Fluctuating asymmetry in the redcollared widow: testing theories of sexual selection.

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Abstract

Sexual selection is usually invoked to explain the evolution of elaborate epigamic characters in animals. However, the mechanism by which female choice operates is poorly understood, and it is not clear whether female choice is purely aesthetic or related to male genotypic quality. It has been suggested that Møller's fluctuating asymmetry (FA) hypothesis may resolve the 'arbitrary trait'-'good gene' debate. However, tests of this controversial hypothesis have yielded equivocal results. I examined the allometric patterns of FA in the redcollared widow in order to test the FA hypothesis. In addition, I documented intrapopulation variation in trait size to determine whether females could distinguish between males on the basis of ornament size and/or symmetry.

Male tail length was found to be more variable in size than other traits, suggesting that sufficient variation exists in ornament size for females to distinguish between males on this basis. In addition, the prediction of the FA hypothesis that ornaments would display higher degrees of asymmetry than non-ornamental traits was supported. However, no significant linear or second-order polynomial relationship was found between trait size and asymmetry for tail, wing and tarsus length. Furthermore, neither tail length or symmetry was correlated with indices of body condition.

Although this might suggest that the FA hypothesis is invalid, I argue that the assumptions of the hypothesis are too simplistic for it to hold true for all species without taking the basic biology of the species into account.

Contents

Introduction

Conspicuous bright colours and extravagant ornamentation are commonplace in the animal kingdom, particularly among bird species. This sexual showiness has fascinated biologists for centuries, and the last thirty years in particular has seen a proliferation of different theories to account for these seemingly non-functional (in terms of survival) epigamic characters. Nonetheless, our understanding of the processes driving the evolution of elaborate male ornamentation is incomplete.

Sexual selection

Darwin introduced the theory of sexual selection to explain the evolution, and function, of extravagant male traits which appear to be detrimental to the bearer. He distinguished between sexual selection and natural selection by saying that "Sexual selection... depends, not on the struggle for existence, but on a struggle between males for possession of females; the result is not death to the unsuccessful competitor, but few or no offspring" (Darwin 1859; cited in Andersson 1994). Darwin (1871) further argued for two different mechanisms by which male ornaments might evolve: (1) male-male competition for mates, and (2) female choice. The former is referred to as intra-sexual selection, and the latter as inter-sexual selection (Krebs & Davies 1992).

Sexual selection research has focused primarily on the role of female choice in driving the evolution of ornaments. Nonetheless, the mechanism by which female choice operates is still a matter of considerable debate (Partridge & Harvey 1986; Bradbury & Andersson 1987; Andersson 1994). Since mate choice determines reproductive success and the genetic constitution of the offspring, animals should actively select their mates rather than mate indiscriminately (Bateson 1983; Dhindsa *et. al.* 1989). But how does the documented female preference for elaborate ornaments (e.g. Andersson 1982; Andersson 1989; Møller 1990) benefit the female? Why do females have a preference for ornaments which have no apparent survival value? Various theoretical constructs have been formulated to answer these questions, and these can be broadly divided into two categories, namely the "arbitrary traits" and the "good gene" models of sexual selection.

The arbitrary traits school of thought maintains that ornaments are arbitrary in the sense that the ornament has no function other than its attractiveness to females (Møller 1993; Andersson 1994). Females choosing males with elaborate ornaments therefore benefit only in that they have attractive sons (Fisher 1930; Majerus 1986; Pomiankowski & Sheridan 1994). On the other hand, the good gene models of sexual selection are based on the idea that when males differ in their quality, either phenotypically or genotypically, females should derive some benefit by mating with the more viable males (Trivers 1972; Lotem 1993). These models therefore propose that ornaments have evolved to provide females with an indication of male viability (Zahavi 1975; Zahavi 1977), and the selective benefit to females who choose elaborately ornamented males is improved health and survival for her offspring (Andersson 1986).

Empirical studies have been unable to distinguish between these two models, and the mechanism by which female choice operates is yet to be clarified.

The fluctuating asymmetry hypothesis

Møller (1990; 1991) introduced the fluctuating asymmetry (FA) hypothesis to explain how females may assess the quality of potential mates. This controversial hypothesis may provide a direct test of whether arbitrary traits or good gene sexual selection is responsible for the evolution of elaborate epigamic characters (Møller & Höglund 1991; Watson & Thornhill 1994). As such, this hypothesis could revolutionize our understanding of the evolution of sexual signals (Jennions & Oakes *in press*).

Fluctuating asymmetry (FA) is a population phenomenon defined as random deviation from perfect bilateral symmetry in a morphological trait, for which differences between the right and left side have a mean of zero and are normally distributed (Polak & Trivers 1994; Watson & Thornhill 1994). Since both sides of a bilaterally symmetrical trait develop as a consequence of the same genome, departure from the *a priori* optimal state (perfect bilateral symmetry) can be regarded as evidence of developmental instability (Polak & Trivers 1994). FA therefore represents an epigenetic measure of the sensitivity of development to factors influencing homeostasis (Palmer & Strobeck 1986; Parsons 1990). In fact, FA is now known to be diagnostic of a wide range of stressors borne during development (Polak & Trivers 1994), since it develops in response to various kinds of environmental (*e.g.* extreme temperatures, food deficiency and radiation) and genetic stress (*e.g.* inbreeding and hybridization) (Parsons 1990). As a general rule, individuals experiencing greater stress during development exhibit higher degrees of FA (Møller & Pomiankowski 1993).

Møller (1990;1991) argued that if FA is an indicator of stress it may be a measure of an individual's ability to produce extravagant ornaments, since only males in good condition will be capable of producing ornaments which are both large and symmetrical. He further argued that in birds tail ornaments reflect a strategic choice on the part of the male, since each male must reach a compromise between tail length and symmetry. The compromise made by each male should be influenced by the genetic quality of the individual male, since poor quality males will incur greater stress during the development of an ornament of a given size, and will therefore have a greater tendency towards asymmetry. This implies that females can use tail length as a reflection of male handicap while simultaneously using the degree of FA as a sign of costly choice when inferring male quality (Møller 1990). Møller argued that this would serve to prevent dishonest signalling by males because a poor quality male who attempted to produce a large ornament would also produce an asymmetrical one, and these males should be disregarded by females. The hypothesis thus predicts a negative relationship between ornament size and FA (Møller 1990).

The FA hypothesis has been a valuable contribution to the sexual selection field. However, the validity of the hypothesis has not been conclusively demonstrated. The relationship between ornament size and the degree of fluctuating asymmetry has been tested for a number of different species. A negative relationship between FA and ornament size has been established for the tail of the barn swallow *Hirundo rustica* (Møller 1990), the trains of peacocks (Manning & Hartley 1991), beetles horns and spurs of birds (Møller 1992). Solberg & Sæther (1993) found a negative relationship between antler symmetry and body mass in the moose *Alces alces*. These results are consistent with the predictions of the FA hypothesis. However, several studies have failed to show the predicted relationship. Examples of species for which there is no negative relationship between ornament size and FA include the paradise whydah *Vidua paradisaea* (Barnard 1994) and the red-billed streamertail *Trochilus polytmus* (Evans *et. al.*1994). Furthermore, Balmford *et. al.* (1993) examined the relationship between tail length and FA for 43 different bird species, and found a significant negative relationship in only two cases. In addition, Oakes & Barnard (1994) have demonstrated that female paradise whydahs do not have any preference for symmetrical tails. In fact, the females appeared to have a greater preference for asymmetry!

The controversy surrounding the FA hypothesis must be resolved if the role of female choice in the evolution of epigamic traits is to be understood. According to Jennions & Oakes (*in press*) there are four approaches which may be used to test the FA hypothesis: (1) the allometric patterns of FA may be examined to determine whether or not sexually selected characters show different relationships between size and symmetry than do other morphological characters; (2) differences in reproductive success, fighting success or survivorship of symmetric and asymmetric individuals can be compared; (3) the direct costs of asymmetry in ornaments can be compared; (4) the symmetry of ornaments can be experimentally manipulated to test female preferences.

The study animal

The subject of this field-based study is the redcollared widow (*Euplectes ardens*). The widow is a small (15.6-25g) bird which feeds on seeds and insects (Maclean 1993). The redcollared widow is polygynous, and highly sexually dimorphic in the breeding season, which is from September to March. The female is a brown-buff colour with brown streaks, while the male is black with a scarlet collar on the lower throat region. Females and non-breeding males have short tails (female $\bar{x}$ =43.4mm; non-breeding male $\bar{x}$=51.6mm), while breeding males have very long tails ($\bar{x}$=218mm). The tail is comprised of twelve retrices and is graduated. Males defend territories on which up to four females breed. Males perform slow display flights with rapidly beating wings and the central retrices depressed and keeled to form an inverted sickle shape (Maclean 1993; Goddard *pers. observ.*) between prominent perches on their territory. Males regularly display their tails when on these prominent perches, flaring the retrices out. The potential for tail symmetry to influence female choice is therefore great.

Males do not invest in any form of parental care (Maclean 1993; Goddard *pers. obs.*), suggesting that the female receives nothing from its mate except genes. No direct benefits are accrued by the female through her choice of mate.

The breeding activity of the redcollared widow is extremely sensitive to environmental conditions, and rainfall in particular (Goddard *pers. obs.*; S. Andersson *pers. comm.*). Indeed, during the 1994-96 breeding season, when rainfall was below average for that time of the year, no nests were found on any of the territories. In addition, nests, which are constructed by the male, are concealed in long grass and are extremely cryptic and difficult to locate. These two points made it difficult to assess the reproductive success of any male. It was also not possible to conduct choice chamber experiments with males who had had tail symmetry manipulated because the stress of captivity quickly resulted in death.

