

ORNAMENT SIZE AND SYMMETRY: IS THE TAIL A RELIABLE SIGNAL OF MALE QUALITY IN THE RED-COLLARED WIDOWBIRD?

KEITH W. GODDARD AND MICHAEL J. LAWES¹

School of Botany and Zoology, University of Natal, Private Bag X01, Scottsville 3209, South Africa

ABSTRACT.—Fluctuating asymmetry (FA) may provide a direct test of whether sexual selection via “arbitrary traits” or “good genes” is responsible for the evolution of epigamic traits, because FA is an epigenetic measure of stress during development. However, tests of the FA hypothesis have yielded equivocal results, and the debate between arbitrary traits and good genes continues. The FA hypothesis predicts a negative relationship between ornament size and asymmetry. In non-ornamental traits, a U-shaped relationship between trait size and asymmetry is expected. We tested these predictions in the Red-collared Widowbird (*Euplectes ardens*) by examining the relationship between size and asymmetry in the length of the tail, tarsus, and wing. We found no significant linear or second-order polynomial relationships between trait size and asymmetry. Furthermore, no relationship existed between asymmetry and two indices of body condition. This suggests that the tail is not a reliable signal of male quality in the Red-collared Widowbird. However, we argue that the assumptions of the FA hypothesis are too simplistic for this conclusion to be drawn with a high degree of confidence. *Received 13 May 1998, accepted 20 August 1999.*

THE DEBATE concerning sexual selection via good genes or arbitrary traits remains one of the most controversial topics in evolutionary biology (Maynard Smith 1991, Andersson 1994). Behavioral ecologists have recently begun studying fluctuating asymmetry (FA) and its correlation with reproductive success in an attempt to evaluate condition-dependent models of sexual selection (Watson and Thornhill 1994) and perhaps resolve the good genes versus arbitrary traits debate (Møller and Höglund 1991). However, findings on the condition dependence of FA have been equivocal (McLachlan and Cant 1995, Andersson and Iwasa 1996), and the question remains: Are the ornamental tails of birds reliable signals of male quality?

Fluctuating asymmetry is a population phenomenon defined as random deviation from perfect bilateral symmetry in a morphological trait, for which mean differences between the right and left side have a mean of zero and are normally distributed (Palmer and Strobeck 1986, Watson and Thornhill 1994). Because both sides of a bilaterally symmetrical trait develop as a consequence of the same genome, FA represents an epigenetic measure of the sensitivity of development to factors affecting homeostasis

(Palmer and Strobeck 1986, Parsons 1990). As a general rule, individuals experiencing greater stress during development exhibit higher degrees of FA (Møller and Pomiankowski 1993, Nilsson 1994, Swaddle and Witter 1994).

Sexual ornaments generally display higher levels of FA than do other morphological traits (Møller and Höglund 1991, Møller 1993). Different morphological characters differ in their susceptibility to environmental and genetic stress because of differences in the extent to which they are buffered developmentally (Møller 1993). Sexual ornaments are assumed to be under intense directional selection and should therefore be less canalized developmentally. Because environmental perturbations tend to have a disproportionate effect on ornamental traits versus other morphological characters (Møller 1992), any stress encountered by an individual during development should be reflected in the degree of FA in ornaments before that of any other trait.

As a result of these characteristics of FA, various authors have suggested that FA provides an indirect measure of fitness (e.g. Palmer and Strobeck 1986, Jones 1987, Hill 1995). Møller (1990) suggested that FA should be a reliable measure of an individual's ability to produce extravagant sexual traits, because only males in good physical condition will be capable of producing ornaments that are large and symmet-

¹ Address correspondence to this author. E-mail: lawes@zoology.unp.ac.za

rical. Therefore, individuals may assess the symmetry of their conspecifics during mate choice because the degree of FA displayed by an individual should reflect its ability to deal with environmental and genetic stress. Indeed, Møller (1990) argued that tail ornaments reflect a strategic choice on the part of the male, because each male must reach a compromise between tail length and symmetry. Because this compromise is assumed to be influenced by the male's genetic quality, females should use ornament size as a reflection of male handicap while simultaneously using symmetry as an indication of costly male choice when inferring male quality (Møller 1990).

