

Food availability and primary feather molt in European starlings, *Sturnus vulgaris*

John P. Swaddle and Mark S. Witter

Abstract: The effects of food quality and overall food intake on molt have been experimentally investigated in a number of species. However, little is known concerning the influence of periodic food availability on molt parameters, although there are some associations in the field. In this study, we experimentally manipulated food availability through food deprivation during the molt of adult and juvenile European starlings, *Sturnus vulgaris*. By monitoring molt scores, wingtip shape, and lengths and length asymmetries of primary feathers during molt, we demonstrated that food deprivation can influence molt. Food-deprived juvenile starlings exhibited slower feather growth rates, although the duration and rate of molt were not affected. There were no differences in wingtip shape between food-deprived and control birds at the end of molt for either adults or juveniles. We also observed erratic reshedding of previously molted primary feathers in juveniles, although this did not appear to be related to the experimental treatments. The results of this study imply that feather growth rates and shedding rates are differentially affected by food availability: growth rates may be decreased when food deprivation occurs, whereas shedding rates are relatively unaffected.

Résumé : Les effets de la qualité de la nourriture et de la quantité totale de nourriture ingérée sur la mue ont été évalués expérimentalement chez plusieurs espèces. Cependant, peu de travaux se sont attardés à l'influence de la disponibilité périodique de la nourriture sur les paramètres de la mue, même si certaines associations ont été déterminées en nature. Dans ce travail, nous avons manipulé expérimentalement la disponibilité de la nourriture en créant des carences alimentaires au cours de la mue chez des adultes et des juvéniles de l'Étourneau sansonnet, *Sturnus vulgaris*. En mesurant les paramètres de la mue, forme du bout de l'aile, longueur des plumes, asymétries dans la longueur des plumes au cours de la mue, nous avons démontré que les carences alimentaires peuvent influencer la mue. Chez les juvéniles privés de nourriture, les taux de croissance des ailes sont plus lents, mais la durée et la fréquence de la mue ne sont pas affectées. La forme du bout de l'aile ne varie pas à la suite d'une carence alimentaire, ni chez les adultes, ni chez les juvéniles. Des cas de mues secondaires erratiques de plumes déjà perdues auparavant ont été observés chez des juvéniles, mais ces cas ne semblent pas avoir été causés par les conditions expérimentales. Il semble donc que les taux de croissance et de rejet des plumes soient affectés différemment par la disponibilité de la nourriture : les taux de croissance peuvent diminuer lorsque des carences alimentaires se produisent, mais les taux de rejet des plumes sont relativement peu affectés.

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Introduction

Avian molt is physiologically costly, not only in total energy terms (e.g., King 1981; Murphy and King 1992; Lindström et al. 1993), but also in the requirements for specific proteins and nutrients (e.g., Newton 1968; Ward 1969; Taylor 1969; Nitsan et al. 1981; Groscolas 1982; Cherel et al. 1988; Murphy and King 1982, 1984a, 1990, 1992). Molt involves the replacement of feathers and their protective sheaths, which can constitute up to 30% of lean dry body mass (Jenni and Winkler 1994). Most of this plumage mass consists of proteins (approximately 90%; Murphy and King 1982, 1986), which can constitute up to 30% of a bird's total protein mass (Newton 1968; Gavrilov and Dolnik 1974; Chilgren 1977; Murphy and King 1986).

As molt is energetically costly, molt parameters may vary with aspects of food quality and availability. Murphy, King,

and colleagues have documented a series of experiments in which they demonstrated that molt of white-crowned sparrows, *Zonotrichia leucophrys gambelii*, can be affected by diet quality (Murphy and King 1984a, 1984b, 1984c, 1987, 1990; Murphy et al. 1988). Specifically, sparrows fed nutritionally deficient diets (deficient in sulfur-amino acids, which are essential for molt) tend to undertake longer molts and suffer a relatively large number of feather deformations (i.e., suffer a reduction in developmental stability) compared with birds fed nutritionally adequate diets (Murphy and King 1987). However, this effect is not always repeatable (e.g., Murphy and King 1984b).

