Reproductive consequences of bilateral asymmetry for individual male red-winged blackbirds

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We used morphological and breeding data from a 2-year field study of red-winged blackbirds (*Agelaius phoeniceus*) to test the hypothesis that males characterized by low levels of bilateral asymmetry (i.e., high developmental competence) realize a reproductive advantage. Specifically, we evaluated each of several distinct components of male reproductive success relative to asymmetry measures made on five bilaterally paired characters. Results of a male removal experiment generally failed to support the prediction that symmetry would be associated with success in competition for access to breeding territories: established territory owners and nonterritorial replacement males were effectively indistinguishable in this regard. Similarly, there was no indication that symmetrical males were more likely to establish territories in high-quality marsh habitat than in marginal upland field habitat. Finally, monitoring of breeding activity in high-quality habitat revealed that male symmetry was generally unrelated to recruitment of social mates (i.e., harem size), the productivity of those mates (average female reproductive success), within-pair paternity (assessed using DNA-based analysis of parentage), or extrapair mating success. Collectively, these results indicate that symmetry is not an important determinant of reproductive success among individual male red-winged blackbirds. This observation, in combination with the results of several other recent investigations, suggests that the fitness consequences of subtle departures from perfect symmetry may be less significant and/or less ubiquitous than initially suggested. *Key words: Agelaius phoeniceus*, bilateral symmetry, extrapair mating, harem size, paternity, territory acquisition, territory quality, red-winged blackbird, reproductive success. *[Behav Ecol 9:232–242 (1998)]*

It has recently become apparent that subtle developmental inconsistencies can have fitness consequences for individuals later in life. Specifically, departures from perfect symmetry in bilaterally paired morphological characters have been shown to influence male mating success in a variety of animal taxa (e.g., Harvey and Walsh, 1993; McLachlan and Cant, 1995; Møller, 1994, 1996; Simmons, 1995; Thornhill, 1992b). Several mechanisms have been proposed to explain the disproportionate success of symmetrical males, but there is currently little consensus regarding the relative importance of these mechanisms (see reviews by Markow, 1995; Polak, 1997). Here we present the results of a study designed both to determine whether symmetrical male red-winged blackbirds (*Agelaius phoeniceus*) realize a reproductive advantage and to identify potential underlying mechanisms by assessing which specific components of reproductive success are associated with male symmetry.

The most frequently discussed hypothesis to explain observed associations between symmetry and male reproductive performance is that females use symmetry as a criterion for mate selection (Møller, 1990; see also Møller, 1992; Møller and Pomiankowski, 1993; Thornhill, 1992a). For the majority of paired characters, perfect symmetry represents the ideal developmental outcome (Palmer and Strobeck, 1986). Thus, departures from symmetry are thought to reflect the inability of individuals to develop normally in the face of contingencies imposed by the environment (Palmer and Strobeck, 1986; Parsons, 1990, 1992). Given heritable variation in the ability of individuals to cope with these contingencies (e.g., Hagen, 1973; Mather, 1953), females that prefer symmetrical males

would obtain mates of high genetic quality and thus enhance the quality of their offspring (Møller, 1992; Thornhill, 1992a). Experimental manipulation of plumage asymmetries in free-living barn swallows (*Hirundo rustica*) and captive zebra finches (*Taeniopygia guttata*) has confirmed that females of these species perceive individual differences in asymmetry and discriminate against asymmetrical males (Møller, 1992, 1993; Swaddle and Cuthill, 1994a).

Møller's (1990) hypothesis describes one of several ways in which asymmetry might influence male reproductive success. Because deviations from perfect symmetry are typically subtle, interpretations that invoke female choice based on symmetry per se are most likely to apply to cases in which individual differences are large and asymmetries particularly conspicuous. Noteworthy in this regard is the observation that secondary sexual characters (e.g., plumage ornaments) often exhibit elevated levels of asymmetry relative to other characters (e.g., Møller and Hoglund, 1991), and studies of sexual ornaments have indeed provided some of the most convincing evidence of female mate selection based on this aspect of morphology (Møller, 1992, 1993; Swaddle and Cuthill, 1994a). However, female preferences for symmetry do not necessarily imply adaptive female choice and might instead reflect perceptual biases toward symmetry in general (Enquist and Arak, 1994; Johnstone, 1994; Ryan et al., 1995). Furthermore, to the extent that departures from perfect symmetry might directly influence the mechanical functioning of certain traits (e.g., those associated with flight performance; see Evans et al., 1994; Møller, 1991; Swaddle et al., 1996), the impact of asymmetry on male mating success might be mediated not by female choice, but rather via effects on the ability of males to compete effectively for mating opportunities (Balmford and Thomas, 1992; Palmer, 1994). Finally, relationships between asymmetry and male reproductive success might arise as incidental by-products of associations between asymmetry and

other male characteristics that confer high reproductive fitness.

