

COMPLETE POST-JUVENILE MOULT IN FIRST-YEAR BLACKCAPS: PROXIMATE CAUSES AND ADAPTIVE IMPLICATIONS

MUDA POST-JUVENIL COMPLETA EN CURRUCAS CAPIROTADAS DE PRIMER INVIERNO: CAUSAS INMEDIATAS E IMPLICACIONES ADAPTATIVAS

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SUMMARY.—Moult is one of the most energy-demanding events in the annual cycle of a migratory bird. As a consequence, moult patterns have evolved that separate moult from other costly life-cycle stages and that exclude unnecessary replacement of the feathers. We studied two Spanish blackcap *Sylvia atricapilla* populations with the aim of elucidating variation and flexibility of their postjuvenile moult pattern. In contrast to most juveniles of this species, which normally undergo a partial moult both in captivity and in the wild, we found complete moult in 2 juvenile blackcaps. Complete moult was also inferred for another 7 birds, which were in active moult. Eight of these birds were trapped at a site in northern Spain and one originated from a partially migratory population from eastern Spain. This bird, held under the same environmental conditions as other 31 juveniles from the same population, moulted all primaries in captivity while the other 31 juveniles invariably undertook a normal partial post-juvenile moult. Therefore, it seems likely that complete post-juvenile moult observed in this bird was not induced by environmental conditions but had a genetic basis. Thus, we show that previously undetected variation among post-juvenile moult patterns is present in wild blackcaps and suggest that variation in the expression of important life-history traits could represent a potential reservoir for adaptive changes. This finding is in line with the great adaptive capacity of blackcap, repeatedly observed both in wild and in captivity.

Key words: adaptive potential, genetic variance, life-history trait, populations.

RESUMEN.—Entre los eventos que componen el ciclo vital de un ave migradora, la muda es de los que requieren un mayor gasto energético. Como consecuencia de esto, los patrones de muda han evolucionado para evitar el solapamiento de la muda con otras fases importantes del ciclo vital, así como para evitar cualquier reemplazo del plumaje que no sea indispensable. En este trabajo estudiamos la muda post-juvenil en dos poblaciones españolas de curruca capirotada *Sylvia atricapilla*, con el

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objetivo de determinar la flexibilidad y la variabilidad de este patrón. Aunque los individuos juveniles de esta especie realizan normalmente una muda parcial tanto en la naturaleza como en cautividad, en nuestro trabajo hemos observado 2 juveniles que realizaron una muda completa y 7 más en que el proceso de muda activa observado era muy probablemente el de una muda completa. Ocho de estas aves fueron capturadas en una localidad del norte de España, mientras que la novena procedía de una población del Levante español. Esta última ave renovó todas las primarias en cautividad, donde fue mantenida bajo las mismas condiciones controladas que otros 31 juveniles procedentes de la misma población, que realizaron la muda parcial habitual para esta especie. Este hecho sugiere que, al menos en este caso, la muda completa observada no fue debida a factores ambientales, sino genéticos. Nuestros resultados demuestran la presencia de una variabilidad hasta el momento no detectada en los patrones de muda post-juveniles de poblaciones silvestres de curruca capirotadas, y consideramos que esta variabilidad en la expresión de un evento del ciclo vital tan importante como la muda, podría representar una reserva potencial de capacidad adaptativa. Nuestros resultados son coherentes con la gran capacidad adaptativa que se ha observado en la curruca capirotada tanto en poblaciones salvajes como en cautividad.

Palabras clave: potencial adaptativo, varianza genética, estrategias vitales, poblaciones.

INTRODUCTION

Life-history theory predicts that life-cycle events should be scheduled in a way that the total fitness of the individual is maximised (Roff, 2002). One way of maximising fitness is to temporally separate events in the life-cycle that demand large amounts of resources. For birds, the most important and energy-demanding life-history stages are: reproduction, moult and, when it occurs, migration (Newton, 2008, 2009). As a consequence, we expect birds to maximize their fitness over the complete life-cycle by optimal scheduling of reproduction, moult and migration (Barta *et al.*, 2006, 2008; Hedenström *et al.*, 2007; McNamara and Houston, 2008).

