

# Food, feathers and fluctuating asymmetries

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## SUMMARY

Nutritional, or energetic, stress has been implicated as a causal factor in the inter-individual differences in levels of fluctuating asymmetry in the elongated tails of male swallows (*Hirundo rustica*). However, there has been no direct experimental test of this hypothesis. We report results from an experiment that has investigated the effects of sequential food deprivations on levels of fluctuating asymmetry in primary feathers and chest plumage of the moulting female European starling (*Sturnus vulgaris*). Birds were housed individually and taken through their full moult by means of photoperiodic manipulation. During this period, some of the birds experienced food deprivations. At regular intervals, we recorded the length of every primary feather, quantified the chest plumage via video-image analysis, and recorded body mass and subcutaneous fat score measurements. We found that increasing levels of nutritional or energetic stress caused larger development asymmetries, which would appear to have increased fitness costs. Primary feather asymmetry showed a negative relation with amount of subcutaneous fat stored during moult and a positive relation with social dominance. This is the first study to show, directly, the importance of energetic stress in the production of feather and plumage asymmetries. Low levels of feather asymmetries were also associated with an indicator of reproductive status (chest 'spottiness'). These findings support the recent literature, suggesting that degree of fluctuating asymmetry, even in traits under stabilizing selection, may reveal aspects of individual fitness value.

## 1. INTRODUCTION

Fluctuating asymmetries (FAs) are the small stress-induced random deviations from perfect symmetry that arise in the development of bilaterally symmetrical traits (Ludwig 1932). These stresses can be either genetic (see, for example, Mather 1953; Tebb & Thoday 1954; Leamy & Atchley 1985) or environmental (see, for example, Beardmore 1960; Parsons 1964; Siegal & Smookler 1973). There are intraspecific differences in the extent to which individuals can resist these developmental accidents (a buffering capacity) which may be heritable (Van Valen 1962; Thornhill 1992). Individuals that can buffer themselves against one kind of stress are also capable of buffering themselves against others (Hoffman & Parsons 1989). This buffering capacity has been equated with certain fitness measures in a wide variety of species (Mitton & Grant 1984; Harvey & Walsh 1993), suggesting that levels of FA can be used as an indicator of individual quality (Russell 1954; Beardmore 1960; Møller 1990).

As levels of FA may reveal aspects of individual quality, it has been proposed that this information is utilized during mate assessment (Møller 1990, 1992, 1993; Swaddle & Cuthill 1993). Through a series of experimental manipulations, Møller has shown that female barn swallows (*Hirundo rustica*) preferentially mate with males that have the most symmetric elongated tail feathers (Møller 1992, 1993). It has been suggested that the individual variation in levels of FA observed in the tails of male swallows is related to the amount of rainfall experienced at the wintering

grounds, where the birds moult and grow these elongated sexual ornaments. This suggests a role for nutritional or energetic stress in the development of plumage FAs. It has been shown that nutritional stress increases levels of FA in species of *Drosophila* (Parsons 1964) and rats (Sciulli *et al.* 1979). However, to date, there is no literature reporting the effects of experimentally manipulated nutritional stress on levels of FA in feather development.

The female European starling (*Sturnus vulgaris*), at the time of mate acquisition, has a dark black chest plumage that is speckled with white spots (Feare 1984). Studies of individual variation in 'spottiness' of this chest plumage has revealed that chest 'spottiness' (number of spots per unit area), in captive birds, is positively correlated with stage of follicular development (A. R. Goldsmith & I. C. Cuthill, unpublished results). Birds with spottier chests (at the beginning of the breeding season) start their ovarian development before those with less spotty chests, and so lay their first clutch earlier. This may give these 'earlier' birds fitness advantages (e.g. opportunity to second brood, as offspring fledge earlier) (Darwin 1871; Fisher 1930; Price *et al.* 1988; Perrins 1991). So it has been postulated that chest spottiness is a reflection of some component of individual quality; higher quality individuals have spottier chests at the beginning of the breeding season (i.e. at the time of mate acquisition).