Aims of the study

This study deals with the phenotypic expression of ornaments in the redcollared widow, and the variation in this expression. However, my primary aim is to test the validity of the FA hypothesis, and determine whether the long tail of the male redcollared widow evolved under good genes or arbitrary traits sexual selection pressure. This is the first study of sexual selection in the redcollared widow, and the first study of FA in any widowbird. I have attempted to answer four questions during the course of this study: (1) are sexual ornaments more variable in size and symmetry than other morphological traits?, (2) is there sufficient variation in ornament size and/or symmetry for females to perceive differences between males on this basis?, (3) is there a negative relationship between tail length and fluctuating asymmetry in the redcollared widow?, and (4) is there a U-shaped relationship between trait size and FA for non-ornamental traits?

This thesis therefore represents a test of the FA hypothesis using the first approach mentioned by Jennions & Oakes (*in press*), an examination of the allometric patterns of FA in the redcollared widow. The sensitivity of the birds to captivity and environmental conditions unfortunately prevented me from conducting choice chamber experiments or comparing the reproductive success of individual birds, although both these approaches were attempted.

Chapter I deals with questions (1) and (2) above, while the last two questions are covered in Chapter II. My final chapter is essentially a review of the FA hypothesis, and my interpretation of it's limitations and how these preclude the universal use of the hypothesis as a means of testing between good genes and arbitrary traits models of sexual selection.

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I. Phenotypic variation and sexual size dimorphism in the Redcollared widow

Abstract

Sexual selection can only be invoked as an explanation for the evolution of elaborate traits if certain preconditions about patterns of variation in that trait are confirmed. I test the prediction that male tail size and symmetry should vary more than other morphological traits and homologous structures in the redcollared widow by documenting intrapopulation variation in trait size, since potential mates and rivals must be able to perceive differences in ornament size if sexual selection is to operate. In addition, patterns of sexual size dimorphism were determined in an attempt to elucidate the possible causes of this dimorphism. Tail length is more variable than other traits for adult males, juvenile males and females. In addition, the degree of fluctuating asymmetry of the tail is greater than for other traits. There appears to be sufficient variation in ornament size and symmetry for females to distinguish between conspecific males. This suggests that sexual selection may be responsible for the evolution of the long tail of male birds. Male birds were significantly larger than females in all body size measures, although males were only slightly bigger than females except for wing length. It seems likely that dimorphism in wing length is an attempt to compensate for the aerodynamic costs of longer tails. No conclusions could be drawn for the cause of size dimorphism in other traits.

Introduction

Sexual selection is often invoked to explain the existence of sexual dimorphism in body size and/or appearance (Andersson 1994). Indeed, the dimorphism prevalent in many polygynous bird species served, in part, as the inspiration for Darwin's (1871) theory of sexual selection. However, field workers are often negligent about verifying preconditions and predictions of theoretical models of sexual selection. Barnard (1994) points out that before sexual selection can be invoked to explain the evolution of dimorphism in trait size the following preconditions must be met : 1) the trait must be heritable and variable; 2) potential mates and rivals must be able to perceive the variation; 3) the trait must tend to confer greater reproductive success on its bearer and his mate. Part of verifying these preconditions is the documentation of patterns of variation in body and ornament size, and determining whether there is sufficient variation in ornament size for conspecifics to perceive differences between individuals.

It is thus vital that the prediction that sexual ornaments vary more in size than other morphological traits (Darwin 1871) be tested (Barnard 1991) before a given trait can be said to have evolved in response to sexual selection. In the light of recent interest in fluctuating asymmetry, it is equally essential that variation in ornament symmetry be documented and compared to symmetry of other bilaterally symmetrical morphological traits. It is also necessary to test the prediction of Møller and Pomiankowski (1993) that sexual ornaments should display higher degrees of FA than other morphological traits.

Most models of sexual selection implicitly assume significant variation among conspecifics (Barnard 1995), but sexual selection may reduce genetic variation in ornament size within a population over time (Cade 1984) since males with smaller ornaments will presumably leave fewer offspring. This reduction may be mirrored by a reduction in genetic variation in fitness (Falconer 1989), although mutations and fluctuating selection may generate additive variation (Hamilton & Zuk 1982). It has also been argued that variation in ornament size may be maintained if ornaments are condition-dependent (Andersson 1986). However, a number of empirical studies of phenotypic variation in ornaments and other morphological traits (*e.g.* Craig 1989; Barnard 1991; Evans & Barnard 1995) suggest that ornament size is not always significantly more variable than other traits.

Sexual selection research has focused primarily on explaining the evolution of elaborate traits, but sexual dimorphism in body size is one of the most common and conspicuous differences between males and females in animals (Höglund 1989; Shine 1989; Andersson 1994). Three main hypotheses for the evolution of sexual size dimorphism (SSD) are proposed (Hedrick & Temeles 1989), namely the sexual selection, intersexual food competition and reproductive role division hypotheses. Of these, the sexual selection hypothesis is the most popular (Shine 1989). Indeed, it has been suggested that the stronger the sexual selection pressure on a species, the more marked the SSD will be (Payne 1984). On the other hand, SSD may merely be an indirect consequence of female preference for large ornaments. For example, dimorphism in wing size in long-tailed birds may be a consequence of males compensating for costly sexually-selected tails (Balmford, Jones & Thomas 1994).

The redcollared widow is markedly dimorphic, as the males possess extremely long tails and there is distinctive dichromatism. Furthermore, the species is polygynous and the male provides no parental care (Maclean 1993). Conventional wisdom would thus suggest that sexual selection is a particularly strong selective force in this species. The redcollared widow is therefore an ideal species to test the prediction that ornaments are more variable in size and symmetry, than traits under stabilizing natural selection pressure.

Materials and Methods

Morphometric data were collected from natural populations during the course of a field study from 1993-1996. The study area was located in Bisley Valley Nature Reserve within the city of Pietermaritzburg municipal boundary, in KwaZulu-Natal (29° 39' S and 30° 23' E; altitude ~870m). Field seasons lasted from October to February.

Birds were captured using mistnets at their night roost, which was situated in a reed bed. Birds were ringed and various morphometric measurements taken. It was occasionally necessary to take birds back to the laboratory to complete measurements. These birds were released at first light the following day. Tarsus and culmen length were measured to the nearest 0.1mm with Vernier's calipers. Wing length, tail length (each retrix) and primary length (9 primaries in each wing) were recorded to the nearest 0.5mm with a metal ruler. Body weight was determined using a Pesola spring balance to the nearest 0.5g.

The degree of fluctuating asymmetry (FA) was measured for tail length, tarsus length, wing length and primary length. Relative asymmetry values were calculated as the numerical value of (R - L) / ((R + L)/2), where R is the length of the right side of the trait and L is the length of the left side (Palmer & Strobeck 1986; Møller 1990). For traits such as the tail or primaries, where there were more than one paired structure, a mean FA value was calculated.

Measured birds were grouped in one of three categories- adult male, brown (juvenile or cryptic) male or female. Adult males were all birds in full nuptial plumage, while brown males were all males without any trace of breeding plumage *i.e.* retaining female colouration. It should be pointed out that since I had no independent way of assessing a bird's age, the distinction between adult and brown male is purely arbitrary with respect to age. Sexual dichromatism made the separation of adult males from the other two groups easy and error free. However, separating females from brown males was subject to error. Females and brown males were differentiated on the basis of wing size, as female wings, according to Maclean (1993), range in size from 60.5-70cm (N=189).

The coefficient of variation (CV) was calculated for each of the measured variables, as an indication of the degree of size variation for that specific trait. CV values for body size characters and tail length were compared to determine whether or not secondary sexual ornaments varied in size more than other morphometric characters. CV values for the degree of fluctuating asymmetry of tail, tarsus, wing and primaries were compared to test the prediction that FA is higher for sexual ornaments than characters under stabilizing natural selection pressure.

One-way analysis of variation (ANOVA), with a one-tailed significance test, was used to determine whether the degree of FA was higher for ornaments than other morphological traits. Where significant differences between FA values were detected, a Least Significant Difference *a priori* multiple range test was used to determine where the difference lay. To avoid Type I errors induced through repeatedly testing the same null hypothesis, multiple analysis of variance (MANOVA) was used to determine whether adult males were significantly larger than females or brown males in any of the traits measured. The test statistic Wilk's lambda (likelihood ratio) varies between 0 and 1 and test the overall significance of the effects of the treatments on the dependent variables. Should this test be significant, the univariate F-tests are consulted to determine which of the factors cause the overall significant effects. Statistical tests were done using either Statgraphics Plus (Version 7.0) or, in the case of MANOVA, Systat for Windows (Version 5).

Results

Phenotypic variation in size and FA

Coefficients of variation for body size measures of adult males (Table 1) ranged from 2.9% to 6.8%, with wing, culmen and tarsus being least variable. This pattern was also observed for females and brown males. Tail length was the most variable character for all three sex categories, followed by body mass. Females showed more variation in body size than either adult or brown males, but this may be an artifact of the difficulties in differentiating between females and brown males. These results concur with those of Barnard (1991) and Craig (1989), since morphological traits vary less in size than the tail, or ornament.

There was considerable variation in the degree of fluctuating asymmetry found in all morphological traits (Table 2). Male tail FA was more variable (CV=105.4%) than primary, tarsus or wing FA (CVs ranging from 55% to 87.6%). Furthermore, tail FA was significantly higher than either tarsus, primary or wing FA (One-way ANOVA: $F_{3,127}$ = 17.977; $P < 0.001$). The variation in wing FA was surprisingly high considering the aerodynamic importance of wing symmetry (*e.g.* Thomas 1993), but this is possibly a consequence of the degree of accuracy of measurement. Since left and right wing length did not differ by more than 1.5mm for any bird, the level of accuracy (0.5mm) is probably inadequate to reliably assess variation in wing symmetry. Nonetheless, as one would expect, wing FA was very low.

