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Bilateral symmetry and social dominance in captive male red-winged blackbirds

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Abstract There has been much recent interest in subtle departures from perfect symmetry in bilaterally paired morphological characters, and the extent to which such departures reflect aspects of individual quality. We used data from aviary contests involving pairs of wild-caught male red-winged blackbirds (*Agelaius phoeniceus*) to test the hypothesis that comparatively symmetrical males are disproportionately successful in intra-sexual competition for food. Although paired contestants showed clear and consistent differences in competitive ability, there was no indication that symmetrical males were competitively superior. Winners and losers of aviary contests were indistinguishable based on asymmetry measures made on each of four bilateral characters (tarsus length, wing chord, and two epaulet dimensions), and for a fifth character (length of outer retriex), asymmetry differences, though significant, occurred in the direction opposite to that predicted. Furthermore, there was no detectable association between male competitive ability and a composite measure that combined asymmetry information across all five characters. Our results, in combination with those of several other recent avian studies, suggest that symmetry is generally a poor predictor of social dominance in birds. This finding is inconsistent with the proposal that symmetry provides a readily obtained, reliable measure of phenotypic quality.

Key words Bilateral symmetry · Dominance · Intra-sexual competition · Red-winged blackbird

Introduction

Subtle departures from perfect symmetry in bilaterally paired morphological characters have recently attracted

considerable attention among behavioral and evolutionary ecologists. Much of this attention relates ultimately to the recognition that, where symmetry is the norm, such departures reflect (at least in part) the inability of individuals to buffer themselves against random developmental errors (for reviews, see Palmer and Strobeck 1986; Parsons 1990, 1992). The link between symmetry and developmental competence has led some authors to suggest that symmetry provides a reliable indication of overall phenotypic (perhaps genotypic) quality, and that symmetry might therefore be an important cue used in mate selection (Møller 1990, 1992; Thornhill 1992a; Møller and Pomiankowski 1993). Møller and Pomiankowski (1993) further proposed that if symmetry is a general quality indicator, symmetrical individuals should be disproportionately successful in direct intra-sexual competition for mating opportunities, as well as in competition for other resources. While the role of symmetry in determining patterns of mate selection and male mating success has received substantial empirical attention (reviewed by Polak 1997), few studies have examined associations between symmetry and competitive success in other contexts. Here we test the hypothesis that comparatively symmetrical male red-winged blackbirds (*Agelaius phoeniceus*) are disproportionately successful in intra-sexual competition for food.

The prediction that symmetry should be positively associated with success in competition for resources has received some empirical support. For instance, Thornhill (1992b) found that male Japanese scorpionflies (*Panorpa japonica*) with low levels of forewing asymmetry were more likely to win intra-sexual fights over nuptial food items (see also Thornhill 1992c; Thornhill and Sauer 1992). Similarly, in two species of ungulates, antler or horn asymmetry has been found to be inversely related to measures of social dominance (Malyon and Healy 1994; Møller et al. 1996). Among avian species that have been studied, however, relationships between symmetry and social dominance are apparently less straightforward. Swaddle and Witter (1994) reported that when captive European starlings (*Sturnus vulgaris*) were

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housed individually during moult, those that developed comparatively high levels of primary feather asymmetry were, in fact, dominant in subsequent contests over food. In contrast, when individuals were maintained in a more competitive environment, no such relationship was apparent (Witter and Swaddle 1994). Similar negative results have since been reported for captive mallards (*Anas platyrhynchos*; Hoysak and Ankney 1996) and American black ducks (*A. rubripes*; Hoysak and Ankney 1996).

