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Periodic food availability and strategic regulation of body mass in the European Starling, *Sturnus vulgaris*

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Summary

1. The hypothesis that European Starlings, *Sturnus vulgaris*, regulate their body mass in response to availability of food was tested in two experiments. The first experiment investigated the response to periodic food deprivations of 6 h, beginning at a random time in the day. The second experiment examined the response to fixed and variable food deprivations, and whether this response differed according to 'season', which was manipulated photoperiodically.

2. In the first experiment, the food deprived birds responded by increasing body mass, in accordance with the adaptive regulation hypothesis.

3. The second experiment demonstrated that the response to food availability differed according to photoperiodic history; birds that were photosensitive responded to a decrease in time available to feed by increasing body mass, whereas birds that were photorefractory did not.

4. Contrary to theoretical predictions, there was no indication that the response to variable time of onset deprivations was larger than the response to deprivations that began at a fixed time of day.

5. It is suggested that different strategies of mass regulation at different points in the annual cycle may be a response to season-specific costs and benefits of fat storage, or may relate to season-specific changes in environmental stochasticity.

Key-words: Body mass, European Starling, food availability, mass regulation, *Sturnus vulgaris*

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Introduction

Birds display large spatiotemporal variation in mass and fat reserves (see Blem 1976, 1990). Regulation of mass has attracted several theoretical (Lima 1986; McNamara & Houston 1990; Houston & McNamara 1993) and empirical (see Witter & Cuthill 1993) studies. Fat reserves usually account for the largest variation in mass, particularly during migration and over winter (Witter & Cuthill 1993). Birds are often fatter and heavier during winter compared with the summer. Within winter, birds are often fatter and heavier during the coldest periods (see Blem 1990). Such relationships indicate that variation in mass is not a 'passive' reflection of environmental food availability or energetic expenditure. Instead, the observed variation in mass is consistent with the hypothesis that birds regulate the size of their energetic reserve, in response to the trade-off between the costs and benefits of fattening (e.g. Lima 1986; Rogers 1987; Ekman & Hake 1990; Rogers, Nolan & Ketterson 1993, 1994; Rogers & Smith 1993; Witter & Cuthill 1993; Witter, Cuthill & Bonser 1994; Witter & Swaddle 1995).

Lima (1986), McNamara & Houston (1990) and Houston & McNamara (1993) have modelled fatten-

ing strategies of small birds in winter. In these models, fat is assumed to be beneficial because it reduces the probability of starvation but costly because of increased energetic expenditure and increased predation risk. These analyses predict that deteriorations in the bird's energetic environment (e.g. decreased predictability of food supply or increased nocturnal energetic expenditure) result in increased fat reserves and body mass. In support of this, Rogers (1987) found that avian species exploiting an unpredictable food source stored more fat than species exploiting more predictable food. Similarly, many field studies have found relationships between weather conditions and fat reserves (see Blem 1976, 1990). Such relations may arise because (1) birds follow a fixed strategy of mass change that is adapted to the local environment (i.e. environmental variables are ultimate factors), (2) they respond directly to environment cues (i.e. environmental variables are proximate factors) or (3) they use some combination of both strategies (see Rogers *et al.* 1993, 1994; Witter & Cuthill 1993). Whilst there has been success at distinguishing proximate and ultimate factors statistically (e.g. Blem & Shelor 1986; Dawson & Marsh 1986), experimental manipulations of the factors of interest provide a direct way to iden-

tify proximate determinants of body mass. Ekman & Hake (1990) found that Greenfinches, *Carduelis chloris*, increased mass in response to an experimental decrease in food predictability. Similarly, Bednekoff (1992) found that Great Tits, *Parus major*, compensated for a decreased time available to feed by increasing body mass. Here, we examine whether European Starlings, *Sturnus vulgaris* L., regulate their body mass in response to manipulated food availability. We investigate decreased feeding time and variability in the time at which food deprivations occur. However, as McNamara (1990) points out, the optimal trade-offs in mass allocation may differ at different points in the annual cycle. Thus, we also investigate seasonal changes in the response to food deprivations, principally during photorefractoriness and photosensitivity (see Nicholls, Goldsmith & Dawson 1988).

Materials and methods

Experiments were performed on wild-caught adult female starlings, housed individually in $0.3 \times 0.3 \times 0.5$ m cages, maintained at a temperature of 20 ± 1 °C. Food (turkey starter crumbs) and water were available *ad libitum*, except as described below. The first experiment examines the changes in mass accompanying decreases in the time available to feed. The second experiment examines the influence of time available to feed, variability in the time at which deprivations begin and whether the response to food availability differs according to photoperiodic conditions.