Moult is costly both because of high energetic and nutritional demands during feather synthesis (Murphy and King, 1992; Lindström *et al.*, 1993; Murphy, 1996; Murphy, 1999) and because of reduced thermoregulation efficiency and aerodynamics of plumage during moult (see, for instance, Schieltz and Murphy, 1997; Swaddle and Witter, 1997; Hedenström and Sunada, 1999; Guillemette *et al.*, 2007). Annual-routine models have been used to investigate whether different patterns of moult

should evolve in birds differing in migration strategy (Barta *et al.*, 2006; McNamara and Houston, 2008). They suggest that there is an optimal moult pattern for each migration strategy. Specifically, these models predict that migrants would gain a maximum benefit from a rigidly programmed moult schedule, while in residents a more flexible organization of life-cycle events is expected. Moreover, an overlap between renewal of primaries and reproduction is predicted to be the optimal strategy only for birds living in habitats with low seasonality, for example, in the tropics (Barta *et al.*, 2006; McNamara and Houston, 2008). In nature, however, it also has been observed in extreme northern breeders. In these birds, which stay only few weeks in the breeding quarters, the overlap between reproduction and primary moult is supposed to be an adaptation to time constraints.

In most cases, deviations between predicted optimal moult strategies and actual moult patterns are probably due to the fact that a strategy is optimal only under very specific conditions and for a very specific group of birds. In passerines, for example, moult strategies generally differ between

juvenile and adult birds (Jenni and Winkler, 1994). Since the energetic costs of moult increase with the extension of moult, we would expect strong selection against unnecessary replacement of the plumage. This probably explains why the general moult pattern among Western Palearctic short-distance migrants is characterised by a partial moult in the first summer of life and a complete moult (i.e. renewal of all the feathers, including the primaries) in following years (Jenni and Winkler, 1994). In late summer, i.e. between reproduction and migration, the feathers of juveniles are only a few weeks old, while the primaries of adults were grown in the previous year and are worn. Therefore, it seems adaptive that juveniles do not renew the wing feathers while adults do. Nevertheless, this is not a general rule because the extent of juvenile moult may vary considerably among different species (Svensson, 1992; Jenni and Winkler, 1994). This may partly be due to phylogenetic constraints on the evolution of moult patterns (Svensson and Hedenström, 1999; Hall and Tullberg, 2004). Phylogenetic constraints on moult pattern variation are consistent with the general finding that phenotypic variation in moult is to a large extent due to genetic differences (Berthold and Querner, 1982; Pulido and Coppack, 2004; I. de la Hera *et al.*, pers. obs.).

One of the model groups for studying the evolution of variation in moult patterns are the Western Palearctic warblers of the family Sylviidae (Svensson and Hedenström, 1999; Hall and Tullberg, 2004) and among these, particularly, the *Sylvia* warblers (Shirihai *et al.*, 2001). The blackcap *Sylvia atricapilla* has been particularly well studied both in captivity and in the wild (Berthold and Querner, 1982; Norman, 1990; Berthold *et al.*, 1990, 1994; Herremans, 1991; Shirihai *et al.*, 2001; Pulido and Coppack, 2004). In this species throughout the whole breeding range and within each subspecies, partial moult among juveniles and complete moult

among adults at the end of the breeding season are the rule (Shirihai *et al.*, 2001). Yet the extent of partial post-juvenile moult may vary both within and among populations, being generally more extensive in southern populations (Jenni and Winkler, 1994). Exceptionally, juvenile blackcaps may also show moult of some external primaries and/or inner secondaries (Shirihai *et al.*, 2001; Blasco-Zumeta, 2012).

Here we use moult data derived from a long-term field study and from a common garden experiment on Spanish blackcaps to draw inferences on the mechanism controlling the occurrence of rare moult patterns and to discuss possible implications for adaptive evolution of this species, particularly in response to climate change. For the first time, we report complete juvenile moult in the blackcap, and discuss its potential control and maintenance.