Despite current interest, existing data on the relationship between asymmetry and male success under natural conditions are limited in several important ways. First, although a number of field studies have demonstrated inverse associations between asymmetry and male mating success, in most instances the underlying mechanisms have not been identified (see, for instance, Polak, 1997). Second, studies of asymmetry and male success thus far have only considered asymmetry in one or two individual characters, despite theoretical and empirical reasons to expect single-character asymmetries to be poor predictors of overall developmental competence (Dufour and Weatherhead, 1996; Palmer, 1994). At present, data on multicharacter asymmetry and male reproductive success are lacking. Finally, not all studies have supported the prediction that males exhibiting high levels of asymmetry are likely to suffer reduced reproductive success (e.g., Eggert and Sakaluk, 1994; Ryan et al., 1995). Thus, additional data are needed to establish the generality of the phenomenon.

We used data from a 2-year field study to assess the consequences of asymmetry for male red-winged blackbirds with respect to intrasexual (i.e., male–male competition) aspects of reproductive success, as well as those aspects presumably influenced by female mating decisions. Redwings are well suited to the goals of this study because individual males show pronounced variation in annual reproductive success (Gibbs et al., 1990; Payne, 1979; Weatherhead and Boag, 1997; Westneat, 1993). This variation arises at a number of levels. First, mating is contingent upon establishing a breeding territory (nonterritorial males collectively account for <5% of all fertilizations; Gray, 1996; Weatherhead and Boag, 1995; Westneat, 1993). Because 35–80% of reproductively competent males fail to acquire a territory in a given year (Searcy and Yasukawa, 1995), competition for territories is intense (see also Beletsky and Orians, 1987b; Eckert and Weatherhead, 1987b; Orians, 1961). Thus, our first objective was to test the prediction that territory owners exhibit low levels of asymmetry relative to their nonterritorial counterparts. To this end, we conducted an experiment in which existing territory owners were removed from their territories and their morphology compared with that of their respective replacements (Eckert and Weatherhead, 1987b; Shutler and Weatherhead, 1991).

Male red-winged blackbird reproductive success also varies as a consequence of large-scale differences in territory quality. Specifically, territories in lowland marshes tend to produce more young than those in upland fields, largely because males defending territories in marsh habitat typically attract more social mates (Case and Hewitt, 1963; Eckert and Weatherhead, 1987a; Weatherhead et al., 1980; although see Ritschel, 1985). Thus, our second objective was to test the prediction that males characterized by low levels of asymmetry would more often be found defending territories in high-quality marsh habitat than in adjacent upland fields.

Among males that succeed in establishing territories in high-quality habitat, variation in reproductive success can also be substantial, in large part because this species is highly polygynous (in eastern Ontario, where the present study was conducted, harem sizes range from 0 to 4; Weatherhead and Boag, 1997). Additionally, extrapair mating is a regular component of reproduction in this species, and extrapair paternity contributes substantially to the success of some males (Gibbs et al., 1990; Gray, 1996; Weatherhead and Boag, 1997; Westneat, 1993). In the context of the present study, this observation has two implications. First, extrapair mating provides an additional avenue through which females might discriminate against asymmetrical males. Second, that many

males realize a net benefit from extrapair mating affirms the importance of assessing parentage when quantifying individual male success in this species (Gibbs et al., 1990; Weatherhead and Boag, 1997). Thus, our third objective was to evaluate each of the following components of success in relation to the levels of asymmetry exhibited by individual males: (1) recruitment of social mates (i.e., harem size); (2) average success of females within harems; (3) within-pair paternity (assessed using DNA fingerprinting); and (4) success in achieving extrapair fertilizations (EPFs). Finally, for a subsample of individuals, we also determined directly the relationship between asymmetry and true annual reproductive success (i.e., accounting for all four components above), confirmed through genetic analysis of parentage.