Experiment 1 was performed on 12 starlings, maintained on a 11L:13D photoperiod. Birds were randomly allocated to two treatment groups: control and food deprived. Birds were arranged so that alternate cages contained control and deprived treatments. The control group remained on *ad libitum* food throughout the experimental period. The deprived group had their food removed for 6 h, beginning at a random time between 'dawn' and 6 h before 'dusk'. These deprivations were performed every other day for 10 days. Body mass was recorded (to 0.1 g, on an electronic balance) for all birds within an hour of 'dawn', every other day, coinciding with the days of food deprivation.

Experiment 2 was performed on 35 starlings, which were initially maintained on an 18L:6D photoperiod to induce photorefractoriness and moult. After moulting began, birds were transferred to a photoperiod of 13L:11D for the food deprivation experiment. This photoperiod was chosen so that birds would not break refractoriness at the end of moult, as would occur on an 11L:13D photoperiod. Birds were then randomly divided into four treatment groups, allowing the investigation of fixed and variable time-of-onset deprivations. The control group (Control, $n=9$) remained on *ad libitum* food throughout the experiment. There were two groups that had their food

removed for 4 h at a fixed time of day; the first group (Morning, $n=8$) had their food removed beginning at 'dawn' and the second group (Afternoon, $n=9$) had their food removed beginning 4 h after 'dawn'. A fourth treatment group (Variable, $n=9$) had their food removed for 4 h either beginning at 'dawn' or beginning 4 h after 'dawn', each with a probability of 0.5. Cages from each treatment were randomly arranged within the room to eliminate position bias. Thus, this design allows the investigation of effects of food deprivation *per se* and variability in the time at which deprivations begin, while controlling for time of day sensitivity to food deprivation. Food deprivations were applied every other day for 15 weeks. Body mass was recorded once per week, with measurements beginning at dawn. Because of the large number of plumage variables also recorded (see Swaddle & Witter 1994), measurements took approximately 5 h on each occasion. Order of measurements with respect to treatment group was randomized, with individual birds being measured in the same order during each session. This design means that time of day will not systematically bias between-group comparisons and within-individual changes during the experiment are not influenced by time of day.

In the second part of this experiment, we examined the hypothesis that response to food deprivation changes according to whether birds are photorefractory or photosensitive. This was achieved by randomly dividing the initial treatment groups into two. Half of the birds in each food treatment had photorefractoriness broken by exposure to short days (8L:16D) for 11 weeks (Goldsmith & Nicholls 1984); birds were then returned to the 13L:11D photoperiod. The remaining birds were maintained on a 13L:11D photoperiod throughout. Food deprivation treatments then recommenced for 3 weeks. Body mass was recorded two or three times per week during this manipulation period, coinciding with the days of food deprivation. All measurements were taken within an hour of 'dawn'. After the end of the food deprivation period, all the birds underwent laparotomies and had the diameter of their largest follicle measured. Maximum follicle diameter is closely related to the mass of the reproductive organs in female starlings (A. R. Goldsmith & I. C. Cuthill, unpublished data); we use this relationship to estimate the contribution of gonadal hypertrophy to the mass changes observed.

In both experiments, body mass has been analysed by mixed-model repeated-measures analysis of variance, using procedure MANOVA on SPSS (SPSS 1988). For experiment 1 and the first part of experiment 2, the main parameter of interest is the Group \times Day interaction; that is, whether there is a significant between-group difference in change in body mass over the course of the experiment. In the second part of experiment 2, the main parameter of interest is the Photoperiod \times Food \times Day interaction; that is, does the response to food availability differ between the two

photoperiodic manipulations over the experiment? Two of the birds in the photorefractory group had become photosensitive by the start of the second part of experiment 2; these were excluded from the analyses. On three occasions during the experiment birds were found to have blocked or broken food hoppers, resulting in low masses on these occasions. All of these events occurred on birds in the deprived treatments, possibly because of their more vigorous feeding behaviour. As a conservative method of maintaining a balanced ANOVA design, these values have been replaced by the mean mass from the weighings immediately before and after (Glantz & Bryan 1990). Throughout the results, values are shown as mean (\pm SE) and P values are based on two-tailed tests of significance.