MATERIALS AND METHODS

Common garden experiment

During the breeding seasons 2010 and 2011, we collected 31 first-year blackcaps from a partially migratory population in eastern Spain, Cocentaina (38° 44' N - 0° 44' W, province of Alicante) and transported them to our experimental facilities in the Casa de Campo, Madrid (40° 25' N; 3° 42' W). This was part of a larger experiment, which aims at studying within and among-population differences in migratory behaviour and life histories in Iberian blackcap populations (Pulido *et al.*, 2011). Our specific experimental cohort was composed of birds taken as chicks from their nest when 7-8 days old (N = 9) or captured as fledglings in their first plumage during the late breeding season (N = 22). As of the date of collection, all birds were maintained under the same environmental conditions (i.e. *ad libitum* food

and water) exposed to the natural and light regime of Madrid, Spain. In the following weeks, we determined individual moult status by quantifying the number of growing feathers both in wings and body. For birds from the 2010 cohort, this was done on September 9, while in 2011 this was done on September 7 and repeated on September 24th.

This common-garden experiment, which minimised among-individual environmental variation, allowed us to study the causes underlying potential differences in moult patterns. In this experiment, all birds experienced identical environmental conditions (e.g. light period, temperature, food, social interactions). As a consequence, any potential phenotypic difference observed must have had other causes (e.g. genetic differences, differences in maternal effects, differences in the environment experienced before collection). Although captive conditions have been reported as potentially affecting moult (i.e. duration of moult in ducks, Butler and McGraw, 2009), to the best of our knowledge, there is no evidence suggesting that captivity may affect moult extension or “type” (i.e. considering complete versus partial moult). Feathers numbers in the text are assigned in descendent order (see, Jenni and Winkler, 1994).

Wild

In order to compare moult extension between birds from the same population studied in captivity and in the wild, we captured and determined the number of renewed feathers in 43 first-year blackcaps from Cocontaina during the breeding seasons (April-August) 2010 and 2011. Age determination in this sample of birds was based exclusively on common plumage observation criteria (Svensson, 1992; Jenni and Winkler, 1994), which cannot identify first-year birds that undertook complete moult in the previous

summer. Therefore, we cannot rule out that juvenile birds with complete moult were overlooked. With regard to migratory behaviour, this population is considered as partially migratory (Morganti *et al.*, 2012).

The other population investigated was located in the Natural Park of Garaio (42° 54' N 2° 32' W, province of Alava, northern Spain). Between 1994 and 2009, 1,726 blackcaps were captured at the local constant-effort ringing station. We obtained information on the extension of moult for 486 of these birds, which were in their first year of life. In this population, birds were aged by the combination of common plumage observation criteria and observation of cranial ossification (Jenni and Winkler, 1994). This population is likely to be completely migratory since there are no winter captures of individuals breeding at this site (Onrubia *et al.*, 2012). Further evidence for the migratory status of this blackcap population comes from recoveries of breeding birds in winter: two breeders from this population were recaptured in the Ebro Valley area, c.a. 200 km south-west to the breeding site and two individuals in north Africa (one in Morocco and other in Algeria, A. Onrubia *et al.*, pers. obs.).

Statistical analyses

We compared moult extension in wild and lab cohorts by computing a chi-square test for each group of feathers (great coverts GC, primary coverts PC, bastard wing BW, carpal feather CC, tertiaries TER). For PC we perform the test using the frequencies of birds that do not renew any feather of the group. Obviously, we excluded birds with complete moult from analyses.

Using Pearson's correlations, we tested whether the number of new and old feathers among the eight wild birds captured in Garaio was related to Julian date.