METHODS

Study populations

This study was conducted at sites located within 20 km of the Queen's University Biological Station, Chaffey's Locks, Ontario, Canada (44°34′ N; 76°20′ W). All data were collected during the breeding seasons (April–July) of 1993 and 1994. Data derive from two main study areas, corresponding to the two broad categories of habitat in which red-winged blackbirds regularly breed (upland field and lowland marsh).

The upland study area comprised a series of isolated or semi-isolated territories distributed along approximately 35 km of paved highway (see Shutler and Weatherhead, 1994, for details). Isolated territories were separated from all other territories by areas uninhabited by red-winged blackbirds, whereas semi-isolated territories shared a common boundary with that of a single neighboring male. Territories in this area typically centered on a small (<200 m²) patch of cattail (*Typha* spp.), but most (>90%) of each defended area was agricultural land, principally pasture or early successional old field.

The lowland study area comprised four small (2–10 ha) marshes, each supporting a breeding population of 4–19 resident males. Two of the marshes were beaver ponds characterized by dense stands of emergent vegetation, chiefly willow (*Salix* spp.) and sedge (*Cyperus* spp.). At a third beaver pond, males defended territories along the perimeter of a large open-water area. Nesting substrate at this site was predominantly cattail. The fourth site, another cattail marsh, was located on the shore of Lake Opinicon. All four marshes had clearly defined perimeters and were surrounded by habitat unsuitable for nesting red-winged blackbirds. The four marshes were within 8 km of each other and were ≥8.5 km from the nearest site in the upland study area.

Male removal

Assessing the potential influence of asymmetry on territory acquisition required comparable samples of territorial and nonterritorial males. Accordingly, in 1994 we experimentally removed existing owners from their territories until we captured their replacement, an approach that has been used extensively (e.g., Beletsky and Orians, 1987b; Eckert and Weatherhead, 1987b; Shutler and Weatherhead, 1991). For this part of the study, we focused exclusively on the upland study area and largely restricted removals to males defending isolated territories. This all but eliminated the possibility that experimentally created vacancies would be annexed by neighboring territory owners. For the few cases in which the focal territory shared a boundary with that of another male (i.e., semi-isolated territories), we determined during subsequent visits whether the original neighbor had annexed the vacant territory and, if so, excluded the site from further study.

We captured resident males using decoy traps (Smith, 1976) or mist nets (with model conspecific male and playback) on selected mornings between 6 May and 15 June. By delaying removals until 6 May (the approximate onset of nesting), we ensured that initial territory ownership was firmly established at the outset of the experiment. Upon capture, each resident male was fitted with a numbered aluminum leg band, measured for bilateral asymmetry (see below), weighed to the nearest 0.5 g using a hand-held Pesola spring scale, and housed in an outdoor aviary with food and water provided ad libitum. Experimentally created vacancies were visited the following morning and each subsequent morning until a replacement male had been captured and processed or until repeated attempts to capture the replacement male had failed. At this point, the original resident was fitted with a unique color combination of aluminum leg bands and released. All males involved in the removal study (both resident and replacement) were at least 2 years old based on plumage (Searcy and Yasukawa, 1995), but otherwise their ages were unknown.

Breeding data

Field methods

We monitored redwing breeding activity continuously at all four lowland study sites during both the 1993 and 1994 field seasons. Beginning 1 April, each site was surveyed every 2–3 days and the area defended by each resident male recorded on a small-scale map. We determined territory boundaries by noting the location of territorial displays and by observing male movements and aggressive interactions. Resident males were captured by mist net, uniquely color-banded for individual recognition, measured, weighed as described above, and released immediately at the site of capture. In 1993, we also obtained a blood sample (80–120 μl) from each individual using jugular venipuncture (Hoysak and Weatherhead, 1991). Blood samples were stored in 900 μl lysis buffer (Seutin et al., 1991) and maintained at 4°C until they could be processed. In each of the 2 years, approximately 90% of resident males were ultimately captured and included in the study.