Results

In the first experiment, there was a between-group difference in change in mass (Fig. 1; Group \times Day, $F_{4,40}=3.03$, $P=0.029$; linear contrast for the Group \times Day interaction, $t_{40}=4.04$, $P=0.0024$; all other contrast terms, $P>0.5$), with the food-deprived birds gradually increasing in mass relative to the controls. By contrast, in the first part of experiment 2 there was no between-group difference in change in mass (Fig. 2; Group \times Day, $F_{33,341}=0.80$, $P=0.780$). However, the period over which we have monitored mass change in this experiment is longer than in experiment 1. Thus, for a more direct comparison, we also analysed between-group differences over the first 3 weeks of the treatment. In this analysis, there is still no indication of a response to food deprivation (Group \times Day interaction, $F_{3,30}=0.09$, $P=0.911$). Thus, there was no response to decreased food availability during moult. However, this experiment also suggests that groups did not differ after moult (between-group difference in change in mass after moult, $F_{3,45}=0.30$, $P=0.823$; Fig. 2), when all birds were still photorefractory. This is examined further below.

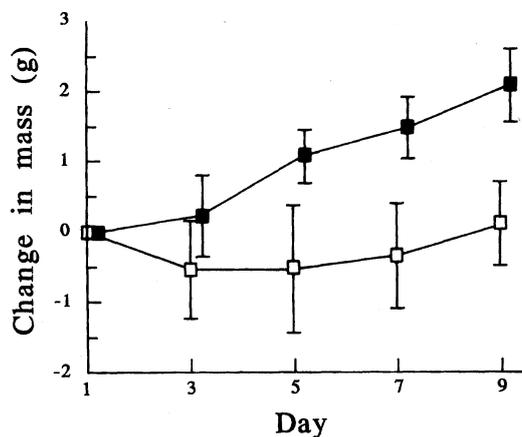


Fig. 1. Mean (\pm SE) change in body mass from experiment 1, in the food-deprived (closed symbols) and control (open symbols) treatment groups.

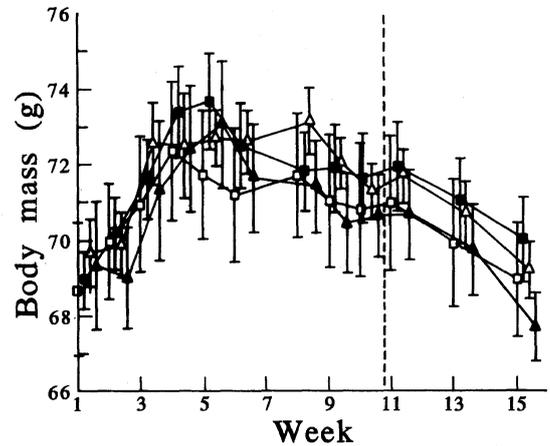


Fig. 2. Mean (\pm SE) body mass from part one of experiment 2, in the control (open squares), morning-deprived (closed squares), afternoon-deprived (open diamonds) and variable-deprived (closed diamonds) treatments. Values from each group have been displaced to the right or left to reduce overlap. The dotted line indicates the time when birds started to end moult.

The changes in body mass associated with the food availability treatments in photorefractory and photosensitive birds are shown in Fig. 3, with associated statistics in Table 1. The two photoperiodic treatment groups differed in change in mass over the experiment; the photosensitive groups increased in mass and the photorefractory groups remained stable. This between-group difference increases linearly over the experiment (linear term of the polynomial contrast; $t_{225}=2.832$, $P=0.009$; other terms, $P>0.5$). Importantly, the significant three-way interaction indicates that this change differs according to the food manipulation. The food deprivations had a significant effect on body mass in the photosensitive group (Food \times Day interaction, $F_{27,99}=1.88$, $P=0.013$) but not the photorefractory group (Food \times Day interaction, $F_{27,126}=1.25$, $P=0.112$). Thus, photosensitive birds responded to food deprivations by increasing mass over time, whereas photorefractory birds did not. However, the photosensitive birds were undergoing gonadal hypertrophy during the experiment, which may contribute to the mass changes observed. To investigate this contribution, maximum follicle diameter was recorded for each bird. Not surprisingly, maximum follicle diameter was larger in the photosensitive birds compared with the photorefractory (Fig. 4; $F_{1,32}=33.24$, $P<0.001$) but there was no effect of the food deprivation on follicle diameter (Food, $F_{3,32}=1.48$, $P=0.243$; Photoperiod \times Food interaction, $F_{3,32}=1.56$, $P=0.224$). We have used these measures of follicle diameter to estimate the mass of the reproductive organs using an empirically derived equation, measured on different birds, relating these two variables [$\log(\text{gonadal mass}) = -2.68 + 0.583 \times \text{Follicle diameter}$; $R^2=71.7\%$, $F_{1,40}=99.05$, $P<0.00001$; A. R. Goldsmith & I. C.

