Female zebra finches prefer males with symmetric chest plumage

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SUMMARY

The level of fluctuating asymmetry in a secondary sexual character is believed to reveal aspects of male quality. Previous investigations have demonstrated that females may pay attention to this information when making mate choice decisions; females prefer symmetric over asymmetric males. However, these studies have involved either manipulation of functionally important flight feathers, or of artificial ornaments. Here, we manipulate an existing secondary sexual plumage trait, one that does not influence flight performance, within the boundaries of natural asymmetry. Through manipulations of chest plumage, we demonstrate that female zebra finches choose to display more and for longer in front of males with symmetric, as opposed to asymmetric, chest plumage.

1. INTRODUCTION

Fluctuating asymmetries (FAS) are the small, randomly produced deviations from perfect symmetry which arise in the development of traits that would otherwise be described as bilaterally symmetrical (Ludwig 1932). These asymmetries arise from the inability of individuals to buffer themselves against environmental and genetic stresses during development (Van Valen 1962; Møller & Pomiankowski 1993; Swaddle & Witter 1994). There are intraspecific differences in the extent to which individuals can resist these developmental accidents, which appear to be heritable (Van Valen 1962; Thornhill & Sauer 1992). It is believed that the level of asymmetry expressed in such traits is a reflection of some component of individual quality (Beardmore 1960; Jones 1987; Møller 1990; Harvey & Walsh 1993). High-quality individuals are more capable of resisting developmental stresses and hence develop more symmetric characters than lower quality individuals (Møller & Pomiankowski 1993).

Models of sexual selection that rely on 'good genes' predict that mate choice should be based on characters that honestly reflect heritable fitness gains (Bradbury & Anderson 1987). It is proposed that the level of FA in bilateral traits provides this information (Møller 1990; Møller & Pomiankowski 1993). It is therefore significant that bilaterally symmetrical secondary sexual ornaments show far greater degrees of asymmetry than ordinary morphological characters and are sufficiently large to be detectable to the eye (Møller & Höglund 1991; Møller & Pomiankowski 1993). It has also been found that levels of FA are negatively correlated with size of these sexual characters (Manning & Chamberlain 1993; Møller & Höglund 1991), indicating that high quality individuals not only invest in ornament growth but also resist the developmental stresses that cause asymmetry.

There is growing evidence to suggest that females do pay attention to symmetry information when making mate choice decisions; they preferentially mate with the most symmetrically ornamented males (Møller 1992, 1993; Swaddle & Cuthill 1994). However, these results can be interpreted in terms of preference for symmetric arbitrary traits (i.e. traits that do not occur naturally on the individual) as manipulations have resulted in extremely abnormal plumage patterns; so far there has been no convincing manipulation of asymmetry levels in an existing secondary sexual character. In this experiment we measure female choice for a symmetry-manipulated secondary sexual trait in male zebra finches (*Taeniopygia guttata*) where the manipulation lies within the natural limits of plumage variation.

Previously, it has been demonstrated that female zebra finches show preferences for males with different coloured leg-bands (Burley *et al.* 1982; J. P. Swaddle, unpublished data) and symmetrically arranged leg-bands (Swaddle & Cuthill 1994). Feil & Curio (1993) have shown that when rate of courtship-song output is equal between competing males, females may rely on the appearance of male plumage and morphological traits to ascertain mate quality. In their observational study, they indicated that males with more chest bars may be preferred over males with less developed chest plumage. In this study we manipulate the asymmetry of male zebra finch chest bars and measure subsequent female sexual preferences for these individuals, in a choice chamber.

