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Notas Breves

STRUCTURAL AND MECHANICAL DIFFERENCES BETWEEN ORIGINAL AND REPLACED FEATHERS IN BLACKCAPS *SYLVIA ATRICAPILLA*

DIFERENCIAS ESTRUCTURALES Y MECÁNICAS ENTRE PLUMAS ORIGINALES Y REEMPLAZADAS EN LA CURRUCA CAPIROTADA *SYLVIA ATRICAPILLA*

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SUMMARY.—Many bird species are able to replace accidentally lost feathers out of the normal moulting periods, but whether such replaced feathers are able to restore the original mechanical properties of the plumage has not been evaluated before. In this study we analysed the structure and mechanical behaviour of the original and replaced feathers of 12 blackcaps *Sylvia atricapilla*. Replaced feathers showed wider rachis and greater density of barbs, but were lighter, shorter and less stiff than original feathers. These results suggest that replaced feathers are not able to fully restore the original functionality of feathers.

RESUMEN.—Muchas aves son capaces de reemplazar las plumas que pierden accidentalmente, pero no se sabe si las nuevas plumas (denominadas plumas reemplazadas) que sustituyen a las originales consiguen restablecer las propiedades mecánicas del plumaje. En este estudio se analizó la estructura y el comportamiento mecánico de las plumas originales y reemplazadas de 12 currucas capirotadas *Sylvia atricapilla*. Las plumas reemplazadas presentaron raquis más anchos y mayor densidad de barbas, pero fueron más ligeras, más cortas y tuvieron menor resistencia a la flexión que las plumas a las que sustituyeron. Estos resultados sugieren que las plumas reemplazadas no son capaces de reestablecer totalmente la funcionalidad del plumaje original.

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Maintaining the plumage in good condition is essential for birds because, among other important functions, feathers determine flight performance and thermoregulatory ability (Ginn and Melville, 1983; Jenni and Winkler, 1994). Apart from the seasonal substitution of feathers (moult), that is a key event in the annual cycle of birds to reset the quality of a plumage deteriorated by physicochemical processes and parasites (Williams and Swaddle, 2003), it is well-known that many bird species are also able to replace accidentally lost feathers out of the normal moulting periods (Lindström and Nilsson, 1988; Svensson, 1992; Møller *et al*., 2006). Such process, called *adventitious replacement* (Willoughby *et al*., 2002), could has been favoured by natural selection because the energetic costs of growing new feathers are lower than the long-term costs of maintaining an incomplete plumage until the following moult.

Moult takes place during certain seasons in which conditions are suitable for satisfying the high nutritional demands of feather production (Jenni and Winkler, 1994). In contrast, adventitious replacement of feathers is an unpredictable event that may occur during periods of food shortage (*e.g*. during wintering period) or when other activities constrain the resources available for feather production (*e.g*. breeding, migration), which would explain why replaced feathers (feathers obtained from adventitious replacement) are typically shorter and lighter than those produced during fledging or moulting periods (Grubb, 2006). Interestingly, such patterns suggest the existence of differences between replaced and original feathers in some structural traits that can contribute to feather quality (such as rachis width or barb density; Dawson *et al*., 2000), yet the implications for plumage functionality of such variation remain to be studied.

In order to explore whether original and replaced feathers show structural and mechanical differences, a sample of tail feathers of free-living blackcaps *Sylvia atricapilla* was analysed. Tail feathers are suitable for these analyses because they are highly susceptible to accidental loss (Møller *et al*., 2006). The study was carried out between September 2006 and March 2007 in several sites of the Campo de Gibraltar region (province of Cádiz, Southern Spain, 36º 01' N, 5º 36' W) within the framework of a more general research project on variation in feather characteristics in relation to migration. Blackcaps were mist-netted monthly in this area during a variable period of time (from 4 to 10 days), and feather loss was caused by us plucking one 5th rectrix feather from each individual. Out of 553 blackcaps sampled for feathers, 31 individuals were recaptured in a subsequent month (time from capture to recapture ranged between 26 and 159 days) of which 12 birds (capture-recapture time between 56 and 159 days) had replaced the removed feather. Of the remaining 19 birds, 18 individuals had growing feathers and one had not replaced the feather when recaptured, and hence could not be included in the final sample. Therefore, this study analysed within-individual variation in the structural characteristics and mechanical behaviour between original and replaced feathers in 12 blackcaps with fully grown replaced feathers, which included 7 juveniles and 5 adults.

