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Mass regulation in juvenile Starlings: response to change in food availability depends on initial body mass

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Summary

1. The adaptive mass-regulation hypothesis suggests that birds should respond to worsening or unpredictable foraging conditions by increasing body mass and energetic reserves. However, previous work on adult European Starlings, *Sturnus vulgaris* L., has revealed that the response to worsening foraging conditions varies according to the seasonal status of the birds. Photosensitive birds respond to decreased time available to feed by increasing mass, whereas photorefractory birds regulate mass at a fixed level. Juvenile Starlings are in a state of photorefractoriness until puberty. In this paper, we examine whether photorefractory juvenile Starlings respond to worsening foraging conditions by regulating mass at a fixed level, like adults, or whether they increase in mass, in accordance with the adaptive regulation hypothesis.
2. Birds were divided into two treatment groups: control and food deprived. Control birds remained on food *ad libitum* throughout the experiment. Food-deprived birds had their food removed for 5 h every other day over a 6-week period. The effects of these manipulations on the resulting changes in body mass and fat reserves were examined.
3. Food-deprived birds increased fat reserves and body mass in comparison with controls. However, the response to food availability depended on the initial body mass of the birds. Birds with the lowest initial mass exhibited the largest response to the manipulation. This may be because birds with low energetic reserves are more severely affected by changes in the availability of food.
4. Juvenile photorefractory Starlings show a response to changes in food availability that is unlike the response of photorefractory adults. We suggest that the mechanism of responding to environmental change, in addition to being modulated seasonally, may be age structured. We speculate that the function of this age effect may be related to the low competitive status of juvenile Starlings. This subdominant age-class may be displaced to less favourable feeding or roosting sites; as a result, they may have to respond flexibly to a rapidly changing and unpredictable energetic environment.

Key-words: Fat reserves, predation, starvation, *Sturnus vulgaris*, trade-off
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Introduction

Birds display large spatiotemporal variation in body mass and fat reserves (see Blem 1976, 1990). Theoretical analyses (Lima 1986; McNamara & Houston 1987, 1990; Houston & McNamara 1993) suggest that this variation is a manifestation of the trade-off between the costs and benefits of fat storage (see Rogers & Smith 1993; Witter, Cuthill & Bonser 1994). Increasing fat reserves is beneficial in terms of reducing the probability of starvation, if food cannot be obtained directly from the environment. However, fattening may also be costly because of, for example, increased risk of predation or increased metabolic expenditure (Witter & Cuthill 1993; Gosler, Greenwood & Perrins 1995; Metcalfe & Ure 1995). Recent comparative and experimental studies support the notion that birds strategically regulate the size of their energetic reserves according to a cost–benefit trade-off. If a comparison is made between species, there is a close fit between fattening strategy and food-resource predictability (Lehikoinen 1986; Rogers 1987). Within species, birds respond to manipulations of the energetic environment, both food availability and temperature, by strategically adjusting body mass and fat reserves (Ekman & Hake 1990; Ekman & Lilliendahl 1993; Hurly 1992; Bednekoff & Krebs 1995; Rogers 1995).

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In addition to these latter findings, Witter, Swaddle & Cuthill (1995) found that the response to periodic food availability in adult Starlings, *Sturnus vulgaris* L., varied according to seasonal status. When photorefractory, the physiological state in which birds are unable to respond to increasing daylength by undergoing gonadal development (see Nicholls, Goldsmith & Dawson 1988), birds regulated body mass at a fixed level as time available to feed decreased. However, when photosensitive, the birds responded to the same manipulations of food availability by increasing mass, in accordance with the adaptive regulation hypothesis. These results support the notion that, within a species, birds may use different strategies of mass regulation at different points in the annual cycle. These data are analogous to previous findings in the Rufous Hummingbird, *Selasphorus rufus*, that response to food deprivation differs according to whether or not birds are breeding (Heibert 1991) and that the response to changes in temperature in Dark-eyed Juncos, *Junco hyemalis*, depends on season (C. M. Wiese, unpublished data, cited in Rogers 1995).