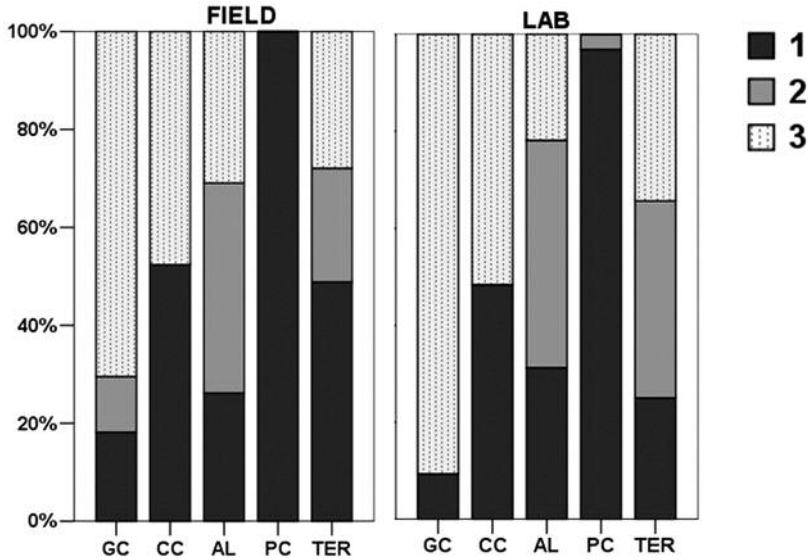


FIG. 1.—Extension of post-juvenile moult in the population of Cocentaina (Alicante, eastern Spain). The two groups represent wild ($N = 43$) and experimental ($N = 31$) birds. Bars represent different groups of feathers. GC: great coverts; BW: bastard wing; CC: carpal feather; PC: primary coverts; TER: tertiaries. 1: all feathers of the group remain unmoulted; 2: some of the feathers of the group new and some old; 3: all feathers of the group renewed. Only for GC 1: one or two retained, 2: three or four retained, 3: all renewed.

[Extensión de la muda postjuvenil en la población de Cocentaina (Alicante, España). Los dos grupos representan aves medidas en el campo ($N = 43$) y en laboratorio ($N = 31$). Las barras representan los diferentes grupos de plumas. GC: grandes coberteras; BW: álula; CC: coberteras carpales; PC: coberteras primarias; TER: terciarias. 1: todas las plumas del grupo sin mudar; 2: algunas de las plumas del grupo nuevas y otras sin mudar; 3: todas las plumas del grupo renovadas. Solamente para la GC: 1: una o dos plumas sin mudar, 2: tres o cuatro sin mudar, 3: todas renovadas.]

RESULTS

Cocentaina birds in captivity (common-garden experiment results)

All birds from both cohorts (2010 and 2011) were actively moulting body plumage when studied at the beginning of September. At this time, moult of greater, median and primary coverts, of the bastard wing and carpal feathers were already completed, so that we could measure the extension of partial moult considering these groups of feathers. Most of the birds (90.6%) renewed all the greater

coverts and one or two bastard wing feathers. About half of the birds also renewed the carpal feather. Only one bird renewed some primary coverts and none renewed all of them (see fig. 1). One male from the 2011 cohort, checked on the 7 September 2011, was apparently undergoing a complete moult, including all the wing feathers, retaining only PC 4 to 9 (see fig. 2 for details on the status of the moult). On the 24th September, we checked this bird again. The inspection of wing feathers corroborated that this bird was undergoing a complete moult and that at this date it was almost completed, except

for inner secondaries that were almost grown (left wing: S6 and S5 status 4; right wing: S6 status 4, S5 and 4 status 3). Data about this bird's migratory restlessness show that the bird had started its preliminary night restlessness on 13th September, and had developed a consistent "migratory activity" in the next few days.

Wild

Cocentaina

Wild birds (N = 43) presented a moult pattern that did not statistically differ from the one shown among experimental birds (Chi-Square tests. GC: $\chi^2_1 = 0.43$, $p = 0.51$;

CC: $\chi^2_1 = 0.04$, $p = 0.89$; PC: $\chi^2_1 = 0.01$, $p = 0.92$; BW: $\chi^2_1 = 0.44$, $p = 0.51$; TER: $\chi^2_1 = 0.19$, $p = 0.66$) (fig. 1).

The lack of significant differences between moult extension in experimental and wild birds suggests that birds in captivity moulted normally, so that patterns observed among these birds are representative of birds in the wild. Considering the whole cohort from Cocentaina pooled (both lab and wild birds), only one out of 74 birds (1.35%), showed complete juvenile moult.

