Sex-dependent response of primary moult to simulated time constraints in the rock sparrow Petronia petronia

Lorenzo Serra, Simone Pirrello, Davide Licheri, Matteo Griggio and Andrea Pilastro

There is growing evidence that moult speed affects plumage quality. In many bird species, males and females differ in terms of breeding effort, survival expectation and the relationship between fitness and plumage quality. Consequently, differences in moult strategies between the sexes can be expected. The aim of this study was to assess whether, under simulated time constraints and with no parental investment in the previous breeding season, males and females differed in: a) timing and duration of primary moult, b) growth rates of individual primary feathers, and c) number of concurrently growing feathers. We investigated the effect of time constraints generated by a treatment consisting of two decreasing photoperiods (slow changing photoperiod, SCP = 2 min day$^{-1}$ and fast changing photoperiod, FCP = 8 min day$^{-1}$) on the primary post-nuptial moult of captive rock sparrows Petronia petronia. Females started to moult on average 14 and 15 days later than males in both experimental groups. Primary moult duration was 10 (FCP) and 24 (SCP) days longer in males than in females, and, within sex, 34 (females) and 48 (males) days longer in SCP birds than in FCP ones. Females renewed a larger number of primaries simultaneously (5.7% in FCP and 12.8% in SCP) and had a higher total daily feather mass grown (9.9% in FCP and 22.4% in SCP), even though daily growth rates of individual primaries did not differ between sexes. As a result, males and females completed their primary moult at the same time within treatment. The observed differences in timing, duration and energy allocation for primary moult between the sexes probably have a genetic basis, as birds did not engage in reproduction during the preceding breeding season.

Life-history theory suggests that organisms are constrained by finite time and energy, so that increased expenditure on one activity necessarily corresponds to reduced allocation for others (Williams 1966). Each year, birds breeding in temperate climates face complex energy trade-offs between the cost of reproduction, feather moult, migration and wintering. These activities are the most demanding in terms of time, have the highest energy costs in the annual cycle and are the principal variables within individual life-histories. Consequently, birds tend to keep them separated in time. Generally, there is a clear relationship between the end of reproduction and the onset of moult, and between the end of moult and beginning of migration or wintering. To compensate for the delay in the optimal timetable, late-breeding birds can make moult overlap with parental care or migration/wintering (Orell and Ojanen 1980, Jenni and Winkler 1994, Hemborg 1999, Siikamaki et al. 1994, Norris et al. 2004), speed up the moultting process (Moore et al. 1982, Morton and Morton 1990, Bojarinova et al. 1999) or suspend the moult (Hall and Fransson 2001).

Due to its high flexibility, avian moult is generally considered as a timing buffer in the annual cycle (Hellm and Gwinner 2006) as it can be fine-tuned to the prevailing time constraints of breeding or migration, events which are probably more readily correlated with fitness than moult. In line with this view, moult patterns are seen as adaptive mechanisms that allow birds to maintain their annual timetables, leading to the large variety of moult strategies (Ginn and Melville 1983, Jenni and Winkler 1994).

Moult pattern adjustments, however, have a cost. Indeed, there is growing evidence that moult speed affects plumage quality, in terms of resistance to wear of flight feathers (Dawson et al. 2000, Serra 2001) and colour of sexual signals (Nilsson and Svensson 1996, Serra et al. 2007, Ferns and Hinsley 2008, Griggio et al. 2009). This suggests that the evolution of moult patterns is influenced not only by time constraints, but also by the effect of the rate of feather growth on plumage quality in relation to flight, insulation, and sexual signalling (Holmgren and Hedenström 1995). It can therefore be expected that each species’ moult strategy (timing, duration and rates of individual feather growth) is adapted to attain the best plumage quality within the constraints imposed by the previous time and energy allocation (e.g. timing of migration and reproduction) and the relationship between moult speed and plumage quality. Considering that in
many bird species males and females are likely to differ in terms of breeding effort, survival expectation and relationship between fitness and plumage quality (because of differences in rate of wear of plumage, or relative importance of plumage in sexual signalling), it may be expected that the two sexes have different moult strategies. Some studies have shown that there are sex-specific moult timing and durations (Siikamäki et al. 1994, Newton and Rothery 2005, Flinks et al. 2008), but it is still unclear if shorter durations are obtained by increasing the growth speed of single feathers, the number of simultaneously growing feathers, or a combination of the two mechanisms.