2. METHODS

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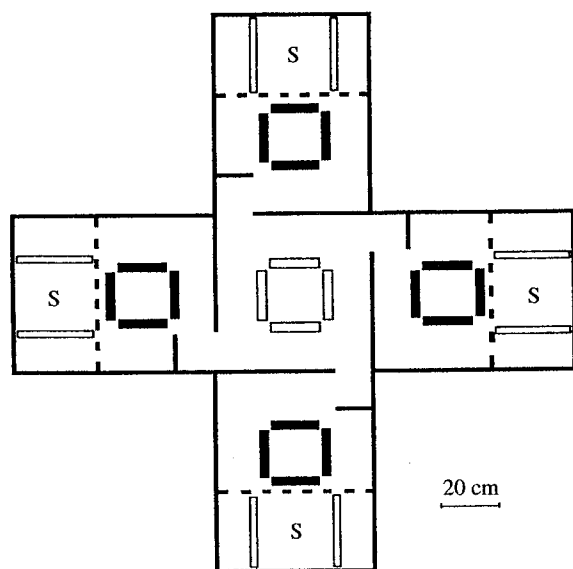*Printed in Great Britain*

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Figure 1. The choice chamber, plan view. Hollow bars represent fixed perches, filled bars represent microswitch perches, dashed lines represent one-way glass, S indicates stimulus cage. Background room illumination was provided by two 80 W fluorescent tubes 1.5 m above the apparatus. In addition, an 8 W fluorescent tube was placed at the back of each stimulus cage to provide an increasing illumination gradient from test to stimulus cages and to ensure correct functioning of the one-way glass.
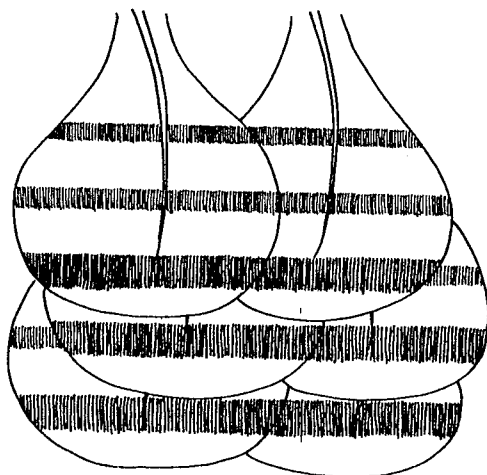

Figure 2. A diagrammatic representation of the typical arrangement of male chest feathers. Each feather has horizontal dark stripes across it that are broader at the feather tip. As the feathers overlap each other, removal of the distal stripe of one feather exposes the slightly thinner stripe of the underlying feather. This results in a disruption of the chest stripe.

divided into two single-sex groups. The cages were maintained in visual, but not acoustic, isolation on a 18:6 L:D photoperiod with food and water *ad libitum* at a constant temperature of 18 °C.

The test apparatus was identical to that used by Swaddle and Cuthill (1994), (see figure 1). The chamber consisted of a central area, where food and water were available *ad libitum*, and four stimulus arms. When in the central area, the test bird was not able to see any of the stimulus com-
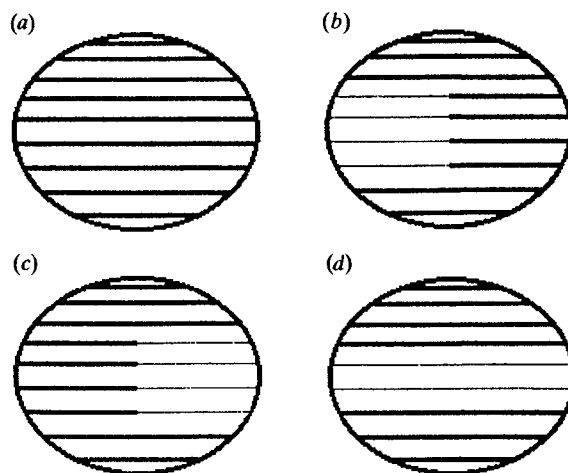

Figure 3. Stylized head-on view of the effect of the treatments on the chest bar plumage of the male zebra finches: (*a*) Symmetry I; (*b*) Asymmetry I; (*c*) Asymmetry II; and (*d*) Symmetry II.