In this paper, the results of an experiment investigating the response of juvenile Starlings to periodic food availability are reported. Juvenile Starlings are in a state of photorefractoriness (see Nicholls *et al.* 1988) until puberty; puberty is synonymous with the first breaking of refractoriness, which takes place in the autumn. Thus, if the state of refractoriness is similar in adults and juveniles, juvenile Starlings should regulate mass and energetic reserves at a fixed level as time available to feed is decreased. However, if this is not the case, juveniles may increase mass and fat reserves under periodic food availability, as predicted by the adaptive regulation hypothesis.

Methods

PROCEDURE

The experiment was done on 22 wild-caught juvenile Starlings. Birds were housed individually in cages 0·3 m × 0·3 m × 0·5 m, held in visual isolation from each other, and maintained at a constant temperature of 20 °C. Photoperiod was adjusted to approximate natural photoperiodic conditions for the time of year (initial photoperiod, 17L : 7D; final photoperiod, 15·5L : 8·5D, reduced in 30 min blocks). Birds were supplied with turkey starter crumbs and water *ad libitum*, except as described below. The 22 birds were randomly allocated to two treatment groups: control ($n = 11$) and food-deprived ($n = 11$). The control group was provided with food *ad libitum* during the experiment. The food-deprived group had their food removed for 5 h, begining at 1030 h, every other day throughout the experiment. Food hoppers were removed manually from the front of each cage; any food on the cage floor was removed at the start of each deprivation period. To control for possible effects of disturbance, food hoppers were similarly removed from the front of control cages, but then immediately returned. The floors of control cages were similarly cleaned of food. Cages from each treatment group were alternated throughout the room to eliminate position bias.

Immediately before the first food deprivation, and then at weekly intervals thereafter, each bird was removed from its cage and the following data were recorded: body mass (to 0·1 g on an electronic balance) and a score of subcutaneous fat (on a scale of 0 to 5) (cf. Helms & Drury 1960). Birds were measured from each treatment group alternately; individual birds were measured in the same order on each occasion. All measurement sessions began at 0900 h. By using this procedure, time-of-day and order biases were eliminated for both within-bird and between-group comparisons. These recordings continued for approximately 6 weeks.

STATISTICAL ANALYSES

Body mass and fat reserves were analysed by repeated-measures analysis of variance (Hand & Taylor 1987), using the procedure MANOVA on SPSS (SPSS 1988). These analyses comprise a between-subjects factor, group (the food-deprivation treatment) and a within-subjects factor, day (day in the experiment). Patterns of change in mass and fat in relation to initial body mass and fat reserves were studied by analysis of covariance, with group as the factor and initial body mass and initial fat score, respectively, as the covariates. Three birds (all from the control group) died during the experiment; these data were excluded from all analyses. Normality of the data or residuals was investigated by normal probability plots. Values are shown as mean (±SE); two-tailed tests of significance are used throughout.