Sexual size dimorphism

Males were bigger than females for all morphometric characters, and adult males were bigger than brown males (Table 1). This size dimorphism was significant for all characters (MANOVA: F =40.260; Wilk's lambda = 0.174; $P < 0.001$). However, SSD is relatively slight in that males are only slightly bigger for skeletal traits, despite the fact that males and females are so noticeably dimorphic in terms of plumage during the breeding season. Males were bigger than females by only 4.5% for culmen, 5.8% for tarsus and 14.8% for wing length. Tail length was obviously much bigger in adult males, and males were consequently 16.2% heavier than females. The size difference between adult and brown males was even smaller. Adult males were bigger than brown males by 1.9% for culmen, 3.8% for tarsus and 6.6% for wing length.

These results are similar to those of Barnard (1995), who found that male paradise and shaft-tailed whydahs only had slight sexual size dimorphism, despite obvious plumage dimorphism.

Discussion

The data support the hypothesis that ornaments are more variable in size than other morphological characters. One of the preconditions for sexual selection to be invoked as an explanation for the evolution of long tails is thus verified. The difference in male intrapopulation trait size variability between secondary sexual characters and other morphological characters (Table 1) suggests that sufficient variation does exist for females to be able to perceive differences in epigamic trait size between males. However, this does not necessarily imply that sexual selection is acting on the population, particularly as the degree of variation necessary for females to be capable of discriminating between males has not been quantified. Nonetheless, the data suggests that it is possible for females to select males on the basis of ornament size.

Furthermore, it should be noted that this phenotypic variation does not necessarily reflect genetic variation, although good gene models assume a direct relationship between phenotypic expression and genetic quality (Andersson 1994). In the case of sexual ornaments, environmental sources of variation include abrasion, the timing and rate of ornament growth, and the overall nutritional condition of the males, although these may all have an underlying genetic component (Barnard 1991). This study did not control for the influence of differential rates of abrasion and growth on the degree of variation in ornament size, as there were insufficient recaptures to calculate mean growth/abrasion rates. These differential rates serve to increase the amount of phenotypic variation females are faced with (Cherry 1990; Barnard 1991), making it easier for females to discriminate between males, but more difficult for females to accurately distinguish between males on the basis of genetic viability. This implies that females cannot use trait size alone as a reliable indication of male quality, unless timing and rate of ornament growth are directly linked to genetic viability. If good genes sexual selection is operating, then females may have to utilize more than one cue (*e.g.* ornament size and symmetry) when assessing male quality to overcome the problems created by differential growth and abrasion rates. However, it should be remembered that for sexual selection to drive the evolution of elaborate ornaments, choosy females only have to do better, on average, than they would by mating randomly (Lotem 1993).

Interpretation of the patterns of variation in ornament size, and determining the implications in terms of the nature of selection on ornaments, is very complex for a number of reasons. Firstly, phenotypic variation is not a good index of genetic variation, as a result of phenomena such as variable developmental environments, polygenic effects, unexpressed alleles and mutations (Barnard 1994). In addition, the assumption that evolutionary history can be inferred from current processes has been questioned (Andersson 1993). It is thus not possible to make inferences about the nature of selection on secondary sexual characters from the data presented here.

There is sufficient variation in tail FA for females to distinguish between males on the basis of symmetry (Table 2), although this does not necessarily imply that females do actually use symmetry as a cue. In order to establish whether or not females are actually using symmetry as a cue when distinguishing between males it is necessary to conduct choice-chamber experiments, where the degree of FA in an ornament is covaried, within natural limits, with tail length. Even if this sort of study has established that females are using symmetry as a cue it is still necessary, however, to determine whether there is sufficient intra-population variation for females to perceive differences between males on the basis of symmetry.

Møller & Pomiankowski (1993) suggested that sexually selected traits should show higher degrees of FA than other morphological traits, since the latter are usually subject to strong stabilizing selection pressure, while the former are assumed to be under intense directional selection pressure. The intensity of directional selection pressure is indirectly proportional to developmental stability (Møller 1993; Møller & Pomiankowski 1993). It is therefore argued that sexual ornaments are less well developmentally canalized than functionally important morphological traits, and subsequently display higher degrees of FA. This prediction is supported by this study, since the tail has a higher degree of FA than any of the other traits measured (Table 2).

While this can be seen as confirmation of the importance of directional selection and disruption of developmental homeostasis in ornament evolution, it goes against some aspects of sexual selection theory (Jennions & Oakes *in press*). The handicap principle suggests, for example, that males express ornaments such that they are condition-dependent. This kind of fine-tuned response to body condition, while requiring some phenotypic plasticity, suggests that a tightly controlled developmental system is required (Jennions & Oakes *in press*). Furthermore, Møller (1990) suggests that males must reach a compromise between tail length and symmetry, and that this compromise should reflect the genetic quality of each male. This argument is the basis for his FA hypothesis, but again it implies the existence of a tightly controlled developmental system which is at odds with the idea that higher FA is a consequence of a breakdown in developmental homeostasis.

Three hypotheses have been put forward to explain the existence of SSD, namely the sexual selection, food competition and dimorphic niche hypotheses (Hedrick & Temeles 1989). In the case of the redcollared widow it is unlikely that either of the latter two hypotheses can satisfactorily explain the existence of the SSD found. The most striking dimorphism between the sexes is found in wing length (Table 1), and this could not be a consequence of either food competition or reproductive role division. It seems likely that sexual selection is responsible for the evolution of this SSD. However, the question remains- is sexual selection directly or indirectly responsible for size dimorphism in this species? If larger body size were a consequence of female preference for larger males, then SSD could be attributed to direct sexual selection. If this was the case then one would expect body size and ornament size to be closely correlated. This does not appear to be the case in the redcollared widow (Fig. 1), so it seems likely that direct sexual selection is not responsible for the evolution of SSD.

Recent work suggests that sexual selection may operate indirectly to cause morphological differences between the sexes. If sexual selection results in the evolution of costly ornaments in one sex, then natural selection may favour the evolution in that sex of other traits which minimize those costs (Balmford *et. al.* 1994). Evans & Thomas (1992), for example, have demonstrated that the aerodynamic costs of long tails in the sunbird *Nectarina johnstoni* are partly offset by increased wing length. This result is supported by across-species studies done by Andersson & Andersson (1994) and Balmford *et. al.* (1994).

While no definite conclusions about the cause of sexual size dimorphism can be drawn from the data presented here, it is suggested that the SSD evident in the redcollared widow can be attributed indirectly to sexual selection. The fact that dimorphism is most evident in wing length intimates that males need longer wings to compensate for the aerodynamic costs of flight with a long tail. This is supported by the fact that wings are longer in adult males than in brown males (Table 1). In addition, the longer wing may help compensate for the aerial display flight of the male widow, which involves slow flying over the territory with rapidly beating wings. The cost of forward flight increases dramatically when speed decreases from normal transport towards slow flight and hovering (Norberg 1990). It is therefore likely that the wing dimorphism can be regarded, in part, as a response to male courtship behaviour. There are thus two indirect sexual selection mechanisms, not mutually exclusive, which may have lead to the evolution of SSD in wing length.

The SSD in tarsus and culmen length, although not as marked as wing dimorphism, are more difficult to explain. It is possible that the larger body size of males is a consequence of male-male contest competition, but there is no direct evidence to support this explanation. However, both Andersson (1993) and Höglund & Lundberg (1987) found that while no mating advantage of body size could be found within leks, established males were indeed larger than non-territorial males. In the redcollared widow it was not possible to determine whether this is the case, since I was not able to ascertain breeding status (*i.e.* territory holder *vs* floater) for all the males whose morphometrics are used in this study.

Conclusions

It would appear that sufficient phenotypic variation in both ornament size and symmetry exists for females to be capable of perceiving differences between males on the basis of either, or both, of these cues. Further work is needed, however, before it can be claimed that females do in fact select males using these features as cues. In addition, no conclusions can be made concerning genetic variation in the population, and any comments on the nature of selection on tail length and symmetry in the redcollared widow would therefore be pure speculation. On the other hand, it can be said that ornaments do vary more in size than other morphological traits. The prediction that ornaments will display higher degrees of fluctuating asymmetry than other bilaterally symmetrical traits is also sustained by the data presented here.

There is significant, but slight, sexual size dimorphism present in this population, with adult males being larger than both females and brown males, and brown males being larger than females. However, the relative roles of natural, intrasexual and intersexual selection in the evolution of this dimorphism remain unclear. It is suggested that wing dimorphism is a consequence of the high aerodynamic costs of the long tail ornament, but the reasons for large general body size are uncertain.

