijk & De Jong 1986).

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STRESZCZENIE

[Porównanie długości, masy i tempa wzrostu sterówek kapturki pomiędzy kolejnymi pierzeniami]

Upierzenie jest regularnie wymieniane podczas całego życia ptaka, przez co zmienne warunki środowiska panujące podczas pierzenia, mogą wpływać na tempo wzrostu czy wielkość piór. Dorosłe osobniki z lokalnej osiadłej lęgowej populacji kapturki były łapane w latach 2001–2007, od każdego pobierano piątą sterówkę. 13 osobników złapano po dwóch kolejnych pierzeniach i porównano długość, masę i tempo wzrostu ich sterówek. Stwierdzono dużą powtarzalność długości i masy piór między kolejnymi pierzeniami, natomiast nie stwierdzono podobnej korelacji dla tempa wzrostu (Fig. 1). Uzyskane wyniki wskazują, że pióra w kolejnych pierzeniach rosną wolniej, a więc czas potrzebny na osiągnięcie przez nie podobnej długości i masy jest większy. Może to być związane ze starzeniem się organizmu, większym lokowaniem zasobów w inne aktywności, lub odzwierciedlać pewne dopasowanie do zmieniających się warunków środowiska.