Garaio

In this locality we captured seven juvenile blackcaps in active primary moult. They

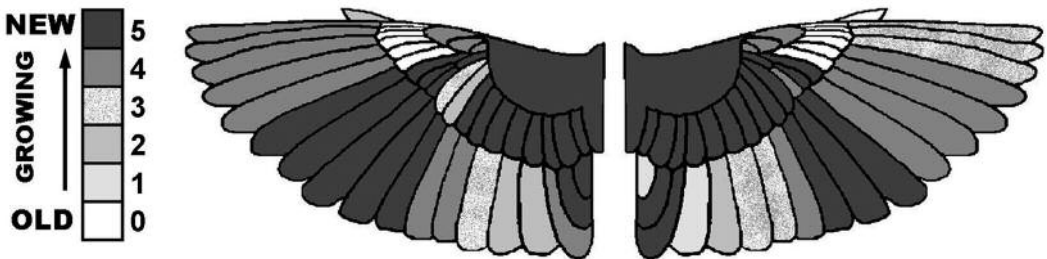


FIG. 2.—Moult status on 7th September 2011 of the captive first-year male showing complete post-juvenile moult (except for PCs 4 to 9 and right P10). The male belongs to the partially migratory population of Cocentaina (Alicante, eastern Spain), and was kept under controlled environmental conditions in captivity. Colours represent the 0 to 5 categories described in Ginn and Melville (1983) with 0 meaning an old feather, 5 a complete grown new one and intermediate numbers meaning progressively more advanced growing stadium. Feathers scored with 4 and 5 can be considered fully functionally to flight. By 24th September 2011 almost all the wing feathers except for few secondaries were fully grown and renewed. Wing shape modified from Blasco-Zumeta (2012).

[Estado de muda el 7 de Septiembre de 2011 del macho de primer año que presentaba muda completa en cautividad (con la excepción de las PC 4-9 y la P10). El macho proviene de la población parcialmente migradora de Cocentaina (Alicante) y se mantuvo en cautividad bajo condiciones ambientales controladas. Los distintos colores de las plumas representan índices de crecimiento según Ginn y Melville (1983), siendo el 0 una pluma sin mudar y el 5 una pluma renovada y completamente crecida. Los índices intermedios representan estadios de crecimiento cada vez más avanzados. Plumaz con un índice de 4 o 5 se pueden considerar plenamente funcionales para el vuelo. El 24 de Septiembre de 2011 todas las plumas de las alas con la excepción de unas pocas secundarias estaban ya completamente crecidas. El esquema del ala se obtuvo con modificaciones de Blasco-Zumeta (2012).]

were identified as “juveniles” from the aspect of the plumage not yet moulted (also the “old” feathers appearing fresh) and by incomplete cranial ossification (following Jenni and Winkler, 1994). A further bird was captured with a completely renewed plumage and classified as “juvenile” by its still incomplete cranial ossification (score 4). Since passerines complete skull ossification within few months of life, we can infer that this bird was born that year and was only a few weeks old. These eight birds were captured between August and October in four different years: 1998 (1 individual), 1999 (1 individual), 2001 (4 individuals) and 2003 (2 individuals). (see table 1 for a complete list with details and raw data on moult status).

We assume that all these birds were born locally because (1) the capture date for six of these birds lies outside the established time window for migration of blackcaps at Garaio (15 Sept-31 Oct; Onrubia *et al.*, 1996), (2) all birds, except one, had a wing length below 75 mm, resembling local breeders, but unlike birds that migrate through the area, which tend to have longer wings, and (3) because of all the birds had low or missing fat deposits (fat-scores 0 or 1 following Kaiser’s 1993 classification).

These birds showed a significant correlation between capture date and progression of moult (new feathers: $r = 0.913$, $p = 0.002$; old feathers: $r = -0.939$, $p = 0.002$; $n = 8$, see fig. 3), supporting the idea that all seven

TABLE 1

List of first-year birds captured in active primary moult at Garaio (Alava, northern Spain). All birds were aged by observation of the contrast between moulting and un-moulted feathers and/or by cranial ossification status (codes ranging from 0 in nestlings to 7 in full adults; Jenny and Winkler, 1994). For each bird, raw data showing the moult progression for primaries is given. Primaries are ordered descendantly and codes means different status of growing from 0 (old feather) to 5 (new feather) following Ginn and Melville (1983).