This hypothesis, which assumes that ornaments are condition dependent, predicts a negative relationship between ornament size and the degree of FA. Although the hypothesis assumes that FA is used directly as a cue by females during mate choice, a negative relationship between ornament size and asymmetry should exist regardless of whether females assess symmetry directly, provided that both the size and symmetry of the ornament are condition dependent. On the other hand, if a trait is under natural selection, one would expect a U-shaped relationship between trait size and FA (Soulé 1982). Thus, examination of allometric patterns of symmetry may allow researchers to determine which ornaments are condition dependent.

To explore the FA hypothesis, it is necessary to determine (1) whether the symmetry of secondary sexual characters is a reliable indicator of individual quality, and (2) whether symmetry is used directly as a cue by conspecifics during mate choice. We aimed to answer the first question by examining the allometric relationship between ornament size and degree of FA in the Red-collared Widowbird (*Euplectes ardens*), which is polygynous and highly sexually dimorphic. Male Red-collared Widowbirds in alternate plumage are black with very long (\bar{x} = 218.1 mm) tails and possess a scarlet collar on the throat. The long tail may be energetically expensive to produce and maintain, although this has not been quantitatively demonstrated. Furthermore, males do not invest in any type of parental care (pers. obs.), suggesting that the female receives nothing from its mate except genes. If this is the case, then a female's choice should be aimed at securing the best possible

genes for her offspring, because no other benefits are accrued through her choice of mate.

STUDY AREA AND METHODS

Morphometric data were collected during October to February, 1993 to 1996. The study area was located in Bisley Valley Nature Reserve within the city of Pietermaritzburg, South Africa (29°39'S, 30°23'E; elevation ca. 870 m). We captured birds in mist nets at night roosts. We banded each bird and measured tarsus and culmen length with Vernier calipers (\pm 0.1 mm) and wing length, tail length (each rectrix), and primary length (nine primaries on each wing) with a metal ruler (\pm 0.5 mm). Body mass was determined using a Pesola spring balance (\pm 0.5 g).

We determined the degree of FA for tail length, tarsus length, wing length, and primary length. Absolute asymmetry values were calculated as the numerical value of the difference between the length of left and right characters (Palmer and Strobeck 1986, Møller 1990). For traits that contained more than one paired structure (i.e. tail length), a mean FA value was calculated. Birds with broken or missing feathers were excluded from the analysis. Repeatability measures were calculated for each of the traits according to the method of Lessels and Boag (1987). Swaddle et al. (1994) suggested that it is not sufficient to determine repeatability measures on the traits themselves and recommended the use of a mixed-model ANOVA to test between measurement error and the asymmetry. However, owing to the large increase in handling time necessary to measure 12 rectrices repeatedly, this method of determining measurement error was not used. For the same reason, only five birds were used to calculate repeatability of FA. Nonetheless, it would appear that repeatability was high for tarsus length (F = 15.59, df = 4 and 5, P < 0.05; repeatability = 0.88) and tail length (F = 23.12, df = 4 and 5, P < 0.05; repeatability = 0.92) but not for wing length (F = 3.36, df = 4 and 5, P < 0.05; repeatability = 0.54). However, we suggest that the low repeatability for wing length is merely a statistical artifact of the method of Lessels and Boag (1987). This measure is based on the variance components derived from a one-way ANOVA and essentially represents a ratio of within-group variance to between-group variance. Because most males had wing lengths of a very similar size (range 3 mm), and wing length was measured to the nearest 0.5 mm, the ratio of between-group to within-group variance did not provide an adequate measure of repeatability.

We tested for departure from normality in asymmetry of wing, tail, and tarsus length using a one-sample Kolmogorov-Smirnov test, and we used a one-sample t -test to determine whether the mean differed significantly from zero. To examine the al-

lometric relationship between trait size and asymmetry, absolute asymmetry was plotted against mean trait size for adult male tarsus length, wing length, and tail length. These relationships were tested with linear and second-order polynomial regression (to test for a U-shaped relationship) as done by Evans et al. (1995). Where appropriate, data that were not normally distributed were transformed.

We used a statistical estimate of body condition in lieu of a direct measure of general body condition. Three different measures of body size (tarsus length, culmen length, and wing length) were entered into a principal components analysis (PCA). The first component derived from the PCA was used as an indication of body size, and body mass was regressed against this first component from the analysis. The residuals were then taken as an estimate of body condition and regressed on both tail length and tail asymmetry.

