

Chest plumage, dominance and fluctuating asymmetry in female starlings.

JOHN P. SWADDLE AND MARK S. WITTER

Behavioural Biology Group, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K.

SUMMARY

It has been proposed that levels of fluctuating asymmetry (FA) may be used in establishing and maintaining dominance hierarchies, as asymmetry reflects aspects of individual quality. However, previous manipulations of FA have failed to reveal that the level or outcome of agonistic intra-sexual interactions are affected by levels of FA. In female European starlings (*Sturnus vulgaris*), correlational data suggest that FA of the speckled chest plumage may be related to dominance status. These data are confounded, however, by total number of spots on the chest and the proportion of the chest that is white, both of which positively covary with chest asymmetry. Thus, we deconfounded the effects of these plumage traits on dominance by experimentally manipulating the number of spots and spot number asymmetry in a factorial design. The results indicated that dominance is influenced by the number of spots on the chest, but not by spot asymmetry. Birds with spottier chests were dominant over birds with experimentally decreased spot number. We suggest that female starlings' chests are exposed to extensive abrasion throughout the breeding season and so are susceptible to damage asymmetries that may mask the 'true' fluctuating asymmetry of the trait. This may devalue the use of chest asymmetry as a quality indicator. Spottier chests may be costly to maintain, in part because of increased susceptibility to abrasion, and so may be a better indicator of quality than asymmetry.

1. INTRODUCTION

Fluctuating asymmetries (FAs) are randomly produced deviations from perfect symmetrical development in bilateral traits (Ludwig 1932). Many studies have linked absolute FA with indicators of individual quality (see, for example, Beardmore 1960; Downhower *et al.* 1990; Harvey & Walsh 1993). Low levels of FA may reveal individuals capable of maintaining developmental homeostasis in the face of stresses during growth. For these reasons, females have been shown to pay attention to symmetry information, particularly in secondary sexual ornamentation, when making mate choice decisions (Møller 1992, 1993; Swaddle & Cuthill 1994*a, b*; but see Enquist & Arak 1994; Johnstone 1994).

The results of investigations of the role of FA in intra-sexual encounters are less consistent. Correlational studies indicate that individuals with low levels of FA are dominant over asymmetric individuals (Thornhill & Sauer 1992; Liggett *et al.* 1993; Manning & Chamberlain 1993; Radesäter & Halldórsdóttir 1993). In contrast, Swaddle & Witter (1994) found that female starlings (*Sturnus vulgaris*) with asymmetric primary feathers were dominant to those with more symmetrical primaries. However, Møller (1992, 1993) found that manipulating levels of asymmetry in male swallows' (*Hirundo rustica*) tails had no effect on level or outcome of aggressive encounters between rival males. In contrast to our previous work on the starling, which

has predominantly examined relations between FA in primary feathers and social dominance (Swaddle & Witter 1994; Witter & Swaddle 1994), here we examine relations between the chest plumage and dominance status.

The European starling has sexually dimorphic chest plumage at the time of mate acquisition. Male starlings have glossy iridescent chest plumage, whereas the female has a dark brown or black chest that is speckled with white spots (Feare 1984). Each individual feather on the females' chest is dark with a white tip, which is slowly abraded during the breeding season. It is these white feather tips that give the breast a spotty appearance. Investigations of between-individual variation in female chest plumage have revealed that chest 'spottiness' (number of spots per unit area) is related to follicular development in captive birds (A. R. Goldsmith & I. C. Cuthill, unpublished results). Females with spottier chests (at the beginning of the breeding season) start their ovarian development, and lay their first clutch, before those with less spotty chests (A. R. Goldsmith & I. C. Cuthill, unpublished results). This may give them fitness advantages, for example, the opportunity to lay a second clutch (Price *et al.* 1988; Perrins 1991). Hence, female chest plumage may reveal aspects of individual quality; higher quality individuals have spottier chests. This type of quality-related trait may act as a signal to settle intra-sexual conflicts without escalation to costly fights (e.g. Järvi & Bakken 1984; Eckert & Weatherhead 1987; Røskaft &

Rohwer 1987; Evans & Hatchwell 1991). Here, we report two experiments that have investigated the role of chest plumage asymmetry in agonistic interactions between female starlings. The first experiment investigated the relation between chest spottiness, chest asymmetry and social dominance in birds with unmanipulated plumage. The second experiment examined these relations further through direct manipulations of the female plumage.

