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Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival

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Life-history theory proposes that costs must be associated with reproduction. Many direct costs are incurred during breeding. There is also evidence for indirect costs, incurred after breeding, which decrease survival and future reproductive success. One possible indirect cost identified in birds is that breeding activity in some way compromises plumage quality in the subsequent moult. Here we propose a mechanism by which this could occur. Breeding activity delays the start of moult. Birds that start to moult later also moult more rapidly—an effect of decreasing daylength. Could this result in poorer quality plumage? We kept two groups of male European starlings, *Sturnus vulgaris*, one on constant long days and the other on decreasing daylengths from the start of moult. Decreasing daylengths reduced the duration of moult from 103 ± 4 days to 73 ± 3 days ($p < 0.0001$). Newly grown primary feathers of birds that moulted fast were slightly shorter, weighed less ($p < 0.05$) and were more asymmetrical. They had a thinner rachis ($p < 0.005$), were less hard ($p < 0.01$) and less rigid ($p < 0.05$). They were also less resistant to wear so that differences in mass and asymmetry increased with time. There was no difference in Young's modulus. Poorer quality plumage will lead to decreased survival due to decreased flight performance and increased thermoregulatory costs. Thus, reproduction incurs costs through a mechanism that operates after the end of breeding.

Keywords: bird; starling; reproductive costs; moult; plumage quality; survival

1. INTRODUCTION

A central tenet of life-history theory is that future reproductive output is negatively influenced by current reproductive effort (Williams 1966; Stearns 1992; Partridge 1989; Jöhnsson *et al.* 1998; Sinervo & Svensson 1998). There are many immediate costs of reproduction, i.e. costs that are accrued during the period of reproductive activity, e.g. production of sexual display and nuptial plumage, gamete production, parental care, increased risk of predation and parasitism, and compromised immunocompetence. Costs of breeding may also be deferred, resulting in decreased over-winter survival (Lindén & Møller 1989; Roff 1992; Daan *et al.* 1996; Nilsson & Svensson 1996) or decreased reproductive output during the next breeding attempt (Røskaft 1985; Gustafsson & Sutherland 1988). Physiological mechanisms that might mediate deferred costs have not been demonstrated.

By experimentally delaying breeding, and hence moult, in blue tits (*Parus caeruleus*), Nilsson & Svensson (1996) showed that 'delayed' birds had higher thermoregulatory costs in the following winter, reduced both over-winter survival and breeding success the following year. They suggested that there was a trade-off between the energetic costs of reproduction and of moult such that the parental effort of late breeding was, in some way, detrimental to the insulative quality of the plumage. Here we propose a mechanism by which breeding may influence feather quality.

Breeding and moult are both energetically demanding (Murphy & King 1992) and hence moult is usually, but not always, delayed until breeding has finished (Morton 1992; Hemborg 1999). Therefore, breeding birds start to moult later than non-breeders, and birds with extended or late breeding moult later than those that curtail breeding activity earlier (Newton 1966; Morton & Morton 1990). Later-moulting birds moult more rapidly (Morton & Morton 1990) because the rate of moult is influenced by the seasonal change in daylength. The start of moult is triggered by long days, but once it has started, decreasing daylength increases the rate of moult (Dawson 1994, 1998). Most species of birds in temperate latitudes moult after the summer solstice and individuals moulting later in the year will be subject to shorter days and a more rapid decrease in daylength during their moult. In this paper, we investigate the effects of the rate of moult, mediated via manipulation of daylength, on feather quality in European starlings, *Sturnus vulgaris*. We propose that a faster moult is detrimental to feather quality and that this will affect future survival and reproduction by increasing thermoregulatory costs and decreasing flight performance (Swaddle *et al.* 1996).