Mixed results notwithstanding, there is some uncertainty regarding which character asymmetries should best reflect individual quality, and hence, be predictive of overall competitive success. Møller and Pomiankowski (1993) have argued that secondary sexual characters may be important in this regard because, for a variety of reasons, such characters are thought to be particularly susceptible to the processes that tend to disrupt precise development (see also Watson and Thornhill 1994). Alternatively, it has been suggested that single character asymmetries in general are likely to be poor predictors of overall developmental competence, and that composite measures that combine information across characters should better reflect underlying individual quality (Palmer 1994). Finally, some authors have argued that only those character asymmetries that might have a direct mechanical impact on performance (e.g., those associated with aerodynamic efficiency) are likely to be predictive of individual competitive success (Eggert and Sakaluk 1994; Palmer 1994). Our approach in the present study was to make no *a priori* assumptions regarding the relative importance of different traits. Rather, our aim was to evaluate male competitive ability relative to asymmetry measures made on each of a variety of paired characters, as well as in relation to a composite (i.e., multi-character) measure that should better reflect asymmetry overall (Palmer 1994; Dufour and Weatherhead 1996). To this end, we used aviary trials to determine the relative dominance of paired contestants forced to compete for access to a limited food supply. We reasoned that the use of an aviary setting would strengthen our test of the central hypothesis by eliminating extrinsic factors that might otherwise obscure individual differences in competitive ability (for discussions, see Eckert and Weatherhead 1987; Shutler and Weatherhead 1991, 1992).

Methods

This study was conducted during the spring of 1994 in conjunction with a broader investigation of red-winged blackbirds breeding in the vicinity of the Queen's University Biological Station, Chaffey's Locks, Ontario (Dufour and Weatherhead 1998a). As part of that investigation, resident males were experimentally removed from territories dispersed along approximately 35 km of rural highway in upland habitat (see Shutler and Weatherhead 1994 for details of the study area). These males were temporarily detained to create vacant territories, thereby inducing the settlement of non-territorial (i.e., non-breeding) replacement males. We used a sub-sample of

both resident ($n = 40$) and replacement ($n = 16$) males as test subjects for the present investigation. All males were at least 2 years old, based on plumage (see Beletsky 1996), but otherwise their ages were unknown.

To assess male competitive ability, we used a study design similar to that employed by Teather and Weatherhead (1995), in which males were housed in pairs and forced to compete, in this case, for access to a limited food supply. In all, 28 replicate contests were conducted, each involving a different pair of males. Paired contestants were captured within 4 h of each other on selected mornings between 6 May and 16 June using decoy traps (Smith 1976) or mist nets. To eliminate the possibility that contestants had recent prior acquaintance with one another, we ensured that paired individuals were obtained from different locales within the general study area. A retrospective analysis based on maps of the study area revealed that source territories for each pair were separated by ≥ 4.5 km. Paired contestants were always matched with respect to their original territorial status (i.e., resident vs. replacement). Within these limits, males were assigned to contests randomly (i.e., without reference to aspects of their morphology).

Within 5 h of capture, contestants were introduced simultaneously to one of six compartments of an outdoor aviary, each measuring $3 \times 2 \times 1.5$ m. Each individual was weighed to the nearest 0.5 g using a Pesola spring scale, measured for bilateral symmetry (see below), and fitted with a single numbered aluminum leg band. To facilitate individual identification during observation sessions, paired contestants were banded on opposite legs. Food (50% cracked corn, 33% millet, 17% commercial chick starter) and water were freely available to both contestants throughout their internment, except as indicated below.

We determined the relative dominance of paired contestants during two replicate observation sessions (trials) conducted approximately 24 and 48 h after initial introduction of the birds to the aviary. To ensure that neither contestant was satiated at the outset of a given trial, we removed all food from the aviary compartment at approximately 2100 hours the evening before the trial and began our observations between 0800 and 1100 hours the following morning (i.e., after 11–14 h of food deprivation). Each trial lasted 1 h. During the trial we recorded the nature and outcome of all aggressive interactions over food, which we restricted to a single, easily monopolized dish located in the center of the compartment. Interactions ranged from threat displays to physical attacks and displacements. The individual that retained control of the food dish following an interaction was considered the "winner" of that interaction, and the individual that won the majority of interactions in a given trial was taken as the winner of that trial (e.g., Eckert and Weatherhead 1987; Shutler and Weatherhead 1991). As an alternative measure of competitive success, we also recorded the total amount of time (to the nearest second) that each individual spent in control of the food dish. Most birds were released within 8 h of the second replicate trial, but for reasons associated with the aims of the removal study, some individuals were detained longer. All birds were released within 7 days of their initial introduction to the aviary.