There is a general lack of unequivocal evidence that food availability influences molt, although a number of researchers have reported an association between molt parameters and natural food availability in the wild (e.g., Ashmole 1962; Ward 1969; Zann 1985; Vaucoulon et al. 1985; Loonen et al. 1991; but see Murphy et al. 1988). There are also cases in which there is contradictory evidence; for example, Meijer (1990) found that food restriction before molt did not influence the onset or duration of molt in captive juvenile European starlings (*Sturnus vulgaris*). To our knowledge, only one study has directly investigated the effect of food abundance

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J.P. Swaddle and M.S. Witter. Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, The Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, U.K. (e-mail: gbza86@udcf.gla.ac.uk).

during molt on plumage replacement: Murphy et al. (1988) manipulated food intake to 60 and 80% of that observed in birds fed ad libitum, and found that molt was prolonged, owing to slower feather shedding and slower feather growth.

The study reported here describes an experimental investigation of the effects of periodic food availability on molt parameters in adult and juvenile European starlings. It was hypothesized that birds subjected to food deprivation undergo a prolonged molt, as the energy required for feather synthesis was more likely to be constrained in these individuals. We were interested in investigating not only the effect of food availability on rates of molt and feather growth, but also the effects of food deprivation on wingtip shape after molt. Wingtip shape is known to influence the costs of flight (see Rayner 1988; Norberg 1990; Lockwood et al. 1997), and hence, deviations in feather growth patterns during molt may cause the bird to incur significant functional costs outside of the molt period.

Materials and methods

Adults

We performed the first experiment on 35 wild-caught adult female European starlings that were caught after postnuptial molt. All birds were housed individually in $0.3 \times 0.3 \times 0.5$ m cages in visual, but not acoustic, isolation in indoor laboratory facilities at a constant 17°C. Birds were housed in accordance with the principles and guidelines of the Canadian Council of Animal Care and provided with water and turkey starter crumbs ad libitum, except as described below. Prior to the experimental manipulations, birds were maintained on a 8 h light (L) : 16 h dark (D) photoperiod and were thus photosensitive (Burger 1947; Farner et al. 1983). The birds were then exposed to long days (18 h L : 6 h D) to induce photorefractoriness and molt (Dawson et al. 1985). They remained on this photoperiod until molting began in all birds (at approximately 10 weeks). After this period, birds were transferred immediately to a 13 h L : 11 h D photoperiod for the duration of the food-deprivation experiment.

Birds were randomly allocated to four treatment groups: control ($n = 8$), morning food deprived ($n = 9$), afternoon food deprived ($n = 9$), and variable-time food deprived ($n = 9$). The control group remained on ad libitum food throughout the experiment. The morning-food-deprived group had their food removed for 4 h, beginning at "dawn" (i.e., when the laboratory lights were switched on). The afternoon-food-deprived group had their food removed for 4 h, beginning 4 h after dawn. The variable-time food-deprived group had their food removed for 4 h either beginning at dawn or 4 h after dawn, each with a probability of 0.5. This experimental design allowed us to investigate the effects of food deprivation per se, time-of-day sensitivity to deprivation, and variability in the time of onset of deprivation. Food deprivation was applied every other day, with occasional "missed days," for 15 weeks.

At approximately weekly intervals, the following measurements were taken on each bird: length of each growing primary feather (to 0.01 cm accuracy with vernier calipers) on both wings, primary molt score (0–45; cf. Ginn and Melville 1983) on both wings, subcutaneous fat score (0–5; cf. Helms and Drury 1960), and body mass (to 0.1 g accuracy on an electronic balance). All body masses were balanced across treatments for time of day. The tips of the primaries were always checked carefully and any damage or wear was noted; values for all such primaries have been excluded from the analyses. This is particularly relevant to measurements of fluctuating asymmetry in feathers (Cuthill et al. 1993; Swaddle et al. 1996). Two of the original 35 birds were excluded from all analyses

because of primary feather damage, precluding accurate measurement of primary length and molt score. Measurements were taken blind of the treatment groups from which the birds came. Measures of wingtip shape were derived from applying Lockwood et al.'s (1997) size-corrected equations for wingtip roundedness and convexity to our individual measurements of primary length.