As the chest plumage of the female starling may be a quality-related signal, and levels of FA have been linked with fitness measures (Russell 1954; Beardmore 1960; Mitton & Grant 1984; Møller 1990; Harvey &

Walsh 1993), we investigated the effects of food deprivations on chest plumage and primary feather asymmetries in the moulting female European starling. We also examined the relations between level of FA, fat reserves and social dominance.

## 2. METHODS

We used 35 wild-caught adult female European starlings, *Sturnus vulgaris*. All birds were housed individually in 0.3 m × 0.3 m × 0.3 m cages, in visual, but not acoustic, isolation. Birds were maintained on water and turkey starter crumbs available ad libitum, except as described below. Before the experimental manipulations, birds were maintained on an 8 h:16 h light:dark (L:D) photoperiod and were thus photosensitive (Burger 1947; Farner *et al.* 1983). The birds were then exposed to long days (18 h:6 h L:D) to induce photorefractoriness and moult (Dawson *et al.* 1985). They remained on this photoperiod until moulting began in all birds (approximately 10 weeks). After this period, birds were transferred to a 13 h:11 h L: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-deprived group had their food removed for 4 h, beginning at 'dawn' (i.e. when the laboratory lights were switched on). The afternoon-deprived group had their food removed for 4 h, beginning 4 h after 'dawn'. The variable-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 the deprivation. Food deprivations were applied every other day, with occasional 'missed days', for 15 weeks.

At approximately weekly intervals, the following measures were taken on each bird: the length of each growing primary (to 0.01 cm, with vernier callipers) on both wings, a score of subcutaneous fat (0 to 5; cf. Helms & Drury 1960), and body mass (to 0.1 g, on an electronic balance). All body mass measurements were balanced across treatments for time of day. The tips of the primaries were always checked carefully, and any damage or wear was noted; all such values have been excluded from the analyses. Also, each week, the chest plumage of each individual, held in the hand, was recorded on videotape. Videos were subsequently digitized by using the Optimas software package (BioScan Incorporated 1992) to calculate the number of spots per unit area (as a measure of 'spottiness') on both sides of the chest. Measurements were taken blind of the treatment groups from which the birds came.

Following the 15 weeks of periodic food deprivations, dominance scores were taken for all birds. This was achieved by randomly allocating the birds to five groups, each containing seven individuals. Each group of seven birds was placed in a cage measuring 0.5 m × 0.5 m × 0.3 m, 4 h before recording dominance interactions. For the first 2 h in these cages, the birds had food and water available ad libitum. After this period, the food was removed for 2 h. Food was then returned and the dominance observations began. All agonistic interactions, over food or otherwise, were recorded for a period of 30 min for each group. Following the observations, all birds were returned to their individual cages. This procedure was repeated five times, once per day, over a period of 8 d. On each occasion, new groups of seven

birds were created by random allocations. A single dominance score was then calculated for each bird from all interactions ((number of interactions won) - (number of interactions lost)); because, over the five observation sessions, dominance was recorded for each bird from interactions with most of the other birds, meaningful comparisons of dominance can be made across all birds.

