

Fluctuating asymmetries, competition and dominance

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SUMMARY

Levels of fluctuating asymmetry (FA) in the primary feathers of European starlings, *Sturnus vulgaris*, have been shown to be sensitive to nutritional and energetic stress. Furthermore, between-individual variation in plumage FA has been found to be related to social dominance, even without social interactions during feather growth, with dominant birds exhibiting the highest levels of FA. Here we examine whether the relation between dominance and FA differs when birds are housed in social groups, under different degrees of competition for food, during moult. We reason that dominants should derive a greater benefit from their social status as competition for food increases. Our results support this proposition. The relation between dominance and FA differed significantly according to the degree of competition for food. However, in no cases did the dominants exhibit lower levels of FA than subdominants. When competition for food was low, dominants had higher levels of FA than subdominants. When competition for food was high, there was no systematic relation between dominance and FA. These results suggest that dominants may only derive a net benefit from their social status, under the circumstances of our experiment, during severe conditions of competition.

1. INTRODUCTION

Fluctuating asymmetries (FAs) are small, random deviations from perfect symmetry which arise due to the inability of individuals to undergo identical development of bilaterally symmetrical traits on both sides of the body (Van Valen 1962). Such asymmetries can arise through either genetic or environmental stress. Individuals generally differ in the extent to which they can buffer themselves against such stresses. As individuals which can buffer themselves against one kind of stress are also capable of buffering themselves against others, levels of FA have been used as measures of individual quality (see, for example, Beardmore 1960; Møller 1990; Møller & Pomiankowski 1993). Previously, we have shown that levels of FA in the feathers of birds are sensitive to nutritional or energetic stress (Swaddle & Witter 1994). We found that levels of FA in the primary feathers of European starlings, *Sturnus vulgaris*, increased when birds were periodically food deprived during moult. However, we also found the surprising result that the most dominant individuals exhibited the highest levels of FA. This result is of interest because of the purported relations between social dominance and individual quality. Although it has been recognized that dominance may entail costs, for example, due to increased metabolic rate (Røskaft *et al.* 1986; Hogstad 1987), frequent involvement in aggressive encounters (Järvi & Bakken 1984) or immunosuppression (Folstad & Karter 1992), dominance is usually considered to result in net benefits, through, for example, enhanced access to food and mates, lower predation risk and increased chances of survival (see, for example, Baker & Fox 1978; Baker *et*

al. 1981; Ekman 1987; Piper & Wiley 1990). Because levels of FA represent a general indicator of individual quality, they may help to identify whether dominants obtain a net benefit through their social status or whether, for example, dominance and subdominance coexist as evolutionary stable strategies (see Maynard Smith 1982). Thus, in this paper, we extend our earlier work (Swaddle & Witter 1994) by examining in more detail the relation between development of FA in primary feathers and social dominance in the starling.

In our original experiment (Swaddle & Witter 1994), birds were housed individually throughout moult. Dominance was determined at the end of this period, after feather growth had been completed. Thus, while the feathers were growing, the birds were not involved in social interactions. For this reason, we proposed that we may have isolated a cost of dominance; for example, although dominants may have some net benefit from their social status when interacting with subdominants, when housed alone dominants may continue to pay the cost of their status (see Johnstone & Norris 1993) without reaping the benefits. In this paper, we test this hypothesis by examining the relation between the development of fluctuating asymmetries in primary feathers and social dominance, in birds housed in social groups under different degrees of competition for food. We reason that, when moulting in social groups, dominants may obtain a net benefit of their status and thus exhibit lower levels of FA. The benefit of being dominant should also vary with the degree of competition for food. As the level of competition for food increases, dominants should experience increasing benefits from their status because their access to food will not be

influenced by the increased levels of competition to the same degree as subdominants (cf. Ekman & Lillendahl 1993). In the discussion, we also consider how factors other than, or in addition to, food availability may influence the development of plumage FA in the competition treatments.