partments. The stimulus arms were constructed so that the female was only in visual contact with one male in each of the four stimulus compartments. One-way glass was placed at the end of the stimulus arms, so that the female (test) bird could see the male (stimulus) bird, but not vice versa. Thus negating any effect that female display characteristics may have on male behaviour. All female birds were pre-exposed to the choice chamber apparatus for a total of 6 h so that they became acclimatized to their novel surroundings. From this initial pool of nine females, the six individuals that moved most actively between stimulus compartments were chosen for the experimental trials. All of these six individuals visited every stimulus compartment during their pre-exposure trials. For the purpose of these pre-exposures, non-experimental males were placed in the stimulus compartments.

The chest feathers of male zebra finches have a distinctive black and white striped pattern (see figure 2). Each feather is predominately white/pale with three or four thin black stripes, with the feather tip always white. We manipulated chest-stripe asymmetry by snipping off, with fine scissors, white feather-tips on one side of the chest, and the feather-tip plus the most distal black stripe of the corresponding feather on the other side. This manipulation resulted in approximately the same mass of feather being removed from both sides of the chest, as the black stripes are very narrow (less than 0.2 mm).

Stimulus males were randomly allocated to four treatment groups (see figure 3): (i) *Symmetry I*, eight white feather-tips were removed from both left and right sides of the chest ($n = 6$); (ii) *Asymmetry I*, eight white feather-tips were removed from the left side of the chest, and eight black-and-white tips from the right ($n = 6$); (iii) *Asymmetry II*, eight white tips were snipped-off the right, and eight black-and-white tips from the left ($n = 6$); and (iv) *Symmetry II*, four white and four black-and-white tips were removed from both sides of the chest ($n = 6$). This experimental design was balanced for the number of feathers snipped-off both sides of the males' chests and allowed us to investigate the effects of both number of black chest bars, as well as chest plumage asymmetry, on female preference. There were six experimental trials, within which all four of the treatment groups were represented equally, so that all treatment groups appeared in every trial. Each male appeared in one trial only. Treatment groups were randomly allocated to stimulus-cage position within the apparatus.

Each experimental trial began by placing four (stimulus) males in the peripheral stimulus cages, one from each of the manipulation groups. A (test) female was released in the central section of the apparatus and was allowed to fly freely between all stimulus compartments during a 2 h acclimatization period. During this period the female visited all stimulus compartments, and so was exposed to all the manipulation groups. The trial then lasted for 5 h: the number of ritualized display jumps performed (see Burley *et al.* 1982) and the total amount of time spent by females in front of each manipulated male was recorded by using microswitch perches placed in every stimulus compartment, which were linked to a BBC microcomputer. Females were randomly allocated to trials and manipulation groups were randomly allocated to stimulus cages. Each male and female was used only once.

Videotaped images of all the male chests were taken immediately prior to and during the manipulations. These videos were subsequently digitized and analysed by using the Optimas software package (BioScan Incorporated 1992) to ascertain the real effect of the manipulations on the chest plumage. All FA measurements were calculated as the absolute difference between trait values on the left and right sides.

On inspection of normal probability plots, the display jump and time data were transformed by a $\ln(x+1)$ transformation to conform with the assumptions of MANOVA. These data were then analysed by MANOVA (SPSS Incorporated 1988) using orthogonal contrasts to compare specific treatments. The data obtained from the videotapes were analysed on Minitab (Ryan *et al.* 1985). Two-tailed tests of probability are used throughout.

3. RESULTS AND DISCUSSION

Analysis of the videotaped data indicated that male chest bar plumage does display FA (refer to Swaddle *et al.* 1994) as the signed asymmetry in number of chest bars of unmanipulated males is normally distributed (Filliben correlation coefficient (Aitken *et al.* 1989) = 0.990, $n = 24$, $P < 0.0001$) around a mean of zero ($t_{23} = 1.64$, $p = 0.11$).