2. METHODS

(a) *Natural chest plumage variation*

In the first experiment, we used thirty five wild-caught adult female starlings, which were housed individually and taken through moult under food manipulation treatments (the same experiment reported in Swaddle & Witter 1994). At the end of moult, birds were randomly assigned to five groups of seven individuals to obtain dominance scores. Each social group was housed in a cage measuring $0.5 \times 0.5 \times 0.3$ m, 4 h before the dominance observations began. Birds were supplied with *ad libitum* food for 2 h. After this period, the food was removed for 2 h. Food was then returned and all agonistic interactions, over food or otherwise, were recorded for a period of 30 min for each group. The majority of the agonistic interactions observed resulted from competition for perch sites. These types of interactions are common amongst groups of female starlings in natural (field and large outdoor aviary) conditions (Feare 1984). After observation, all birds were returned to their individual cages. This procedure was repeated five times, once a day, over an eight day period. On each occasion, new groups of seven birds were created by random allocations. All birds were assigned a novel coloured leg-band combination, to facilitate individual recognition. A single dominance score was calculated for each bird by subtracting the number of interactions lost from the number of interactions won. Over the five observation periods, dominance was recorded for each bird from interactions with most other birds, allowing meaningful comparisons of dominance across all birds.

Chest spottiness, absolute spottiness asymmetry ($|L-R|$), whiteness and absolute whiteness asymmetry measures were obtained for each bird by analysis of video images taken of the starlings' chest plumage on the day of the first observations. All chest plumages were filmed in identical lighting conditions with specified camera settings and all birds were held vertically at the same distance from the lens. The video images were digitized using the Optimas software package (BioScan Incorporated 1992) to calculate the number of spots per unit area and proportion of white area to black on both sides of the chest. The midline of the chest was determined from a vertical line drawn from the midpoint of the bill, when the bird was held vertically. These spottiness and whiteness measurements were subsequently shown to be highly repeatable (spottiness, $F_{4,32} = 21.48$, $p < 0.0001$; whiteness, $F_{4,32} = 24.786$, $p < 0.0001$; see Swaddle *et al.* 1994) and exhibit the properties of FA, i.e. a normal distribution (Filliben Correlation coefficients, i.e. correlations of raw data with predicted normal probability scores (Aitken *et al.* 1989), spottiness, $r = 0.959$, $n = 33$, $p < 0.0001$; whiteness, $r = 0.955$, $n = 33$, $p < 0.0001$) around a mean of zero (one sample *t*-tests, spottiness, $t_{32} = 0.93$, $p = 0.180$; whiteness, $t_{32} = 0.62$, $p = 0.270$).

(b) *Manipulated chest plumage*

The second experiment was performed on thirty two wild-caught adult female starlings, housed in large outdoor

aviaries with approximately 50 non-experimental individuals. Aviaries were exposed to natural photoperiod; the experiment was performed in June 1994. At this time, birds were in full breeding plumage (i.e. immediately pre-moult). Birds were randomly assigned to four treatment groups. The manipulations altered the chest plumage by partially or wholly removing white feather tips, with fine scissors, from corresponding positions on the left and right sides of the chest. The groups were as follows: (i) spotty symmetric, ss, where four complete and twelve partial feather tips were removed from both sides of the chest; (ii) spotty asymmetric, sa, eight whole and eight partial tips were snipped off on one side, and sixteen tips were partially removed on the other (manipulations randomly assigned to left and right sides); (iii) less-spotty symmetric, ls, eight whole and eight partial tips were removed from both sides; (iv) less-spotty asymmetric, la, twelve whole tips and four partial tips were removed from one side of the chest whilst four whole and twelve partial tips were removed from the other (manipulations randomly assigned to left and right sides). This experimental design was balanced so that the same numbers of feathers were manipulated between all treatment groups and this allowed us to investigate the effects of spottiness and spottiness asymmetry on social dominance. In the first experiment, number of spots on the females' chests ranged from 39–92 (mean = 68.1, s.e. = 2.45), and the mean absolute spottiness asymmetry ranged from 0–18 (mean = 6.20, s.e. = 0.80). The manipulations in the second experiment increased asymmetry by eight spots between symmetric and asymmetric treatments. Similarly, the number of spots on the chest was reduced by eight in the spotty treatment and by 16 in the less spotty treatment. Thus, these manipulations represent values that are within the natural range observed in female starlings.