2. METHODS

We performed the experiment on 48 wild-caught juvenile European starlings, *Sturnus vulgaris*, of undetermined sex. All individuals were randomly allocated to 12 groups of four birds, housed in cages measuring 0.5 m × 0.5 m × 0.3 m, which were maintained in visual isolation. At the start of the experiment, birds were under natural photoperiod (approximately, 17 h:7 h light:dark), and all birds had already shown signs of moulting. Photoperiod was then adjusted throughout moult, in 30 min blocks, to approximate natural daylength conditions. Alternate cages were allocated to two treatment groups, high competition and low competition, with degree of competition being manipulated by differential access to food. In both cases, food (turkey starter crumbs) and water were available ad libitum. However, the low-competition group could obtain food from two feeders, a single small feeder which could only be accessed by one bird at a time, and a long open feeder which all birds could access simultaneously. The high-competition group could obtain food only from a single small feeder. The long open feeding tray was present in the high-competition cages, but it did not contain food. Thus this manipulation alters degree of competition for food without simultaneously changing the amount of open or perching space available in each treatment, which may itself influence the number of dominance interactions. At weekly intervals, beginning the day before the competition treatments began, the following measures were taken on each bird: the length of each primary feather which had completed growth (to 0.01 cm, with vernier callipers) on both wings, a score of subcutaneous fat (0–5; cf. Helms & Drury 1960), and body mass (to 0.1 g, by using 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 (see Cuthill *et al.* 1993). We originally intended to continue taking measurements until the completion of moult. However, because of the large number of birds which suffered damaged or abraded outer primaries in the later stages of moult, we curtailed the experiment while birds were still growing primaries 8 and 9. All of the analyses presented here have been done on primaries 1 to 6, which did not suffer from such damage.

During the first week of the experiment, dominance scores were taken on all cages. All agonistic interactions, over food or otherwise, were recorded for a period of 15 min for each group. The identities of the birds involved in each interaction were noted, together with the outcome of the competition. These data were used to give each bird a dominance score (number of interactions won minus number of interactions lost) for each bird in each cage.

These data were then used to examine the effects of competition for food and social dominance on the development of plumage asymmetries and primary length. A detailed analysis of the effects of the manipulation on body mass and fat reserves will be reported separately (M. S. Witter & J. P. Swaddle, unpublished results). We examined whether the asymmetry data conformed to the properties of fluctuating asymmetries (i.e. a normal distribution with a mean of zero) by normal probability plots and one-sample *t*-

tests (see Swaddle *et al.* 1994). As the distribution of signed asymmetries closely approximated a normal distribution (correlation coefficients of normal plots, $r = 0.886\text{--}0.993$, $n = 48$, $p < 0.001$ in all cases), and did not differ significantly from a mean of zero ($t_{48} = 0.48\text{--}1.28$, $p < 0.20$ in all cases), the asymmetries measured were assumed to be fluctuating asymmetries. Previously, we have demonstrated that our measures of primary asymmetry are high repeatable (intra-class correlation coefficient, $r_1 = 0.91$, $F_{9,30} = 43.69$, $p < 0.0001$; see Swaddle & Witter 1994). Treatment effects on log-transformed median primary asymmetries have been analysed by analysis of variance or covariance, with the factors Treatment (high or low competition), Cage (each of the 12 cages) and, where appropriate, the covariates Dominance (dominance score), Fat (mean fat score during moult) and Mass (mean body mass during moult). Inspection of the normal probability plots of the residuals from these analyses showed that the assumptions of the parametric statistical tests were fulfilled in these cases. Results are shown as mean ± s.e., and two-tailed tests of significance have been used throughout.

3. RESULTS

The manipulations of competition for food successfully influenced the number of aggressive interactions in each treatment group (figure 1*a*); there were significantly more interactions in the high-competition group compared with the low-competition group ($F_{1,34} = 16.59$, $p < 0.001$). The manipulation of competition also influenced levels of plumage FA (figure 1*b*). Primary asymmetry was significantly higher in the high-competition treatment ($F_{1,34} = 8.23$, $p = 0.007$). The relation between dominance and FA also differed