To quantify individual differences in asymmetry, on each male we measured both the left and right elements of five bilaterally paired morphological characters (all measurements made by K.W.D.). Non-ornamental characters included tarsus length, wing chord, and "tail length", i.e., length of the outer retriex (see Dufour and Weatherhead 1996 for complete character descriptions). Secondary sexual characters included the length of the red portion and total length of the epaulet, a bilaterally paired plumage ornament (see Searcy and Yasukawa 1995). Tarsus and epaulet measures were made using callipers (± 0.1 mm), whereas wing chord and tail length were measured with modified rulers (± 1 mm). All characters were measured twice. In an analysis based on a more extensive sample of males (including those used in the present study, see below), asymmetry scores derived from these measures showed moderate to high repeatability [intra-class correlation coefficients for signed asymmetry scores (i.e., left – right), range among characters: 0.72–0.92; corresponding values for absolute (i.e., unsigned), asymmetry scores: 0.67–0.91; all P values < 0.0001]. Nevertheless, to improve precision of measurement, we used the mean value

computed across replicate measures as the basis for all computations (Bailey and Byrnes 1990; Yezerinac et al. 1992). Feather characters were inspected for evidence of breakage or wear, and any showing such damage were excluded from the analysis. Consequently, sample sizes vary among individual tests.

Previous authors have identified a number of technical difficulties associated with quantifying asymmetry variation at the individual level (Palmer and Strobeck 1986, 1992; Palmer 1994). In particular, it has been suggested that directional asymmetry (departures of the mean left – right value from zero) and antisymmetry (evidenced by a platykurtic frequency distribution of left – right values) may compromise the use of bilateral variation as a measure of developmental competence. Thus, Palmer (1994) has argued that all characters should be assessed for departures from “ideal fluctuating asymmetry”, wherein left – right values are normally distributed about a mean of zero. Because the ability to detect such departures increases with increasing sample size, we addressed these issues in an analysis based on a more extensive sample of males ($n = 119$) captured throughout the 1993 and 1994 breeding seasons. This sample included all individuals used in the present study, as well as 63 additional males that had been defending territories within 20 km of the biological station. Details of the analysis are presented elsewhere (Dufour and Weatherhead 1998a), so here we merely summarize the key results. In brief, all characters were in qualitative agreement with the criteria for ideal fluctuating asymmetry: distributions of signed asymmetry values were either normal or only slightly non-normal, and all were approximately centered on a mean of zero. Formal testing revealed no evidence of antisymmetry in any character, though several characters showed slight but statistically significant directionality. To eliminate the biasing effects of these directional tendencies, individual signed asymmetry scores were adjusted to a mean of zero before conversion to absolute values (Palmer 1994). Absolute asymmetry for each character was thus computed according to the equation:

$$\text{absolute asymmetry} = |d_i - \bar{d}|$$

where d_i is the signed asymmetry score for individual i , and \bar{d} is the corresponding mean value computed across all individuals in the sample. Because distributions of absolute asymmetry scores were positively skewed, all scores were transformed to square roots for analysis [preliminary inspection of normal quantile plots (SAS Institute 1994) had revealed that the square root transformation was, for all five characters, the most effective transformation to normality among those recommended by Sokal and Rohlf 1981:pp 423–427]. Within a given character, absolute asymmetry was unrelated to character size [i.e., $(\text{left} + \text{right})/2$], so correction for size dependence was not required (Palmer 1994).

Elsewhere we have shown that, in red-winged blackbirds, asymmetry measures made on different characters covary at the individual level, though correlations among characters are generally weak (Dufour and Weatherhead 1996). While these observations support the existence of an organism-wide asymmetry property (*sensu* Soulé 1967), they also imply that individual character asymmetries are likely to be poor predictors of this property. Thus, in the present study, we tested our central prediction (i.e., that symmetrical males are competitively superior) in two ways. First, to retain the maximum amount of information, we compared winners and losers of aviary contests with respect to the levels of absolute asymmetry exhibited at each individual character. Second, we evaluated male competitive success in relation to a composite measure that should better reflect asymmetry overall. Composite scores were computed by first ranking males according to their levels of absolute asymmetry at each individual character, and then by summing these ranks across characters to obtain a composite measure for each male. Ranks were computed based on all 108 males in the broader sample that had non-missing values for all five characters. Among males included in the present study, composite scores ranged from 121 to 471, with high values indicating high levels of asymmetry relative to other males in the sample.