One bird was randomly chosen from each of the four groups, and placed in a metal cage, measuring $0.5 \times 0.5 \times 0.3$ m, so that eight groups of four birds were formed, and all treatment groups were represented by one individual in each cage. Within each group, birds were randomly assigned two novel coloured leg-bands, allowing individual recognition. The group cages were placed within a larger outdoor aviary. The birds were supplied with *ad libitum* food and water for 2 h. Food was removed for 1.5 h, and then returned when the dominance observations began. Dominance scores, during 30 min observation periods, were then determined as described for experiment 1. Dominance scores were ranked to obtain a dominance hierarchy of one to four for each group of four birds. Four was the most dominant bird, and one was the least dominant.

(c) *Statistical analyses*

Analyses for the first experiment were performed on residual data, partitioning out the effects of the food deprivation groups (see Swaddle & Witter 1994). The spottiness and whiteness data were analysed on MINITAB (Ryan *et al.* 1985) by linear regression. As a result of the particular half-normal distribution of unsigned absolute asymmetry data (see Swaddle *et al.* 1994), the relations between dominance and spottiness asymmetry and whiteness asymmetry were investigated by non-parametric Rank Spearman Correlations (Siegel & Castellan 1988). Two individuals were excluded from these analyses due to extensive feather damage. The data from the second experiment were analysed by Friedman non-parametric two-way analysis of variance (Siegel & Castellan 1988), investigating the effects of the manipulations on dominance rank, blocked by cage. This analysis treated each group as an independent statistical unit, not each individual, to avoid

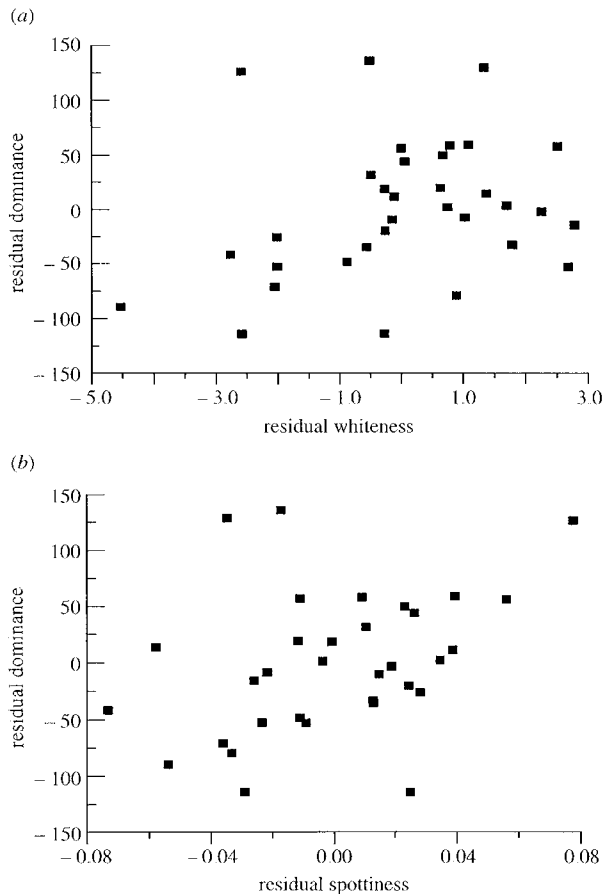


Figure 1. Social dominance versus (a) proportion of white area to black on the chest plumage ('whiteness') and (b) number of spots per unit area ('spottiness'), from experiment 1. Values control for effects of treatment group. Each data point represents one individual.

pseudoreplication (Hurlbert 1984). Two-tailed tests of probability have been used throughout.