All breeding males were in full adult plumage and were therefore at least 2 years old. However, because all four breeding populations had previously been monitored (and breeding adults banded) as part of a long-term investigation (Weatherhead and Boag, 1997) and because male red-winged blackbirds exhibit extremely high breeding-site fidelity (e.g., Beletsky and Orians, 1987a; Searcy, 1979a; Weatherhead, 1995), we had complete breeding histories for all males included in this part of the study. Moreover, because most male redwings first establish territories when they are 2 or 3 years old (Orians and Beletsky, 1989; Shutler and Weatherhead, 1994), breeding experience provides a surrogate measure of age. Thus, for this particular sample of males, we measured male age as the amount of breeding experience (in years) accrued by the beginning of the appropriate breeding season.

After female settlement and nest initiation, we conducted systematic searches of each marsh every 2–3 days to locate new nests and to monitor the progress of nests already found. Most nests (90% of 194, years pooled) were discovered during nest construction or egg laying; all were found before the eggs hatched. That no nests were discovered beyond incubation suggests that few nests, if any, went undetected. Nests were initially assigned to resident males on the basis of location. In all but one instance, the identity of the putative male parent was later confirmed (often repeatedly) through direct observation of nest defense behavior. We checked nests every 2–3 days and, in 1993, obtained blood samples (50–70 μl) from all nestlings when they were 4–6 days old. In both years, we

continued to monitor nests as long as they remained active. Nestlings were assumed to have fledged if (1) fledglings were observed at or near the nest at the appropriate stage of the nesting cycle (i.e., 9–12 days after hatching) or (2) the nest was found empty after a minimum brood-rearing period of 9 days had elapsed, and there was no indication that the nest had been disturbed by a predator.

During the 1993 field season, we also endeavored to capture, color band, and obtain blood samples from all females associated with active nests. Some females were captured opportunistically during the prenesting period (i.e., during attempts to capture males), but most were caught in nets set near their nests during incubation or brood rearing. In all, 58 of 72 nesting females (81%) were captured in 1993. We made no attempt to capture females in 1994.

We defined harem size as the total number of individual females nesting on the territory of a given male in a particular breeding season (e.g., Weatherhead, 1995; cf. Searcy and Yasukawa, 1995). For data collected in 1993, harem size could be determined directly because most females were individually marked. For the 1994 data, we used nesting chronologies to estimate harem size indirectly as the maximum number of simultaneously active nests (e.g., Weatherhead and Boag, 1995). Analysis based on the 1993 data confirmed that our indirect measure was an excellent predictor of true harem size as defined herein (simple linear correlation: $r = .93$, $n = 35$, $p < .0001$). Average success of females within the harem was taken as the total number of fledglings raised per female on the territory of a given male (Weatherhead, 1995).

Parentage analysis

We determined the true parentage of nestlings sampled in 1993 using standard multilocus DNA fingerprinting techniques (Burke and Bruford, 1987; Jeffreys et al., 1985a,b; see Burke, 1989, for an overview). Fingerprinting protocols and gel scoring procedures were virtually identical to those described by Yezerinac et al. (1995), so here we simply outline those methods and summarize key results (details provided in Dufour, 1996). For logistic reasons, parentage analysis was restricted to samples obtained at our two most productive study sites. This subsample was composed of 143 nestlings from 42 broods, collectively reared on the territories of 26 males. For all but three of the broods, the attending female had been sampled and was included in the analysis as well.

Nuclear DNA was isolated using phenol-chloroform extraction, and a 5-μg sample from each individual was digested with the restriction endonuclease Alu I. DNA fragments were sorted according to size using agarose gel electrophoresis and transferred by Southern blotting to an Immobilon nylon membrane. DNA profiles (i.e., "fingerprints") were produced by hybridization of the transferred fragments with each of two radioactively labeled minisatellite probes: Jeffreys 33.15 (Jeffreys et al., 1985a) and per (Shin et al., 1985). We compared profiles from nestlings and their putative parents with the aid of a computerized scoring system developed specifically for the analysis of electrophoretic gels (National Center for Supercomputing Applications, Champagne, Illinois). To facilitate comparison, we always ran samples from nestlings and their putative parents on the same gel.

We used information on both the frequency of novel fragments (i.e., nestling bands that could not be ascribed to either social parent) and the degree of band-sharing between individuals (Wetton et al., 1987) to identify genetically mismatched young. For female–offspring dyads ($n = 134$), band-sharing coefficients were normally distributed (Shapiro-Wilk $W = 0.98$, $p = .24$), averaged 0.51 (range: 0.32–0.80), and did not covary with the number of novel fragments detected in the nestling's DNA profile. These patterns suggest that all 134

nestlings were the true descendants of the female attending the nest, consistent with other studies of parentage in red-winged blackbirds (e.g., Gibbs et al., 1990; Gray, 1996; Westneat, 1993).