2. MATERIAL AND METHODS

(a) *Experimental design*

Wild, juvenile starlings were caught during the summer of 1996 and kept in outdoor aviaries at Monks Wood (52° N). In mid-May 1998, when natural daylength was 17 h 10 min, two groups of eight randomly selected males were moved indoors, into two identical rooms on an artificial daylength of 18 h. Illumination was provided by cool fluorescent tubes: lights on, 03.00; lights off, 21.00. No birds had begun to moult at this time. One week later, some birds in each group had dropped their first primary feather. For one group of birds, daylength was then

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reduced by 1 h each week until, after six weeks, it reached 12 h (figure 1). The other group remained on 18-hour days. The progress of moult was recorded at weekly intervals, on the same day for all birds. In the case of the decreasing daylength group, this was 7 d after the last decrease in daylength. A dropped primary feather was scored as 1, a quarter-, half- or three-quarter regrown feather was scored 2, 3, or 4 respectively, and a fully regrown feather was scored 5 (Newton 1966). A bird that had moulted and fully regrown all nine primary feathers therefore had a moult score of 45. As soon as each individual had finished moulting, the left and right seventh primary feathers were plucked and stored. Waiting until the moult score was 45, i.e. when the ninth primary appeared to be fully grown, ensured that the seventh primary had indeed fully grown, while at the same time allowing little time for subsequent wear. At the end of September, by which time all birds had finished moulting, they were returned to outdoor aviaries. Natural daylength then was 12 h 40 min. In late November, the eighth primary was plucked from the right wing. In mid-May 1999, i.e. just before birds were due to start moulting again, the ninth primary was plucked from both wings of each bird. The experiment was carried out under Home Office licence PPL 80/1211.

To compare experimental moult rates with the rate under natural daylengths, moult was also recorded in another group of males from the same cohort. This group remained in the outdoor aviary. Feather quality of these birds was not assessed because they had not been held in identical conditions and so were not directly comparable.

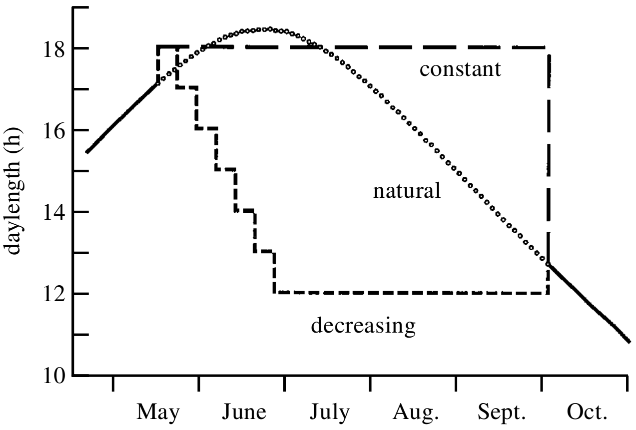

Figure 1. Experimental design. Two groups of starlings were moved from an outdoor aviary in mid-May (natural daylength of 17 h 10 min) to indoor rooms on 18 h days. One group remained on 18 h days until the end of September (constant). For the other group, daylength was reduced by 1 h each week until it reached 12 h in late June, and then remained at 12 h until the end of September (decreasing). Both groups were then moved back outdoors (natural daylength 12 h 40 min). For comparison, another group remained outdoors exposed to natural daylengths throughout (natural). Data on natural daylength including civil twilight at 52° N were obtained from H. M. Nautical Almanac Office. The maximum natural rate of decrease in daylength is 30 min per week.

(b) *Feather measurements*

The seventh primaries were carefully examined for wear. Any in which the tip was not complete were ignored. The aim was to assess the quality of new feathers rather than effects due to subsequent wear. Both the left and right feathers were weighed to the nearest 0.1 mg and length was measured to the nearest 0.1 mm. Unsigned asymmetry was assessed as the difference in mass and length between the left and right feathers from each individual. These feathers were then used for tests of stiffness and hardness. The eighth primaries were plucked in November and weighed. In this case, all feathers were used irrespective of whether the tips had been damaged, the aim being to assess the effects of wear. These feathers were then used to measure Young's modulus (E), which is the ratio of the tensile stress to the tensile strain. The ninth primaries, plucked in May, were also weighed irrespective of damage, and asymmetry between left and right feathers was recorded. The dorsoventral diameter of the rachis was measured to the nearest 0.02 mm at 1 cm intervals from the base of each feather.