All analyses were conducted using JMP (version 3.1) statistical software (SAS Institute 1994). Statistical significance was accepted

at $P \leq 0.05$. Means are presented in original units ± 1 SE. Two-tailed probabilities are reported throughout.

Results

Before addressing our central objective, we first sought to determine the extent to which results of the aviary contests were consistent between replicate trials, as well as the extent to which our two measures of competitive ability were in agreement. In 25 of the 28 contests (89%), the contestant that won the majority of aggressive interactions in the first trial also won the majority of interactions in the second trial (mean proportion of interactions won by the “winner”: 0.86 ± 0.027 and 0.86 ± 0.030 for trials 1 and 2, respectively; mean number of interactions scored per trial: 21.3 and 23.9). In each of these same contests, the contestant that won the majority of interactions in a given trial also spent the greatest amount of time at the food dish. On average, the margin of victory was substantial (mean time spent at the food dish by winners and losers, respectively, and corresponding paired difference tests: trial 1, 28.0 ± 2.43 vs. 10.6 ± 1.60 min, paired $t = 5.48$, $df = 24$, $P < 0.001$; trial 2, 29.2 ± 2.65 vs. 10.4 ± 1.66 min, paired $t = 5.27$, $df = 24$, $P < 0.001$). Thus, for these contests, we concluded that dominance relationships were stable, and accordingly, we pooled results across trials for subsequent analysis.

For the three remaining contests, results were somewhat less consistent, both within and between replicate trials; we therefore consider these cases on an individual basis. In the first contest, one contestant (SX) won only 2 of 10 aggressive interactions in the initial trial, but nevertheless spent appreciably more time at the food dish (42.8 min vs. 12.5 min for his opponent). In the second trial, this individual won all 20 aggressive interactions, and again clearly monopolized the food dish (42.1 vs. 10.3 min). Thus, in this instance we assigned the victory to contestant SX. A similar situation occurred in the second contest, wherein one contestant won the majority of aggressive interactions in only one of the two replicate trials (number of interactions won: trial 1, 35 of 39; trial 2, 11 of 28), but nevertheless monopolized the food dish in both trials (40.3 and 27.2 min for trials 1 and 2, respectively, vs. 13.3 and 10.3 min for his opponent). Again, we concluded that the individual that monopolized the food dish in both trials was the winner of the contest overall. In the final contest, a winner could not be unambiguously assigned, as results for both aggressive interactions and time spent at the food dish were inconsistent between replicate trials. This contest was therefore excluded from further analysis. In total, then, we retained for analysis 27 of the 28 original pairs of contestants.

Before testing the specific prediction that symmetrical males are competitively superior, we first evaluated several other potential morphological correlates of social dominance. Previous studies of captive male red-winged

blackbirds have indicated that both epaulet length and overall body size (measured as wing length) may be important in this regard (Searcy 1979; Eckert and Weatherhead 1987). In the present study, however, there was no evidence that either of these factors influenced the outcome of competitive interactions. Winners and losers did not differ with respect to the length of the red portion of the epaulet (computed as the mean length of the left and right elements; paired $t = 0.34$, $df = 26$, $P = 0.735$), total epaulet length (paired $t = 0.32$, $df = 26$, $P = 0.749$), or body size (i.e., wing chord; paired $t = 0.62$, $df = 26$, $P = 0.544$). Thus, in the present instance, statistical control of these variables was not required.

Results of the aviary contests generally failed to support the prediction that symmetrical males realize a competitive advantage. In the analysis based on individual characters, only one of the five comparisons revealed a significant asymmetry difference between winners and losers, and in this instance the direction of the difference was opposite to that predicted (Table 1). That is, winners had, on average, high rather than low levels of tail feather asymmetry relative to their opponents (Table 1). This difference remained significant ($P < 0.05$) when the experimentwise type I error rate was controlled using sequential Bonferroni adjustment (Rice 1989). There was no detectable difference between winners and losers with respect to asymmetry overall (mean composite scores: 271 ± 17.2 and 269 ± 14.9 , respectively; paired $t = 0.11$, $df = 21$, $P = 0.913$).