[Lista de las aves de primer año capturadas en muda activa de primarias en Garaio (Álava, España). La edad de estas aves se asignó según la observación de los contrastes entre plumas mudadas y sin mudar y/o a través de la observación del estado de osificación craneal (códigos entre 0 en los pollos hasta 7 en los adultos; Jenny y Winkler, 1994). Se da el estado de la muda de primarias de cada individuo. Las primarias se ordenaron de forma descendente y se utilizaron los índices de crecimiento en una escala de 0 (pluma sin mudar) a 5 (pluma completamente crecida) siguiendo Ginn y Melville (1983).]

Month	Day	Year	Sex	Body moult	Primary moult	Primary status (P1 to P10)	Skull ossification
August	4	2001	♂	Localized	Active	5543210000	2
August	7	1999	Unknown	Extensive	Active	5421000000	2
August	15	1998	Unknown	Extensive	Active	5543100000	3
August	16	2003	♂	Extensive	Active	5543100000	2
August	23	2001	♂	Extensive	Active	5554310000	3
September	6	2003	♀	Extensive	Active	5555543100	2
September	30	2001	♂	Completed	Active	5555554321	4
October	14	2001	♀	Completed	Completed	5555555555	4

birds we report here were performing a complete moult. Further support for this idea comes from the fact that these birds were moulting primaries in the normal progression as at the start of complete moult process (from inner to outer primaries), while juveniles with accidentally moulted primaries are normally renewing the external ones (Jenni and Winkler, 1994; Shirihai *et al.*, 2001).

The percentage of juvenile birds showing complete or active moult of inner primaries in Garaio was 1.65% (8 out of 486), which does not statistically differ from the frequen-

cy observed in the Cocentaina population ($\chi^2_1 = 0.03$, $p = 0.85$).

DISCUSSION

Our study suggests that a small proportion of Spanish blackcaps undergo a complete post-juvenile moult. This moult pattern found at low frequencies in two different Spanish populations, was not environmentally determined, as demonstrated in our common-garden experiment, but is likely to have a genetic basis.

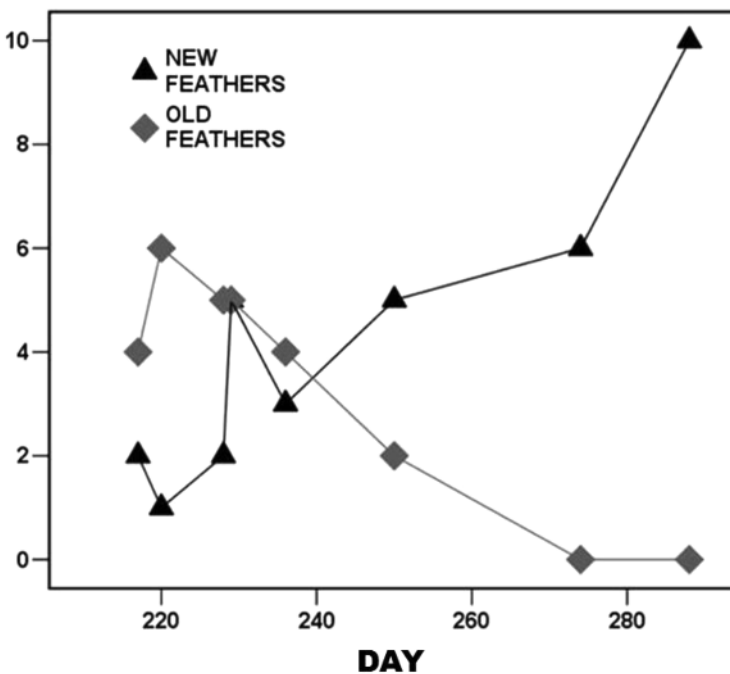


FIG. 3.—Moult progression in the 8 wild birds captured in Garaio (Alava, Spain) between 1998 and 2003. Black triangles show numbers of completely grown feathers while empty square show numbers of feathers of the previous generation (i.e. first plumage feathers). Day 220 corresponds to 8th August in non-leap years.

[Progresión de la muda en 8 aves silvestres capturadas en Garaio (Álava, España) entre 1998 y 2003. Los triángulos negros representan el número de primarias completamente crecidas, mientras que los cuadrados grises representan el número de primarias de la generación anterior (primer plumaje). El día 220 corresponde al 8 de Agosto en años no bisiestos.]