RESULTS

Do these structures exhibit fluctuating asymmetry?—The criterion for determining whether a morphological trait exhibits FA is that the difference between the right and left sides must be normally distributed and have a mean of zero (Palmer and Strobeck 1986). Wing ($D = 0.16$, $n = 28$, $P = 0.49$), tarsus ($D = 0.16$, $n = 24$, $P = 0.60$), and tail ($D = 0.17$, $n = 41$, $P = 0.20$) asymmetry were normally distributed. In addition, the mean values did not deviate from zero for any of the traits (wing, $t = 1.64$, $n = 28$, $P = 0.10$; tarsus, $t = -1.17$, $n = 24$, $P = 0.30$; tail, $t = 1.47$, $n = 41$, $P = 0.15$). Thus, we assume that all of these traits exhibited FA.

Does asymmetry vary with trait size?—The degree of fluctuating asymmetry and trait size were not linearly correlated for any of the traits we measured. Despite the predictions of Møller (1990) that ornament size and asymmetry should be negatively correlated, the linear regression model showed that no predictable relationship existed between FA and tail length ($F = 1.48$, $df = 1$ and 40 , $P = 0.23$; $R^2 = 0.036$; Fig. 1). Similarly, no significant linear relationship existed between FA and trait size for tarsus length ($F = 0.14$, $df = 1$ and 23 , $P = 0.70$, $R^2 = 0.007$) or for wing length ($F = 0.30$, $df = 1$ and 27 , $P = 0.61$, $R^2 = 0.013$). In addition, no significant second-order polynomial relationships occurred between trait size and FA for any of the traits (tail, $F = 1.55$, $df = 1$ and 40 , $P = 0.22$, $R^2 = 0.0007$; tarsus, $F = 1.15$, $df = 1$ and 23 , $P = 0.34$, $R^2 = 0.0009$; wing, $F = 0.91$,

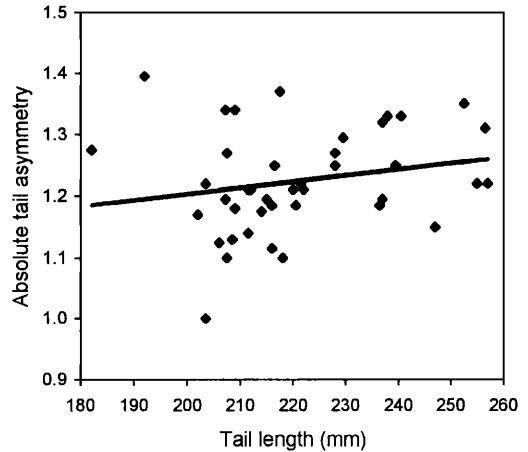


FIG. 1. Tail asymmetry as a function of tail length in the Red-collared Widowbird.

$df = 1$ and 27 , $P = 0.42$, $R^2 = 0.0007$), so the relationship between trait size and asymmetry cannot be described by a U-shaped function for any of the traits we measured.

We note that we could not control for the stage of tail growth owing to the low recapture rate, which made it impossible to determine mean rates of growth or abrasion. However, for a number of reasons it is unlikely that this compromised the data. First, our morphometric data gave no indication that asymmetry changes in any predictable manner as the season progresses. To determine how tail length and asymmetry change as the breeding season progressed, we arbitrarily assigned 1 September as day 1 in the season as birds were caught and measured. Tail length and relative asymmetry were then regressed (multiplicative regression) against day of the season. A very good fit was obtained when tail length was plotted against day of the season ($F = 119.03$, $df = 1$ and 58 , $P < 0.001$, $R^2 = 0.676$; Fig. 2), but not when asymmetry was regressed against day of the season ($F = 0.536$, $df = 1$ and 58 , $P > 0.05$, $R^2 = 0.009$; Fig. 3). This suggests that although tail length grows predictably, asymmetry does not change predictably enough to make controlling for stage of tail development essential when determining the allometric relationship between ornament size and FA. Second, at the time when females are choosing mates, presumably on the basis of male ornamentation, very few males have well-developed tails, and no males have tails that are close to being fully developed. Fi-

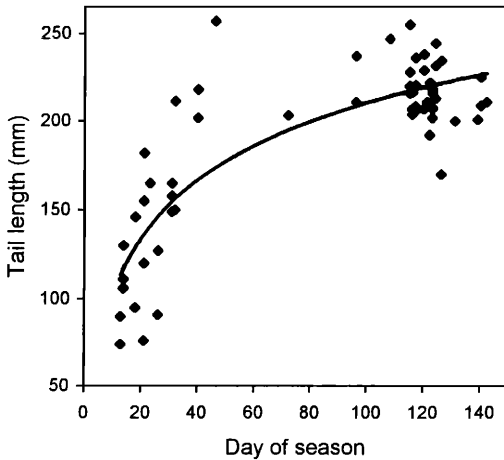


FIG. 2. Tail length of the Red-collared Widowbird as a function of time of season. Day 1 equals 1 September.