Results

Birds exhibited strong longitudinal increases in both body mass and fat score during the experiment (mass, $f_{6,102} = 30{\cdot}78$; $P < 0{\cdot}001$; fat, $f_{6,102} = 6{\cdot}28$, $P < 0{\cdot}001$) (Fig. 1). Levels of fat reserves differed by treatment group; birds that were periodically food deprived exhibited increased fat reserves in comparison with control birds (group, $f_{1,17} = 6{\cdot}82$, $P = 0{\cdot}018$; group × day interaction, $f_{6,102} = 1{\cdot}03$, $P = 0{\cdot}411$) (Fig. 1a). Although body mass tended to diverge between groups (Fig. 1b), this change was not significant (group, $f_{1,17} = 0{\cdot}97$, $P = 0{\cdot}340$; group × day interaction, $f_{6,102} = 1{\cdot}04$, $P = 0{\cdot}406$). However, evidence that food availability did influence mass is provided by the between-individual patterns of change within treatment groups. Ekman & Hake (1990) reported that the strength of response to unpredictable food availability in Greenfinches, *Carduelis chloris*, depended on body mass at the start of the experiment. The same relation is evident in the present data (Fig. 2). For simplicity, this is illustrated here with respect to change in mass and fat score observed over the experiment; the more appropriate statistical analysis is given below. Relations between change in mass over the experiment and initial body mass differed by treatment group (group, $f_{1,15}=6{\cdot}78$, $P=0{\cdot}020$; initial mass, $f_{1,15}=11{\cdot}56$, $P=0{\cdot}004$; group × initial mass, $f_{1,15}=6{\cdot}08$, $P=0{\cdot}026$) (Fig. 2b). In other words, birds with a lower mass at the beginning of the experiment increased mass to a greater extent than birds with a higher mass at the beginning of the experiment. This relation differed according to food availability; birds that were periodically food deprived increased in mass to a greater extent compared with control birds, when initial mass was controlled for. As Ekman & Hake (1990) explain, this result is consistent with the view that birds with an initially low mass have to respond to changes in food availability more strongly than birds with higher mass, because they are less well buffered against environmental change. The same analysis on mean change in fat score reveals similar relations, although in this case the test for homogeneity of slopes is not significant (group, $f_{1,15}=4{\cdot}63$, $P=0{\cdot}048$; initial fat score, $f_{1,15}=21{\cdot}63$, $P<0{\cdot}001$; group × initial fat score, $f_{1,15}=1{\cdot}52$, $P=0{\cdot}236$) (Fig. 2a). Lack of an interaction between initial fat score and treatment group, in this case, is perhaps not surprising given the initial low variation in fat score (see Fig. 2a). There is a potential difficulty with this method of analysis, however. Change in mass (or fat) is biased towards a negative relation with initial mass, because it is calculated as 'change in mass' = 'final mass' − 'initial mass'; this may have been a problem in previous analyses (see, for example, Ekman & Hake 1990). The appropriate solution is to examine total body mass or fat (rather than change in mass or fat) after the period of manipulation with initial body mass or fat as a covariate. In this case, the conclusions remain unchanged; the response to the experimental manipulations of food availability differ according to initial body mass ($f_{1,15}=6{\cdot}08$, $P=0{\cdot}026$).

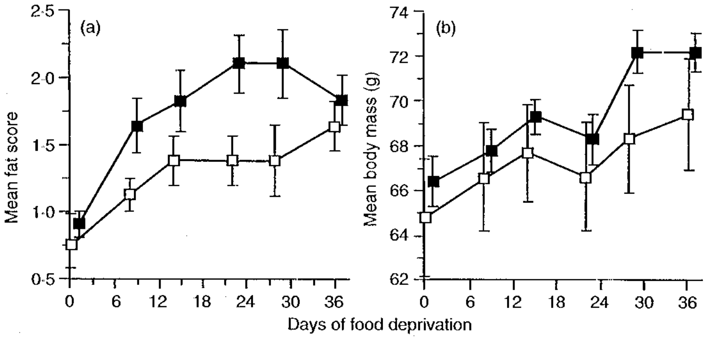

Fig. 1. Mean (±1SEM) (a) fat score and (b) body mass in the food-deprived (filled symbols) and control (open symbols) treatment groups. Values have been displaced by one day to reduce overlap.