Juveniles

Twenty-two wild-caught juvenile European starlings were housed in conditions identical with those in the first experiment, but experienced natural photoperiodic cues to induce molt, as birds were caught in their first summer. Throughout the experiment, the juveniles were maintained on a photoperiod that simulated natural daylight and was reduced in 30-min blocks every 2 weeks, starting at 17.5 h of light and decreasing to a 13 h L : 11 h D photoperiod at the end of molt. Birds were randomly allocated to two treatment groups: control ($n = 11$) and food deprived ($n = 11$), which were identical with the control and morning-food-deprived groups described above, except that food was removed for 5 h. On days between deprivation days and at the end of molt, we recorded the same plumage and body-composition measurements as described in the first experiment, except that only primaries 5, 7, and 9 (in ascending order from proximal to distal) were measured. This step was taken to reduce the handling time of birds.

Three juveniles died within the first 2 weeks of the experiment, reducing the sample size of the control group to eight. Five individuals were observed to redrop primaries on both left and right wings that had already regrown during molt; hence, these individuals were excluded from wingtip-shape analyses and the regrown feathers were not included in individual estimates of asymmetry. All measurements were taken blind of the treatment groups from which the birds came, and body masses were controlled across treatment groups for time of day.

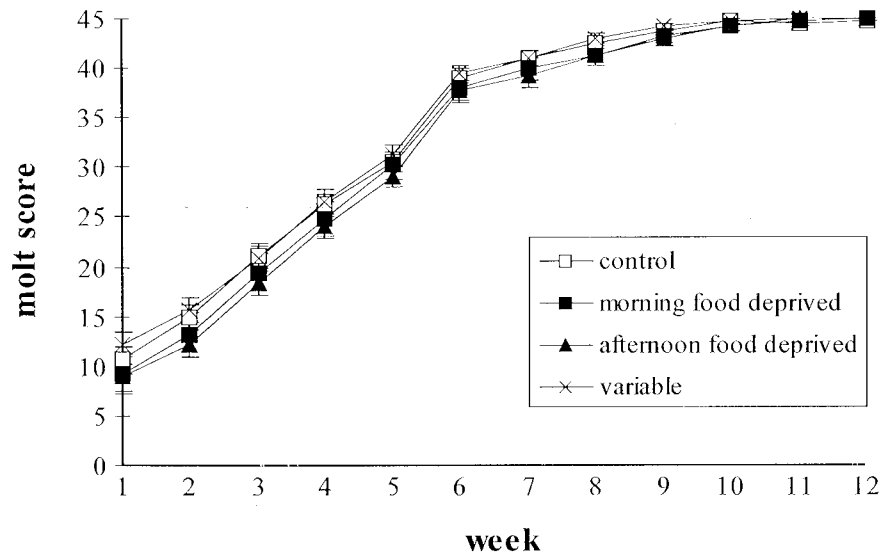
Statistical analyses

The data were used to examine the effects of food deprivation on molt, individual feather growth, juvenile primary feather asymmetry (fluctuating asymmetry; see Ludwig 1932), and wingtip shape after molt. The relationships between molt parameters, wingtip shape, and fat reserves were also examined. Analyses of the effects of food deprivation on absolute (left–right) asymmetry of adult starling primaries and the relations between the manipulations and body mass regulation in both adults and juveniles have been reported elsewhere (Swaddle and Witter 1994; Witter et al. 1995; Witter and Swaddle 1997).

Asymmetry was defined as the absolute difference in length between left and right primaries. Analyses of three repeated length measurement of left and right primaries 3 and 4 revealed that primary asymmetry was highly repeatable (mixed-model analysis of variance (ANOVA) constructing F test by the ratio of the individual \times side mean square to the combined individual \times side \times repeat and individual \times repeat mean squares: primary 3, $F_{9,361} = 1592.55$, $P < 0.00001$; primary 4, $F_{9,361} = 558.04$, $P < 0.0001$; Swaddle et al. 1994). All but two primaries (2 and 8) in the juvenile experiment displayed a characteristic half-normal distribution (Anderson–Darling normality test, $a^2 < 0.501$, $P > 0.1$; see Minitab Incorporated 1994) around a mean of zero (one-sample t test, $t < 1.58$, $P > 0.1$); hence, primaries 2 and 8 were excluded from the asymmetry analyses (Palmer 1994; Swaddle et al. 1994). For each bird, median asymmetry values across the remaining primaries were used in the analyses.