Frequency and geographic distribution of complete juvenile moult in the blackcap

Generally, juvenile blackcaps moult 3-10 great coverts (50% of the juveniles renew 10). The bastard wing generally remains un-moulted, or with a single feather renewed (c.a 30% of the cases). Two to three tertial feathers are renewed. The carpal feather, the primary coverts and the tail feathers are only seldom renewed (less than 10% of the cases) (Jenni and Winkler, 1994; Shirihai *et al.*, 2001). Exceptionally, juvenile blackcaps may also show moult of external primaries and/or inner secondaries (0.2% out of 1,891 individuals, Shirihai *et al.*, 2001). Despite the large amount of studies on captive birds, complete juvenile moult in blackcaps has not been previously observed. Berthold *et al.* (1990) reported post-juvenile moult extension based on about 2,000 juveniles in southern German blackcaps held in captivity between 1968 and 1970. They found 2% of these birds showing a moult that included all tertiaries and the inner secondary, but they never observed a single bird with a complete moult. However, Berthold *et al.* (1990) did not consider blackcaps of southern Europe in their study. Likewise, Shirihai *et al.* (2001) did not report any complete moult among juvenile blackcaps, although mostly they studied birds from the Mediterranean area (about 2,000 birds from NE Spain). To our knowledge, the most extensive juvenile moult hitherto reported in blackcaps are birds moulting 1 to 5 external primaries and 1 to 3 inner secondaries (Shirihai *et al.*, 2001; Blasco-Zumeta, 2012).

This study is the first report of juvenile blackcaps moulting inner primaries and, for one population at least, we could demonstrate that the progression of moult observed in the wild is in the right chronological order expected for a complete moult. This strongly suggests that this moult pattern is a rare but regular phenomenon in Iberian populations. In general, it is very likely that the incidence

of complete post-juvenile moult in blackcaps (and other species) is higher than reported here, since the method for ageing birds is based on the assumption that juvenile blackcaps do not undergo a complete moult, and systematic check of cranial ossification is done at very few ringing stations. A juvenile bird is normally identified by the presence of feathers from different generations in the wing. Therefore, juveniles that conducted a full moult will be considered adults and remain undetected. Apart from birds captured in first plumage and maintained in captivity, only data from constant effort sites with high numbers of recaptures between seasons could detect such unusual moult patterns. This is corroborated by the fact that at the same site in northern Spain (Natural Park of Garaio, see above), where we found first evidence for juvenile blackcaps moulting full plumage, the first juvenile Cetti's warbler *Cettia cetti* with complete moult was detected (A. Onrubia *et al.*, pers. obs.).

The fact that all blackcaps with complete juvenile moult are from southern populations is in line with a general pattern found in European Passerines, i.e. that birds from southern populations have a more extended moult (e.g. Gargallo and Clarabuch, 1995; and see Jenny and Winkler, 1994). An adaptive explanation for this pattern could be that in southern European populations conditions at the breeding sites remain favourable during a longer time than in the north. As a consequence, the cost of replacing flight feathers in juveniles is probably lower in the south. At higher latitudes, birds have to leave the breeding areas early and endure long migratory flights. If the extent of moult is controlled by these selection factors, recent environmental changes observed in Europe and elsewhere, which involve a lengthening of the growing season (Menzel and Fabian, 1999; Linderholm, 2006), could lead to an increase of the frequency of complete moult among first-year passerines.

Control of moult extent in the captive bird: genetic or environmental factors?

Intraspecific variation in the extent of post-juvenile moult is also found in other species of the genus *Sylvia*. It is especially variable in the sardinian warbler *Sylvia melanocephala*, in which early-hatched birds have a more extensive moult, which may be complete in some cases (Gauci and Sultana, 1979). This pattern was also observed in other passerines belonging to the Turdidae, Paridae and Fringillidae (Noskov *et al.*, 1999; Bojarinova *et al.*, 1999), suggesting that hatching date is an important determinant of moult extension.

For the blackcaps with complete juvenile moult described in our study, the hatching date is only known for the bird studied in captivity. This bird, however, could be considered as born late in the season (birth date: 7th June, 2011, the median hatching date for 9 nests from the same population in 2011: 28th May), which makes it unlikely that hatching date is the explanation for complete moult in this blackcap.