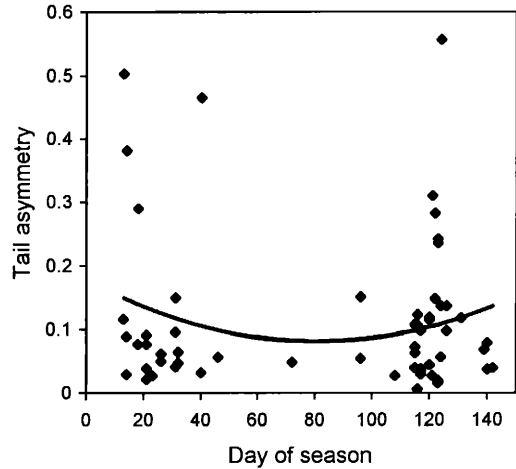


FIG. 3. Tail asymmetry of the Red-collared Widowbird as a function of time of season. Day 1 equals 1 September.

nally, females have to make their choice on the basis of what is available at that time, and females do not themselves control for stage of growth when assessing the degree of symmetry.

Are tail length and/or tail FA condition dependent?—The three different measures of body size were plotted using PCA, and the first principal component accounted for 39.67% of the variance. The regression models between estimated body condition and tail length ($F = 0.127$, $df = 1$ and 32 , $P = 0.72$, $R^2 = 0.004$) and estimated body condition and tail asymmetry ($F = 0.328$, $df = 1$ and 32 , $P = 0.57$, $R^2 = 0.010$) were not statistically significant. This suggests that neither tail length nor tail FA are condition dependent. However, body mass may have been a poor measure of body condition because we did not control for differences in the amount of crop contents, which may lead to considerable short-term variation in body mass.

DISCUSSION

The predictions of Møller's (1990) FA hypothesis were not supported by our study, because males with longer tails did not demonstrate lower levels of asymmetry. According to Møller (1993), these results indicate that the tail ornament of the Red-collared Widowbird is under arbitrary-traits sexual selection pressure, because the tail is not a condition-dependent

ornament. However, the interpretation of allometric patterns of symmetry is not quite as straightforward as Møller suggests. In fact, a number of problems with the inherent assumptions of the FA hypothesis confuse the interpretation of these patterns.

The prediction of a negative relationship between ornament size and asymmetry is based on the assumption that trait size and asymmetry are under intense directional selection pressure, because males should attempt to optimize size and symmetry simultaneously (Møller 1993). However, all models of sexual selection predict that at equilibrium, sexual selection favoring increased ornament elaboration is balanced by selection for reduced ornament size through the negative effects that large ornaments have on viability (Balmford and Read 1991, Kirkpatrick and Ryan 1991). At equilibrium, an ornament should be considered to be under two opposing forms of directional selection (Møller and Pomiankowski 1993). This does not necessarily apply to ornament symmetry because both sexual selection and natural selection should select for increased symmetry. Nonetheless, it is possible that the allometric relationship between ornament size and asymmetry will differ depending on whether an ornament and its associated signaling system have evolved to equilibrium. Ideally, the lack of a negative relationship between ornament size and asymmetry should not be interpreted as evidence that an orna-

ment is not condition dependent unless one has knowledge of whether the signal is in a state of equilibrium. However, this is not a practical approach because of the inherent difficulties in determining whether any given ornament has evolved to a state of equilibrium.

Furthermore, if asymmetry imposes direct fitness costs on the individual in terms of decreased viability or higher energetic costs (e.g. Evans et al. 1994), then it does not necessarily follow that high-quality males will have lower levels of asymmetry. Grafen (1990) pointed out that in a stable signaling system, a handicap can result in higher-quality males having lower viability than males of medium quality. This situation would arise if the benefits of increased ornament size exceeded the costs of decreased viability. In this case, it is assumed that decreased viability will be reflected by increased asymmetry. This raises two important points. First, the relative costs and benefits of ornament elaboration will differ from species to species, thus complicating the interpretation of allometric relationships between size and FA. If, for example, the potential reproductive benefits of possessing large ornaments outweigh the costs of asymmetrical ornamentation, males may attempt to maximize ornament size even if this means developing asymmetrically.