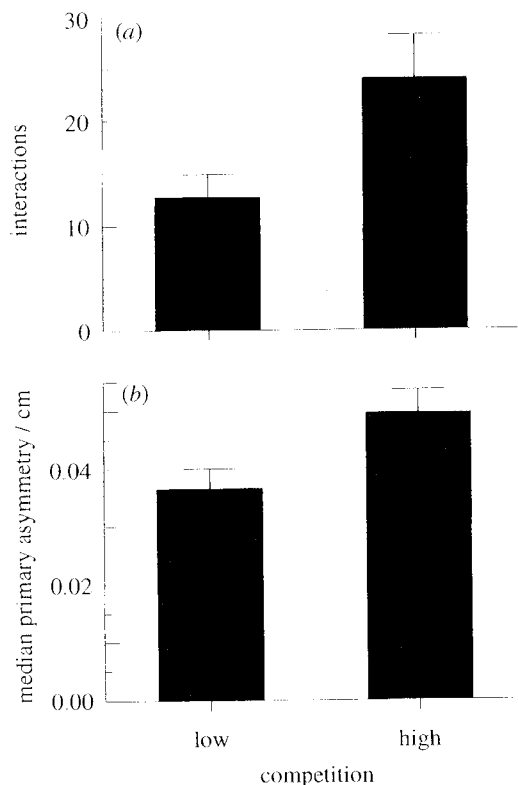


Figure 1. Mean ± s.e. (a) Number of competitive interactions, and (b) median primary asymmetry, across primaries, in the low and high competition groups.

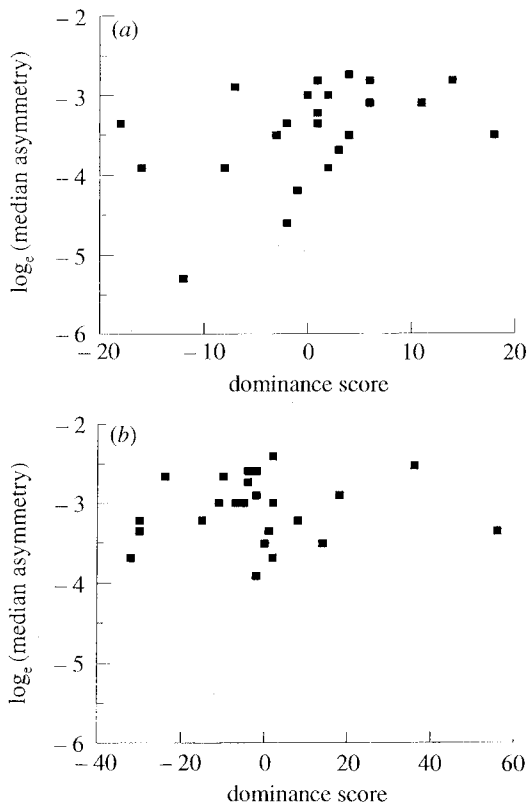


Figure 2. Median primary asymmetry against dominance score in (a) the low-competition group (\log_e (median asymmetry) = $-3.46 \pm 0.117 + 0.031 \pm 0.014$ (Dominance score); $F_{1,22} = 4.91$, $p = 0.037$), and (b) the high-competition group (\log_e (median asymmetry) = $-3.08 \pm 0.086 + 0.0017 \pm 0.0044$ (Dominance score), $F_{1,22} = 0.15$, $p = 0.700$). Higher dominance scores represent more dominant individuals (see text for details).

according to the degree of competition for food (Group by Dominance, $F_{1,34} = 6.63$, $p = 0.015$). In the low-competition treatment, dominants exhibited the highest levels of FA, as reported by Swaddle & Witter (1994), whereas, in the high-competition group, there was no relation between dominance and FA (figure 2). Swaddle & Witter (1994) also found that birds with the highest fat reserves during moult exhibited the lowest levels of FA. However, we could find no relation between fat and FA in this data set (\ln (median asymmetry) = $-0.008 \pm 0.271 + 0.005 \pm 0.161$ (Fat score), $F_{1,46} = 0.00$, $p = 0.977$), although there was a non-significant trend for the birds with higher body mass to exhibit higher levels of asymmetry (\ln (median asymmetry) = $-2.189 \pm 1.303 + 0.029 \pm 0.017$ (Body mass), $F_{1,46} = 2.83$, $p = 0.099$).