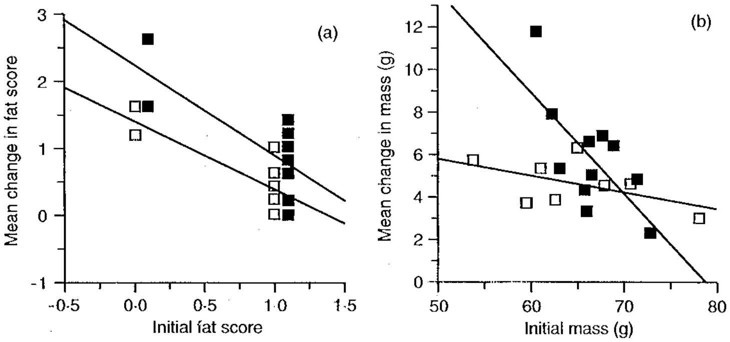

Fig. 2. Mean change in (a) fat score and (b) body mass during the experiment, plotted against initial fat score and body mass, respectively, in food-deprived (filled symbols) and control (open symbols) treatment groups. Each treatment group's scores have been displaced by 0·1 to reduce overlap. Within groups, some points represent more than one value. Lines are least-squares linear regressions calculated separately for each treatment group. For the control group in (a), change in fat score = 1·40 (±0·264) − 1·03 (±0·304) × initial fat score; $r^2=65{\cdot}8\%$, $f_{1,7}=11{\cdot}53$, $P=0{\cdot}015$. For the food-deprived group in (a), change in fat score = 2·24 (±0·376) − 1·37 (±0·378) × initial fat score; $r^2=59{\cdot}3\%$, $f_{1,10}=13{\cdot}10$, $P=0{\cdot}006$. The two slopes do not differ significantly from each other ($f_{1,15}=0{\cdot}44$, $P=0{\cdot}515$). For the control group in (b), change in body mass = 9·51 (±3·396) − 0·0756 (±0·052) × initial body mass; $r^2=26{\cdot}0\%$, $f_{1,7}=2{\cdot}11$, $P=0{\cdot}197$. For the deprived group in (b), change in body mass = 37·4 (±10·970) − 0·475 (±0·167) × initial body mass; $r^2=48{\cdot}0\%$, $f_{1,10}=8{\cdot}30$, $P=0{\cdot}018$. The two slopes differ significantly from each other ($f_{1,15}=6{\cdot}08$, $P=0{\cdot}026$).

Discussion

These results provide further support for the hypothesis that birds strategically regulate their body mass, as predicted by theoretical analyses of avian mass regulation (see, for example, Lima 1986; McNamara & Houston 1990). Although the specific predictions of these models differ (see Houston & McNamara 1993), they have in common the prediction that deteriorations in a bird's energetic environment are associated with increased mass and energetic reserves, provided that food availability does not directly limit fat deposition. However, these models alone cannot indicate the mechanism by which birds regulate their energetic reserves. For example, birds may adjust their reserves in direct response to environmental change. Alternatively, they may follow a fixed pattern of mass change (seasonal sliding set-points) (Mrosovsky & Sherry 1980), shaped by selection pressure for changes in reserve requirements. Birds may also use a combination of both strategies: they may exhibit seasonal changes in reserves that are fine tuned by recent experience. Rogers, Nolan & Ketterson (1994) have usefully referred to these strategies as 'responders', 'predictors' and 'responder–predictors', respectively. The optimal strategy may depend on the nature of environmental change (see Witter & Cuthill 1993; Witter *et al.* 1995). For example, in environments that suffer sudden large drops in food availability, previous experience may be a poor indicator of future requirements. However, if decreased food availability tends to occur at particular times of year, a fixed strategy of mass change may provide a more effective means of avoiding starvation than responding directly to change in food availability. Field data suggest that different species may follow different strategies. Some species appear to regulate mass in response to recent experience (see, for example, Jenni & Jenni-Eiermann 1987), whereas others regulate mass in anticipation of requirements (see, for example, King & Mewalt 1981; Dawson & Marsh 1986).