In the laboratory, feathers were weighed using a Mettler Toledo ® AG-245 digital balance (0.01 mg of instrumental repeatability). The overall feather length and the maximum dorso-ventral width of the rachis at the base of the feather vane were measured using a digital calliper (Mitutoyo ® 500, resolution 0.01 mm). The density of feather barbs was estimated with the aid of a magnifier (10 × magnification), counting the number of barbs on a 10-millimetre section located at the centre of the feather. Finally, in this same section of the feather, the maximum length of the inner feather barbs was measured using a graph paper at three different sites (at the centre of the feather and 5 mm up and down from the centre). The mean value of these three measurements of barb length was used in the analyses.

In addition to these previous traits, the quality of feathers was directly estimated by measuring the dorso-ventral bending stiffness of feathers. Bending stiffness is an important mechanical property of feathers because it transmits the aerodynamic forces to the musculoskeletal system during flight (Videler, 2005). This property of feathers was obtained using a MTS ® 810 machine adapted for that purpose (Borgudd, 2003; Weber *et al.*, 2005), in which the proximal part of feather shaft (*calamus*) was inserted into the clamp of the test device until the beginning of the rachis. The clamp was filled with silicon to avoid damage on the calamus. The test was designed following the same procedure described in de la Hera *et al*. (2010). Thus, the test took 3 minutes for each feather, and recorded the force that is necessary to apply every 1.5 seconds at 31 millimetres from the rachis base to bend the feather 0.05 millimetres, causing and overall feather deformation of 6 millimetres. Such a procedure provided 120 measurements of force and displacement for each feather that allowed estimating the bending stiffness from the slope of the force-displacement regression line. Thus, the steeper the force-displacement slope, the higher the value of bending stiffness.

Repeated measures ANOVA were conducted to analyse within-individual variation between original and replaced feathers in the aforementioned feather traits. In spite of the small sample size, adult and juvenile blackcaps were distinguished in the analyses because their original feathers are produced under different developmental and ecological conditions (*e.g*. juveniles produce their flight feathers simultaneously during the fledging period, while adults do it sequentially during a complete moult process; Svensson, 1992; Jenni and Winkler, 1994). Such circumstance could cause variation in the structure and quality of feathers between age-classes (Jenni and Winkler, 1994), which could interact with the comparison between original and replaced feathers. Additionally, in order to explore for the individual contribution to variation in feather traits, the correlations between the traits of original and replaced feathers were also analysed, but including the age of blackcaps as a factor (ANCOVA).

Feather length, feather mass, barb length and bending stiffness were greater in adult than in juvenile blackcaps in both original and replaced feathers, but age had no significant effect on rachis width (table 1, fig. 1). On the other hand, replaced feathers of juveniles were denser than replaced feathers of adults, but barb density was similar between age classes in original feathers, leading to a significant interaction between age and type of feather (table 1). After controlling for the effects of age, replaced feathers were shorter, lighter and less stiff, but showed a wider rachis and greater density of barbs, than original feathers (table 1, fig. 1). In contrast, barb length did not differ between original and replaced feathers (table 1). Interestingly, variation in structural traits and bending stiffness of replaced feathers was better predicted by the scores of such traits in the original feathers than by the age of birds (table 2, fig. 1). The only exception for this pattern was barb density, for which the scores of replaced feathers were more associated with the age of blackcaps than with the scores of original feathers (table 2, fig. 1).