Female zebra finches perform more display jumps in front of males which have symmetrically manipulated chest plumage ($F_{3,15} = 3.99$, $p = 0.028$; contrast, Symmetry I and II versus Asymmetry I and II, $t = 2.92$; $p = 0.010$; see figure 4*b*). They also spend longer in front of symmetrical males ($F_{3,15} = 5.27$; $p = 0.011$; contrast, Symmetry I and II versus Asymmetry I and II, $t = 3.64$; $p = 0.002$; see figure 4*a*). There was no preference for males with more chest bars, either in amount of display jumps (contrast, Symmetry II versus Symmetry I, $t = 1.02$; $p = 0.326$), or time spent displaying (contrast, Symmetry II versus Symmetry I, $t = 0.89$; $p = 0.388$). There was also no 'sided' preference between asymmetry treatments for number of display jumps (contrast, Asymmetry I versus Asymmetry II, $t = 1.56$; $p = 0.140$), or time spent displaying (contrast, Asymmetry I versus Asymmetry II, $t = 1.33$; $p = 0.203$).

It would appear that asymmetry of chest plumage may be an important criterion when making mate choice decisions. Symmetry is preferred as, when the number of chest bars removed is kept constant between treatments, the symmetrically manipulated birds were

preferred over both of the asymmetric treatments. When levels of asymmetry are equal between treatment groups, there is no preference for a greater number of chest bars.

Previous findings have suggested that, in mate choice situations, males with more chest bars may be preferred over males with fewer bars (Feil & Curio 1993). These results do not support that hypothesis as Symmetry I birds were not preferred over Symmetry II birds. Symmetry I males did not have any black feather bars removed, whereas Symmetry II males had as many black bars removed as males in the asymmetric treatments. This result also indicates that mass of feather removed during the manipulation did not affect female choice, as the Symmetry I birds had slightly less of their plumage removed than Symmetry II birds, and yet were not preferred.

Alternatively, as the chest feathers overlie each other, the manipulation may not have resulted in an actual reduction of number of chest stripes. If the black bar of the top feather is removed, a smaller black bar of the underlying feather is exposed in its place (see figure 2). We tested for this *post-hoc* hypothesis by examining the videotaped images of the male finch chests. There were no differences between treatment
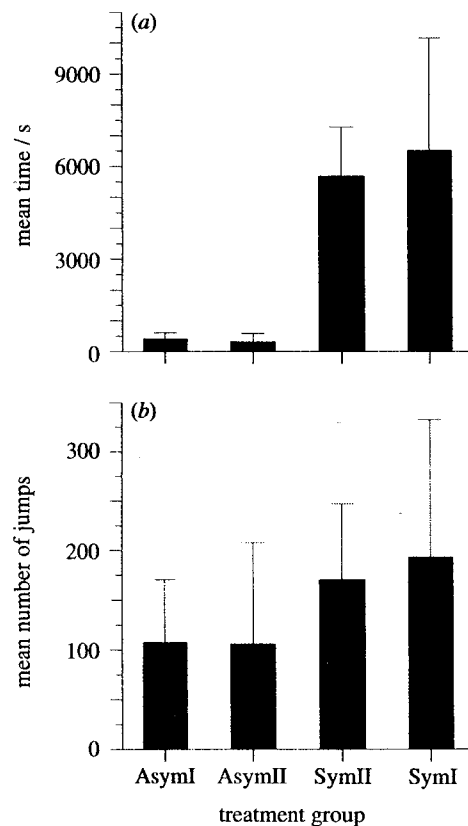

Figure 4. (*a*) Mean time (+s.e.) spent by female zebra finches displaying in stimulus compartments containing males from the different treatment groups. There is a strong preference for males with symmetrically manipulated chest plumage ($F_{3,15} = 5.27$, $p = 0.011$). (*b*) Mean number of display jumps (+s.e.) performed by female zebra finches in stimulus compartments containing males from the different treatment groups. More jumps were performed in front of symmetrically treated males ($F_{3,15} = 3.99$; $p = 0.028$).