(i) *Stiffness*

The stiffness of each seventh primary feather, plucked at the end of the moult, was measured using a modification of Purslow & Vincent's (1978) method. Ten grams ('the weight') were attached to the rachis 65 mm from the proximal end of each feather (about two-thirds along its length), and the vertical (downward) and horizontal (towards the trailing edge) deflections were measured. The proximal end of the calamus was fixed into a hole in a brass block with cyanoacrylate adhesive (RS Components, Corby, UK) so that it emerged at a point corresponding to the insertion point of the feather into the skin of the bird's wing (*ca.* 10 mm from the proximal end). The brass block was mounted in a stand beside two pieces of graph paper (attached to vertical boards), with the dorsal surface of the feather uppermost and that part of the feather to which the weight was to be attached parallel to the ground. The weight was attached to the rachis by means of a short piece of cotton. Some barbs and barbules had to be separated in order to insert the cotton. These, and any other unzipped barbules on the rest of the feather, were smoothed back into place before releasing the weight and measuring the deflection. The weight was removed and the measurement repeated ten times.

(ii) *Hardness*

The hardness of each seventh primary feather was measured using Bonser's (1995) method. A 10 mm section of rachis was removed from each feather at the point of insertion into the wing. This was split into dorsal and ventral halves, and the medullary foam scraped away. The dorsal half was mounted on to a block of Perspex with cyanoacrylate adhesive. The hardness of the upper surface of the upper half was measured with a Leitz 'Wetzlar' miniload machine using a load of 5 g. The indenter was allowed to remain on the specimen for 15 s and the indentation was measured after a further 45 s. Ten indentations were measured in this way.

(iii) *Young's modulus*

Young's modulus was assessed in the eighth primary feathers plucked in late November. The proximal 5 mm of the rachis were removed from each feather and a strip 25 mm in length cut longitudinally from the rachis. The strip was cut sufficiently narrow so that curvature of the cross-section of the strip was negligible. Each end of the strip was glued using a cyanoacrylate gel adhesive to a tab of aluminium 1 mm thick, which was folded over to sandwich the strip. The mean specimen length remaining non-encapsulated was 9.55 ± 0.01 mm (s.e.m., $n = 16$). Specimens were clamped in the tensile test grips of a Davenport-Nene T10 test frame (Davenport-Nene Ltd, Wellingborough,

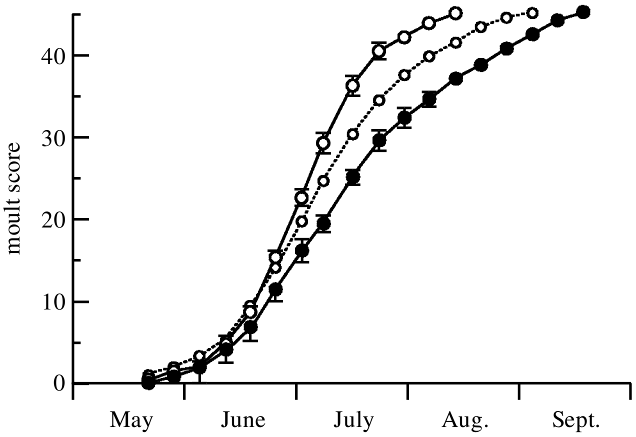

Figure 2. Change in moult score in two groups of experimental starlings ($n = 8$, solid lines). One group was held under a constant daylength of 18 h (solid circles). The other group was exposed to daylengths that decreased by 1 h each week from the beginning of moult, in mid-May, until daylength was 12 h, six weeks later (open circles). Each point represents the mean ± s.e.m. The duration of moult in slow-moulting birds was 103 ± 4 d compared with 73 ± 3 d for fast-moulting birds ($p < 0.0001$). Moult duration in birds under natural changes in daylength (broken line) was 85 ± 2 d.