The positive association between tail feather asymmetry and male competitive success was unexpected. To explore this association in greater detail, we determined whether males with comparatively high levels of tail feather asymmetry were more likely to win aviary contests by a disproportionately large margin of victory. Specifically, we used simple linear correlation to evaluate the relationship between the proportion of aggressive interactions won by the "winner" and the degree to which the winner was more asymmetrical than his opponent (i.e., the signed difference between their respective asymmetry scores, computed as winner – loser). The relationship was weak and non-significant ($r = -0.25$, $n = 22$, $P = 0.261$). Thus, although relative tail feather asymmetry did distinguish winners and losers (Table 1), it did not predict the decisiveness of the victory.

Table 1 Levels of character asymmetry (mm) exhibited by winners and losers in paired aviary contests over access to food. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements. All comparisons are based on 27 pairs of individuals, except that for tail length, which is based on 22 pairs

Character	Asymmetry				t^a	P
	Winners		Losers			
	Mean	SE	Mean	SE		
Tarsus length	0.22	0.058	0.23	0.033	-0.84	0.407
Wing chord	0.64	0.090	0.76	0.122	-0.63	0.535
Tail length	1.79	0.470	0.62	0.112	3.12	0.005
Epaulet length – red	1.16	0.159	1.13	0.159	0.17	0.868
Epaulet length – total	1.18	0.180	1.39	0.243	-0.52	0.606

^a Paired difference test (two-tailed) based on sqrt-transformed asymmetry values

Discussion

Our results indicate that, when housed in pairs, male red-winged blackbirds generally show clear and consistent differences in competitive ability. Our findings also indicate, however, that these differences are, for the most part, unrelated to measures of male developmental competence (i.e., departures from perfect symmetry). In each of five separate tests based on individual characters (including both ornamental and non-ornamental traits) we found no evidence to support the prediction that comparatively symmetrical males realize a competitive advantage. In fact, for one character (length of the outer retrix), we found just the opposite: males with comparatively symmetrical tail feathers were actually less likely to succeed in competition for food. Additionally, there was no indication that male competitive success was related to composite (i.e., multi-character) asymmetry, arguably the most reliable measure of developmental competence used here (Palmer 1994). In sum, our results offer little support for the suggestion that developmental asymmetries can be used to predict individual competitive success, at least among male red-winged blackbirds housed in captivity. This observation is inconsistent with the more general hypothesis that symmetry provides a measure of overall phenotypic quality (e.g., Møller 1990, 1992; Møller and Pomiankowski 1993).

Reasons for the observed positive association between tail feather asymmetry and male competitive success are unclear, though the result is not without some precedent. Swaddle and Witter (1994) found a similar association among captive European starlings, reporting that individuals with relatively high levels of primary feather asymmetry were competitively superior (i.e., dominant). In the case of the starling data, however, the result may have been a direct consequence of the particular conditions under which individuals had developed their plumage asymmetries. Specifically, all individuals used in the study of Swaddle and Witter (1994) had moulted their primary feathers in captivity, during a period of experimental food deprivation. Because birds were housed individually throughout this period (and dominance assessed in subsequent trials), Swaddle and Witter (1994) proposed that, during moult, dominant individuals had incurred certain costs associ-

ated with their social status (e.g., a high metabolic rate), but in the absence of social interaction, were unable to reap the corresponding benefits. This ostensibly resulted in increased developmental stress among dominants, and ultimately, increased levels of primary feather asymmetry, hence the relationship between symmetry and social status (see also Witter and Swaddle 1994). Such a mechanism, however, is unlikely to account for the positive association between tail feather asymmetry and dominance reported here, because all individuals used in the present study had developed their plumage asymmetries under natural conditions (i.e., before capture and introduction to the aviary). It is possible (albeit statistically improbable) that the association between tail feather asymmetry and dominance observed in our study was a spurious artifact (i.e., type I error). Our finding that relative tail feather asymmetry did not predict the *degree* to which dominant individuals defeated their opponents lends some support to this interpretation. Regardless, our results for tail feather asymmetry, as well as those for the other characters we measured, are clearly inconsistent with the hypothesis that symmetry and social dominance are positively related.