Although we found the above effects on primary asymmetry, we could find no evidence that degree of competition for food influenced mean primary length ($F_{1,34} = 0.39$, $p = 0.536$; figure 3a). Similarly, there was no relation between fat score and mean primary length ($F_{1,46} = 0.00$, $p = 0.972$). However, there was a significantly positive relation between body mass primary length (Primary length = $6.461 \pm 0.503 + 0.015 \pm 0.006$ (Body mass), $F_{1,46} = 5.32$, $p = 0.026$; figure 3b), probably due to the relation between body size and wing area. As predicted for morphological traits under stabilizing selection, there was no relation

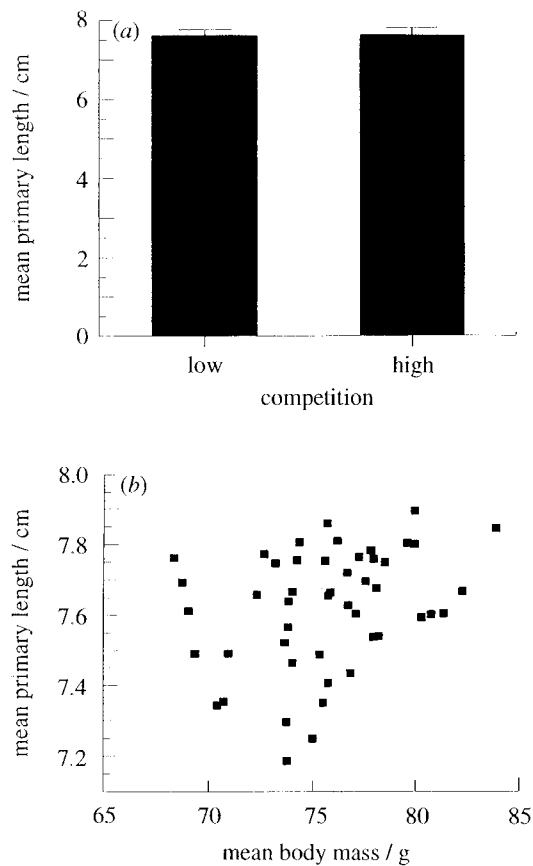


Figure 3. Mean (\pm s.e., where appropriate) primary length against (a) treatment group and (b) body mass.

between primary length and asymmetry (controlling for individual and feather differences, $F_{1,234} = 1.20$, $p = 0.275$) and the effects of treatment group and dominance on primary FA hold when primary length is included in the analysis as a covariate (Group, $F_{1,33} = 7.61$, $p = 0.009$; Dominance, $F_{1,33} = 6.31$, $p = 0.17$; Group by Dominance, $F_{1,33} = 6.77$, $p = 0.014$).

4. DISCUSSION

The manipulation of competition for food significantly influenced the degree of FA in the primary feathers of starlings. Birds which experienced increased levels of competition exhibited higher levels of plumage FAs, suggesting that increased competition can result in greater stress during moult. Importantly, however, this effect differed according to dominance status. In the low-competition treatment, there was a positive relation between FA and dominance score, i.e. the most dominant individuals exhibited the highest levels of FA. This result is consistent with our earlier findings (Swaddle & Witter 1994). However, in the high-competition treatment there was no significant relation between dominance score and asymmetry. We explained our previous findings by suggesting that dominants may have exhibited higher levels of asymmetry, when housed individually, because they continued to pay a cost of dominance (see Johnstone & Norris 1993) but did not reap the benefits of their social status (Swaddle & Witter 1994). We proposed that, when housed in groups, dominants may exhibit lower

levels of asymmetry. This specific prediction has not been borne out by the current experiment. However, our present results show that the relation between FA and social dominance varies according to the prevailing environment. Dominants appear to be affected less than subdominants by increased competition for food (cf. Ekman & Lillendahl 1993).