These data were then used to examine the effects of food deprivation on the development of plumage asymmetries and the relation between the development of asymmetries, dominance and fat reserves. Analysis of the effects of the manipulation on other aspects of moult will be reported separately (J. P. Swaddle & M. S. Witter, unpublished results; Witter *et al.* 1994). We examined whether the asymmetry data conformed to the properties of fluctuating asymmetries (i.e. a normal distribution with a mean of zero) by Kolmogorov-Smirnov one-sample tests (Siegel & Castellan 1988). As the distribution of signed asymmetries did not differ from a normal distribution for both the chest plumage and primary feather data, the asymmetries measured were assumed to be fluctuating asymmetries (chest spottiness asymmetry,  $Z = 0.651$ ,  $n = 35$ ,  $p = 0.79$ ; range of scores for primary feather asymmetry,  $Z = 0.628$ -1.297,  $n = 31$ -33,  $p = 0.070$ -0.83). The repeatability of the asymmetry measures was analysed by the intraclass correlation coefficient ( $r_1$ ) method (Zar 1984), using signed asymmetry data. Repeatability of the chest plumage asymmetry was investigated by taking five measures of 'spottiness' asymmetry from five individuals. Repeatability of primary asymmetry was investigated by taking four measures of primary asymmetry from 10 birds. Both measures of asymmetry were highly repeatable (primary,  $r_1 = 0.91$ ,  $F_{9,30} = 43.69$ ,  $p < 0.001$ ; chest,  $r_1 = 0.96$ ,  $F_{4,20} = 124.0$ ,  $p < 0.0001$ ). The measures of asymmetry were then used to compare levels of absolute, rather than relative, plumage asymmetry (see Cuthill *et al.* 1993) between the food treatment groups. Because of the particular 'half-normal' frequency distribution of absolute fluctuating asymmetry, and the difficulty of normalizing this distribution by transformation, we have used non-parametric statistics (see Siegel & Castellan 1988) for most of the between-group analyses. Between-individual relations between the log-transformed median value of primary asymmetry across the nine primaries, mean fat score during moult, and dominance score have been analysed by stepwise-multiple regression; inspection of the normal probability plots of the residuals from these analyses suggest that the assumptions of the parametric statistical tests were fulfilled in these cases. All statistical analyses were done on MINITAB (Ryan *et al.* 1985). Two-tailed tests of significance have been used throughout. In the results, two of the original 35 birds have been excluded from all analyses because of primary damage, precluding measurement of asymmetry.

## 3. RESULTS AND DISCUSSION

The manipulations of food availability significantly affected the final asymmetry of the primary feathers (Kruskal-Wallis,  $H = 11.51$ , d.f. = 3,  $p = 0.01$ ; figure 1*a*). Levels of asymmetry were higher in the variable-food-deprived group compared with the control and fixed-time food deprived groups. The fixed-time food deprived groups also exhibited higher levels of asymmetry than the control group. Thus food deprivation per se increases levels of primary asymmetry, as does variability in the time of food deprivation; however, there was no evidence that the time of food deprivation influences the level of primary asymmetry, at least over

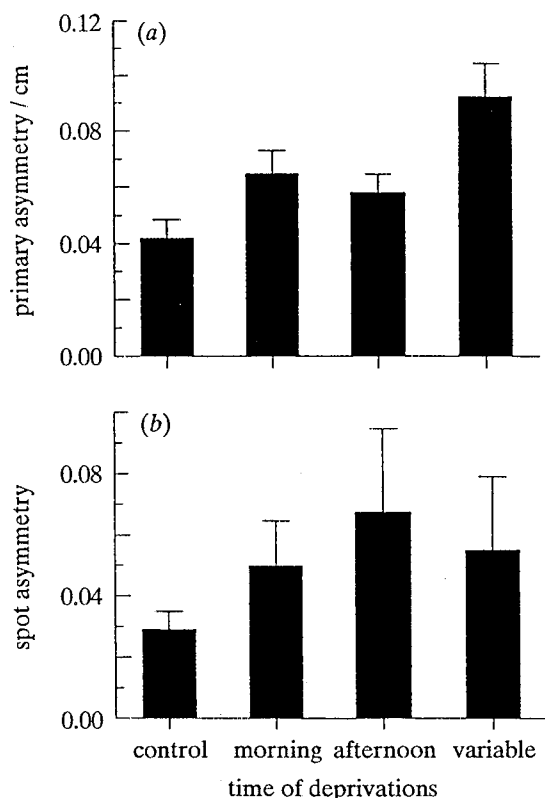


Figure 1. (a) Mean (+s.e.) asymmetries of the primary feathers for all birds in each of the four treatment groups. Each bird is represented by a single value, the median asymmetry of the nine primary feathers. Pairwise tests, control against fixed-time deprivations,  $W = 64.5$ ,  $p = 0.0165$ ; morning against afternoon deprived,  $W = 93.5$ ,  $p = 0.5075$ ; fixed against variable deprivations,  $W = 196.5$ ,  $p = 0.025$ . (b) Mean (+s.e.) asymmetries of the chest plumage for all birds in each of the four treatment groups at the end of moult.