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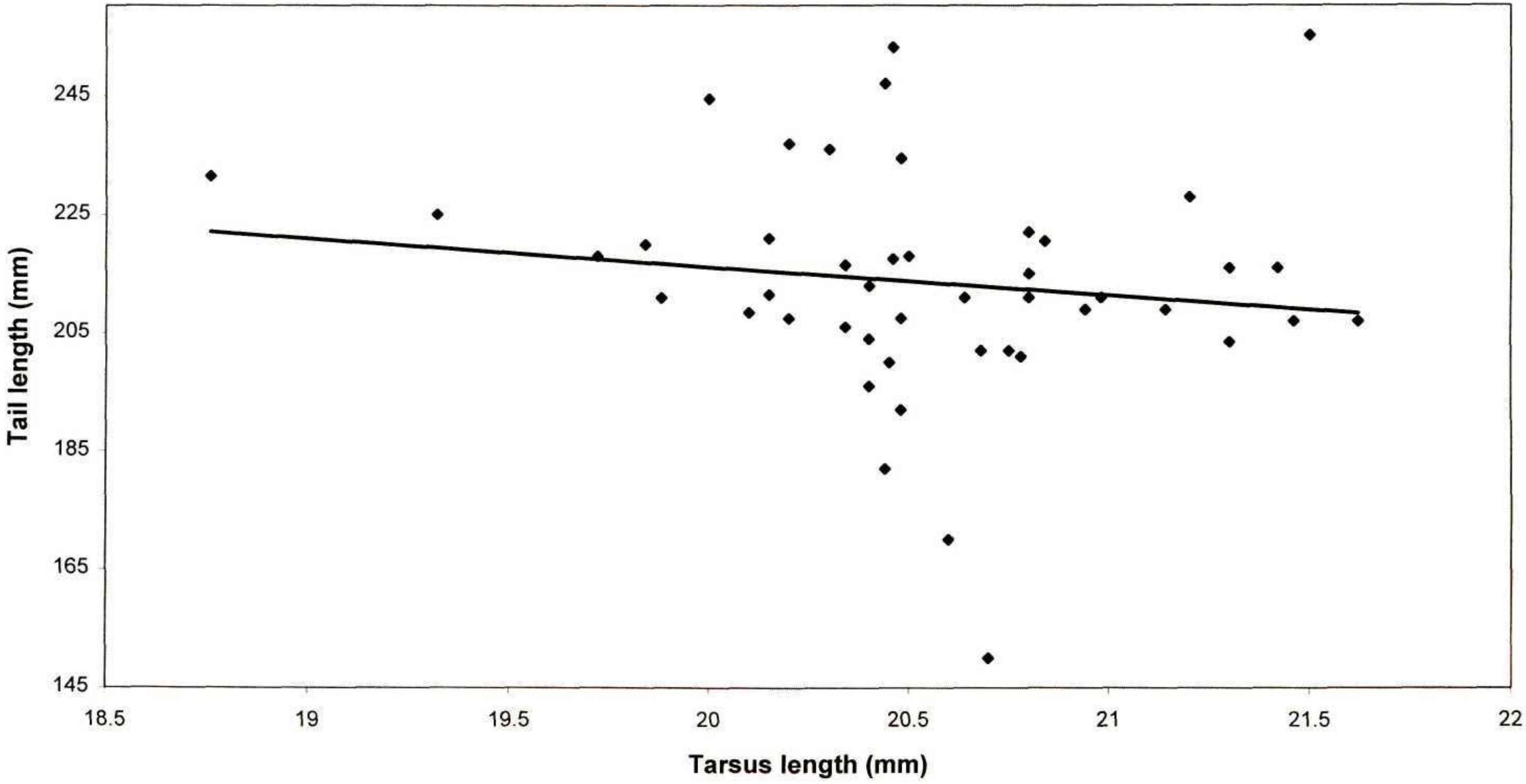
Table 1. Variation in adult male, brown male and female body size

	Culmen length	Tarsus length	Wing length	Tail length	Mass
Adult male					
N	52	55	58	41	51
Mean	9.78	20.69	76.11	218.06	21.97
S.D.	0.38	0.99	2.24	15.51	1.49
CV(%)	3.8	4.8	2.9	7.1	6.8
Brown male					
N	27	27	27	28	23
Mean	59	19.94	71.41	51.38	20
S.D.	0.36	0.99	1.32	4.95	1.14
CV(%)	3.7	5	1.9	9.6	5.7
Female					
N	58	58	58	57	54
Mean	9.34	19.49	66.28	45.83	18.9
S.D.	0.38	1.04	2.32	3.49	1.32
CV(%)	4	5.3	3.5	7.6	7

Table 2. Variation in the degree of fluctuating asymmetry

	Primary asymmetry	Tail asymmetry	Wing asymmetry	Tarsus asymmetry
Adult male				
N	39	41	28	24
Mean	0.021	0.097	0.017	0.01
S.D.	0.012	0.103	0.015	0.008
CV(%)	55	105.4	87.6	78.9

Fig. 1 Tail length as a function of tarsus length



II. The relationship between ornament size and symmetry: does the tail reliably signal male quality in the Redcollared Widow?

Abstract

It has been suggested that fluctuating asymmetry (FA) may provide a direct test of whether "arbitrary traits" or "good gene" sexual selection is responsible for the evolution of epigamic traits, since fluctuating asymmetry is an epigenetic measure of stress during development. However, tests of the FA hypothesis have yielded equivocal results, and the arbitrary trait-good gene debate continues. The FA hypothesis predicts a negative relationship between ornament size and asymmetry. In non-ornaments, a U-shaped relationship between trait size and asymmetry is expected. I tested these predictions in the redcollared widow (*Euplectes ardens*), a polygynous, sexually dimorphic bird. The relationship between trait size and asymmetry was measured for tail, tarsus and wing length. No significant linear or second-order polynomial relationships between trait size and asymmetry were found. Furthermore, no relationship was found to exist between asymmetry and two indices of body condition. This suggests that the tail does not reliably signal male quality in the redcollared widow. However, I argue that the assumptions of the FA hypothesis are too simplistic for this conclusion to be drawn with any confidence.

Introduction

The debate between good genes and arbitrary traits sexual selection remains one of the most controversial topics in evolutionary biology (Pomiankowski 1987; Maynard Smith 1991; Andersson 1994). Behavioural 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 & Thornhill 1994), and perhaps resolve the good genes versus arbitrary traits debate (Møller & Höglund 1991). However, findings on the condition-dependence of FA have been equivocal (*e.g.* McLachlan & Cant 1995; Andersson & Iwasa 1996), and the question remains: do the ornamental tails of birds reliably signal male quality?

FA 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 & Strobeck 1986; Polack & Trivers 1994; Watson & Thornhill 1994). Since 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 & Strobeck 1986; Parsons 1990; Palmer 1996). In fact, FA is known to be diagnostic of a large range of stressors borne during development (Polack & Trivers 1994), as it develops in response to various kinds of environmental and genetic stress

(Leary & Allendorf 1989; Parsons 1990). As a general rule, individuals experiencing greater stress during development exhibit higher degrees of FA (*e.g.* Møller & Pomiankowksi 1993; Nilsson 1994; Swaddle & Witter 1994). In addition, both the likelihood of an individual developing asymmetrically and the degree of FA in an individual seem to have a heritable basis (Soulé 1982; Leamy 1984; Palmer & Strobeck 1986; Thomas *in press*).

Sexual ornaments generally display higher levels of FA than other morphological traits (Møller & Höglund 1991; Møller 1993a;b). Different morphological characters differ in their susceptibility to both environmental and genetic stress because of differences in the extent to which they are buffered developmentally (Møller 1993b). Sexual ornaments are assumed to be under intense directional selection pressure, and should therefore be less well canalized developmentally. Since they are relatively developmentally unstable, environmental perturbations will have a disproportionate impact on ornamental traits relative to other morphological characters (Møller 1992). Any stress encountered by an individual during development should thus be reflected in the degree of ornament FA before that of any other feature. In addition, many polygynous birds, which are traditionally regarded as being under stronger sexual selection pressure (Krebs & Davies 1992), have both eclipse and nuptial plumage. The ornaments of these birds are produced just prior to the onset of the breeding season, and any information conveyed by FA is thus likely to represent recent stress.

As a result of these characteristics of FA, various authors have suggested that

FA may provide an indirect measure of fitness (*e.g.* Palmer & Strobeck 1986; Jones 1987; Hill 1995). Møller (1990) suggested that FA should thus be a reliable measure of an individual's ability to produce extravagant sexual traits, since only males in good physical condition will be capable of producing ornaments which are both large and symmetrical. Individuals may, therefore, assess the symmetry of their conspecifics during mate choice, in order to gauge mate quality, as the degree of FA displayed by an individual should reflect his ability to deal with environmental and genetic stress. Indeed, Møller (1990) argues that tail ornaments reflect a strategic choice on the part of the male, since each male must reach a compromise between tail length and symmetry. Since 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 irrespective of whether females directly assess symmetry, provided the ornament is condition-dependent. On the other hand, if a trait is under natural selection pressure one would expect a U-shape relationship between trait size and FA (Møller 1993a;b; Watson & Thornhill 1994). Examination of allometric patterns of symmetry may thus allow researchers to determine which ornaments are condition-dependent (Jennions & Oakes *in press*).

In order to explore the FA hypothesis it is necessary to answer two fundamental questions: (1) is secondary sexual character symmetry a reliable indicator of individual quality?, and (2) is symmetry used directly as a cue by conspecifics during mate choice? (Jennions & Oakes *in press*). This study aims to answer the first question by examining the allometric relationship between ornament size and the degree of FA in the Redcollared Widow *Euplectes ardens*, a polygynous and highly sexually dimorphic Euplectid (Maclean 1993). Traditional wisdom suggests that highly polygynous animals are subjected to more intense sexual selection pressure than monogamous animals (Darwin 1871; Møller 1990; Møller & Pomiankowksi 1993), because the potential advantage to an attractive male, in terms of reproductive success, is greater for polygynous animals (Krebs & Davies 1992). Male redcollared widows, when in nuptial plumage, are black with very long tails ($\bar{x}$= 218.06 mm) and possess a scarlet collar on the throat region. The tail, which is comprised of twelve retrices, is graduated and the potential for tail asymmetry to influence female choice is considerable. The long tail may be energetically expensive to produce and maintain, although this has not been quantitatively demonstrated. Furthermore, the 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 female choice should be aimed at securing the best possible genes for her offspring, since no other benefits are accrued through her choice of mate.