The effects of treatment group on the rates of molt and feather growth were investigated by repeated-measures analysis of variance (SPSS Inc. 1988) with within-subject factor time (time during experiment) and between-subjects factor group (treatment groups). The relations between wingtip shape and treatment group were inves-

Fig. 1. Adult molt scores (mean \pm SE) throughout the experiment. See the text for details of the treatment groups. There are no differences in rates of molt of adult female starlings between treatment groups.



tigated by means of ANOVA (Minitab Incorporated 1994). The relations between wingtip shape, time taken to grow feathers, body mass, and subcutaneous fat stores were investigated by means of linear regression (Minitab Incorporated 1994). Analyses of the effects of treatment groups on primary feather asymmetry were performed using a Kruskal–Wallis nonparametric one-way ANOVA (Siegel and Castellan 1988). Two-tailed tests of significance are used throughout.

Results

Adult molt

There was no effect of food deprivation on the rate of molt, as changes in molt scores over time did not differ between the groups ($F_{[33,319]} = 0.65$, $P = 0.935$; see Fig. 1). Additionally, food deprivation did not appear to influence the shape of the wingtip after molt had been completed, in terms of either wingtip roundedness ($F_{[3,23]} = 0.86$, $P = 0.478$) or wingtip convexity ($F_{[3,23]} = 1.52$, $P = 0.236$). There was also no relation between wingtip shape and residual body mass (roundedness: $F_{[1,25]} = 0.77$, $P = 0.389$; convexity: $F_{[1,25]} = 2.23$, $P = 0.148$) or between wingtip shape and residual subcutaneous fat (roundedness: $F_{[1,25]} = 0.96$, $P = 0.336$; convexity: $F_{[1,25]} = 0.21$, $P = 0.647$) after the effects of the manipulations had been controlled for.

Juvenile molt

The food-deprivation treatments did not influence the rates of molt observed in the juvenile birds, as changes in molt score over time did not differ with treatment group ($F_{[16,272]} = 0.54$, $P = 0.927$; Fig. 2). Nor did the food-deprivation treatments affect wingtip shape in juveniles after molt (roundedness: $F_{[1,12]} = 0.41$, $P = 0.533$; convexity: $F_{[1,12]} = 0.38$, $P = 0.548$). Wingtip shape was also not related to juvenile residual body mass (roundedness: $F_{[1,12]} = 1.27$, $P = 0.281$; convexity: $F_{[1,12]} = 0.24$, $P = 0.636$) or juvenile residual subcutaneous fat stores (roundedness: $F_{[1,12]} = 1.02$, $P = 0.333$; convexity: $F_{[1,12]} = 0.84$, $P = 0.379$) after the effects of the manipulations were controlled for.

Damage, abrasion, and feather redropping during molt significantly reduced the sample sizes for growth rates of primaries 5 and 9, therefore we only present feather growth analyses for primary 7. There are no a priori reasons to suspect that food deprivation differentially alters growth rates of different primaries. We found a significant effect of the food-deprivation treatments on the growth rate of primary 7 (Fig. 3). In food-deprived birds, this primary feather grew at a slower rate than in controls (log-transformed percent growth: $F_{[26,416]} = 3.06$, $P < 0.001$), so control birds completed growth of this feather earlier than food-deprived birds ($F_{[1,16]} = 4.71$, $P = 0.045$). The time taken to complete growth of primary 7 was not related to residual mass or fat when the effects of the manipulation were controlled for (mass: $F_{[1,16]} = 0.66$, $P = 0.429$; fat: $F_{[1,16]} = 0.07$, $P = 0.790$).

Surprisingly, median primary feather asymmetry was not significantly affected by food deprivation (Kruskal–Wallis, $H = 2.46$, $df = 1$, $P = 0.117$), which contradicts our findings for adult starlings in the first experiment (Swaddle and Witter 1994).

Redropped feathers

Five juveniles were observed to redrop primaries on both sides of the wing that had already grown during molt. This did not represent a restarting of molt, as redropping did not start with primary 1. Asymmetry of these feathers did not appear to be greater than the median asymmetry of other primaries on these individuals (Friedman's nonparametric two-way ANOVA, $S = 1.80$, $df = 1$, $P = 0.180$). Four other individuals were observed to redrop previously molted feathers in this erratic way, although these birds did not redrop primaries on both left and right wings and, hence, asymmetry values could not be calculated.