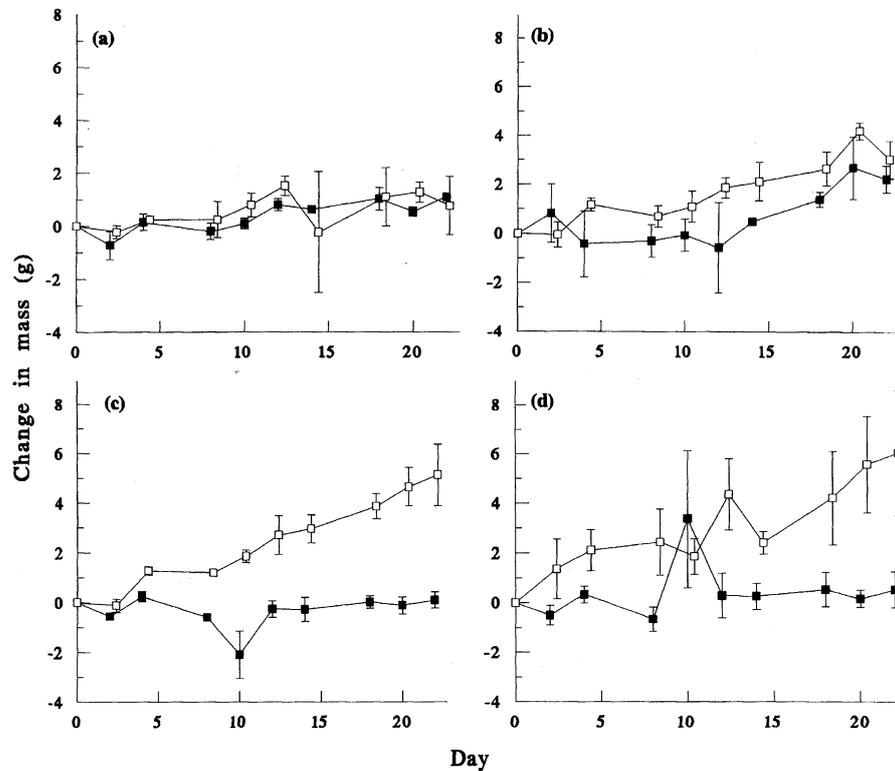


Fig. 3. Mean (\pm SE) change in body mass from part two of experiment 2 in (a) control, (b) morning-deprived, (c) afternoon-deprived and (d) variable-deprived treatment groups, in photosensitive (open symbols) and photorefractory (closed symbols) birds.

Cuthill, unpublished data]. Estimated gonadal mass was then subtracted from the mass of each bird. We then investigated whether between-group differences in change in mass remained after removing the mass of the gonads.

Controlling for mass of the gonads yields conclusions that are qualitatively similar to the total body mass analysis. That is, photosensitive birds responded to decreased time available to feed by increasing body mass, whereas photorefractory birds did not (Photoperiod \times Food interaction, $F_{3,32} = 3.90$, $P = 0.020$; Fig. 5). Comparing photoperiodic treatments separately, food deprivations significantly influenced mass in the photosensitive group ($F_{3,14} = 3.92$, $P = 0.032$) but not in the photorefractory group ($F_{3,11} = 1.92$, $P = 0.185$). Pairwise analyses of the photosensitive group, using the Tukey *post hoc* multiple comparisons test, revealed that the afternoon and variable deprived treatments increased in mass compared with controls ($P < 0.05$). None of the other pairwise comparisons was significant ($P > 0.166$, in all cases). These data indicate that (1) there is time-of-day sensitivity to food deprivations, with afternoon and variable deprivations having a more profound effect than morning deprivations, (2) there is no influence of variability in the time at which deprivations begin and (3) photosensitive and photorefractory female starlings respond differently to identical food deprivation regimes.