This study supports the idea that replaced feathers are shorter and lighter than original feathers, as had been previously reported (Grubb, 2006). However, replaced feathers had a wider rachis and greater density of barbs than original feathers and did not differ in barb length, which suggests that mass decrease in replaced feathers is mainly caused by reduction in the overall size of feathers, and not by differences in the structural complexity/density compared to original feathers. In spite of the observed differences between adult and juvenile original feathers (Jenni and Winkler, 1994), and although the majority of feather traits analysed in this study differ between original and replaced feathers, significant positive correlations between the scores of replaced and original feathers were detected for all traits (except for barb density). Such relationship shows that most feather traits have a strong individual component in the blackcap, not only during the normal periods of feather production (Berthold and Querner, 1982; de la Hera *et al*., 2009), but also when new feathers grow up to replace accidentally lost ones.

TABLE 1

Results of the repeated measures ANOVAs of feather traits between original and replaced feathers and controlling for the age (juvenile and adult birds) of blackcaps.
[Resultados de los ANOVA de medidas repetidas entre plumas originales y reemplazadas, y controlando por la edad (aves juveniles y adultas) de las currucas capirotadas.]

	Age		**Type of feather**		**Age × type of feather**	
	$F_{1,10}$	P	$F_{1,10}$	*P*	$F_{1,10}$	*P*
Feather length	10.54	0.009	33.95	< 0.001	4.56	0.058
Feather mass	5.46	0.042	10.55	0.009	1.88	0.2
Raquis width	3.28	0.1	10.23	0.01	3.88	0.077
Barb density	1.7	0.222	21.82	< 0.001	6.9	0.025
Barb length	14.37	0.004	1.87	0.202	1.05	0.33
Stiffness	18.73	0.001	13.83	0.004	3.59	0.088

TABLE 2

Results of the ANCOVAs analysing the relationship between original and replaced feathers in feather traits and considering the age (juvenile and adult birds) of blackcaps.
[Resultados de los ANCOVA que analizaron la relación entre los rasgos de plumas originales y reemplazadas considerando la edad (aves juveniles y adultas) de las currucas capirotadas.]

	Age		**Scores of original feathers**		
	$F_{1,9}$	P	Beta	$F_{1,9}$	*P*
Feather length	2.55	0.145	0.715	17.1	0.003
Feather mass	1.08	0.327	0.774	18.32	0.002
Raquis width	2.58	0.142	1.034	16.90	0.003
Barb density	5.75	0.04	0.307	1.4	0.267
Barb length	1.04	0.335	0.693	8.9	0.02
Stiffness	0.52	0.487	1.062	6.5	0.03