3. RESULTS

Analysis of the data from the first experiment indicated that chest whiteness is positively related to social dominance (residual dominance = $0.0 + 674$ residual whiteness, $r^2 = 9.9\%$, $F_{1,31} = 4.53$, $p = 0.041$; see figure 1a). There was a similar, but non-significant, trend between spottiness and dominance (residual dominance = $0.0 + 9.99$ residual spottiness, $r^2 = 4.5\%$, $F_{1,31} = 2.49$, $p = 0.124$; see figure 1b). That is, individuals with whiter or spottier chest plumage tended to be dominant. There was also an indication of a positive relationship between chest plumage asymmetry and social dominance (whiteness asymmetry, $r_s = 0.357$, $n = 33$, $p = 0.035$; spottiness asymmetry, $r_s = 0.273$, $n = 33$, $p = 0.113$). However, chest spottiness/whiteness and chest asymmetry were almost positively related (whiteness, residual whiteness asymmetry = $0.0 + 0.184$ residual whiteness, $r^2 = 8.6\%$, $F_{3,31} = 4.02$, $p = 0.054$; spottiness, residual spottiness asymmetry = $0.0 + 0.165$ residual spottiness, $r^2 = 8.5\%$, $F_{1,31} = 3.99$, $p = 0.055$), so it is not possible to disentangle the relative importance of spottiness from spottiness asymmetry and whiteness from whiteness

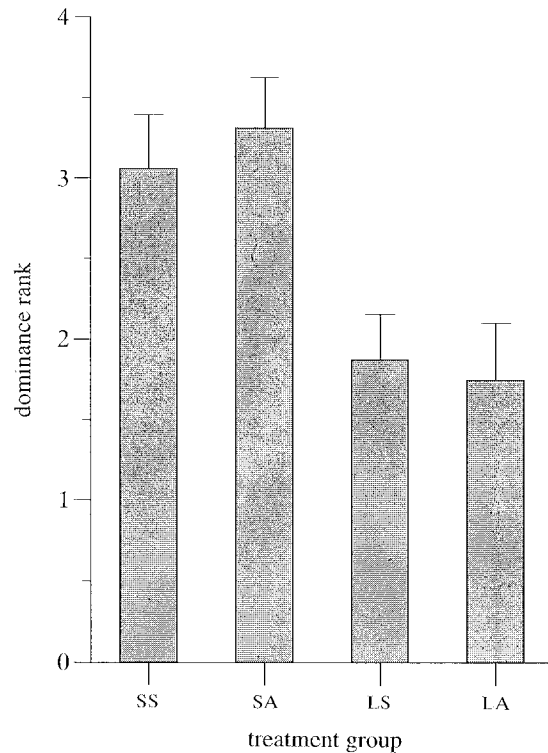


Figure 2. Mean (and s.e.) dominance rank of female starlings from the different treatment groups in experiment 2: ss, spotty symmetric; sa, spotty asymmetric; ls, less-spotty symmetric; la, less-spotty asymmetric.

asymmetry. In an attempt to tease apart these effects statistically, we performed further regression analyses on residual data controlling for chest spottiness/whiteness and chest asymmetry in turn. There was no effect of asymmetry once chest spottiness/whiteness were controlled for (whiteness asymmetry, residual dominance = $0.004 + 1.62$ residual whiteness asymmetry, $r^2 = 0.1\%$, $F_{1,31} = 0.03$, $p = 0.872$; spottiness asymmetry, residual dominance = $-0.005 - 0.205$ residual spottiness asymmetry, $r^2 = 2.9\%$, $F_{1,31} = 0.93$, $p = 0.343$). However, there were indications of a relationship between spottiness/whiteness and dominance when asymmetry was controlled for (whiteness, residual dominance = $0.1 + 20.5$ residual whiteness, $r^2 = 10.7\%$, $F_{1,31} = 3.72$, $p = 0.063$; spottiness, residual dominance = $0.0 + 19.6$ residual spottiness, $r^2 = 9.8\%$, $F_{1,31} = 3.36$, $p = 0.077$). This provides weak evidence that overall spottiness and whiteness may play a more important role in establishing and maintaining dominance hierarchies than asymmetry. However, it does not rule out the possibility that dominance is influenced by other (unmeasured) variables that may covary with these aspects of plumage. In experiment two, we have removed these possible confounding influences by experimentally manipulating the chest plumage directly.

In experiment two, there was a significant effect of the chest manipulations on dominance rank ($S = 9.62$; d.f. = 3; $p = 0.022$; see figure 2). There was no difference in dominance between the symmetric and asymmetric treatments (sa and la versus ss and ls, $S = 0.00$; d.f. = 1; $p = 1.00$). However, there was an effect of spottiness (ss and sa versus ls and la, $S =$

4.50; $d.f. = 1$; $p = 0.034$); spottier birds were dominant over less-spotty birds. There was no evidence of an interaction between spottiness and spottiness asymmetry (difference between ss and sa versus difference between ls and la, $S = 1.00$, $d.f. = 1$, $p = 0.318$).