Discussion

The results support the hypothesis that starlings can respond to a decrease in the time available to feed by increasing mass. This accords with the results of Ekman & Hake (1990) and Bednekoff (1992). Together, these data indicate that birds are able to regulate their body mass in direct response to environmental change, suggesting that avian mass is a plastic life-history trait (see Rogers *et al.* 1993). Importantly, the present data also demonstrate that the response to food availability differs according to the photoperiodic conditions: photosensitive starlings responded to a decrease in the time available to feed by increasing body mass, whereas photorefractory birds did not. The specific responses to food deprivations in photorefractory birds may differ according to whether they were moulting. There was no evidence of a response to food deprivation (either increase or decrease in mass) when the birds were moulting. In fact there was a longitudinal trend over the first half of moult for all birds to increase in mass, regardless of treatment group. This longitudinal change may have obscured any between-group differences. However, in the second part of experiment 2, the body masses of control birds were stable. At this point, there were clear differences according to photoperiodic history; photosensitive birds responded to the food deprivations by increasing mass and photorefractory birds responded by decreasing mass.

Table 1. ANOVA on body mass from the second part of experiment 2. Food refers to the four food availability treatments; day refers to day in the experiment; photoperiod refers to the pre-trial photoperiodic manipulation

| Factor | df | F | P |
|--------------------------|---------|-------|--------|
| Food | 3, 25 | 0.40 | 0.751 |
| Photoperiod | 1, 25 | 5.50 | 0.027 |
| Day | 9, 225 | 16.47 | <0.001 |
| Food × photoperiod | 3, 25 | 1.09 | 0.373 |
| Food × day | 27, 225 | 0.96 | 0.528 |
| Photoperiod × day | 9, 225 | 4.79 | 0.001 |
| Food × photoperiod × day | 27, 225 | 1.65 | 0.028 |

The most likely interpretation of the changes in body mass observed are that they represent changes in fat reserves. Changes in body mass may reliably reveal changes in lipid reserves (e.g. McEwan & Whitehead 1984; Johnson *et al.* 1985; Ekman & Hake 1990), because non-fat components of birds often remain the same during fat deposition (e.g. Connell, Odum & Kale 1960; Rogers & Odum 1964; Helms *et al.* 1967; Mascher & Marström 1976) but generally not during migration (Marsh 1984) and reproduction (Moreno 1989). In the second experiment, the photosensitive birds were undergoing gonadal hypertrophy, which would contribute to changes in mass. However, significant between-group differences in body mass remained after removing the mass of the gonads. Thus, the changes observed may represent strategic adjustments of energetic reserves. However, regardless of which components of body mass are changing, these data indicate that natural variation in avian body mass observed in the field may be a response to changes in food availability.

Contrary to theoretical predictions (Lima 1986; McNamara & Houston 1990), the birds did not

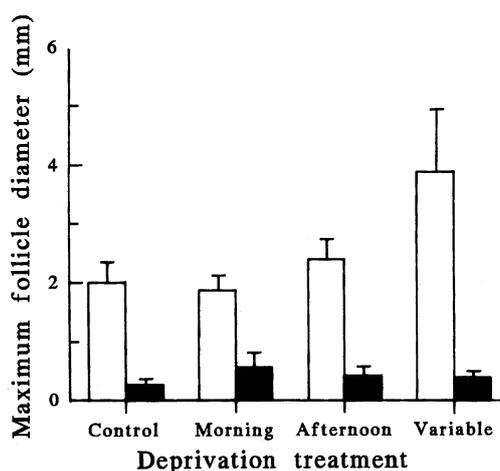


Fig. 4. Mean (\pm SE) maximum follicle diameter in photosensitive (open bars) and photorefractory (closed bars) birds in each of the four food treatments (Control, control group; Morning, deprived from dawn; Afternoon, deprived from 4 h after dawn; Variable, deprived either from dawn or 4 h after dawn) from the second part of experiment 2.

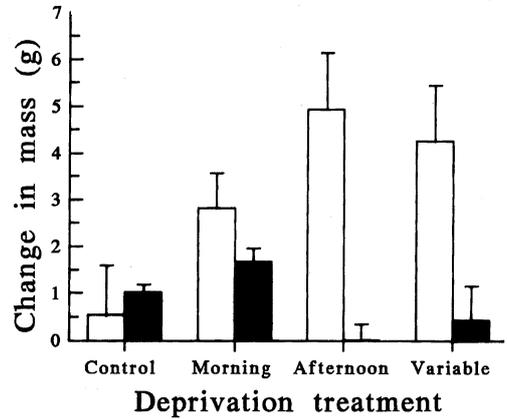


Fig. 5. Mean (\pm SE) change in body mass, controlling for gonadal mass, in photosensitive (open bars) and photorefractory (closed bars) birds in each of the four food treatment groups (Control, control group; Morning, deprived from dawn; Afternoon, deprived from 4 h after dawn; Variable, deprived either from dawn or 4 h after dawn) from the second part of experiment 2.