In contrast to the situation for nestlings and their social mothers, the distribution of band-sharing coefficients for male–offspring dyads was distinctly bimodal (range for each of two non-overlapping distributions: 0.05–0.24 and 0.31–0.71; $n = 29$ and 105, respectively). Additionally, the DNA profiles of nestlings with low paternal band-sharing coefficients were invariably characterized by high numbers of novel fragments (range: 3–13; range for nestlings with high paternal band-sharing: 0–3). Thus, the two measures used for parentage exclusion were in near perfect agreement. Of the 134 nestlings for which both types of information were available, 29 had DNA profiles that were incompatible with those of their respective social fathers. We concluded that these nestlings were sired by extrapair males. Of the additional nine nestlings for which DNA was only available for the putative male parent, eight had paternal band-sharing coefficients ranging from 0.44 to 0.57, and one had a value of only 0.18. Given no evidence of intraspecific brood parasitism, we concluded that this last nestling was also the result of an EPF. Thus, 30 of 143 nestlings (21%) were identified as sired by an extrapair male, well within the range reported from a long-term study of the same population (Weatherhead and Boag, 1995).

To identify extrapair sires, we compared the DNA profiles of excluded nestlings with those of all males resident on the same marsh, again using band-sharing coefficients and novel fragments for diagnosis. With one exception, the procedure unambiguously identified a single male as the true genetic sire (band-sharing coefficients $\geq$0.40 with $\leq$2 novel bands). The exceptional nestling could not be assigned to any resident male and was therefore presumably sired by a nonterritorial floater (see Weatherhead and Boag, 1995). Consistent with previous studies (Gibbs et al., 1990; Gray, 1996; Westneat, 1993), most extrapair sires (77%) defended adjacent territories.

Male morphology

To assess variation in asymmetry, we measured both the left and right elements of five bilaterally-paired morphological characters on each male (complete character descriptions provided in Dufour and Weatherhead, 1996): tarsus length, wing chord, "tail length" (i.e., length of the outer retrix), and both the length of the red portion and total length of the epaulet, a bilaterally paired display character used extensively by males in both inter- and intrasexual interactions (Searcy and Yasukawa, 1995). Tarsus and epaulet measures were made to the nearest 0.1 mm using callipers, whereas wing chord ($\pm$ 1 mm) and tail length ($\pm$ 1 mm) were measured with modified rulers. We measured all characters twice (nonconsecutively) to permit assessment of measurement error and to improve precision of measurement for subsequent analysis (see below). Measurements made on feather characters showing evidence of breakage or wear were excluded from analysis, resulting in slightly different sample sizes among the various tests.

Asymmetry for each character was initially taken as the signed difference between the size of the left and right elements (i.e., with information on the direction of departure from perfect symmetry retained). To assess the level of measurement error associated with signed asymmetry scores, we employed a method that we have used previously (Dufour and Weatherhead, 1996), in which replicate left-minus-right values are entered in a one-way, model II ANOVA (individuals as treatment levels) and the total variability for a given character

partitioned into its within and among-individual components (see also Yezerinac et al., 1992). This preliminary analysis was based on all 119 territorial males (both resident and replacement) captured over the 2 years of study. Consistent with the results of a similar analysis based on an independent sample of males (Dufour and Weatherhead, 1996), all characters showed measurable departures from perfect symmetry—that is, significant among-individual variability (all model p values $< .0001$). Character-specific levels of measurement error (i.e., the within-individual variance component, expressed as a percentage of the total variance) ranged from 8.1% to 28.3%. An equivalent analysis based on absolute (i.e., unsigned) asymmetry scores similarly revealed significant among-individual variability at each character (all model p values $< .0001$), with levels of measurement error in this instance ranging from 8.6% to 33.2%. While these values are generally within the range of those thought to be acceptable for studies of asymmetry variation (Palmer, 1994), the moderately high levels of measurement error associated with some characters highlight the importance of minimizing the effects of measurement error in subsequent analysis. Accordingly, for each individual we used the mean value computed across replicate measures as the basis for all subsequent calculations (Bailey and Byrnes, 1990; Yezerinac et al., 1992).