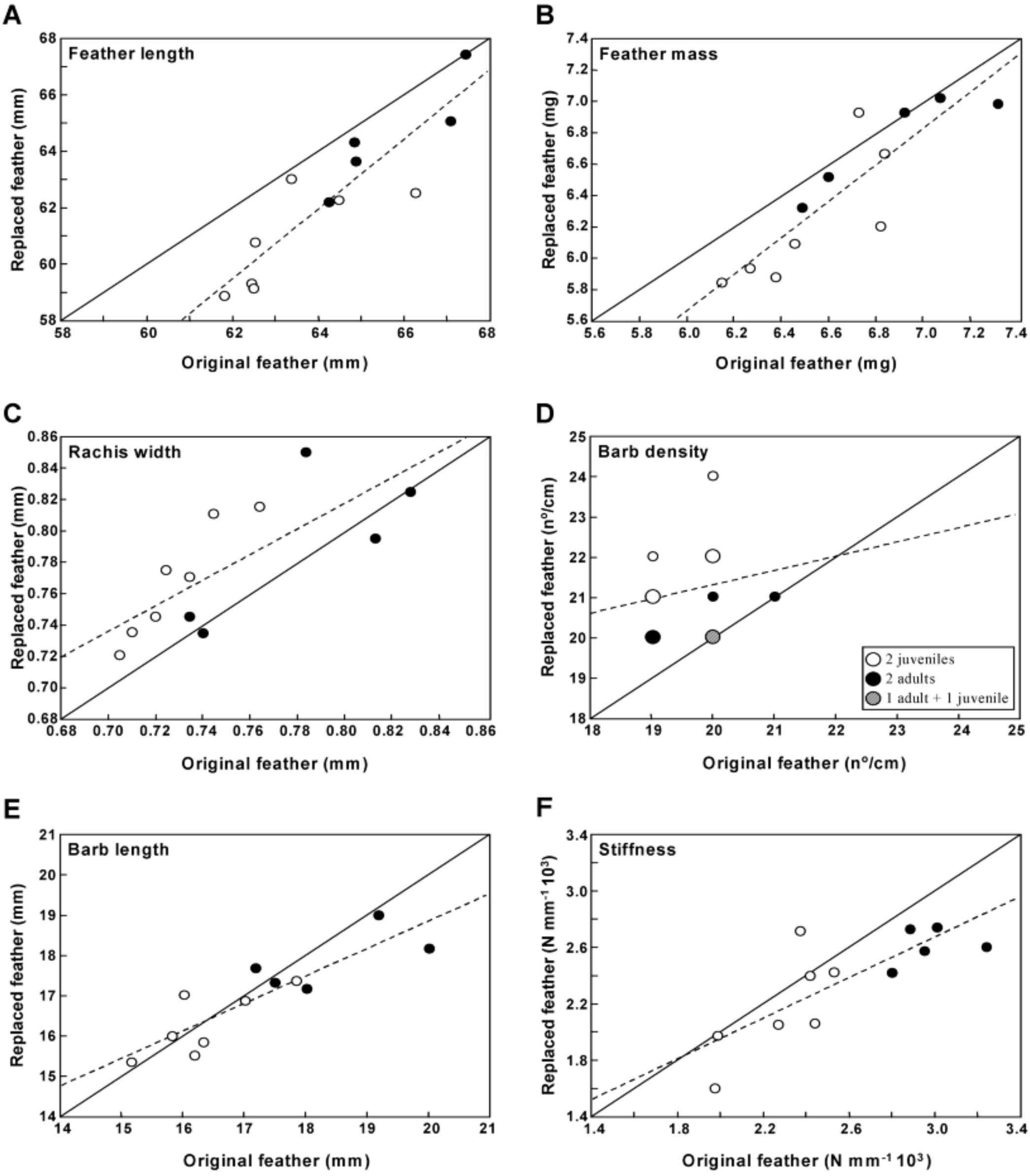

FIG. 1.—Relationship between original and replaced feathers in length (A), mass (B), raquis width (C), barb density (D), barb length (E) and bending stiffness (F). Adult and juvenile blackcaps are represented by filled dots and open circles, respectively (see additional box in graph D for overlapped cases). Each graph shows the identity line (solid line) and the observed regression line (broken line).

[Relación entre las plumas originales y las reemplazadas en la longitud total (A), masa (B), anchura del raquis (C), densidad de barbas (D), longitud de las barbas (E) y resistencia a la flexión (F). Las currucas capirotadas adultas y juveniles se representan con círculos negros y blancos respectivamente (véase recuadro adicional en gráfico D para los casos solapados). Cada gráfico muestra la recta de identidad (línea continua) y la recta de regresión observada (línea discontinua).]

Interestingly, this study reports variation in the mechanical behaviour of replaced and original feathers. The fact that replaced feathers had reduced bending stiffness compared to original feathers reveals that adventitious replacement, while necessary to repair feather losses outside moult periods, is not able to fully restore the original mechanical performance of feathers. According to these results, losing feathers may be costly not only because of the aerodynamic costs of feather gaps (Hedenström and Sunada, 1999), but also because of the potential reduced quality of replaced feathers. The latter effect may have fitness implications in species for which feather quality determines flight performance or mating success, and therefore deserves further investigation.

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