Materials and Methods

Morphometric data were collected from a natural population during the course of a field study from 1993-1996. The study area was located in Bisley Valley Nature Reserve within the City of Pietermaritzburg municipal boundary in KwaZulu-Natal, (29° 39' S and 30° 23' E; altitude ~870m). Field seasons lasted from October to February.

Birds were captured using mistnets at their night roost. Each bird was ringed and various morphometric measurements were taken. Tarsus and culmen length were measured to the nearest 0.1mm with Vernier's calipers. Wing length, tail length (each retrix) and primary length (9 primaries in each wing) were recorded to the nearest 0.5mm with a metal ruler. Body weight was determined using a Pesola spring balance to the nearest 0.5g.

The degree of FA was determined for tail length, tarsus length, wing length and primary length. Relative asymmetry values were calculated as the numerical value of (the difference between the length of left and right characters) / (the length of the left side plus the right side/2) (Palmer & Strobeck 1986; Møller 1990). For traits such as the tail or primaries, where there were more than one paired structure, a mean FA value was calculated. Repeatability measures were calculated, according to the method of Lessels & Boag (1987), for measures of each of the traits (Table 1). Swaddle *et. al.*

(1994) suggest that it is not sufficient to determine repeatability measures on the traits themselves, and recommend that a mixed-model ANOVA to test between measurement error and the asymmetry itself is more appropriate. However, due to the large increase in handling time necessary to measure each retrix repeatedly, this method of determining measurement error was not used, in order to minimize the stress on the animal. For the same reason, only five birds were used to calculate repeatability of FA. Nonetheless, it would appear that repeatability is high for both tarsus and tail length, but not for wing length (Table 1). However, I suggest that the low repeatability for wing length is merely a statistical artifact of the method of Lessels & Boag (1987) for testing repeatability. 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. Since most males had wing lengths of a very similar size (range of 3mm) and wing length was measured accurate to 0.5mm , the ratio of between and within group variance does not provide an adequate measure of repeatability.

If asymmetry values are to qualify as fluctuating asymmetry the frequency distribution of left minus right values should not differ from a normal distribution with a mean of zero (Palmer & Strobeck 1986). To test departure from normality a Komolgorov-Smirnov one-sample test was used, while a one-sample t-test was used to test whether the mean differed significantly from zero. For both these tests, the absolute values of the asymmetry were not used, as this would obviously change the outcome of the tests considerably. These tests were done for wing, tarsus and tail asymmetry.

In order to examine the allometric relationship between trait size and asymmetry, relative asymmetry (absolute value) was plotted against mean trait size for adult male tarsus, wing and tail. These relationships were tested for both linear and second-order polynomial regression (to test for a U-shaped relationship), as done by Evans *et. al.* (1995). Where appropriate, data which were not normally distributed were transformed.

No direct measure of the general body condition of the birds was recorded, but two different statistical estimates of body condition were used. First, Andersson, S. (1994) suggests that body condition can be calculated as the residual from a linear regression of log (body mass) on 3X log (tarsus length). Tarsus length is considered the most adequate univariate measure of size (Freeman & Jackson 1990), because growth of the tarsometatarsal bone is completed when young altricial birds leave the nest (Craig 1989). The calculated regression line between body mass and tarsus length thus represents the average relationship between body weight and size. If one assumes that weight is an indication of body condition, then the residuals of the regression can be used as an estimation of the condition of each bird. Log-transformations were used to remove the underlying effects of different dimensionality of mass (volume) and tarsus (length) (Andersson, S. 1994). Both tail length and tail FA were regressed against this estimate in order to determine whether either was related to body condition.

A second method, which does not rely on a single univariate measure of body size, was also used to estimate body condition. Three different measures of body size (tarsus length, culmen length and wing length) were plotted on the first two principal co-ordinates of 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 of the analysis. The residuals were then taken as an estimate of body condition, and regressed on both tail length and tail asymmetry.

All data analysis was done using Statgraphics Ver. 7.

Results

Do these structures demonstrate fluctuating asymmetry?

The criteria for determining whether or not a morphological trait demonstrates fluctuating asymmetry are that the differences between right and left side must be normally distributed with a mean of zero (Palmer & Strobeck 1986). Wing, tarsus and tail asymmetry are all normally distributed (wing: D= 0.16, P= 0.49, n=28; tarsus: D= 0.16, P=0.6, n= 24; tail: D= 0.17, P=0.204, n=41). In addition, one-sample t-tests showed that the mean did not deviate from zero for any of the traits (wings t= 1.643, P= 0.1, n= 28; tarsus t= -1.167, P= 0.3, n=24; tail t= 1.472, P= 0.15, n= 41). I shall therefore proceed with the assumption that all of these traits do demonstrate fluctuating asymmetry.

Does asymmetry vary with trait size?

The degree of fluctuating asymmetry and trait size were not linearly correlated for any of the traits. Despite the predictions of Møller (1990) that ornament size and asymmetry should be negatively correlated, the calculated linear regression model shows clearly that there is no predictable relationship between FA and tail length ($F_{1,40} = 0.001$; $P = 0.97$; $r^2 = 0.00$ %; see Fig. 1). Similarly, there was no significant linear relationship between FA and trait size for tarsus ($F_{1,23} = 0.16$; $P = 0.69$; $r^2 = 0.74\%$) or wing ($F_{1,27} = 0.28$; $P = 0.59$; $r^2 = 1.08\%$). There were no significant second order polynomial relationships between trait size and FA for any of the traits (tail: $F_{1,40} = 0.096$, $P = 0.93$, $r^2 = 0.005\%$; tarsus: $F_{1,23} = 1.15$, $P = 0.34$, $r^2 = 0.09\%$; wing: $F_{1,27} = 0.91$, $P = 0.42$, $r^2 = 0.07\%$), so the relationship between trait size and asymmetry cannot be described by a U-shaped function for any of the measured traits.

It should be pointed out that this study did not control for the stage of tail growth, due to the low recapture rate which made it impossible to determine mean growth or abrasion rates. However, it is unlikely that this has compromised the data, for a number of reasons. First, my morphometric data do not give any 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, I arbitrarily assigned the 1 September as day 1 in the season. As birds were caught and measured they were assigned the relevant day of the season from day 1. Tail length and 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 ($F = 119.03$; $df = 58$; $P < 0.001$; $r^2 = 67.62$ %), but not when asymmetry was regressed against day of the season ($F = 0.536$; $df = 58$; $P > 0.05$; $r^2 = 0.93$ %). This suggests that while 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 (see Figs. 2 & 3). 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 which are close to being fully developed. Finally, females have to make their choice on the basis of what is available at that point in 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?

When tail length is regressed against the residuals from the relationship between log (mass) and 3X log (tarsus) there is no significant relationship ($F_{1,32} = 0.418$; $P = 0.52$; $r^2 = 1.33\%$). Similarly, there is no significant relationship between tail FA and this index ($F_{1,32} = 0.832$; $P = 0.369$; $r^2 = 2.62\%$). Similar results were obtained using the PCA method of estimating body condition. The three different measures of body size were plotted using PCA, and the first principal component accounted for 39.67 % of the variance. The resultant regression models between body condition estimate and tail length ($F_{1,32}$ = 0.127; P = 0.72 ; r^2 = 0.41%) and body condition estimate and tail asymmetry ($F_{1,32}$ = 0.328; P = 0.57; r^2 = 1.05%) were not statistically significant. This suggests that neither tail length nor tail FA are condition-dependent. However, body mass may provide a confounded measure of body condition. The effects of differential crop fill, which may lead to considerable short-term variation in body mass, were not controlled for. Considering the fact that mass did not differ much between male birds (range of 3.5g), it is essential that body mass is recorded accurate to at least 0.1g and that differential crop fill is factored out if body mass is to be used to estimate body condition.

Discussion

The predictions of Møller's (1990) FA hypothesis are not supported by this study, as males with longer tails do not demonstrate lower levels of asymmetry. What does this lack of a negative relationship between ornament size and FA mean in terms of sexual selection theory? According to Møller (1993a;b), these results indicate that the tail ornament in the redcollared widow is under arbitrary traits sexual selection pressure, since the tail is not a condition-dependent ornament. However, the interpretation of allometric patterns of symmetry is not quite as simplistic as Møller would have us believe. There are, in fact, a number of problems with the inherent assumptions of the

FA hypothesis which confuse the interpretation of these patterns.

The prediction of a negative relationship between ornament size and asymmetry is based upon the assumption that both trait size and asymmetry are under intense directional selection pressure, since males should be attempting to optimize both size and symmetry (Møller 1993b). 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 which large ornaments have on viability (Kirkpatrick & Ryan 1991; Balmford & Read 1991; Jennions & Oakes *in press*). At equilibrium, an ornament should be considered as being under two opposing forms of directional selection (Møller & Pomiankowski 1993). This does not necessarily apply to ornament symmetry, since both sexual selection and natural selection pressure should select for increased symmetry. Nonetheless, it is possible that the allometric relationship between ornament size and asymmetry will differ depending on whether or not an ornament, and its associated signalling system, has evolved to equilibrium. For example, if ornament size is being constrained by natural selection a U-shaped relationship, conventionally associated with stabilizing natural selection (Watson & Thornhill 1994), might be expected. Ideally, the lack of a negative relationship between ornament size and asymmetry shouldn't be interpreted as evidence that an ornament is not condition-dependent unless one has some 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 does impose some form of direct fitness cost on the individual in terms of decreased viability or higher energetic costs (*e.g.* Evans *et. al.* 1994), it doesn't necessarily follow that high quality males will have lower levels of asymmetry (Jennions & Oakes *in press*). It has been pointed out by Grafen (1990) that in a stable signalling system a handicap can result in better quality males having lower viability than medium quality males. This situation would arise if the benefits of increased ornament size exceed 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 then males may attempt to maximize ornament size even if this means developing asymmetrically.