Because sexes take different advantage of plumage quality, and both sexual signals and survival rate outside the breeding period seem negatively correlated to the differential sexual investment in the preceding breeding season, we set up an experiment in which the effect of reproductive costs was eliminated in order to identify the sexual component of moult patterns which is not related to the parental investment. To simulate the effect of late breeding, and hence the need of a faster moult, we introduced a time constraint by manipulating the daily rate of photoperiod decrease. The effect of photoperiod on moult is well known: long photoperiods act as a trigger for the start of moult, while rapid decreases in photoperiod increase moult speed (Noskov et al. 1985, Dawson 1994, 1998). For this purpose, a flock of captive bred rock sparrows Petronia petronia, with no previous breeding experience, was used to investigate sexual differences under simulated time constraints in: a) timing and duration of primary moult, b) growth rates of individual primary feathers and c) number of concurrently growing primaries.

The rock sparrow Petronia petronia, a small-sized passerine, is an unusual species in which brood desertion can occur in both sexes, parental investment is highly variable and there is sexual conflict over parental care (Griggo et al. 2003, Griggo and Pilastro 2007). This species undergoes a complete post-nuptial moult (Cramp and Perrins 1994). In a previous study, we demonstrated that moult duration had a strong influence on the expression of plumage sexual signals (the yellow throat patch and the white terminal spots on the rectrices) in the rock sparrow (Serra et al. 2007). In this study, we analysed the growth rates of individual primary feathers from the same birds used in above-mentioned experiment with the aim of investigating how time constraints affect flight feather moult. The only result shared by the two papers is the overall moult duration of primary moult, which was used in Serra et al. (2007) as a proxy for body and tail feather moult durations, to demonstrate that our photoperiod manipulation was effective in changing feathers’ growth rates.

Material and methods

Housing condition

Our experimental birds were 25 rock sparrows (15 males and 10 females, all sexed by DNA analysis). Birds were caught as juveniles soon after fledging in mist-nets near L’Aquila (42°23’N, 13°18’E), central Italy, between 6 and 8 August 2003 and then kept in individual indoor cages (58 × 33 × 31 cm) in Ozzano Emilia, Bologna (44°28’N, 11°30’E).

Birds completed their first moult by November 2003 and did not breed in spring 2004. On 25 June 2004, at the first onset of primary moult in two individuals, birds – which were kept at 18 h light and 6 h darkness (18L: 6D) two weeks prior to onset of moulting – were divided into two neighbouring rooms and exposed to two photoperiods which decreased at different rates. The starting photoperiod was local natural day-light conditions (data from: <http://aa.usno.navy.mil>). Eight males and five females, hereafter referred to as ‘slow-changing photoperiod’ birds (SCP), were exposed to a 2 min day−1 decrease, while seven males and five females, hereafter called ‘fast-changing photoperiod’ birds (FCP), to an 8 min day−1 decrease (Fig. 1). For more details in housing conditions, see Serra et al. (2007).

Primary moult recording

Primary moult was checked every seven days (checking dates) from 25 June 2004 (the date when the first bird was observed in active primary moult) to the end of the primary moult (no birds in moult: 20 October in FCP birds, 23 December in SCP birds). Primary moult was recorded according to Ashmole (1962): old feathers were scored 0, new feathers 5 and growing feathers from 1 to 4 depending on their stage of growth. We assumed that the starting date of primary moult was the checking date before the first primary scoring ≥1 was observed. Primaries were numbered from the innermost (P1) to the outermost (P9). The vestigial 10th primary was excluded from the analyses. Nine stages of primary moult progression were identified by the sequential shedding of primaries from P1 to P9, each stage being hereafter referred to as ‘point of moult progression’. For each point, the number of simultaneously growing primaries (NSGP) was counted.