groups for number of chest bars (ANOVA (Ryan *et al.* 1985), $F_{3,20} = 2.21$, $p = 0.118$) or for bar number asymmetry (Kruskal-Wallis (Siegel & Castellan 1988), $H = 0.84$, d.f. $= 3$, $p = 0.839$). This may account for the lack of difference in attractiveness between Symmetry I and Symmetry II males. However, our manipulation does result in a disruption of the chest bar pattern, as the underlying stripe is thinner (see figure 3). There was an indication that chest bars in the Asymmetry I, Asymmetry II and Symmetry II treatments were thinner overall, as Symmetry I males had 'whiter' chests than Asymmetry I males (ANOVA, $F_{1,10} = 12.07, p = 0.006$), Asymmetry II males (ANOVA, $F_{1,10} = 7.83$, $p = 0.019$) and Symmetry II males (ANOVA, $F_{1,10} = 6.85$, $p = 0.026$). There were no difference in chest whiteness between Asymmetry I, Asymmetry II and Symmetry II birds (ANOVA, $F_{2,15} = 1.11$, $p = 0.354$). Whiteness was calculated as the proportion of white to black on each male chest. This may represent a measure of overall chest bar size, as number of chest bars did not differ significantly between treatment groups. 'Whiteness' asymmetry was lower in symmetric treatments as opposed to asymmetric treatments (Kruskal-Wallis, $H = 7.18$, d.f. $= 3$, $p = 0.067$; see below). So, it would appear that our manipulations, at the very least, would have resulted in symmetric and asymmetric disruptions of the chest plumage, where symmetric patterns are preferred over asymmetric patterns (refer to figure 3 for a diagrammatic representation of the differences between the treatments).

Prior to the manipulations, male chests exhibited a range of absolute whiteness asymmetry between 0.009 and 0.224 (median, 0.084; standard deviation, 0.047). Experimental alterations of plumage resulted in the following median whiteness asymmetries: Symmetry I, 0.030; Asymmetry I, 0.151; Asymmetry II, 0.164; Symmetry II, 0.070. These manipulations are within the natural range of asymmetry values normally observed in male zebra finch chest plumage. This is the first experiment that has manipulated levels of asymmetry within natural limits and so the results can not be interpreted in terms of avoidance of mutant phenotypes; females are genuinely choosing symmetry over asymmetry.

Previous experiments that have attempted to investigate the effects of levels of FA on mate choice decisions have either confounded the asymmetry manipulation with aspects of flight performance (Møller 1992) or can be interpreted in terms for preference for symmetric arbitrary traits (Møller 1993; Swaddle & Cuthill 1994). In the first of these experiments, Møller (1992) manipulated levels of asymmetry in the tails of male swallows (*Hirundo rustica*) and recorded indirect measures of subsequent female choice (order of pairing, date of egg laying, and number of fledglings produced per pair). He found that males with symmetric tails paired earlier, mated with females that laid their first clutch earlier, and produced more offspring, than asymmetric males. However, increasing tail asymmetry detrimentally affects aerial manoeuvrability (Møller 1991; Thomas 1993; Evans *et al.* 1994), and so females could have

been choosing 'better fliers' without paying direct attention to tail asymmetry. With this particular criticism in mind, Møller (1993) conducted another experiment in which his manipulation of tail asymmetry did not affect aspects of aerial performance. He painted male swallow tails with combinations of white and black correction fluid to give 'apparent' symmetric and asymmetric tail length treatments. Even ignoring that the density differences between his different coloured solutions might create turning forces about the axis of symmetry and may affect flight performance, we suggest that his manipulation did not result in 'apparent' tail loss.