Second, there 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 lower quality individuals (Enquist 1985; Zahavi 1987; Grafen 1990). Jennions & Oakes (*in press*) point out that almost no work has been done to identify the costs of increasing ornamental symmetry, and yet the FA hypothesis can only be valid if these costs exist, and if they are greater for low quality males. There is empirical evidence to suggest that high quality males display lower levels of asymmetry, but this only constitutes indirect evidence that there is a cost to developing symmetrical ornaments. Furthermore, in terms of the possession of symmetrical ornaments, the available experimental evidence suggests that asymmetry is far more costly than symmetry in the case of the ornamental tails of birds. Møller (1991)experimentally manipulated the degree of FA in the tail of the Barn Swallow (*Hirundo rustica*), and showed that maneuverability was negatively correlated with asymmetry. Similar results were obtained by Evans *et. al.* (1994) for the red-billed streamertail (*Trochilus polytmus*). In fact, the theoretical and empirical evidence that asymmetry in birds is energetically expensive is so compelling that various authors (*e.g.* Balmford *et. al.* 1993; Evans 1993) have suggested that negative relationships between trait size and asymmetry would be expected purely as a consequence of natural selection. This suggests that asymmetry would in fact constitute more of a handicap than symmetry would. If the tail were a handicap, and an expensive signal was required by females, it could be argued that high quality males should be more asymmetrical than low quality males. There is sufficient evidence to refute this argument, but it does illustrate 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.

The above-mentioned issues mean that while a negative relationship between size and asymmetry could be regarded as evidence that an ornament is condition-dependent, the absence of such a relationship does not necessarily imply that the ornament is not condition-dependent. The issue is complicated further by the suggestion of some authors (Palmer & Strobeck 1986; Balmford *et. al.* 1993; Evans 1993; Evans *et. al.* 1994; 1995) that the mechanical constraints of FA on flight performance in birds may be sufficiently high that natural selection alone can explain negative relationships between FA and the size of ornamental tails. Experimental manipulation of tail length and symmetry in the red-billed streamertail has shown that the aerodynamic effects of FA are dependent on the length of the tail, having more pronounced adverse effects on maneuverability as tail length increases. There is thus evidence to support the idea that natural selection alone may be responsible for negative relationships between tail length and FA in birds. The fact that such a relationship may be selectively advantageous because of mechanical and aerodynamic factors would not , however, preclude the assessment of such patterns by interacting individuals (Evans *et. al.* 1994). Indeed, Evans (1993) argues that the mechanical effects of asymmetry may act to enforce honest advertising by ensuring that males do not grow their tail ornaments longer than they are capable of without losing symmetry. Nonetheless, this evidence does cast doubt on the integrity of the theoretical assumptions upon which the FA hypothesis is based.

A U-shaped relationship is predicted for traits which are considered to be under natural selection pressure, such as wing symmetry or tarsus symmetry. The fact that none of the measured traits in the redcollared widow display a U-shaped relationship between size and asymmetry is therefore quite puzzling. The fact that there is no U-shaped relationship between trait size and asymmetry for tarsus and wing, in particular, is difficult to explain since these traits are presumably not under sexual selection pressure but are purely products of natural selection. However, it should be pointed out that larger samples might yield results which fit the expected U-shaped function better. This applies particularly to wing symmetry, which is likely to be under especially strong stabilizing natural selection pressure due to the aerodynamic importance of symmetrical wings. Since male widows have to deal with large cumbersome tails during the breeding season I submit that wing length is under extremely tight developmental control, and relatively few males will possess asymmetrical wings. It has been suggested (see Chapter I) that wing size dimorphism in the redcollared widow is a consequence of the aerodynamic costs of the large tail in males, emphasizing the importance of natural selection in determining wing size. Very large sample sizes are probably needed to detect individuals with asymmetrical wings.

While Evans *et. al.* (1995) found that there is a U-shaped relationship between tail length and the degree of FA in the red-billed streamertail, this was not the case for the redcollared widow. This suggests that the allometric relationship between ornament size and FA in the redcollared widow is not a consequence of selection to control for errors in development *i.e.* natural selection is probably not shaping tail shape.

Furthermore, the lack of a negative relationship between FA and body condition strongly suggests that symmetry is not used as a cue for female choice in the redcollared widow.

According to Møller 's (1990) FA hypothesis the lack of a negative relationship precludes the possibility that the tail evolved under good genes sexual selection pressure. However, I suggest that this is not necessarily the case. Because the redcollared widow is polygynous the potential benefits 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 redcollared widow, but it has been demonstrated in the longtailed widow *Euplectes progne* (Andersson 1982) and in Jackson's widow *Euplectes jacksoni* (Andersson 1989; Andersson 1992). I therefore submit that male redcollared widows attempt to maximize tail length, even if this means incurring asymmetrical development, because marginal increases in tail length may potentially 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 impact on maneuverability and consequently energy budgets (Balmford *et. al.* 1993; see also Møller 1991; Evans *et. al.* 1994). FA will therefore increase the costs of cheating, because the impact of FA on maneuverability increases with tail length (Evans *et. al.* 1994), and the tail can thus be regarded as a conditional handicap which 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 is essentially just another good genes sexual selection model, and tests of the hypothesis can only establish in which species the hypothesis holds true. Where the predictions are not met, there are too many other conflicting issues involved for one to state with any confidence that the ornament is not condition-dependent . It is clear from this study, however, that asymmetry cannot be regarded as a reliable indicator of male quality in the redcollared widow, although this does not preclude the possibility of tail length being condition-dependent.

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Table 1 Repeatability estimates for morphological traits used in this analysis

Tarsus	Wing	Tail
$F_{4,5} = 15.59$ $P < 0.005$ repeatability = 0.88	$F_{4,5} = 3.36$ $P > 0.05$ repeatability = 0.54	$F_{4,5} = 23.12$ $P < 0.05$ repeatability = 0.92