4. DISCUSSION

It has been suggested that FAs reveal aspects of individual quality, and that this information is used when making mate choice decisions (Møller 1992, 1993; Swaddle & Cuthill 1994*a, b*). Furthermore, correlational studies have indicated that individuals with lower levels of FA are more likely to win intra-sexual encounters (Thornhill 1992; Liggett *et al.* 1993; Radesäter & Halldórsdóttir 1993; but see Swaddle & Witter 1994; Witter & Swaddle 1994). Experimental manipulations of plumage FA, however, have failed to find evidence that level of asymmetry influences intra-sexual encounters (Møller 1992, 1993). Our data support the latter findings. In the first experiment, there was a weak indication of a relation between asymmetry and dominance, but this was confounded by chest spottiness/whiteness. In the second experiment, where overall spottiness and spottiness asymmetry were deconfounded experimentally, we found that spottiness *per se* influenced dominance, whereas spottiness asymmetry did not. These results indicate that overall chest spottiness may be more important as a signal in intra-sexual interactions than spottiness asymmetry. We expect selection pressures to favour the evolution of preferences for the most reliable indicators of individual quality. In this case, spottiness may be a more reliable indicator of condition than spottiness asymmetry, because female starlings appear to make use of chest spottiness in establishing and maintaining dominance hierarchies. This naturally raises two related points.

1. Does chest asymmetry reflect some aspect of individual quality and if so why is it not used as a cue in agonistic intra-sexual encounters?

2. Why might chest spottiness convey useful information about quality or dominance if spottiness asymmetry does not? We address each of these points below.

Chest asymmetry may not be used during intra-sexual encounters either because starlings are unable to perceive chest plumage asymmetries or because chest asymmetry does not convey reliable quality-related information. There are reasons for believing that both effects may be important. Firstly, symmetry in dot texture patterns may be relatively difficult to perceive and assess in comparison with spottiness *per se*. It has been shown that humans find these symmetries difficult to detect (see, for examples, Wagemans *et al.* 1992). Also, the symmetry information used by the visual system in this kind of symmetry detection falls in a very narrow central strip, approximately 1° wide (Jenkins 1982), and the manipulations may have fallen outside this focal area. Thus, birds may not pay attention to the symmetry information because it is difficult to detect, whereas spottiness *per se* is more easily assessed and may reliably indicate condition.

There appear two broad reasons why chest asymmetry may not relay reliable information about quality. Firstly, it is possible that the chest plumage of the female starling, as a whole trait, does not exhibit 'true' FA as it is made up of a large number of individual feathers. This sort of composite trait may show the statistical properties of FA (a normal distribution around a mean of zero) but may not be under the same developmental processes as a single bilateral trait (cf. Evans & Hatchwell 1993). Thus, it may be more relevant to consider single chest-feather whiteness and lengths. However, starlings do moult their chest plumage in bilateral feather tracts, so there is some justification in viewing the chest as a bilateral composite trait that exhibits FA. Furthermore, asymmetries in composite plumage traits, such as the ocellus number of peacocks, have previously been shown to be negatively related to degree of ornamentation, which may influence mate choice decisions (e.g. Manning & Hartley 1991). Secondly, and perhaps more importantly, the female chest plumage suffers continual abrasion, particularly during the breeding season when the bird is entering and leaving nesting sites. Females start the breeding season with extremely spotty chests. These spots are formed by white feather tips that are slowly abraded, decreasing overall chest spottiness. This form of damage asymmetry may mask the 'true' FA of the females' chests (cf. Cuthill *et al.* 1993) throughout most of the year.

Importantly, the ability to resist damage and abrasion may be related to individual quality. Feathers, or areas of feathers, without melanin abrade more rapidly than darker feathers with a high melanin content (Averill 1923; Bergman 1982; Burt 1986). Therefore, white feather tips may be difficult to maintain as they are susceptible to damage and wear (cf. Bonser & Witter 1993). This damaged plumage may incur energetic thermoregulatory costs (see, for example, Brush 1965). Thus, while the speckled chest of the starling may be beneficial in terms of reduced conspicuousness for predation (see, for example, Baker & Parker 1979), costs of increased abrasion may act against extensive development of non-melanic plumage areas. Such costs may enforce the honesty of a plumage signal based on chest spottiness (cf. Johnstone & Norris 1993). Thus, degree of spottiness in the chest plumage may represent a measure of an individual's ability to resist damage and abrasion. This may occur because only those individuals that are best able to resist abrasion can afford to pay the cost of developing highly speckled plumage, or degree of spottiness directly reveals the amount of abrasion that has occurred. Because asymmetry in spot patterns may be difficult to detect, assessment of overall chest spottiness may represent a more straight-forward method of assessing damage and abrasion avoidance than, say, examining the extent of damage asymmetries.