In failing to support the prediction that symmetrical males are competitively superior, our results corroborate those of previous studies that have investigated relationships between symmetry and social dominance in birds (Swaddle and Witter 1994, 1995; Witter and Swaddle 1994; Hoysak and Ankney 1996; see also Swaddle 1996). Available evidence from avian studies is also largely inconsistent with the proposal that symmetry should be associated with success in direct intra-sexual competition for mates. For instance, Møller (1992, 1993) reported that male barn swallows (*Hirundo rustica*) with experimentally reduced levels of tail feather asymmetry were no more likely to engage in or win intra-sexual encounters over females. Similarly, in a recent study of red-winged blackbirds, comparatively symmetrical males were apparently no more likely to succeed in competition for breeding territories, a prerequisite for successful reproduction in this species (Dufour and Weatherhead 1998a). Thus, while avian studies have provided some of the most convincing evidence that symmetry may be important in determining patterns of mate selection (Møller 1992, 1993; Swaddle and Cuthill 1994a,b), as yet there is little evidence from birds that symmetry might also play a role in determining the outcome of intra-sexual interactions. This observation suggests some limits to the general significance of symmetry as a correlate of fitness at the individual level (cf. Clarke 1995).

Our results also have implications regarding the extent to which symmetry reliably reflects aspects of underlying individual quality (Møller and Pomiankowski 1993). Elsewhere we have shown that in red-winged blackbirds, character asymmetries are generally unrelated to measures of male health (nutritional condition and parasitic infection), viability (between-year survival),

or parental quality, i.e., nest defence effort (Dufour and Weatherhead 1998b). In the present investigation, we found no evidence to indicate that symmetry is positively associated with success in intra-sexual competition for food. Thus, results of the present study extend our earlier findings in suggesting that, for red-winged blackbirds, symmetry appears not to provide a reliable indication of overall phenotypic quality. While this conclusion obviously does not preclude the possibility that symmetry conveys quality-related information in other species (see, for instance, Thornhill 1992b; Møller et al. 1996), it does suggest that generalizations regarding the importance of symmetry in this regard may be somewhat premature. Why symmetry should be indicative of individual quality in some species and not in others remains to be determined.

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References

- Bailey RC, Byrnes J (1990) A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. *Syst Zool* 39:124–130
- Beletsky L (1996) The red-winged blackbird: the biology of a strongly polygynous songbird. Academic Press, London
- Clarke GM (1995) Relationships between developmental stability and fitness: applications for conservation biology. *Conserv Biol* 9:18–24
- Dufour KW, Weatherhead PJ (1996) Estimation of organism-wide asymmetry in red-winged blackbirds and its relation to studies of mate selection. *Proc R Soc Lond B* 263:769–775
- Dufour KW, Weatherhead PJ (1998a) Reproductive consequences of bilateral asymmetry for individual male red-winged blackbirds. *Behav Ecol*, in press
- Dufour KW, Weatherhead PJ (1998b) Bilateral symmetry as an indicator of male quality in red-winged blackbirds: associations with measures of health, viability, and parental effort. *Behav Ecol*, in press
- Eckert CG, Weatherhead PJ (1987) Ideal dominance distributions: a test using red-winged blackbirds (*Agelaius phoeniceus*). *Behav Ecol Sociobiol* 20:43–52
- Eggert A, Sakaluk SK (1994) Fluctuating asymmetry and variation in the size of courtship food gifts in decorated crickets. *Am Nat* 144:708–716
- Hoysak DJ, Ankney CD (1996) Correlates of behavioural dominance in mallards and American black ducks. *Anim Behav* 51:409–419
- Malyon C, Healy S (1994) Fluctuating asymmetry in antlers of fallow deer, *Dama dama*, indicates dominance. *Anim Behav* 48:248–250
- Møller AP (1990) Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim Behav* 40:1185–1187
- Møller AP (1992) Female swallow preference for symmetrical male sexual ornaments. *Nature* 357:238–240