Previously, we have shown that adult Starlings do not increase body mass in response to periodic food availability when photorefractory (Witter *et al.* 1995). The results presented here suggest that this is not the case in juvenile Starlings in a state of photorefractoriness. Juvenile Starlings respond to decreased time available to feed by increasing their fat reserves and mass, in a manner similar to that observed in photosensitive adults. Thus, the apparent seasonal modulation of the response to food availability is not inextricably linked to the state of photorefractoriness. The present results, together with our previous findings, suggest that Starlings exhibit both age-class and seasonal differences in their response to changes in the availability of food. As reported by Ekman & Hake (1990), between-individual differences in the response to the manipulation were related to initial body mass. Birds with low initial masses gained more mass during food deprivation, compared with heavier birds. Heavier birds, with higher energetic reserves, may be less affected by the period of food deprivation (cf. Swaddle & Witter 1994), and so respond to a lesser degree (see Ekman & Hake 1990). In Witter *et al.* (1995) we did not explicitly examine the relation between initial mass and between-individual differences in mass change during food deprivations. However, a retrospective analysis has revealed that there was no relation between change in mass and initial mass in our previous experiments, even in cases where birds responded to the manipulations of food availability by increasing mass (Fig. 3). Why the response to changes in food availability appear to be state dependent in juveniles but not adults is unclear, but it perhaps further emphasizes the discrepancy between adults and juveniles in their response to identical manipulations.

What functional explanations might account for why photorefractory juveniles increase in mass when time available to feed decreases, whereas photorefractory adults do not? As considered above, Witter & Cuthill (1993) suggested that the nature of environmental stochasticity may be a particularly important determinant of the strategy of mass regulation. It is likely that foraging stochasticity is age-class-structured in Starlings. Juvenile Starlings are known to exploit food resources different from those of adults (Brown 1974; Feare 1980). Further, because juvenile Starlings are generally subdominant to adults, they are often displaced to less favourable feeding habitats and may suffer more variable foraging success (see Feare 1984). Similarly, subdominants may be forced to occupy less favourable roosting sites (Summers, Westlake & Feare 1986; Swingland 1987), resulting in increased energy expenditure or increased variability in energetic expenditure. Decreased energetic gain, increased variability in gain, increased energetic expenditure and increased variability in expenditure are all predicted to increase the benefits of maintaining higher fat reserves (Lima 1986; McNamara & Houston 1990). Social dominance is known to be an important determinant of fattening (Ekman & Lilliendahl 1993; Witter & Swaddle 1995), most probably because of dominance-dependent access to food (but see Witter & Swaddle 1995). Because the composition of the social environment may be variable over time, low dominance status may increase the benefits of responding flexibly to changes in the energetic environment. Dominant age or sex classes, with a reduced probability of being interrupted or displaced from favoured food or roost sites, may exist in an intrinsically more predictable energetic environment. In these cases, fixed trajectories of mass change may be sufficient to match current reserves with changing energetic requirements. Thus, although dominance status may directly influence the accumulation of fat reserves, age-class differences in social status may also be an important selection pressure in creating different strategies of response to environmental change.

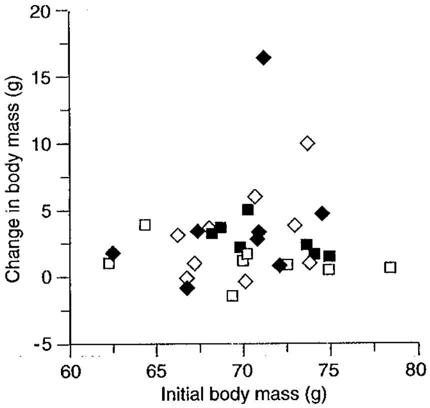

Fig. 3. The mean change in body mass plotted against initial body mass in adult Starlings experiencing four food availability treatment groups: control (open squares), morning-deprived (filled squares), afternoon-deprived (open diamonds) and variable-deprived (filled diamonds) treatments (see Witter *et al.* [1995] for details of the treatment groups). There were no significant relations between change in body mass and initial body mass for any of the treatment groups considered separately ($f_{1,6-8}<4{\cdot}74$, $P>0{\cdot}081$, in all cases); the relations between change in mass and initial mass did not differ significantly from each other in different treatments ($f_{1,25}=1{\cdot}21$, $P=0{\cdot}327$). Data are taken from Witter *et al.* (1995).

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