Measurement error notwithstanding, previous authors have identified a number of technical difficulties associated with quantifying asymmetry at the individual level. In particular, Palmer and Strobeck (1992) have argued that tendencies toward greater development on one side or the other can compromise the use of asymmetry as a measure of developmental competence and that tests for directional asymmetry and antisymmetry should be routinely employed. The authors further stressed that choice of an appropriate asymmetry index depends critically on the relationship between asymmetry and character size (see also Palmer, 1994). For the characters used here, both of these issues have already been addressed in a separate analysis based on an independent sample of males (Dufour and Weatherhead, 1996). Thus, here we present only the key results of a similar analysis based on the sample of individuals included in the present investigation. In brief, all character asymmetries were in qualitative agreement with the criteria for ideal fluctuating asymmetry: frequency distributions of left-minus-right values were either normal or only slightly non-normal (based on inspection of normal quantile plots; SAS Institute, 1994), and all were approximately centered on a mean of zero. Formal testing revealed no evidence of antisymmetry (i.e., platykurtosis) in any of the characters measured (one-tailed t tests of H_o: $\gamma_2 \geq 0$, all p values $> .25$; see Sokal and Rohlf, 1981). However, three of the characters showed slight but significant ($p \leq .05$) directionality, that is, departures of the mean left-minus-right value from zero (Table 1). A fourth departure was significant at $p \leq .1$ (Table 1). For all characters, mean deviations from perfect symmetry were moderate, ranging from 3.2% to 12.7% of the maximum individual value (Table 1). Nevertheless, to eliminate the biasing effects of these directional tendencies, we adjusted individual signed asymmetry scores to a mean of zero before converting them 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 (as expected; see Swaddle et al., 1994), all scores were transformed to square roots for

Table 1

Statistics describing the distribution of signed asymmetry scores[a] (mm) for each of five bilaterally paired morphological characters

Character	n	Asymmetry			t^c	p
		Mean	SE	Max[b]		
Tarsus	119	0.09	0.032	−1.50	2.67	.009
Wing	119	0.13	0.082	−2.50	1.60	.113
Tail	109	−0.35	0.200	−11.00	−1.77	.080
Epaulet, red	118	−0.85	0.150	−6.70	−5.68	<.001
Epaulet, total	119	−0.64	0.150	−5.45	−4.27	<.001

[a] Computed as the difference between the size of the left and right elements.

[b] Maximum departure from perfect symmetry (in either direction).

[c] Two-tailed test of H_o: $\mu = 0$.

analysis [a preliminary analysis revealed that the square root transformation was, for all five characters, clearly the most useful transformation to normality among those recommended by Sokal and Rohlf (1981)]. Absolute asymmetry in a given character was unrelated to character size [i.e., (left + right)/2; simple linear regression based on transformed asymmetry values, all p values >.30], so correction for size dependence was not required (Palmer, 1994).

Elsewhere we have shown that, in red-winged blackbirds, statistically significant concordance exists among asymmetry measures made on different characters (Dufour and Weatherhead, 1996). While this suggests that the effects of developmental stability are, to some extent, "organism-wide" in this species, correlations among characters are nonetheless typically weak (Dufour and Weatherhead, 1996). Thus, in addition to evaluating asymmetry variation at each individual character, we also computed a composite index that should better reflect overall developmental competence (Palmer, 1994; Watson and Thornhill, 1994). Specifically, for each character we ranked individuals according to their absolute asymmetry scores and, for each individual, took the sum of these ranks as a measure of asymmetry overall. As such, composite asymmetry scores were only available for those individuals for which measurements were available for all five characters. Composite scores were normally distributed (Shapiro-Wilk W = 0.98, $n = 108$, $p = .37$) and ranged from 121 to 471, with high values indicating high levels of asymmetry relative to other individuals in the sample.