![Figure 1. Changes in daylight experienced by birds. Daylight decrease from 16L: 8D in FCP birds (8 min day−1, dotted line) and SCP birds (2 min day−1, dashed line). Natural local conditions were expressed both as the period between sunrise-sunset (solid line) and dawn-dusk (dashed-dotted line). FCP birds were kept at constant daylight of 7L: 17D from 16 September onwards.](image-url)
Feather measurements

Two weeks after the end of the moult in each group, all primaries of both wings were plucked. Birds were not injured and new feathers grew completely within 2–7 weeks from extrusion. The following measurements were taken for each primary of the right wing: maximum rachis length with an electronic dialler (accuracy: 0.1 mm), dry mass (accuracy: 0.0001 g) and area (accuracy: 0.01 mm²). The daily increment in mass and length of each primary, hereafter referred to as ‘daily feather mass grown’ (DFMG) and ‘daily feather length grown’ (DFLG), were calculated by dividing feather mass and length by moult duration of each feather, i.e. assuming a constant growth from tip to base (Murphy and King 1986, Prum and Williamson 2002, Dawson 2003). The ‘total daily feather mass grown’ (TDFMG) was calculated as the sum of DFMG for each point of moult progression. The ‘total primary mass’ (TPM) was calculated as the sum of the mass of each primary (P1–P9) at the end of the moult.

The proportion of feather mass grown at each moult score (1 to 5) was obtained by applying five correction factors (0.125, 0.375, 0.625, 0.875, 1) as proposed by Underhill and Zucchini (1988). Feathers were dried in a convection oven for 24–48 h at 70°C (Underhill and Joubert 1995) before measuring dry mass. Areas were calculated with UTHSCSA Image Tool software (<http://ddsdx.uthscsa.edu/dig/download.html>) from TIFF-files obtained by feather scanning at 300 dpi.

Spectrometry

We measured spectral reflectance (at ca 0.34 nm intervals) on the dorsal side of the outer vane of the extruded primaries of the right wing with an Ocean Optics S2000 Spectrometer (range 180–1024 nm). A fibre-optic measuring probe was used to transfer the light from a halogen lamp to the feathers and to pass the light reflected back to the spectrometer. The probe was held at a 90° angle to the feather surface and ambient light was excluded with a black PVC tube that held the probe tip at a distance of 3 mm from the surface. Spectra were recorded with OOIBase32 software, setting standards to a white-standard and dark before each measurement session. Teflon tape was assumed as a qualified white-standard as it gave a strong (>94%) and diffuse reflectance in the 300–700 nm wavelengths (Fig. 2). Spectral reflectance of each feather was measured against a white teflon tape background. Five consecutive measurements were taken from the tip, centre and base of the outer vane and averaged for each primary. Reflectance against a white background is a measurement that mimics feather light absorbance and was used here as an index of ‘primary’ darkness, as primary colour is correlated to density of melamins. Reflectance spectra were restricted to wavelengths between 300 and 700 nm and total reflectance was calculated as the summed reflectance in the investigated range (Saks et al. 2003).

Statistical analyses

Two ‘general linear models’ (GLM) were applied to model the effect of sex and treatment (factors) on moult strategy.
both treatment and sex on the overall duration of primary moult was also detected (Table 1). Primary moult duration was longer in males than in females in both treatments: 10 days (11%) in FCP birds and 24 days (17%) in SCP birds. Within sex, primary moult duration was 48 days (35%) longer in SCP than in FCP males, and 34 days (30%) longer in SCP than in FCP females. However, as a combined effect of starting date and duration, moult completion date did not differ between sexes, but was significantly later for SCP birds (on average, SCP males completed their moult 54 days later (34%) than FCP males and SCP females 42 days later (28%) than FCP females (Table 1).

**Moult duration of individual primaries and total feather mass production**

The moult duration of individual primaries was not significantly affected by treatment or sex, although it was close to statistical relevance (Fig. 3a–b, Table 2). On average, moult duration of individual primaries was 4.3% and 6.1% shorter in females than in males (within FCP and SCP birds, respectively), and 3.9% and 5.7% shorter in SCP than in FCP birds (within males and females, respectively).