UK). A 50 N load was used to apply a peak load of 9 N with a test speed of $1\,\mathrm{mm\,min^{-1}}$. The slow test speed and consistent specimen lengths were chosen to limit the possible influence of viscoelastic effects on the measured modulus (Bonser & Purslow 1995). The Young's modulus of the specimen was calculated from the steepest, linear section of the resulting load–displacement curve. All specimens were conditioned at room temperature and humidity for 24 h prior to testing.

(c) *Statistical analyses*

Differences in each measurement between the two treatment groups were assessed with two-tailed Student's *t*-tests except in the case of asymmetries. The standard deviations of asymmetries were markedly unequal and Mann–Whitney tests were used instead.

3. RESULTS

Exposing birds to decreasing daylengths significantly accelerated the rate of moult (figure 2). Birds held under constant long daylength completed their moult in mid-September, a duration of 103 ± 4 d. Those under decreasing daylengths finished in mid-August, taking only 73 ± 3 d ($p < 0.0001$). Another group of birds, which was held in outdoor aviaries for comparison with the experimental groups, showed a rate of moult intermediate between the experimental groups. These birds completed moult by the end of August, duration 85 ± 2 d.

(a) *Feather mass and dimensions*

Two of the eight birds in each group had damaged tips to their seventh primaries. Amongst the remaining six birds in each group, the mean mass was 7.5% greater ($p < 0.05$) in slow-moulting birds (figure 3*a*). Slow-moulting birds also showed less asymmetry in feather mass (figure 3*b*), although the difference was not quite significant. Mean feather length was greater in the slow-moulting birds (104.4 ± 0.8 mm compared with 101.0 ± 1.9 mm) and slow-moulting birds showed less asymmetry in feather length (1.0 ± 0.3 mm compared with 1.8 ± 0.6 mm) although neither of these differences was statistically significant.