Whilst correction fluid has a high, and flat, spectral reflectance across human-visible wavelengths (and is therefore perceived as white), reflectance drops dramatically below about 425 nm and is minimal in the ultraviolet (UV) (Vos *et al.* 1992). Furthermore, under polarized light, it exhibits selective reflection in the UV, dependent on the angle of viewing (Vos *et al.* 1992). UV sensitivity appears to be ubiquitous in diurnal birds including swallows (Bennett & Cuthill 1994), and UV reflectance is common in many species' plumage, including the swallow (Burkhardt 1989; Bennett & Cuthill 1994). 'Colour' manipulation of avian plumage based on human perception is thus completely without justification (Bennett *et al.* 1994). These properties create a number of specific problems that apply to Møller's (1993) experiment.

Under a clear blue sky, as would be found in Denmark in late spring and early summer, polarized UV light is abundant. Barn swallows are aerial insectivores and take part in elaborate courtship flights; they are, therefore, constantly changing direction in the air. To the eye of a female swallow, white correction fluid would most probably appear as 'flashing lights', changing in brightness and hue, at the ends of the male tail; certainly not as apparent tail loss. However, Møller's (1993) result still stands, there was a preference for the symmetric treatment and it is the interpretation of these results that requires clarification. These findings can be explained as either avoidance of abnormal plumage traits or as a general preference for symmetry in an existing secondary sexual trait. Swaddle & Cuthill (1994) demonstrated that female zebra finches preferred males which were wearing symmetrically arranged leg bands, indicating a preference for a symmetric arbitrary trait on the basis of visual cues alone. These studies provided important results in their own right; if symmetry is preferred, then there must be coevolutionary consequences for signal design.

In this experiment we have provided clear evidence that females exhibit a preference for symmetry in an existing sexually dimorphic character. As our manipulations are within the range of natural asymmetries observed in male zebra finch chest plumage, this preference may be a true reflection of females assessing males on the basis of the asymmetry of a condition-revealing secondary sexual trait. However, the functional importance of this trait is unclear and it may not be a reliable indicator of male quality. Females may prefer symmetric males because they have a pre-

disposed bias toward symmetric signalling structures. It is well known in the psychological literature that humans display a preference for the most average member of a set of signals (see, for example, Strauss 1979; Younger & Gotlieb 1988). In cases where signalling traits display FA (characterized by a normal distribution centred around zero asymmetry), symmetry will be average and so may be preferred for this reason. Comparative investigations of animal cognitive systems have revealed that some animals may also have a predisposed preference for symmetry (Rensch 1957, 1958).

The functional importance of male chest bar plumage requires further experimental investigation. As this trait results from a complex pattern of overlapping feathers, there may be a considerable cost to maintenance. Birds that maintain their chest plumage in better condition will, as a result, probably have more symmetric chest bars.

Whatever the basis of the preference, it is clear that the choice of symmetric birds was determined solely by visual cues, as there were no other differences between treatment groups. These findings, along with the substantial literature indicating that asymmetry is negatively related to fitness measures (see, for example, Beardmore 1960; Jones 1987; Møller 1990; Harvey & Walsh 1993), strongly suggests that females do assess and use sexual ornament FA information in mate choice decisions and choose symmetrically ornamented males over asymmetric males.

REFERENCES

Aitken, M., Anderson, D., Francis, B. & Hinde, J. 1989 *Statistical modelling in GLIM*. Oxford University Press.

Beardmore, J. A. 1960 Developmental stability in constant and fluctuating temperatures. *Heredity* **14**, 411–422.

Bennett, A. T. D. & Cuthill, I. C. 1994 Ultraviolet vision in birds: what is its function? *Vision Res.* **34**, 1471–1478.

Bennett, A. T. D., Cuthill, I. C. & Norris, K. N. 1994 Sexual selection and the mismeasure of colour. *Am. Nat.* **144**, 848–860.