The overall duration of primary moult (from P1 to P9, Table 1) was shorter in FCP birds and in females because they simultaneously grew a larger number of primaries (Table 3, Fig. 4a–b). On average, females had 5.7–12.8% (in FCP and SCP birds, respectively) more concurrently growing primaries than males, and FCP birds had 61.7–51.6% (in males and females, respectively) more than SCP birds.

Total daily feather mass grown (TDFMG) was significantly affected by sex and treatment, with females on average producing 9.9% and 22.4% (in FCP and SCP birds, respectively) more feather mass than males, and FCP birds on average producing 56.9% and 40.8% (in males and females, respectively) more feather mass than their SCP counterparts (Table 3, Fig. 4c–d).

**Final primary length, area and mass**

At the end of the moult, individual primary length and mass were 2.0–3.8% (range P1–P9) and 4.7–8.7% greater in males than in females, while no differences were found for primary area. No significant effect of treatment was detected on these variables, although mean values of P1–P9 were larger in FCP than SCP birds in only 4 out of 54 comparisons (93%) (Fig. 3c–h, Table 2). The total primary mass (TPM) measured at the end of the moult was significantly different both for treatment and sex (treatment: $F_{1,21} = 5.974$, $p = 0.023$; sex: $F_{1,21} = 9.065$, $p = 0.007$). On average, SCP birds produced 5.97% and 7.03% more feather mass than FCPs for males and females, respectively.

**Final reflectance and daily growth rates of individual primaries**

Primary reflectance was 5.7–16.1% (range P1–P9) greater in SCP than in FCP birds (i.e. primaries of SCP birds were less dark), and no sex differences were found (Fig. 3i–j, Table 2). The daily primary increment in length (daily feather length grown, DFLG) and mass (daily feather mass grown, DFMG) were respectively 1.3–13.4% (range P1–P9) and 0.2–15.8% greater in SCP than in FCP birds; no effect of sex was found (Fig. 3k–n, Table 2).

**Discussion**

The effect of a difference in the decrease of day length on the overall duration of primary moult was significant for both treatment and sex, as already reported in Serra et al. (2007), and observed differences were within the range of variation known for natural populations of other species (Serra 2001), and for similar experiments with captive birds (Dolnik and Gavrilov 1980, Dawson 1994, 2004, Hall and Fransson 2000, Hall 2002). The shortening of moult duration of primaries, observed in birds experiencing the faster decrease in photoperiod, was due to a simultaneous growth of a larger number of primaries in both sexes, females renewing a larger number of feathers simultaneously than males did. The same effect on moult duration and pattern was observed in several experiments with various species, and seems to be a general moult reaction to time constraints (Dolnik and Gavrilov 1980, Hall and Fransson 2000, Dawson 2004). Although sex differences in timing (i.e. females start moulting later than males) or duration (females make a faster moult) of moult have been described in both free-living populations (Ginn and Melville 1983, Jenni and Winkler 1994, Sii kamaki et al. 1994, Newton and Rothery 2005) and captive birds (Wingfield and Farner 1979, Meijer 1991), the observation that sexes differ in their primary shedding rate has not — to our knowledge — previously been described.