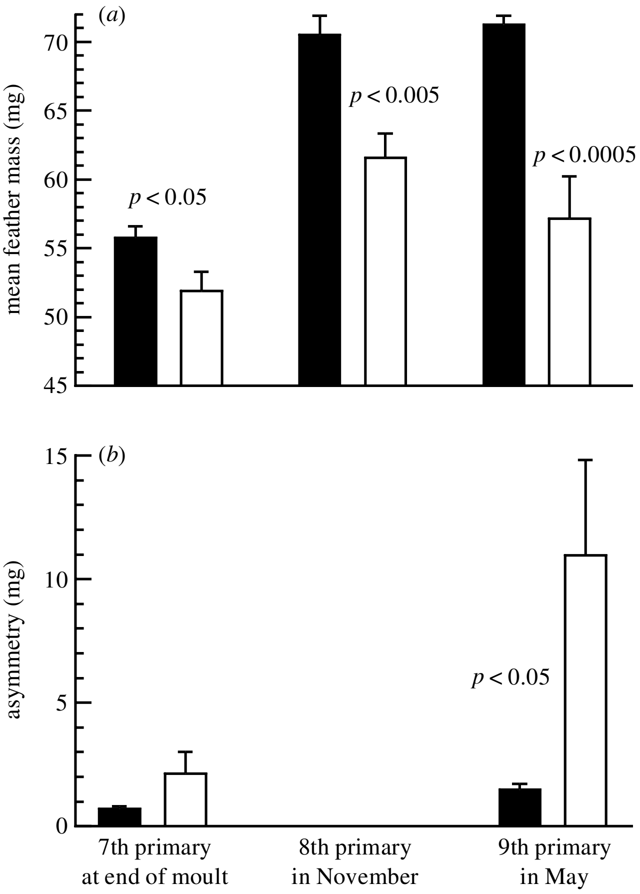

Figure 3. (*a*) Mean mass and (*b*) asymmetry (absolute difference in mass between the left and right primary feathers) of the seventh primary feather immediately after the end of moult ($n = 6$ in each group), the eighth primary in November ($n = 8$ in each group) and the ninth primary in May, immediately before the next moult ($n = 8$ in each group) from starlings that had moulted during constant long days (solid bars) or decreasing daylength (open bars). Each bar represents the mean ± s.e.m. (Asymmetry was not assessed on the eighth primary.)

The eighth primary feathers, plucked in November, showed a greater difference, 14.5% ($p < 0.005$), in mass between the two groups (figure 3*a*), and the ninth primaries, taken in May, before the next moult, showed a further increase in difference, 25% ($p < 0.0005$). There was also a greater difference in asymmetry in the mass of these feathers (figure 3*b*). Presumably the initial differences in feather mass and symmetry immediately after moult became exaggerated through the effects of subsequent wear and damage. The dorsoventral width of the rachis was highly significantly less (between $p > 0.005$ and $p < 0.0001$) at each of the measurement points in the feathers from fast-moulting birds (figure 4). Thus, for example, the width 30 mm from the feather base in feathers from fast-moulting birds was the same as the width 40 mm from the base in feathers from slow-moulting birds.

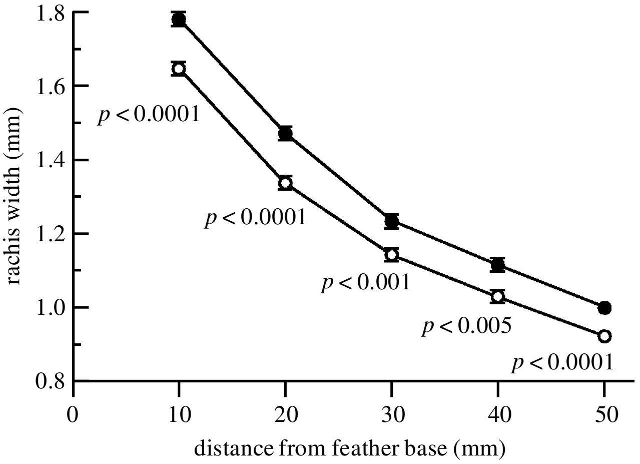

Figure 4. The dorsoventral width of the rachis of the ninth primary feather as a function of the distance from the base of the feather from starlings that had moulted during constant long days (solid circles, $n = 8$) or decreasing daylength (open circles, $n = 8$). Each point represents the mean ± s.e.m.

(b) *Physical properties of feathers*

The repeatability (Lessells & Boag 1987) of the vertical ($r = 0.997$, $F_{26,243} = 10.470$, $p < 0.0001$) and horizontal deflections ($r = 0.992$, $F_{26,243} = 3.438$, $p < 0.0001$) was high. The seventh primaries of fast-moulting birds were significantly ($p < 0.05$) less rigid under dorsal load than slow-moulting ones—they deflected 29% further, on average, in the downward direction. They also deflected 3% further towards the trailing edge, but this difference was not significant (figure 5). The repeatability of the hardness measurements was only moderate ($r = 0.550$, $F_{26,243} = 34.0$, $p < 0.001$), the surface of the rachis being too uneven to obtain more consistent measurements. The dorsal rachis of the seventh primary of slow-moulting birds was on average 24% harder ($p < 0.01$) than that of fast-moulting birds (figure 5). There was no difference in Young's modulus (E) for the eighth primary between the two groups: slow-moulting $E = 2.3 \pm 0.2$ GPa; fast-moulting $E = 2.6 \pm 0.2$ GPa.