the two time periods tested. If we assume that the food deprivations cause a certain degree of nutritional stress during development (Parsons 1964; Sciulli *et al.* 1979; Meijer 1990), it would appear that the lack of predictability of the food supply in the variable-deprived group increased the level of nutritional stress from that experienced by the fixed-time groups (cf. McNamara & Houston 1990; Witter & Cuthill 1993). This relative increase in stress resulted in greater asymmetries in the variable-deprived group. These data suggest that nutritional stress, caused by the food deprivations, could play an important role in the production of primary feather asymmetries.

Beyond reflecting differences in the ability to resist nutritional stress during development (which may be fitness related), higher levels of FA may themselves have direct fitness consequences, as the increased levels of primary asymmetry observed in the food-deprived birds may affect the aerodynamic properties of the wings, and so decrease aerial performance (Thomas 1993). This reduction in flying ability would incur costs that could directly affect individual fitness (Møller 1991), further suggesting that increased levels of FA are associated with lower fitness.

The experimental manipulations of food availability did not appear to affect chest plumage asymmetry to

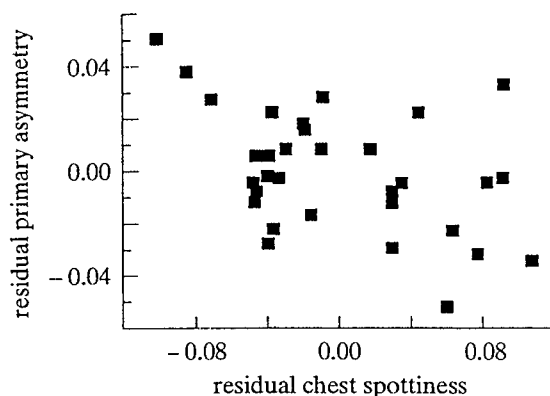


Figure 2. Mean primary asymmetry against mean chest spottiness for each bird, controlling for the effects of treatment group. Residual primary asymmetry =  $(0.000 \pm 0.0035) - (0.00386 \pm 0.0012)$  (residual chest spottiness),  $R^2 = 25.2\%$ ,  $F_{1,32} = 10.42$ ,  $p = 0.003$ .

the same magnitude ( $H = 0.60$ , d.f. = 3,  $p = 0.90$ ; figure 1b). There was an apparent trend for individuals in the food-deprived groups to have greater chest asymmetry than controls, but there was no additional effect of variability.

There was a negative relation between primary asymmetry and chest spottiness when controlling for the effects of treatment group (figure 2). The spottiest birds had the most symmetrical primary feathers. As spottiness is associated with advanced follicular development in captive starlings (see Introduction), it would appear that these putatively high-quality individuals, identified by their spotty chests, are best able to resist developmental stress and grow the most symmetrical primary feathers. This result suggests that levels of FA in primary feathers, even though they are under strong stabilizing selection to be symmetrical (Møller & Pomiankowski 1993), may be correlated with aspects of direct fitness value. However, these asymmetries are very small, and it is improbable that these FAs are used in individual assessment.