A delay of 8–24 days in the onset of moult by females in comparison to males has been described in some passerines (Newton and Rothery 2005, Flinks et al. 2008), and it is thought to be associated with a stronger maternal reproductive investment, with males more willing to invest in
Figure 3. The effect of sex and treatment on moult duration of individual primaries (a–b), primary length (c–d), area (e–f), mass (g–h), reflectance (i–j), daily feather length grown (k–l), daily feather mass grown (m–n). Empty dots = slow changing photoperiod birds (SCP), solid dots = fast changing photoperiod birds (FCP). Means ± SD are shown. See Table 2 for statistical analysis.
moult than in parental care (Bensch et al. 1985, Runfeldt and Wingfield 1985, Siikamäki et al. 1994, Svensson and Nilsson 1997). Indeed, despite the prevalence of the biparental care system in birds, females tend to provide more parental care than males (Ligon 1999). In the rock sparrow, males contribute less than females to nestling feeding (Grigio et al. 2005, Grigio and Pilastro 2007) and defence (Grigio et al. 2003). Females might hence have developed a moult pattern which allows them to complete their moult by the same time as males, even if they start later. Time of moult completion is a key factor in the annual cycle, because it affects migration time in migratory species and annual survival (Holmgren and Hedenström 1999). In our experiment, there was no previous parental investment, and hence, moult patterns reflected only intrinsic differences between the sexes, suggesting that the delayed onset of moult observed in females has a genetic component in the rock sparrow and is not completely influenced by proximate factors (e.g. end of breeding). Considering the implications of moult strategy on sexually selected ornaments in this species (Serra et al. 2007), it is possible that the observed difference in onset of moult between males and females is correlated with different selective pressure on plumage quality.

The duration of moult of individual primaries, even if only nearly significantly different between treatments, suggested the existence of a trade-off between the number of simultaneously growing primaries (NSGP) and the growth rates of individual primaries, as FCP birds, which showed a higher number of simultaneously growing feathers, had slower growth rates (mm day$^{-1}$ and mg day$^{-1}$) and longer moult durations of individual primaries. As a combined result of feather growth rates and number of concurrently growing feathers, the total daily feather mass grown (TDFMG) was higher in FCP birds. They therefore completed the moult in a shorter time, but paid a higher daily energy cost. This is an obvious cost of fast moulting, imposed by the seasonal time constraints experienced by migrant birds (Bensch et al. 1991, Norris et. al. 2004) and populations wintering at northern latitudes (Serra et al. 2006). The duration of moult of individual primaries was shorter in females (although marginally non-significant), but it was not associated with higher growth rates (below). This difference was probably entirely due to the longer length of males’ primaries, as the 4.1 mm average difference in wing length (Serra et al. 2007) can easily explain the average difference of 1.2–1.5 days in moult duration of individual primaries between sexes, within treatment, and by the respective average daily length growth (2.7 and 2.9 mm day$^{-1}$ for FCP and SCP females, respectively). Females, as FCP birds, had a higher total daily feather mass grown (TDFMG) than males even if sexes did not differ in daily growth rates of individual primaries. In this case, the higher total daily energy cost paid by females for moulting was entirely due to the number of simultaneously growing feathers.

Primary length, mass and area were not significantly affected by treatment in the rock sparrow, even if averages were larger in SCP than in FCP birds in both sexes for almost all primaries. This pattern is confirmed by the larger total primary mass (TPM) in SCP birds and is in line with previous findings on starlings *Sturnus vulgaris*, in which primaries of fast-moulting birds were shorter, weighed less and were more asymmetrical (Dawson et al. 2000, Dawson 2004). Similarly, in lesser white-throats *Sylvia curruca*, fast-moultng birds had shorter wings (Hall and Fransson 2000, but see Hall 2002). Our data suggest that both sexes adjust some growth parameters (average daily growth rate of individual primaries, number of simultaneously growing primaries and total daily production of feather mass) in

### Table 2. Results of LMMs on seven variables taken on individual primaries (P1–P9, see statistical analysis in ‘Methods’). DFMG = daily feather mass grown, DFLG = daily feather length grown.

<table>
<thead>
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<th>Treatment</th>
<th>Sex</th>
<th>Primary</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>DF</td>
<td>p</td>
</tr>
<tr>
<td>Length</td>
<td>2.68</td>
<td>1.22</td>
<td>0.12</td>
</tr>
<tr>
<td>Mass</td>
<td>2.32</td>
<td>1.22</td>
<td>0.14</td>
</tr>
<tr>
<td>Area</td>
<td>0.20</td>
<td>1.22</td>
<td>0.66</td>
</tr>
<tr>
<td>DFMG</td>
<td>11.84</td>
<td>1.22</td>
<td>0.002</td>
</tr>
<tr>
<td>DFLG</td>
<td>8.06</td>
<td>1.22</td>
<td>0.01</td>
</tr>
<tr>
<td>Reflectance</td>
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<td>1.22</td>
<td>0.02</td>
</tr>
<tr>
<td>Moult duration</td>
<td>3.42</td>
<td>1.22</td>
<td>0.08</td>
</tr>
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</table>

### Table 3. Result of GLMs on the number of simultaneously growing primaries (NSGP) and the total daily feather mass grown (TDFMG) (see statistical analysis in ‘Methods’). $^1$ = partial squared Eta.