4. DISCUSSION

Exposing starlings to decreasing daylengths after the start of moult decreased the duration of moult, as has been demonstrated before (Dawson 1994, 1998), and resulted in poorer quality primary feathers. The new primaries of the faster-moulting birds were shorter, had a narrower rachis, were lighter and less rigid than those of birds moulting more slowly, and consisted of softer keratin. There was greater asymmetry between left and right wing feathers. Differences in mass, length and asymmetry increased with time after moult, indicating less resistance to wear.

The only measured parameter unaffected by the speed of moult was Young's modulus. This property depends on the structure of the feather keratin and appears to be similar across a wide range of species, leading to the suggestion that keratin structure is biochemically conservative (Bonser & Purslow 1995; Bonser 1996). If keratin synthesis, and hence structure, are indeed conserved, then increasing the speed of moult is more likely to influence the quantity, rather than the quality, of keratin produced. Feather rigidity is a function of Young's modulus and the second moment of the rachis cross-sectional area. Young's modulus did not differ between feathers from fast- and slow-moulting birds, but cross-sectional area, as estimated by rachis dorsoventral width, was less in the feathers from fast-moulting birds, making them less rigid.

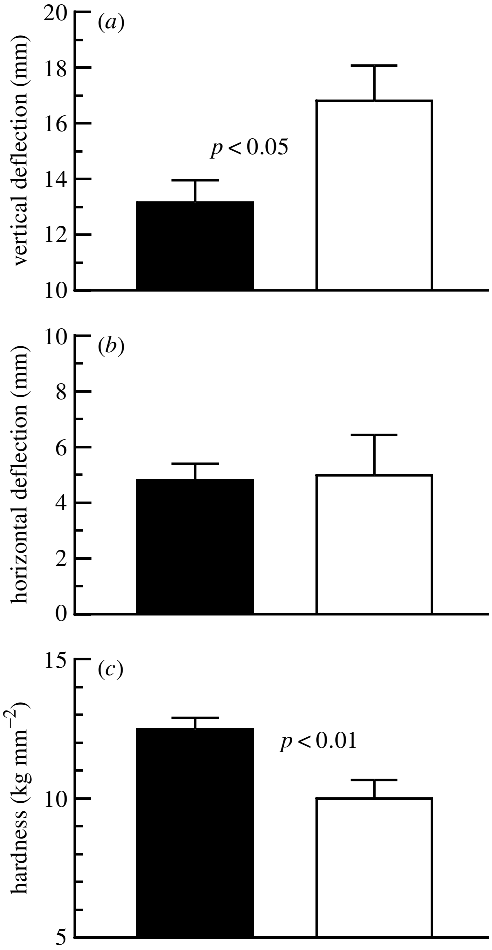

Figure 5. (a) Vertical deflection, (b) horizontal deflection and (c) hardness of the seventh primary feather from starlings that had moulted during constant long days (solid bars) or decreasing daylength (open bars). Each bar represents the mean ± s.e.m. for seven feathers.

A reduction in plumage quality may influence survival by decreasing flight performance and increasing thermoregulatory costs. The changes recorded in the primaries of the fast-moulting birds were indicative of a loss of flight performance in terms of both take-off speed and manoeuvrability (Metcalfe & Ure 1995; Swaddle *et al.* 1996). Nilsson & Svensson (1996) suggested that the reduction in over-winter survival and subsequent breeding success of late-moulting blue tits were caused by increased thermoregulatory costs due to poorer feather quality. However, Nolan *et al.* (1992) found no difference in over-winter survival of dark-eyed juncos, *Junco hyemalis*, in which moult was delayed by testosterone implants, although, not surprisingly, survival was markedly reduced in birds that were prevented from moulting. The subsequent breeding performance of the late-moulting juncos was not reported. We did not measure thermoregulatory ability in starlings or assess the quality of the contour feathers, but it does not seem unreasonable to suppose that birds with a short duration of moult, which had poorer quality primary feathers, also had poorer quality contour feathers.