Of the nine birds that displayed this feather-redropping phenomenon, five were from the control group and four from the food-deprived group. This indicates that feather redropping was not directly influenced by the experimental treatments ($\chi^2 = 1.27$, $df = 1$, $P = 0.260$).

Fig. 2. Juvenile molt scores (mean \pm SE) throughout the experiment. See the text for details of the treatment groups. There are no differences in rates of molt of juvenile starlings between treatment groups.

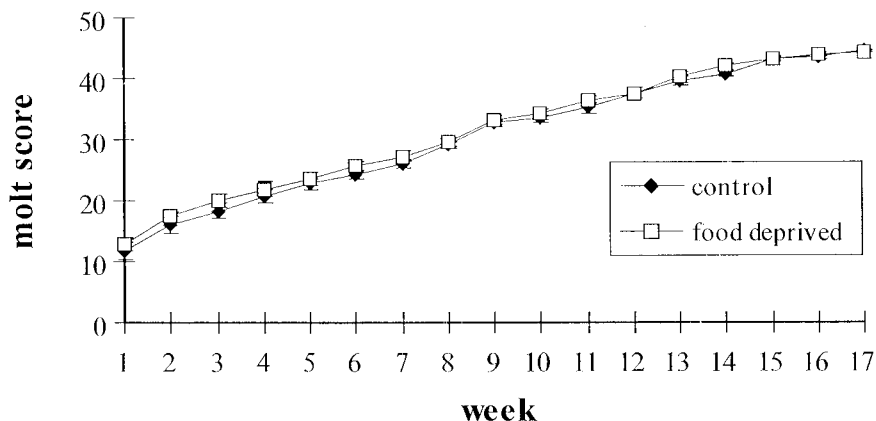
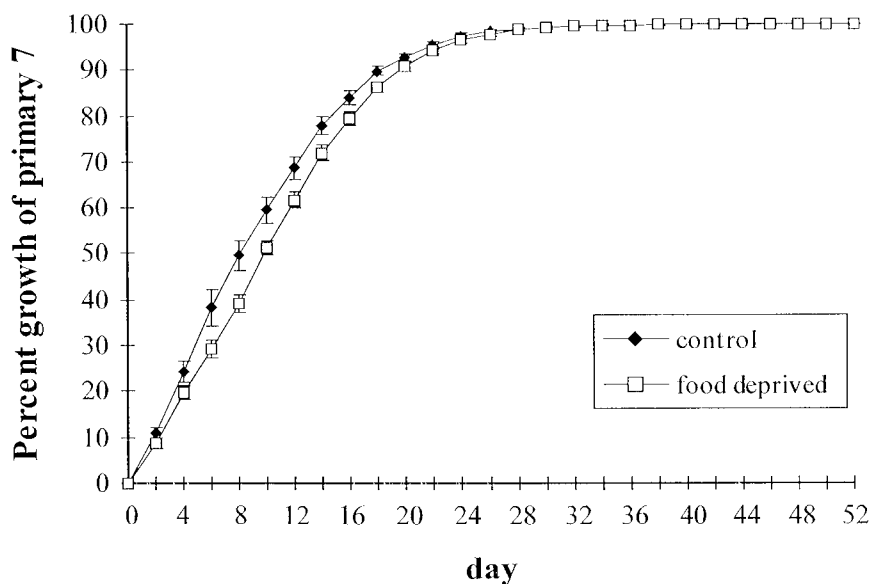


Fig. 3. Percent growth of primary 7 in juvenile starlings (mean \pm SE) throughout the experiment. See the text for details of the treatment groups. The feathers of food-deprived birds grew at a slower rate.



Discussion

Food deprivation had no effect on the change in molt score over time in either the adult or juvenile starlings. However, food availability affected growth rates of juvenile starlings. Food-deprived juveniles experienced slower primary feather growth and, hence, feathers of food-deprived birds took longer to reach their final length. Unfortunately, we did not collect detailed enough information to investigate the effects of food deprivation on feather growth rates in the adult birds. Molt scores are not particularly sensitive for discriminating differences in feather growth rates; however, molt scores are relatively more influenced by feather shedding and the early stages of feather growth (see Ginn and Melville 1983). Therefore, these data may indicate that primary feathers were shed and started regrowing at relatively equivalent intervals between treatment groups, whereas complete regrowth of individual feathers appeared to occur at a slower rate in food-deprived birds.