respond to variability. To date, there are no unequivocal demonstrations of a response to variable food availability. Although Bednekoff (1992) found that Great Tits responded to variable length food deprivations to a greater extent than birds on a constant food deprivation schedule with the same mean period of deprivation. However, this may have been a response to the 'worse conditions' experienced in the variable treatment rather than a response to variability *per se* (see Bednekoff 1992). Similarly, Ekman & Hake's (1990) manipulation of food 'predictability' involved changes in time available to feed, variability and predictability, so it is unclear which proximate factor was important. The finding that starlings developed larger fluctuating asymmetries in their primary feathers when given variable food deprivations compared to fixed deprivations (Swaddle & Witter 1994) supports the hypothesis that variability is stressful. Thus, it is surprising that no response to variability was found in body mass.

The response to changes in food availability differed according to whether the birds were photorefractory or photosensitive. Photosensitive starlings responded to decreased time available to feed by increasing body mass, whereas photorefractory birds, post-molt, tended to decrease mass. Analogous seasonal modulation of mass regulation has been reported for Rufous Hummingbirds, *Selasphorus rufus* (Heibert 1991). Heibert (1991) found that during the spring Rufous Hummingbirds increase in mass in response to food deprivations but during the summer mass either declines or shows no change. Heibert (1991) suggested that the hummingbirds were diverting all available resources to reproduction, rather than depositing fat (cf. Wingfield 1988). Lack of increase in mass in response to changes in food availability during molt may have a similar functional explanation. For

example, it may be more costly to divert resources away from feather growth, perhaps because moult is delayed, than to reduce the risk of starvation by storing more fat. An additional ultimate factor may be that the costs of fattening are higher during moult because of increased flight costs, resulting from a decrease in wing area or increase in water content (cf. King & Murphy 1985). Increasing body mass and fat reserves by changes in food intake is only one possible response to a deterioration in the energetic environment. An alternative is to decrease metabolic requirements. This could be achieved by changes in behaviour (see Witter & Cuthill 1993), changes in metabolic rate (e.g. Buttemer, Astheimer & Wingfield 1991) or changes in the amount of metabolically active tissue (e.g. Heldmaier 1989). Thus, while the decrease in mass observed in response to food deprivations in photorefractory starlings could simply be a 'passive' reflection of decreased time available to feed, it may reflect a strategy to reduce energetic requirements.

This seasonal modulation of the response to food availability is also consistent with previous findings on the corticosterone stress response (see Harvey *et al.* 1984). Levels of plasma corticosterone and the sensitivity of the stress axis change seasonally, particularly during reproduction and moult (Wingfield, Vleck & Moore 1992). Data on wild-caught starlings support this view; levels of corticosterone are lower in starlings during a period coinciding with photorefractoriness (Dawson & Howe 1983). If the corticosterone stress response is related to periodic food availability, as field data suggest (e.g. Wingfield 1988, Astheimer, Buttemer & Wingfield 1992), then this represents one likely mechanism through which this seasonal modulation occurs. Corticosterone levels are known to be associated with both food-intake rate and metabolic expenditure (Astheimer *et al.* 1992); the changes in body mass observed may have arisen through either process.

Against the functional explanations suggested above, for the starling example, is that birds continued to show no response after moult was completed. Witter & Cuthill (1993) argued that the nature of environmental stochasticity may be important in determining whether it is better for a bird to respond directly to environmental cues or follow an endogenous strategy of mass change. For example, in environments that are prone to sudden fluctuations in food availability, previous experience may be a poor indicator of future requirements. If decreased food availability tends to occur at particular times of year, a fixed strategy of fattening may be a better method of avoiding starvation than responding to environmental change. It is feasible that environmental stochasticity changes during the year to favour both predictive and responsive strategies (Witter & Cuthill 1993). Field data suggest that different species may follow different strategies. Some species appear to regulate mass in response to recent experience (e.g. Jenni & Jenni-Eiermann 1987),

while others regulate mass in anticipation of requirements (e.g. King & Mewaldt 1981; Dawson & Marsh 1986). The data presented here suggest that birds may use different strategies of mass regulation at different points in the annual cycle.

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