- Møller AP (1993) Female preference for apparently symmetrical male sexual ornaments in the barn swallow *Hirundo rustica*. *Behav Ecol Sociobiol* 32:371–376
- Møller AP, Pomiankowski A (1993) Fluctuating asymmetry and sexual selection. *Genetica* 89:267–279
- Møller AP, Cuervo JJ, Soler JJ, Zamora-Munoz C (1996) Horn asymmetry and fitness in gemsbok, *Oryx g. gazella*. *Behav Ecol* 7:247–253
- Palmer AR (1994) Fluctuating asymmetry analyses: a primer. In: Markow TA (ed) *Developmental stability: its origins and evolutionary implications*. Kluwer, Dordrecht, pp 335–364
- Palmer AR, Strobeck C (1986) Fluctuating asymmetry: measurement, analysis, patterns. *Annu Rev Ecol Syst* 17:391–421
- Palmer AR, Strobeck C (1992) Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of statistical tests. *Acta Zool Fenn* 191:57–72
- Parsons PA (1990) Fluctuating asymmetry: an epigenetic measure of stress. *Biol Rev* 65:131–145
- Parsons PA (1992) Fluctuating asymmetry: a biological monitor of environmental and genomic stress. *Heredity* 68:361–364
- Polak M (1997) Parasites, fluctuating asymmetry, and sexual selection. In: Beckage NE (ed) *Parasites: effects on host hormones and behaviour*. Chapman and Hall, New York
- Rice WR (1989) Analysing tables of statistical tests. *Evolution* 43:223–225
- SAS Institute (1994) *JMP statistics and graphics guide*. SAS Institute, Cary
- Searcy WA (1979) Morphological correlates of dominance in captive male red-winged blackbirds. *Condor* 81:417–420
- Searcy WA, Yasukawa K (1995) Polygyny and sexual selection in red-winged blackbirds. Princeton University Press, Princeton
- Shutler D, Weatherhead PJ (1991) Owner and floater red-winged blackbirds: determinants of status. *Behav Ecol Sociobiol* 28:234–241
- Shutler D, Weatherhead PJ (1992) Surplus territory contenders in male red-winged blackbirds: where are the desperados? *Behav Ecol Sociobiol* 31:97–106
- Shutler D, Weatherhead PJ (1994) Movement patterns and territory acquisition by male red-winged blackbirds. *Can J Zool* 72:712–720
- Smith DG (1976) An experimental analysis of the function of red-winged blackbird song. *Behaviour* 56:136–156
- Sokal RR, Rohlf FJ (1981) *Biometry: the principles and practice of statistics in biological research*, 2nd edn. Freeman, New York
- Soulé ME (1967) Phenetics of natural populations. II. Asymmetry and evolution in a lizard. *Am Nat* 101:141–161
- Swaddle JP (1996) Reproductive success and symmetry in zebra finches. *Anim Behav* 51:203–210
- Swaddle JP, Cuthill IC (1994a) Female zebra finches prefer males with symmetric chest plumage. *Proc R Soc Lond B* 258:267–271
- Swaddle JP, Cuthill IC (1994b) Preference for symmetric males by female zebra finches. *Nature* 367:165–166
- Swaddle JP, Witter MS (1994) Food, feathers, and fluctuating asymmetries. *Proc R Soc Lond B* 255:147–152
- Swaddle JP, Witter MS (1995) Chest plumage, dominance and fluctuating asymmetry in female starlings. *Proc R Soc Lond B* 260:219–223
- Teather KL, Weatherhead PJ (1995) The influence of age and access to females on dominance in captive male brown-headed cowbirds (*Molothrus ater*). *Can J Zool* 76:1012–1018
- Thornhill R (1992a) Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*: Mecoptera). *Behav Ecol* 3:277–283
- Thornhill R (1992b) Fluctuating asymmetry and the mating system of the Japanese scorpionfly *Panorpa japonica*. *Anim Behav* 44:867–879
- Thornhill R (1992c) Fluctuating asymmetry, interspecific aggression and male mating tactics in two species of Japanese scorpionflies. *Behav Ecol Sociobiol* 30:357–363
- Thornhill R, Sauer P (1992) Genetic sire effects on the fighting ability of sons and daughters and mating success of sons in a scorpionfly. *Anim Behav* 43:255–264
- Watson PJ, Thornhill R (1994) Fluctuating asymmetry and sexual selection. *Trends Ecol Evol* 9:21–25
- Witter MS, Swaddle JP (1994) Fluctuating asymmetries, competition, and dominance. *Proc R Soc Lond B* 256:299–303
- Yezerinac SM, Loughheed SC, Handford P (1992) Measurement error and morphometric studies: statistical power and observer experience. *Syst Biol* 41:471–482

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