In summary, we have found that the chest plumage of female starlings influences the outcome of agonistic interactions. Chest spottiness is known to be related to one aspect of individual quality (timing and rate of follicular development) and may also reliably reveal an individual's ability to resist plumage damage and

abrasion. The present data further indicate that the number of spots on the chest is positively related to dominance status; spot asymmetry was not related to dominance. Spot asymmetry may not influence dominance measures because it is difficult to perceive or because levels of chest FA are masked by damage asymmetries. Thus, spottiness *per se* may represent a more reliable indicator of individual quality. This increased dominance status may convey fitness advantages to the individuals with better chest plumage.

We are grateful to Innes Cuthill, Andy Bennett, Tim Guilford, Henrik Smith and an anonymous referee for helpful comments and discussions, and to Julian Partridge for assistance with video image analysis. We would also like to thank Rob Massie and Sadie Iles for all the routine maintenance of our birds. J.P.S. was funded by a SERC research studentship and a NERC research fellowship, M.S.W. was supported by a NERC research fellowship and a NERC grant GR3/8924 awarded to Innes Cuthill.

REFERENCES

- Aitken, M., Anderson, D., Francis, B. & Hinde, J. 1989 *Statistical modelling in GLIM*. Oxford University Press.
- Averill, C. K. 1923 Black wing tips. *Condor* **25**, 57–59.
- Baker, R. R. & Parker, G. A. 1979 The evolution of bird coloration. *Phil. Trans. R. Soc. Lond. B* **287**, 63–130.
- Beardmore, J. A. 1960 Developmental stability in constant and fluctuating temperatures. *Heredity* **14**, 411–422.
- Bergman, G. 1982 Why are the wings of *Larus fuscus fuscus* so dark? *Ornis. Fenn.* **59**, 77–83.
- BioScan Incorporated. 1992 *Optimas 4.02*. Edmonds, Washington: BioScan Incorporated.
- Bonsler, R. C. H. & Witter, M. S. 1993 Indentation hardness of the bill keratin of the European starling. *Condor* **95**, 736–738.
- Brush, A. 1965 Energetics, temperature regulation and circulation in resting, active and defeathered California quail, *Lophortyx californicus*. *Comp. Biochem. Physiol.* **15**, 399–421.
- Burt, E. H. 1986 An analysis of physical, physiological, and optical aspects of avian colouration with emphasis on wood-warblers. *Ornithol. Monogr.* **38**, x+126.
- Cuthill, I. C., Swaddle, J. P. & Witter, M. S. 1993 Fluctuating asymmetry. *Nature, Lond.* **363**, 217–218.
- Downhower, J. F., Blumer, L. S., Lejeune, P., Gaudin, P., Marconato, A. & Bisazza, A. 1990 Otolith asymmetry in *Cottus bairdi* and *C. gobio*. *Polskie Archiw. Hydrobiol.* **37**, 209–220.
- Eckert, C. G. & Weatherhead, P. J. 1987 Ideal dominance distributions: a test using red-winged blackbirds (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.* **20**, 143–152.
- Enquist, M. & Arak, A. 1994 Symmetry, beauty and evolution. *Nature, Lond.* **372**, 169–172.
- Evans, M. R. & Hatchwell, B. J. 1991 An experimental study of male adornment in the scarlet-tufted malachite sunbird: I. the role of pectoral tufts in territory defence. *Behav. Ecol. Sociobiol.* **29**, 413–420.
- Evans, M. R. & Hatchwell, B. J. 1993 New slants on ornament asymmetry. *Proc. R. Soc. Lond. B* **251**, 171–177.
- Feare, C. 1984 *The starling*. Oxford University Press.
- Harvey, I. F. & Walsh, K. J. 1993 Fluctuating asymmetry and lifetime reproductive success are correlated in males of the damselfly *Coenagrion puella* (Odonata: Coenagrionidae). *Ecol. Entomol.* **18**, 198–202.