A direct role for energetic stress in the development of asymmetries is further suggested by the negative relation between fat reserves and primary asymmetry when the effects of treatment group and dominance have been controlled for (figure 3a). The birds with the most symmetrical primary feathers had the highest mean fat reserves during moult. Although we have not manipulated fat levels in this experiment, and so do not know the direction of any causal arrows between fat and asymmetry, we propose that this relation demonstrates the importance of nutritional stress in the production of feather asymmetries. If we take the *a priori* stance that food deprivations create nutritional or energetic stress during development (Parsons 1964; Sciulli *et al.* 1979; King & Murphy 1985; Meijer 1990), these data suggest that individuals with low fat reserves experienced greater energetic stress due to the same food deprivations than those with large reserves. When energy stores are large, the food deprivations do not exert as much stress during development as when energetic reserves are low. The increased level of developmental stress incurred by individuals with lower levels of subcutaneous fat resulted in greater

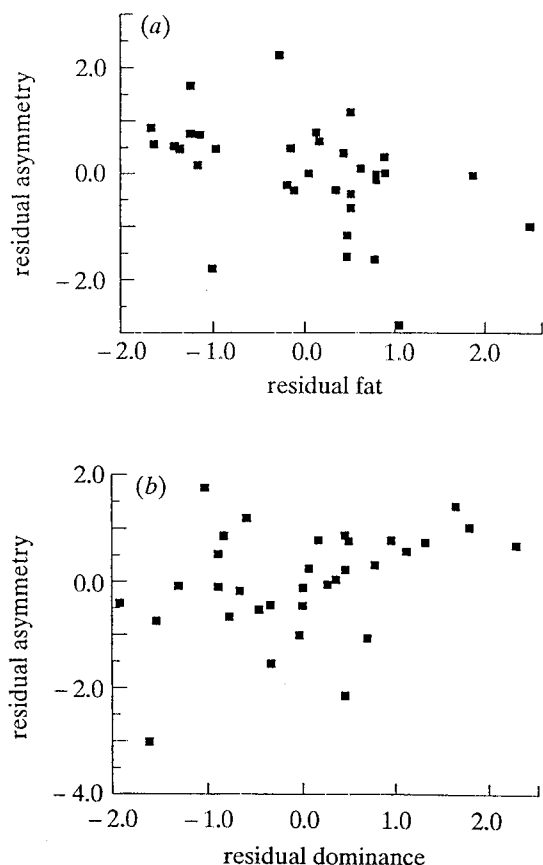


Figure 3. (a) Primary asymmetry against mean fat score over moult, controlling for effects of treatment and dominance on both variables, (b) primary asymmetry against dominance score (higher dominance scores represent more dominant individuals; see text for details), controlling for treatment and fat on both variables. Stepwise-multiple regression of log<sub>e</sub> (median primary asymmetry) on group, fat, dominance score and all interaction terms gave the following model:  $\log_e(\text{median primary asymmetry}) = (-2.601 \pm 0.353) + (0.196 \pm 0.071)(\text{group}) - (0.492 \pm 0.191)(\text{fat score}) + (0.003 \pm 0.001)(\text{dominance score})$ ,  $R^2 = 38.1\%$ ,  $F_{3,32} = 7.57$ ,  $p = 0.001$ . (Constant,  $t = 7.37$ ,  $p < 0.001$ ; group,  $t = 2.76$ ,  $p = 0.010$ ; fat score,  $t = 2.58$ ,  $p = 0.015$ ; dominance score,  $t = 2.18$ ,  $p = 0.038$ .)

primary feather asymmetries. Birds with larger fat reserves experienced less energetic stress and developed more symmetrically. The data do not provide unequivocal evidence for this interpretation, but they do lend support to the hypothesis that energetic stress and developmental homeostasis are intimately linked. Only by experimental manipulations of lipid reserves will we be able to disentangle the way in which fat and asymmetry are related.