Fig.1 Tail asymmetry regressed against tail length

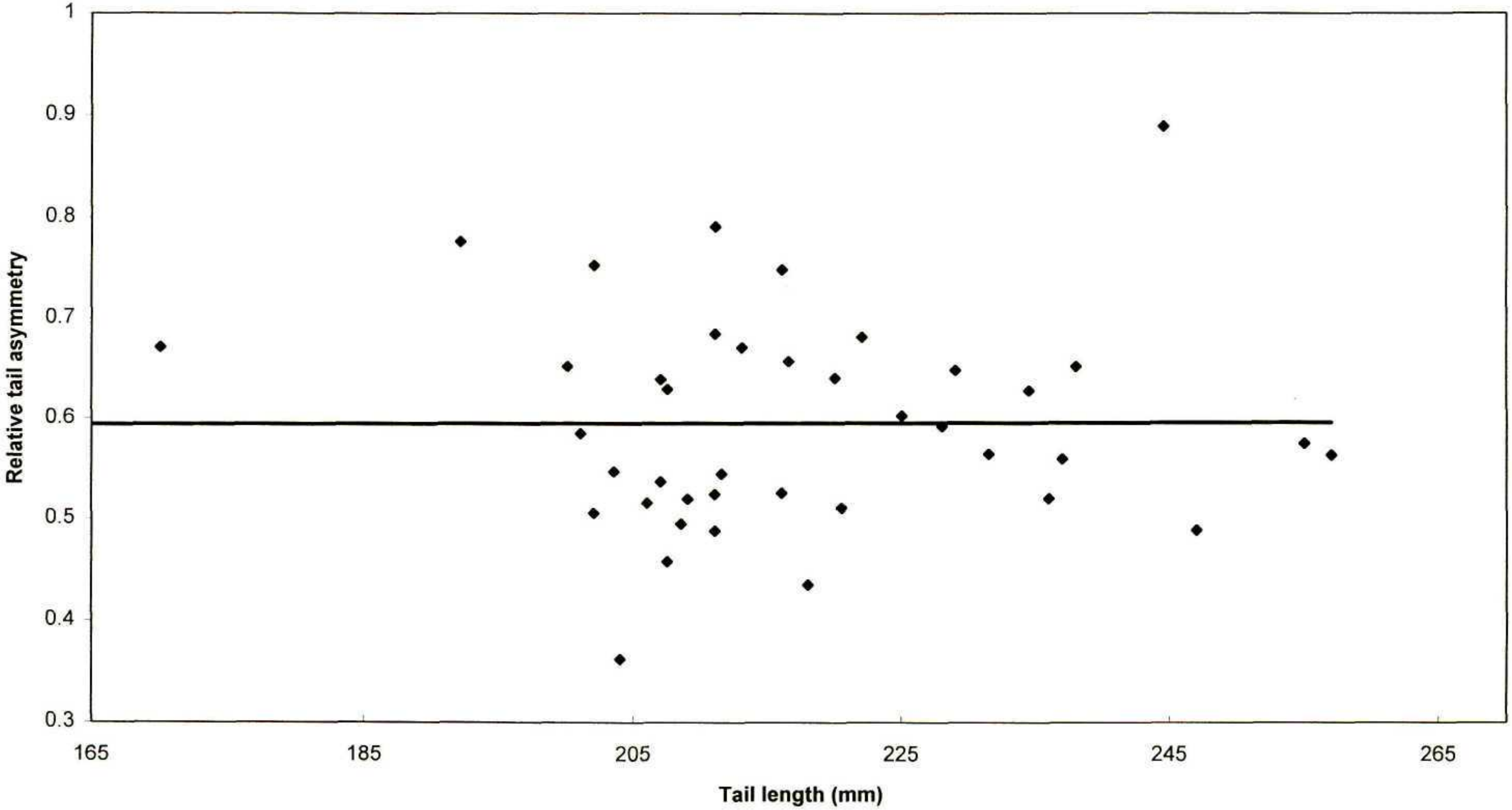


Fig.2 Tail length regressed on time of season

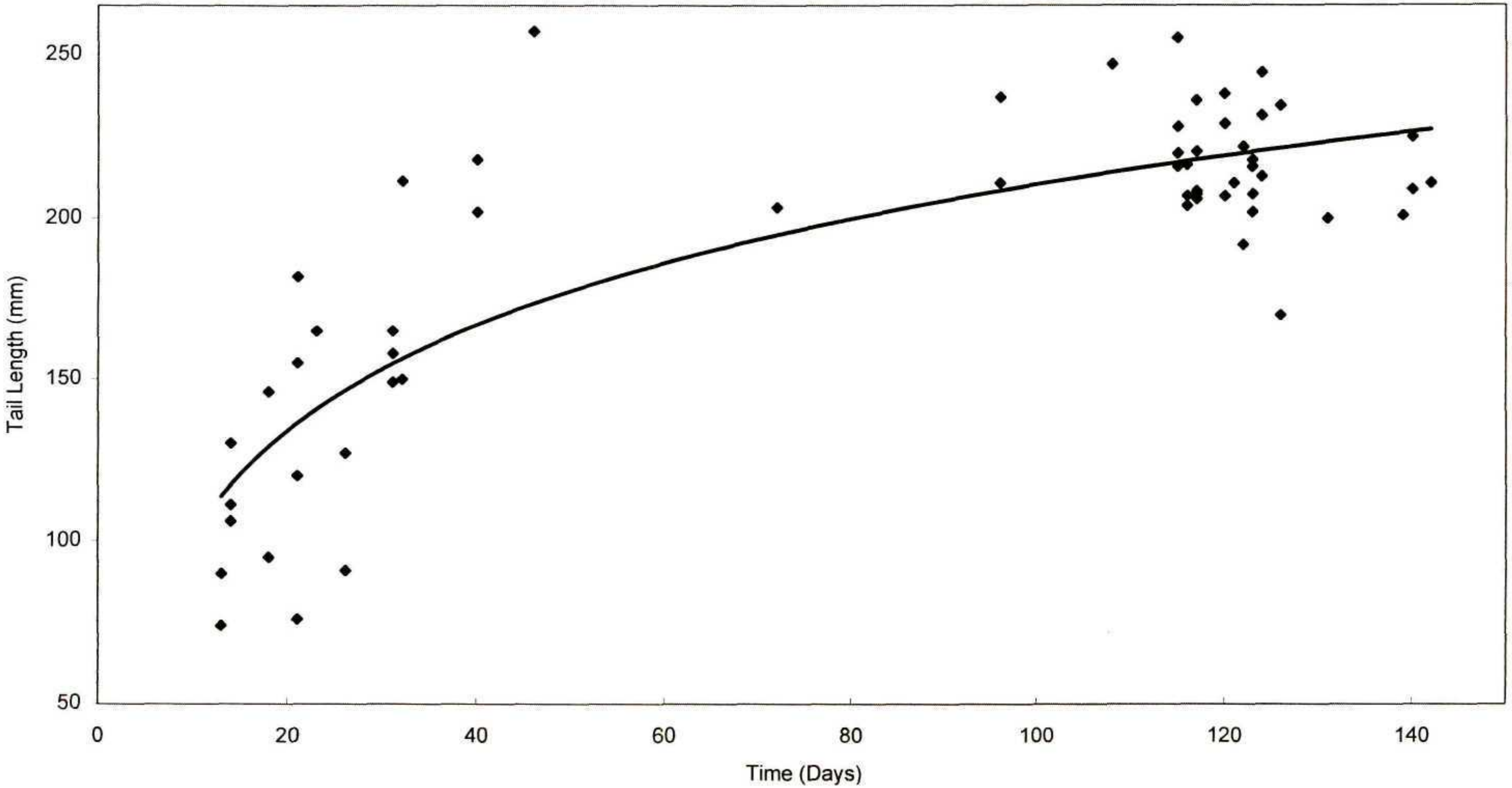
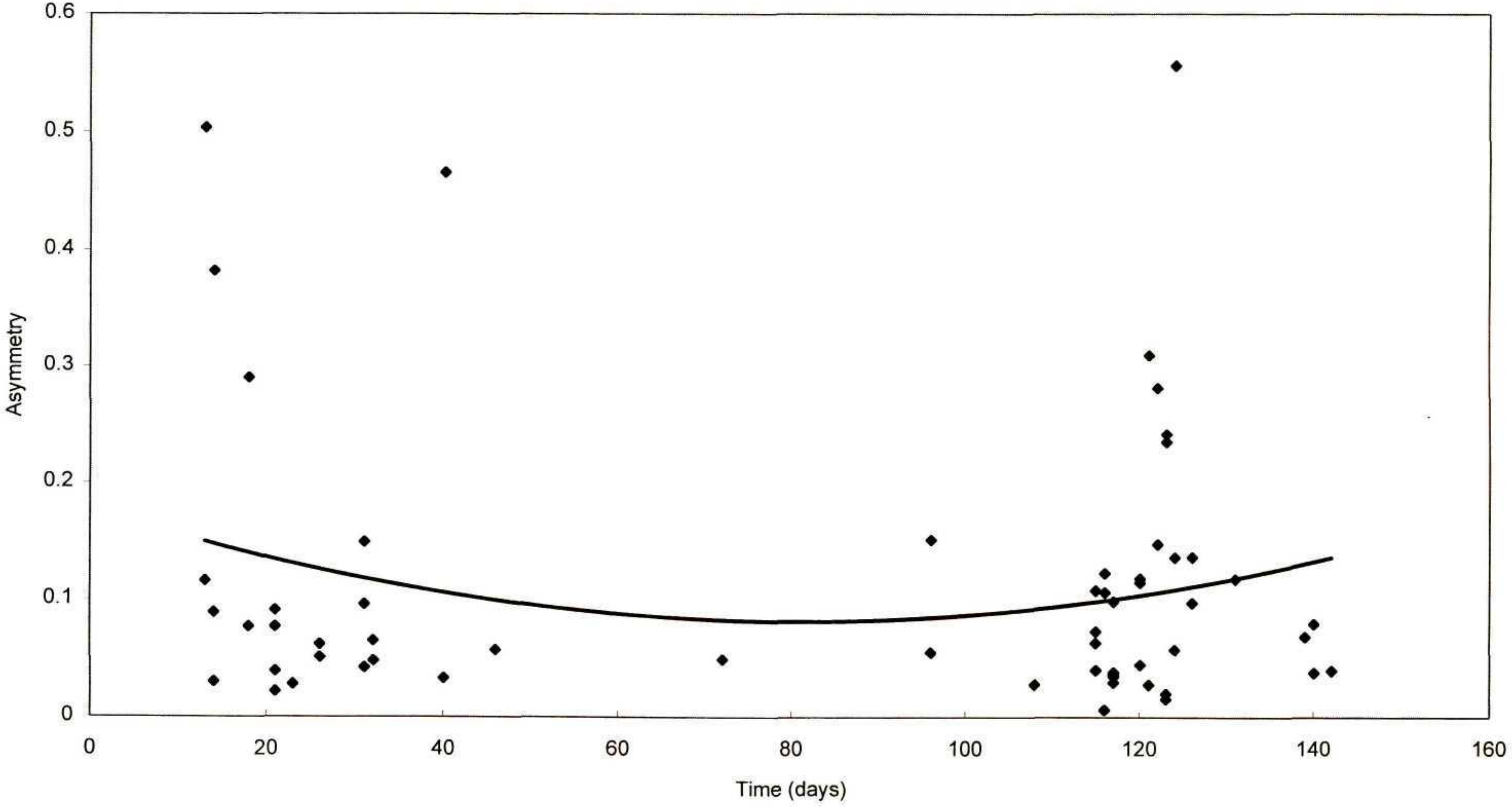


Fig. 3 Tail asymmetry regressed on time of season



III. Should polygynous birds have long symmetrical tails?

Abstract

The fluctuating asymmetry (FA) hypothesis has received considerable attention in the last few years, particularly as a potential means of distinguishing between arbitrary traits and good gene sexual selection. However, the hypothesis remains to be validated as tests of the hypothesis have yielded contradictory results. Here I suggest that these contradictions can, to a large extent, be resolved by taking into account the simplistic assumptions of the hypothesis. I suggest that monogomous and polygynous species will have different costs and benefits associated with a given ornament, and that certain ornaments may well be under strong natural selection pressure. I conclude that the FA hypothesis, as it stands, is too simplistic for it to apply universally. However, I argue that this does not necessarily negate the usefulness of the hypothesis. Indeed, by taking into account the basic biology of a given species the FA hypothesis may still yield useful information about the selection forces driving the evolution of epigamic characters.