BioScan Incorporated 1992 *Optimas 4.02*. Edmonds, Washington: BioScan Incorporated.

Bradbury, J. W. & Anderson, M. B. 1987 *Sexual selection: testing the alternatives*. Chichester: Wiley.

Burkhardt, D. 1989 UV vision: a bird's view of feathers. *J. comp. Physiol. A* **164**, 787–796.

Burley, N., Krantzberg, G. & Radman, P. 1982 Influence of colour banding on the conspecific preferences of zebra finches. *Anim. Behav.* **30**, 444–455.

Evans, M. R., Martins, T. L. F. & Haley, M. 1994 The asymmetrical cost of tail elongation in red-billed streamertails. *Proc. R. Soc. Lond.* B **256**, 97–103.

Feil, B. & Curio, E. 1993 Phenotypical traits and female choice in Timor zebra finches. *Proceedings of XXIII International Ethological Conference*, p. 244.

Harvey, I. F. & Walsh, K. J. 1993 Fluctuating asymmetry and lifetime mating success are correlated in males of the damselfly *Coenagrion puella* (Odonata: Coenagrionidae). *Ecol. Ent.* **18**, 198–202.

Jones, J. S. 1987 An asymmetrical view of fitness. *Nature, Lond.* **325**, 298–299.

Ludwig, W. 1932 *Das Rechts-Links Problem im Tiereich und bein 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.

Møller, A. P. 1990 Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim. Behav.* **40**, 1185–1187.

Møller, A. P. 1991 Sexual ornament size and the cost of fluctuating asymmetry. *Proc. R. Soc. Lond.* B **243**, 59–62.

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.

Møller, A. P. & Höglund, J. 1991 Patterns of fluctuating asymmetry in avian feather ornaments: implications for models of sexual selection. *Proc. R. Soc. Lond.* B **245**, 1–5.

Møller, A. P. & Pomiankowski, A. 1993 Fluctuating asymmetry and sexual selection. *Genetica* **89**, 276–279.

Rensch, B. 1957 Ästhetische Faktoren bei Farb- und Formbevorzugungen van Affen. *Z. f. Tierpsychol.* **14**, 71–99.

Rensch, B. 1958 Die Wirksamkeit ästhetischer Faktoren bei Wirbeltieren. *Z. Tierpsychol.* **15**, 448–461.

Ryan, B. F., Joiner, B. I. & Ryan, T. A. 1985 *MINITAB Handbook*, 2nd edn. Boston: PWS-Kent.

Siegel, M. I. & Castellan, N. J. 1988 *Nonparametric statistics for the Behavioral sciences*, 2nd edn. Singapore: McGraw-Hill.

SPSS Incorporated 1988 *SPSSx User's guide*, 3rd edn. Chicago: SPSS Inc.

Strauss, M. 1979 Abstraction of prototypical information by adults and 10-month-old infants. *J. exp. Pscyhol.: Hum. Learn. Memory* **5**, 618–632.

Swaddle, J. P. & Cuthill, I. C. 1994 Female zebra finches prefer symmetric males. *Nature, Lond.* **367**, 165–166.

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.

Thomas, A. L. R. 1993 The aerodynamic costs of asymmetry in the wings and tails of birds: asymmetric birds can't fly round tight corners. *Proc. R. Soc. Lond.* B **254**, 181–189.

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.

Van Valen, L. 1962 A study of fluctuating asymmetry. *Evolution* **16**, 125–142.

Vos Hzn, J. J., Coemans, M. A. M. J. & Nuboer, J. F. W. 1992 Intensities following selective reflection and transmission of polarized light. In *On the perception of polarized light by the homing pigeon* (ed. M. Coemans & J. Vos). Universiteit Utrecht.

Younger, B. A. & Gotlieb, S. 1988 Development of categorization skills: changes in nature or structure of infant form categories? *Devl. Psychol.* **24**, 611–619.