- Hurlbert, S. H. 1984 Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**, 187–211.
- Jarvi, T. & Bakken, M. 1984 The function of variation of the breast stripe of the great tit (*Parus major*). *Anim. Behav.* **39**, 967–975.
- Jenkins, W. 1982 Redundancy in the perception of bilateral symmetry in dot textures. *Percept. & Psychophys.* **32**, 171–177.
- Johnstone, R. A. 1994 Female preference for symmetrical males as a by-product of selection for mate recognition. *Nature, Lond.* **372**, 172–175.
- Johnstone, R. A. & Norris, K. 1993 Badges of status and the cost of aggression. *Behav. Ecol. Sociobiol.* **32**, 127–134.
- Liggett, A. C., Harvey, I. F. & Manning, J. T. 1993 Fluctuating asymmetry in *Scatophaga stercoraria* L.: successful males are more symmetrical. *Anim. Behav.* **45**, 1041–1043.
- Ludwig, W. 1932 *Das rechts-links Problem in Tierreich und beim Menschen*. Berlin: Springer.
- Manning, J. T. & Chamberlain, A. T. 1993 Fluctuating asymmetry, sexual selection and canine teeth in primates. *Proc. R. Soc. Lond. B* **251**, 83–87.
- Manning, J. T. & Hartley, M. A. 1991 Symmetry and ornamentation are correlated in peacock's trains. *Anim. Behav.* **42**, 1020–1021.
- Møller, A. P. 1992 Female swallow preference for symmetrical male sexual ornaments. *Nature, Lond.* **357**, 238–240.
- Møller, A. P. 1993 Female preference for apparently symmetrical male sexual ornaments in the barn swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.* **32**, 371–376.
- Perrins, C. M. 1991 Tits and their caterpillar food supply. *Ibis* **133**, 49–54 (Suppl. 1).
- Price, T. D., Kirkpatrick, M. & Arnold, S. J. 1988 Directional selection and the evolution of breeding status in birds. *Science, Wash.* **240**, 798–799.
- Radesäter, T. & Halldórsdóttir, H. 1993 Fluctuating asymmetry and forceps size in carwigs, *Forficula auricularia*. *Anim. Behav.* **45**, 626–628.
- Roskoff, E. & Rohwer, S. 1987 An experimental study of the function of the epaulets and the black body colour of male red-winged blackbirds. *Anim. Behav.* **35**, 1070–1077.
- Ryan, B. F., Joiner, B. I. & Ryan, T. A. 1985 *MINITAB handbook*, edn 2. Boston: PWS-Kent.
- Siegel, S. & Castellan, N. J. 1988 *Nonparametric statistics for the behavioural sciences*, edn 2. Singapore: McGraw-Hill.
- Swaddle, J. P. & Cuthill, I. C. 1994a Preference for symmetric males by female zebra finches. *Nature, Lond.* **367**, 165–166.
- Swaddle, J. P. & Cuthill, I. C. 1994b Female zebra finches prefer males with symmetric chest plumage. *Proc. R. Soc. Lond. B* **258**, 267–271.
- Swaddle, J. P. & Witter, M. S. 1994 Food, feathers and fluctuating asymmetry. *Proc. R. Soc. Lond. B* **255**, 147–152.
- Swaddle, J. P., Witter, M. S. & Cuthill, I. C. 1994 The analysis of fluctuating asymmetry. *Anim. Behav.* **48**, 986–989.
- Thornhill, R. 1992 Fluctuating asymmetry, interspecific aggression and male mating tactics in two species of Japanese scorpionflies. *Behav. Ecol. Sociobiol.* **30**, 357–363.
- Thornhill, R. & Sauer, P. 1992 Genetic sire effects on the fighting ability of sons and daughters and mating success of sons in a scorpionfly. *Anim. Behav.* **43**, 255–264.
- Wagemans, J., Van Gool, L., Swinnen, V. & Van Horebeek, J. 1992 Higher-order structure in regularity detection. *Vision Res.* **33**, 1067–1088.
- Witter, M. S. & Swaddle, J. P. 1994 Fluctuating asymmetry, competition and dominance. *Proc. R. Soc. Lond. B* **256**, 299–303.

Received 24 February 1995; accepted 14 March 1995