There was a positive relation between levels of primary asymmetry and social dominance when controlling for the effects of treatment group and fat score (figure 3b). The most asymmetric birds were the most dominant. Intuitively, this may appear to be a surprising result if there is a net benefit to being dominant (e.g. Ekman 1987). However, it is important to remember the role of social dominance within the context of the experimental conditions. Birds were housed individually throughout the entire period of their moult. Effectively, we may have teased out one of the costs of being dominant (see Johnstone & Norris

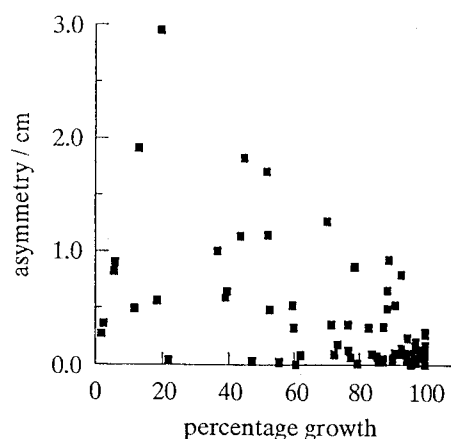


Figure 4. Mean primary asymmetry against percentage growth for primary four, controlling for individual differences. Rank Spearman correlation coefficient,  $r_s = -0.482$ ,  $n = 107$ ,  $p < 0.0001$ . Spearman rank correlation coefficients were calculated for all primaries:  $P_1$ ,  $r_s = -0.233$ ,  $n = 99$ ,  $p = 0.019$ ;  $P_2$ ,  $r_s = -0.660$ ,  $n = 97$ ,  $p < 0.001$ ;  $P_3$ ,  $r_s = -0.721$ ,  $n = 96$ ,  $p < 0.0001$ ;  $P_5$ ,  $r_s = -0.403$ ,  $n = 118$ ,  $p = 0.0005$ ;  $P_6$ ,  $r_s = -0.588$ ,  $n = 123$ ,  $p < 0.0001$ ;  $P_7$ ,  $r_s = -0.664$ ,  $n = 161$ ,  $p < 0.0001$ ;  $P_8$ ,  $r_s = -0.543$ ,  $n = 147$ ,  $p < 0.0001$ ;  $P_9$ ,  $r_s = -0.425$ ,  $n = 136$ ,  $p \neq 0.0001$ .

(1993) for discussion), as there were no social interactions. We believe that the observed relation between primary asymmetry and dominance may be a manifestation of the relation of dominance and metabolic rate. It has previously been reported that dominant individuals have higher metabolic rates than subdominants (Røskaft *et al.* 1986; Hogstad 1987). Birds with higher metabolic rates (dominants) may be affected more by the same food deprivation régime than those with lower metabolic rates (subdominants). This relative increase in the energetic stress for dominant individuals results in a loss of developmental control and increased levels of FA. This hypothesis is further supported by the substantive literature reporting the negative relation between levels of FA and metabolic rates (see Mitton & Grant (1984) for review). However, the relation between asymmetry and dominance is undoubtedly complex and requires closer examination. Currently, we are investigating the development of feather asymmetries in birds housed in social groups.

We examined the change in level of FA during the growth of individual primary feathers. As a primary grows it becomes progressively more symmetric (figure 4). This increase in symmetry is associated with reduced growth rates as the feather reaches its final length (J. P. Swaddle & M. S. Witter, unpublished results). Our data suggest that there is a compromise of developmental control, early in a feather's development, in favour of increased growth rates, which can be explained functionally. When a primary feather is small, there are relatively small costs in being asymmetric, as the feather does not contribute much to the aerodynamic properties of the wing, nor does it create large moments about the axis of symmetry (cf. Evans & Hatchwell 1993). It may be more important for the individual to grow the primary feathers as quickly as possible, and so increase the surface area of

the wing. However, as the feather elongates, the costs of asymmetry increase and so the primary is constrained to be symmetrical as it nears full development (Evans & Hatchwell 1993).

In conclusion, it would appear that the food manipulations did create greater levels of FA in the feathers of female starlings. This implies a causal role for nutritional or energetic stress in the production of these asymmetries. Birds under greater nutritional stress exhibit greater levels of FA. As feather asymmetries showed a negative relation with a correlate of reproductive development (spotty chests), we provide further evidence to support the growing consensus that low levels of FA may reveal aspects of high quality. Developmental stresses, at energetically crucial stages of a bird's life cycle (e.g. during moult), can have profound effects on feather growth and may affect overall fitness.

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