Free-living starlings around Monks Wood normally raise only one brood per year (Dawson & Goldsmith 1985). Eggs are laid in mid-April and young fledge in late May. Consequently, there may be little effect of breeding activity on the start of moult. Indeed, mean start date of moult in free-living birds, an unknown proportion of which would have bred, was not significantly later than that of non-breeding birds in outdoor aviaries (I. Wyllie, unpublished data). However, in some localities in the UK the first clutch is laid sufficiently early to permit a second brood to be raised (Feare 1984). In this case, the second clutch is laid in late May, which means young are not fledged until early July (Feare 1984; Dawson & Goldsmith 1985). Presumably this would significantly delay the start of moult, and birds from such localities have been found still moulting in November, well after the end of moult in non-breeding birds (Feare 1984). This is likely to have a significant effect on the rate of moult: daylength in November is considerably shorter than the 12 h to which the fast-moulting experimental birds were exposed.

Data on the rate of moult in free-living birds are rare, probably because of the difficulty of re-trapping the same individuals over the period of moult. Morton & Morton (1990) showed that in mountain white-crowned sparrows, *Zonotrichia leucophrys* ssp. *oriantha*, late-moulting birds tended to moult more rapidly. The duration of moult in non-breeding males exceeded that of late-breeding females by 16 d, compared with a difference of 30 d between our two treatments. Newton (1966) showed that in bullfinches, *Pyrrhula pyrrhula*, the spread of moult start dates appeared to be greater than completion dates, which implies a faster rate of moult in late-moulting individuals. In juvenile great tits, *Parus major*, the start of moult is related to hatch date and later-moulting birds moult more rapidly (Bojarinova *et al*. 1999). Our experiment exaggerated the difference in the rate of decrease in daylength that would be experienced between non-breeding and late-breeding birds. However, the resultant differences in feather quality were marked and significant. In free-living birds, the differences may be less pronounced, but nevertheless are likely to represent a significant cost of breeding, and particularly of late breeding in multi-brooded species where breeding activity extends beyond the (summer) solstice.

One criticism of the experimental design is that decreasing daylength once per week, as opposed to a smaller decrease each day, could have resulted in stress-induced fault bars in the feathers. This could have affected wear and consequently asymmetry, but should not have affected initial feather mass or length. However, analysis of figures 1 and 2 shows that the last decrease in daylength was in late June when the moult score was 15. All of the results reported in this study refer to primaries 7, 8 and 9. Primary 7 would not have started to grow until the moult score was at least 20, and the others later again. None of the differences reported in this study could therefore have been due to abrupt decreases in daylength. Both groups of birds were on constant, but different, daylengths during the period when the relevant feathers were being grown.

The duration of moult is affected by daylength. It does not appear to be affected by nutrition. Severe food deprivation, sufficient to cause a 20% reduction in body mass in starlings, did not affect the overall duration of moult, but it did slow the growth rate of individual feathers (Meijer 1991; Swaddle & Witter 1997). The rate of individual feather growth was not measured in our study, so it is unclear whether the increased moult rate resulted from an increase in the rate of growth of each feather or an increase in the number of feathers being regrown at any one time. In either case, the consequent decrease in feather quality may have resulted from a constraint on whole-body protein synthesis and/or a limit on the rate at which keratin could be deposited in the growing feathers (Murphy & Taruscio 1995).

In conclusion, the experimentally induced decrease in the duration of moult resulted in a significant reduction in primary feather quality. A decrease in the duration of moult will be experienced by breeding birds compared with non-breeders, and especially by late-breeders, because of the effects of decreasing daylength after the summer solstice. Thus, a loss of plumage quality due to the decreased duration of moult may be one mechanism by which costs of breeding are deferred beyond the end of the current reproductive season. To our knowledge, this is the first demonstration of such a mechanism.

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