There are several possible mechanisms through which this increased competition for food may act. The most obvious is differential access to food. As competition for food increases, subdominants may be unable to obtain sufficient quantities of food, or experience a more unpredictable supply of food (Gosler 1987; Ekman & Lillendahl 1993; Witter & Cuthill 1993), which results in increased nutritional or energetic stress. Swaddle & Witter (1994) showed by experimental manipulation that both time available to feed and predictability of food supply influence degree of primary FA in starlings. However, altering competition for food may influence degree of FA through other aspects of the manipulation. For example, involvement in aggressive interactions *per se* (without differential access to food) may result in greater stress and increase levels of FA in the high-competition group. Between-group differences in number of aggressive interactions might also influence activity levels and energetic expenditure, which might affect degree of FA (see Mitton & Grant 1984). Although FA was not significantly related to the number of aggressive interactions (regression of asymmetry on interactions, controlling for effects of treatment and dominance on both variables by ANCOVA, $F_{1,33} = 1.91, p = 0.174$), this cannot be taken as strong evidence against an effect of interactions *per se* as it is only correlational. An important alternative explanation, rarely acknowledged in the literature, is that there may be a change in dominance between the two contexts of high and low competition. There is evidence to suggest that relations within a dyad or social group can be different in altered contexts (Hand 1986). Therefore dominance of an individual and the dominance structure of groups can change when the context of the interactions change (Lee 1983). The costs of losing an encounter over food may differ according to both degree of competition and dominance status. For example, dominants may only use their enhanced competitive ability when competition for food is very high. Subdominants may win more encounters under low competition (and thus have a higher 'dominance score') if the cost of losing is substantially higher than for a dominant. Therefore to decide on the mechanism through which increased competition affects FA it will be necessary to disentangle changes in aggressive interactions, dominance status and differential access to food experimentally.

Because females pay attention to FA information when making mate choice decisions (Møller 1992*a*, 1993*a*; Swaddle & Cuthill 1994*a, b*), it has been suggested that FA may play a signalling role in the development and maintenance of dominance hierarchies through intrasexual competition (Møller 1992*b*; Manning & Chamberlain 1993; but see Møller 1992*a*, 1993*a*). In our experiment, however, we did not directly manipulate either dominance or levels of

FA; therefore, it is not possible to draw conclusions concerning the presence or direction of any causal links between asymmetry and dominance. This is a problem that has not been addressed so far in the literature, and will be investigated in a separate manipulation experiment.

Morphological traits under stabilizing selection exhibit a particular U-shaped (or flat, if extreme phenotypes are rare) relation between FA and trait size (Møller & Pomiankowski 1993). Møller (1993*b*) has suggested that, within each trait size level, the 'higher quality' individuals exhibit lower levels of FA. So, at the extremes of the population where the variance in asymmetry is relatively large, it may be fairly straightforward to distinguish between 'high' and 'low' quality individuals. However, at average trait sizes (i.e. in the middle of the U-shaped curve) there is little variance in asymmetry, and so estimating the quality of individuals on the basis of FA information may be more difficult. It is conceivable, under this theoretical framework, that a 'low quality' individual with average trait size displays less FA than a 'higher quality' individual at the population trait-size boundary. Asymmetry alone will not be an accurate indicator of quality. Thus we propose that the use of relations between feather FAs and extent of plumage development (or size) in the field may provide a measure of quality that is reliable, simple to assess, and more straightforward than investigations of survivorship; such data may indicate whether dominants are at a net advantage from their status under natural conditions. FA may be a particularly useful indicator of quality because the ability of individuals to buffer themselves against different environmental stresses is often correlated. It is quite possible, however, that some of the benefits of dominance derived in natural circumstances, such as enhanced access to mates or lower predation risk, are not manifested in lower levels of FA. This would have to be examined empirically for the utility of this approach to be verified.

Our data show that degree of primary FA is influenced by manipulations of competition for food. Further, we have also shown that the relation between FA and dominance varies under different experimental conditions. Given the large literature suggesting that levels of FA are negatively related to aspects of individual quality (Jones 1987; Møller 1990, 1993*b*; Harvey & Walsh 1993), the relation between social dominance and FA is of particular interest. Our results demonstrate that the benefits or costs of dominance vary with experimental manipulations of degree of competition for food. However, in neither treatment group did the dominants exhibit lower levels of FA, even when feather length was controlled for, suggesting that more extreme manipulations of competition are required for dominants to obtain a net benefit from their social status. The results also demonstrate that a lack of a relation between dominance and FA (for example, as found in the high-competition group in this experiment) cannot be taken as evidence that dominance is unimportant in determining asymmetry; different dominance-mediated influences on FA may mask each other under certain circumstances.

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