Environmental conditions experienced by individual birds, and conditions experienced in captivity, are known to affect the speed of the moult in ducks (Butler and McGraw, 2009). Therefore, in principle, it would be possible that conditions experienced by blackcaps in captivity could induce complete moult. However, we have no reason to assume that this was the case with the blackcap from Cacentaina, which had a complete juvenile moult. There is strong evidence that captivity does not influence the extent of moult (i.e. number of feathers moulted), as our data show (fig. 1), as other studies on blackcaps demonstrate (Berthold *et al.*, 1990), and as reported for non-passerine species (Cieslak and Kwiecinski, 2009). Moult extent was normal in all bird that we held in captivity. The high moult intensity (6 and 7 primaries in active moult) found in the juvenile bird with complete moult is only

slightly higher than the one that we registered for adults captured in active complete moult in the same population (mean number of primaries active moulting: 4, N = 3, our pers. obs.). Moreover, it has to be considered that feathers with even a minimum trace of the “waxy sheath” (defined in Ginn and Melville, 1983) were scored as “in moult” even if they were fully grown and fully functional. Thus, we can consider the high moult intensity found in the juvenile blackcap held in captivity consistent with moult intensities in the wild. We can also exclude that physical condition may have induced complete moult: the bird undergoing complete moult presented good physical conditions (fat score: 1; muscle score: 2; weight: 17.31g), similar to that shown by the other experimental birds measured on the same date (median fat score: 1; median muscle score: 2; mean body mass \pm C.I. 95%: 16.72 g \pm 0.39, N = 20).

The above mentioned evidences allow us to largely exclude environmental or physical conditions as causes of the observed moult pattern, endogenous genetic control remaining as the best explication for the observed phenomenon. Since we can exclude that environmental effects induced complete moult in the blackcap held in captivity, we need to infer other possible causes for the difference in the extent of moult found among individuals held in captivity. In principle, there are three possible explanations for the differences found in the common-garden experiment: (1) genetic effects, (2) maternal effects and (3) early common-environment effects (in the specific case, before the age of 8 days). Unfortunately, our experiment does not allow distinguishing between these factors. However, in view of other studies demonstrating additive genetic effects on winter moult extent (de la Hera *et al.*, pers. obs.), and on the timing and duration of postjuvenile moult (e.g. Gwinner and Neusser, 1985; Helm and Gwinner, 1999; Pulido and Coppack, 2004), and no evidence

for early environment or maternal effects (Larsson, 1996), we think that it is likely that the extent of moult is genetically controlled.

CONCLUSIONS

A main implication of this study is that previously undetected genetic and phenotypic variation in a life-history trait may exist in wild blackcap populations. If this variation is not phenotypically expressed (cryptic variation) it could be due in part to rare recessive alleles or, alternatively, to “genetic assimilation” (i.e. the expression of variation only under particular environmental conditions). Clearly, this unexpressed variation is difficult to detect and will largely remain undetected.

Because genetic variance is the prerequisite for adaptive evolution (Falconer and Mackay, 1996), the knowledge of existing genetic variability among traits gives a measure of the extent of the adaptive potential of a species (i.e. blackcap) or population.

We hypothesise that in blackcap populations, not only juvenile moult patterns, but many other traits, may show undetected phenotypic and genetic variation at low frequencies, producing a great extent of adaptive potential. This hypothesis is in line with the large potential of blackcaps for rapid evolutionary change (Berthold *et al.*, 1992; Pulido and Berthold, 2003; Bearhop *et al.*, 2005; Pulido and Berthold, 2010). If moult represents “a changeable event playing the part of the buffer in the annual cycle” (Noskov *et al.*, 1999), the existence of variation in this trait could be particularly important for the adaptation to novel environmental conditions.

Apart from describing a new pattern of moult in the blackcap, our results are an example of previously undetected phenotypic variation present at low frequency in wild populations of birds. This variation may be crucial for populations to adapt to rapid

environmental changes. Specifically, we expect that changes in selection regimes due to climate warming will favour individuals having a complete postjuvenile moult. Thus, we predict that the frequency of this moult pattern in blackcaps will increase.

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