<table>
<thead>
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<th>Factors</th>
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<th>Covariate</th>
</tr>
</thead>
<tbody>
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<td></td>
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<td>DF</td>
<td>p</td>
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<tr>
<td>NSGP</td>
<td>94.90</td>
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<tr>
<td>TDFMG</td>
<td>70.96</td>
<td>1,342</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
order to maintain final feather length and mass as stable as possible. Primary length and mass are probably of great importance for flight, as recent studies have demonstrated that slower growth rates lead to higher quality primaries (Dawson et al. 2000, Serra 2001). Hence, if a delayed moult leads to a higher energy cost per unit of time (Bensch et al. 1985), it does not necessarily produce less durable or lower quality feathers soon after moult. However, it has been shown in starlings that the negative effect of fast moulting on feather mass is weak (7.5%) at the end of moult and tends to increase appreciably after 2 (14.5%) and 7 months (25%) (Dawson et al. 2000).

FCP birds, and marginally females, had a higher number of concurrently growing primaries, which implies a potentially higher daily metabolic cost for feather synthesis. However, the slower growth rate of individual primaries of FCP birds suggests that they probably tried to reduce energy costs of feather synthesis or were limited in their ability to achieve feather synthesis. The lack of sexual differences in the daily growth parameters suggests that females and males have the same structural requirements for primaries, assuming growth rate as a honest indicator of feather quality (Dawson et al. 2000, Serra 2001).

FCP birds had lower spectral reflectance, i.e. primaries were darker, and there were no sexual differences. This suggests that slower growth rates lead to the inclusion of higher pigment densities during feather development (Prum and Williamson 2002). Higher melanin densities have been postulated to give better resistance to feather abrasion, to decrease wear and to cause lower barb breakage (Burtt 1986, Bonser 1996), and hence, to be an important factor in determining optimal moult duration (Serra 2001). Furthermore, this may explain the progressive feather mass reduction observed after moult in fast moulting starlings (Dawson et al. 2000). In our experiment, the reflectance of primary feathers seems to be constrained by feather growth rates. Although the different colourations observed between feather parts (i.e. feather tip vs base) have been explained as an adaptation linked to the protective function of melanin in feather barbs (Gill 1995), our results suggest that differing intensity of colouration between feather parts might simply be a consequence of developmental mechanisms. The same mechanism might be true for variation in reflectance along a feather tract, as occurs in our case between inner and outer primaries. Different rates of feather growth might therefore be the cause of the colour pattern in the primaries of waders (Charadrii), and in other species where the longest outermost primary is clearly darker than the others. The different scaling relationships between length and mass of primaries recently described for 120 bird species (Dawson 2005, Serra and Underhill 2006) probably has a tight correspondence to reflectance, because the ratio between mass and length is directly related to follicle size, and thereby to growth rates (Serra and Underhill 2006).

In conclusion, we identified two sex-dependent moult patterns, featured by a different allocation of time and energy, which allowed birds of the two sexes to 1) grow feather at the same rate, and probably obtain feathers of the same quality (as far as this correlates with feather density), and 2) complete the moult at the same time, and hence have an expectation of similar winter survival rates.

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undertaken (capture, maintenance in captivity and experimental treatments) under the combined prescriptions of Art. 4 (1) and Art. 7 (5) of Italian law 157/1992, which regulate studies on wild bird species. This research was partly funded by the Univ. of Padua (‘Fondi di ricerca ex-60%’ to AP).

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