Tails of birds have been the focus of numerous studies of fluctuating asymmetry (FA) because of their potential role in sexual selection (Andersson & Iwasa 1996). These studies have attracted considerable attention since evidence substantiating the FA hypothesis could be regarded as direct evidence of "good genes" sexual selection (*e.g.* Møller 1990; Møller 1994). However, findings on the condition-dependence of FA have been equivocal and controversial, and the debate between good genes and arbitrary traits sexual selection continues (*e.g.* McLachlan & Cant 1995; Andersson & Iwasa 1996). Here I question whether the relationship between tail length and FA predicted by the fluctuating asymmetry hypothesis can reasonably be expected to hold true for all mating systems. I believe that the contradictory evidence pertaining to fluctuating asymmetry in birds can, to a large degree, be resolved by (1) considering monogamous and polygynous species to have different costs and benefits of mate choice, and (2) emphasizing that tail shape and size in birds is under strong natural selection pressure even when it is an epigamic character.

While it is generally accepted that sexual selection is stronger in polygynous than monogamous species (Møller & Pomiankowski 1993), I believe that workers in the FA field have prematurely assumed that the relative costs and benefits of epigamic characters are equal for polygynous and monogamous species. This is evident in the prevalent expectation that the predictions of the FA hypothesis (as stated by Møller 1990;1993) should hold for both monogamous and polygynous species. We feel that the expression of an ornament will be influenced by the relative costs and benefits of possessing such an ornament. If these costs and benefits differ for different mating strategies, then predictions about the nature of an ornament must take the biology of the species into account.

In addition, I suggest that the FA hypothesis' implicit assumption that the long tails of birds are subject to stronger sexual selection than natural selection pressure is too simplistic. Structures which are aerodynamically functional, such as the lift generating surface of the tail (Thomas 1993), will have an optimum size and shape based on the biology of the animal (Evans 1993). Despite the fact that the long tails of birds may be epigamic characters, the aerodynamic importance of the tail will ensure that it is under strong selection pressure towards the aerodynamic optimum. For example, experimental manipulation of tail length and symmetry in the Red-billed Streamertail *Trochilus polytmus* has shown that the aerodynamic effects of FA are dependant on the length of the tail, having more pronounced adverse effects on manoeuvrability as tail length increases (Evans *et. al.* 1994). In addition, Møller (1991) has shown that manoeuvrability during flight is negatively correlated with the degree of FA in the Barn Swallow *Hirundo rustica*. This evidence suggests that individuals with long tails may be forced into greater symmetry by the mechanical constraints of FA (Evans *et. al.* 1994;1995). It could, in fact, be argued that the costs of asymmetry are sufficient for natural selection alone to determine patterns of FA in birds' tails (Palmer & Strobeck 1986; Thomas in press).

It has been suggested by Evans *et. al.* (1994;1995) that the relative costs of FA will determine whether a negative relationship exists between ornament size and asymmetry in a given species. The costs of FA will depend on the shape of the tail

(Balmford *et. al.* 1993) and the extent to which a species of bird relies on flight, which will in turn be influenced by the proportion of time spent flying and the dichotomy between insectivorous and granivorous feeding. On the other hand, the benefits of moving away from the aerodynamically optimum tail design will depend to a large extent on the potential benefits of marginal increases in tail length. These benefits are likely to be influenced primarily by variance in male mating success. While these points have been raised by various authors (*e.g.* Evans *et. al.* 1994;1995), I feel the implications in terms of sexual selection and quality signalling theory have been overlooked.

I suggest that the exact role which FA will play in sexual selection and mate choice will, in the case of birds, be dependent primarily on whether the species is monogamous or polygynous, since this dichotomy will largely determine the benefits of moving away from the aerodynamically optimum tail design. Traditionally, polygynous species have been regarded as having higher variance in reproductive success than monogamous species (Trivers 1972; Payne 1984), although this view is being challenged by recent evidence on extra-pair copulations (EPCs) in monogamous species (*e.g.* Birkhead & Møller 1992). Hill *et. al.* (1994), on the other hand, suggest that there is too little evidence in support of the idea that EPCs generate large variation in male reproductive success for us to assume that it applies to all, or most, monogamous species. Perhaps most importantly, Hill *et. al.* (1994) found no relationship between male ornamentation and the probability of being cuckolded. In a further example, Ligon & Zwartjes (1995) found that the reproductive strategy of female

Red Junglefowl appears to be procurement of multiple paternity within a single brood of offspring. When exposed to males of different ornament size, females mated preferentially with the "superior" male, but did nonetheless engage in EPCs with the "inferior" male. It would thus appear that female Junglefowl, while having a preference for superior ornaments when choosing a social mate, do not discriminate between males when seeking EPCs. It could be argued, therefore, that while EPCs can cause variation in male reproductive success, there is no evidence that larger ornaments improve the chances of a male acquiring extra-pair offspring. The variation in reproductive success which can be attributed to ornament size thus appears to be lower for monogamous than polygynous males.

In the case of monogamous bird species, particularly those which rely on flight to a large degree, the relative costs of moving away from the aerodynamically optimum tail design will thus be high. Each male can only acquire one female on the basis of ornament size, and there is therefore little advantage to growing the tail so long that the male can no longer maintain symmetry. The marginal increase in reproductive success achieved by developing a larger tail will be outweighed by the aerodynamic costs incurred through asymmetrical flight. A negative relationship between tail length and asymmetry should thus arise, as predicted by both the FA (Møller 1990) and the mechanical constraints hypotheses (Evans *et. al.* 1994;1995)

This has important implications in terms of honest signalling of male quality. Evans (1993) argues that the mechanical effects of FA will serve to reinforce honest signalling. The mechanical constraints on FA will serve to increase the costs of cheating to males with a tendency towards asymmetry (*i.e.* low quality males), and thus reinforce honest signalling. It is a prerequisite of good gene models of sexual selection that the costs of advertising be greater for low than high quality males (Grafen 1990; Møller 1993). The mechanical constraints hypothesis thus provides a mechanistic explanation of how this situation may arise, but only where the costs of asymmetrical flight are high enough to enforce a negative relationship between tail length and FA. The fact that such a relationship may be selectively advantageous because of mechanical and aerodynamic factors does not preclude the assessment of such patterns by interacting individuals (Evans *et. al.* 1994). The degree of FA is not in itself a signal (as predicted by the FA hypothesis), it is a consequence of signal design which has an impact on the signaller (Evans 1993). The degree of FA will, however, still convey information about the signaller, but only if viewed in conjunction with ornament size (Evans 1993; Evans *et. al.* 1994).

This suggestion ties in with current signalling theory. Perception of signals is unlikely to be error-free (Johnstone & Grafen 1992; Johnstone 1994), and signal receivers should assess several signals reflecting the same information in order to minimize perceptual error. Tail ornaments should be considered as compound structures with size and the degree of FA as non-independent components of tail design (Evans *et. al.* 1994). I suggest that where the costs of asymmetry are sufficiently high to enforce a negative relationship between these two components, females should use both components as independent indicators of male quality.

The case of polygynous or promiscuous bird species is somewhat different.

Mating success is assumed to be highly variable for these species, and the potential benefit to a male who develops a large tail are great, provided the females have a preference for long tails. The males of these species may attempt to maximize tail length, even if this means incurring aerodynamic costs through asymmetrical development, because marginal increases in tail length may increase reproductive success considerably. I suggest that the aerodynamic costs of asymmetry will be lower than the potential reproductive benefits of possessing a long tail for polygynous species (particularly those which do not rely on flight to a large degree), and no negative relationship between ornament size and FA will arise. FA will thus not be a reliable signal of male quality. It follows that, under these circumstances, female birds will not use FA as a cue when choosing males and should therefore not have a preference for symmetrical ornaments. Nonetheless, FA will serve to increase the costs of cheating and thus reinforce honest signalling because the aerodynamic costs of asymmetrical traits will still impact negatively on the energy budgets of the males. In this case I suggest that long tails are classic conditional handicaps, and it is in fact the degree of FA which makes the possession of such an ornament a handicap. Females will, on average, be choosing good quality males if they have a preference for long tails because of the handicap of FA.

I hypothesize that:

(1) there should be a negative relationship between ornament size and asymmetry in monogamous species

(2) females of monogamous species should have a preference for symmetrical

ornaments

(3) there should not be a negative relationship between ornament size and asymmetry in polygynous/promiscuous species

(4) polygynous/promiscuous females should not have a preference for symmetrical ornaments

This hypothesis can only be tested by doing interspecific comparisons of the relationship between tail length and the degree of FA and preference for or against symmetrical ornaments. At present too few studies have dealt with either of these issues for the hypothesis to be tested with any degree of confidence. However, I feel that the possibility of differential relative costs of epigamic characters for monogamous and polygynous species needs to be explored. If there are differences between these mating strategies in the costs and benefits of possessing elaborate ornaments, then the FA hypothesis does not consider the biology of each species sufficiently for it to apply universally. I suggest that the role played by FA will be dependent on a number of biological considerations for each species. Firstly, whether or not an ornament is functional will determine whether stabilizing selection pressure influences patterns of FA in that trait. This will in turn influence the extent to which FA can be considered to mechanically constrain the development of ornaments. Secondly, the relative costs and benefits of possessing asymmetric ornaments will determine how reliable a signal FA is for any given species. In species where the mechanical costs of asymmetry are sufficient to enforce a negative relationship between ornament size and asymmetry (generally monogamous species), FA will provide a mechanistic explanation for how the costs of advertising are higher for low quality males, while simultaneously providing females with an additional signal to assess. In species where the potential benefits of possessing large ornaments outweigh the costs of asymmetrical ornaments (generally promiscuous/polygynous species), FA will not serve as a reliable signal and will therefore not be directly assessed by females. However, FA will make the possession of a long tail a handicap, and so enforce honest signalling by imposing severe costs on poor quality males who attempt to produce large ornaments. In this situation FA may not enforce honesty as adeptly as when a negative relationship exists between ornament size and asymmetry, since the potential benefits to males are so high. It is expected that multiple ornaments may evolve for these species.

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