In contrast to these findings, Murphy and King (1984c)

found that feather shedding rates of white-crowned sparrows, but not feather growth rates, were influenced by the nutritional content of food. Murphy et al. (1988) illustrated that both shedding and feather growth rates can be influenced by malnutrition during molt, but that shedding rates are more phenotypically plastic. Our results are therefore somewhat surprising, as molt scores were not influenced by food deprivation, and decreased food availability appeared to slow growth of individual feathers. This apparent discrepancy may indicate interspecific variability of mechanisms controlling molt processes. However, it is also possible that molt is influenced in a different manner by manipulations of diet quality and manipulations of food availability per se.

Molt is undoubtedly energetically and physiologically costly. The increases in oxygen consumption during molt have been frequently estimated as being 9–35% greater than premolt levels (see review in King 1981), therefore it may not be surprising that food deprivation affects molt parameters. However, it appears that shedding rates are fairly robust in the starling, and only growth rates of individual feathers are

influenced by a reduction in food availability. This may indicate that the mechanisms controlling shedding and feather growth rates can be independent at some level. This is supported by Murphy et al.'s (1988) finding that growth rates and shedding rates respond differently to malnutrition in white-crowned sparrows.

Although molt was not prolonged in the food-deprived birds, the reduction in feather growth rates may still mean that these individuals incur significant functional costs. As the growth of individual feathers is slower (at least for the juveniles), food-deprived birds will possess shorter primary feathers for a longer period during molt. This relative reduction in primary feather length compared with controls will reduce flight performance (Swaddle et al. 1996; Swaddle and Witter 1997), as there will be a relative reduction in lift and thrust generated by these smaller wing areas (see reviews in Pennycuik 1975; Norberg and Rayner 1987; Norberg 1990). Additionally, at the early stages of development, the primary feathers of starlings are significantly more asymmetric than at later stages (Swaddle and Witter 1994). Hence, slow-growing primaries will be relatively more asymmetric for a longer period of time. The small asymmetries that are observed during feather regrowth have significant effects on the flight performance of these birds, most notably decreasing their ability to perform aerial maneuvers (Swaddle et al. 1996). Decreased aerial maneuverability is likely to influence individual survival, owing to a decreased ability to avoid aerial predators and a reduction in ability to capture aerial prey (see references in Witter et al. 1994).

The normal pattern of primary feather molt in juvenile birds (i.e., sequentially from proximal to distal) was observed to be frequently disrupted by the reshedding of primaries that had already regrown during molt. This occurred with equal frequency in the control and food-deprived birds, and these redropped feathers did not appear to be less developmentally stable than other feathers on the wing, although sample sizes were small. Eccentric molts (molt is initiated in the middle of the usual molt tract) and interrupted molts (molt stops and then restarts at same point along the wing) have been observed in adult and juvenile starlings in the field (Evans 1985) and laboratory (Schleussner 1990). However, the nonsequential pattern of reshedding a single or symmetric pair of feathers that we observed has not been documented to our knowledge. One possible explanation of this erratic pattern is that it represents a form of fright molt (e.g., van der Meulen 1939; Wagner 1962), where an external stressor causes the feathers to be redropped in this peculiar way. However, this erratic molt is not likely to be due to physical damage to the feathers, because in five out of the nine cases, redropped feathers were observed on both wings at the same time. Therefore, there may be a nonspecific factor (e.g., extensive handling) that causes a general disturbance of the mechanisms which control molt in these individuals, and the reshedding phenomenon could occur through neurally mediated relaxation of the muscles at the feather bases (Stettenheim 1972). This suggested mechanism is speculative and it is not clear how common this form of erratic molt is in the wild and in other species.

There is a whole suite of environmental influences that may affect molt. For example, food availability and quality, temperature, photoperiod, unpredictable onset of breeding, breed-

ing success, level of parental care, social interactions, climatic conditions, and parasitic infection have all been implicated as having an influence on molt (see reviews in Payne 1972; Jenni and Winkler 1994; also see Langston and Hillgarth 1995). Therefore, experimental investigations that isolate possible factors are crucial to understanding the array of molt patterns and tactics exhibited by bird species. The results of the experiment reported here indicate that a decrease in periodic food availability (in the context of the food-deprivation treatments) reduces primary feather growth rates of starlings but does not affect the overall rate or duration of molt.

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