The second point is the question of what constitutes more of a handicap, symmetry or asymmetry? If a trait is to be an honest signal of quality, then it must be costly to produce and maintain, and increased ornamentation (or in this case symmetry) must impose a greater marginal cost on low-quality individuals (Enquist 1985, Grafen 1990). Almost no work has been done to identify the costs of increasing ornamental symmetry, but the FA hypothesis can be valid only if these costs exist and if they are greater for low-quality males. Furthermore, in terms of the possession of symmetrical ornaments, the experimental evidence suggests that asymmetry is far more costly than symmetry in the case of the ornamental tails of birds (e.g. Møller 1991, Evans et al. 1994). The evidence that asymmetry in birds is energetically expensive is so compelling that various authors have suggested that negative relationships between trait size and asymmetry would be expected purely as a consequence of natural selection (e.g. Balmford et al. 1993, Evans 1993). This

suggests that asymmetry constitutes more of a handicap than symmetry. If the tail were a handicap, and an expensive signal was required by females, then high-quality males should be more asymmetrical than low-quality males. Sufficient evidence exists to refute this argument, but the argument illustrates the inherent difficulties in interpreting allometric data pertaining to FA. Clearly, more work is needed to determine the costs associated with developing ornaments with increased symmetry, and how these costs compare with the mechanical costs of possessing an asymmetrical ornament.

A U-shaped relationship is predicted for traits that are considered to be under natural selection pressure, such as wing symmetry or tarsus symmetry. Thus, the fact that none of the traits we measured in Red-collared Widowbirds displays a U-shaped relationship between size and asymmetry is quite puzzling. The absence of a U-shaped relationship between trait size and asymmetry for wing length, in particular, is difficult to explain because wing symmetry is likely to be under especially strong stabilizing natural selection owing to the aerodynamic importance of symmetrical wings. Because male widowbirds frequently fly from one vantage point to another within their territories during the breeding season, we submit that wing length is under such extremely tight developmental control that relatively few males will possess asymmetrical wings. Very large sample sizes are probably needed to detect individuals with asymmetrical wings.

Evans et al. (1995) found that a U-shaped relationship existed between tail length and degree of FA in the Streamertail (*Trochilus polytmus*), but this was not the case for the Red-collared Widowbird. This suggests that the allometric relationship between ornament size and FA in the Red-collared Widowbird is not a consequence of selection to control for errors in development; i.e. natural selection probably is not "shaping" tail shape.

According to Møller's (1990) FA hypothesis, the lack of a negative relationship between tail size and FA precludes the possibility that the tail evolved under good-genes sexual selection pressure. However, we suggest that this is not necessarily the case. Because Red-collared Widowbirds are polygynous, the potential bene-

fits to a male who develops a large tail are great, assuming that females have a preference for long tails. This assumption has not been quantitatively tested in the Red-collared Widowbird, but it has been demonstrated in Long-tailed Widowbirds (*E. progne*; Andersson 1982) and in Jackson's Widowbirds (*E. jacksoni*; Andersson 1989, 1992). Therefore, we submit that male Red-collared Widowbirds attempt to maximize tail length even if this means incurring asymmetrical development, because marginal increases in tail length potentially may yield large reproductive benefits. A negative relationship between ornament size and asymmetry would not be expected under these circumstances. However, it is important to realize that the asymmetry in tail shape would have a negative effect on maneuverability and consequently on energy budgets (Balmford et al. 1993; see also Møller 1991, Evans et al. 1994). Therefore, FA will increase the costs of cheating, because the effect of FA on maneuverability increases with tail length (Evans et al. 1994), and the tail can thus be regarded as a conditional handicap that has evolved under good-genes sexual selection pressure.

It is clear that FA cannot be regarded as an easy means of determining which ornaments are condition dependent and which evolved under arbitrary-traits sexual selection. The FA hypothesis essentially is just another good-genes model of sexual selection, and tests of the hypothesis can only establish for which species the hypothesis holds true. Where the predictions are not met, too many conflicting issues are involved for one to state with any confidence that the ornament is not condition dependent. It is clear from our study, however, that asymmetry cannot be regarded as a reliable indicator of male quality in Red-collared Widowbirds, although this does not preclude the possibility that tail length is a condition-dependent trait.

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