In addition to asymmetry, we also considered several other male characteristics that might be expected to influence male success. Two attributes that have previously been identified as important determinants of male reproductive success in our study population are male age and overall body size (Weatherhead and Boag, 1995). Methods for estimating male age (where possible) have already been described (see "Breeding data" above). As a measure of body size, we used tarsus length, computed as the average length of the left and right elements. We chose tarsus length in this instance because data from our study population indicate that, unlike size measures made on other external characters (e.g., wing and tail), tarsus length covaries with size of the skeleton (Dufour and Weatherhead, 1998; see also Freeman and Jackson, 1990; Rising and Somers, 1989). Finally, because some evidence suggests that energy balance might influence the ability of male red-winged blackbirds to defend territories and/or perform epigamic displays (Searcy, 1979b), we also considered nutritional condition as a potential source of variation in male success. Condition for each individual was taken as the residual from a multiple linear regression equation describing the dependence of body

mass on both date of capture (days since 31 March) and body size [model: mass = 49.9 − 0.09 (date) + 0.74 (tarsus); model $R^2 = .19$, $n = 119$, $p < .0001$].

Data analysis

All analyses were performed using JMP (version 3.1) statistical software (SAS Institute, 1994). With the exception of analyses pertaining to territory acquisition (where paired-sample comparisons were required), our basic analytical approach was to evaluate each component of male success in relation to character or composite asymmetry using generalized linear modeling procedures (McCullagh and Nelder, 1989), controlling effects of additional variables (i.e., breeding experience, size, and/or individual condition) where appropriate. Thus, where the response variable was continuous (e.g., harem size), we used multiple linear regression, specifying asymmetry and other male characteristics as predictors. For categorical response variables (e.g., marsh versus upland habitat), we developed binary logistic regression models and evaluated the significance of predictors using likelihood ratio tests (SAS Institute, 1994). All models were developed separately by character. Further details are provided with individual results. All means are presented in original units ± 1 SE.

RESULTS

Territory acquisition

Between 6 May and 15 June 1994, we removed and detained 41 resident males that had been defending isolated or semi-isolated territories in upland habitat. Of the resulting vacancies, 33 were subsequently reoccupied, with replacement usually occurring within 48 h. Two of the remaining eight vacancies were annexed by neighboring resident males, one was reoccupied by a former resident that had been removed from another territory, and five vacancies, all created after 5 June, were never filled. Of the 33 replacement males, 24 were eventually captured and processed. Consistent with previous studies of territory acquisition in red-winged blackbirds (e.g., Eckert and Weatherhead, 1987b; Shutler and Weatherhead, 1991; Yasukawa, 1979), territory owners and their nonterritorial counterparts were indistinguishable based on size (paired-sample comparison of residents and replacements based on tarsus length: $t = 0.11$, df = 23, $p = .91$). There was some suggestion that residents were in better condition than replacement males, but the difference was marginally nonsignificant (paired-sample t test based on residual body mass: $t = 1.93$, df = 23, $p = .07$). Furthermore, simple logistic regression (with resident versus replacement as the binary response variable) revealed that condition explained only 5.1% of the "uncertainty" in territorial status (see SAS Institute, 1994). Given that the influence of condition was apparently weak and only approached statistical significance, and because statistical control in this instance would have required that we ignore the paired nature of the data, we elected not to control for condition in analyses of territory ownership relative to asymmetry.

Paired-sample comparisons provided little evidence that territory owners were more symmetrical than their nonterritorial counterparts (Table 2). Although two of the five comparisons (by character) revealed marginally nonsignificant ($p \le .1$) asymmetry differences between residents and replacements, in both instances the direction of the difference was opposite to that expected (i.e., for these characters, resident males had higher rather than lower levels of asymmetry than replacement males; Table 2). Similarly, among resident–replacement pairs for which asymmetry measures were available for all five

Table 2

Comparison of resident (territorial) and replacement (floater) male red-winged blackbirds with respect to levels of asymmetry[a] (mm) exhibited at each of five bilaterally paired morphological characters

| Character | Status | n | Asymmetry | | t[b] | p |
			Mean	SE		
Tarsus	Resident	24	0.23	0.037	0.57	.575
	Replacement	24	0.30	0.074		
Wing	Resident	24	0.83	0.133	1.79	.087
	Replacement	24	0.53	0.104		
Tail	Resident	20	1.17	0.276	0.49	.631
	Replacement	20	1.32	0.270		
Epaulet, red	Resident	24	1.31	0.182	0.11	.913
	Replacement	24	1.45	0.241		
Epaulet, total	Resident	24	1.41	0.223	1.86	.076
	Replacement	24	0.97	0.170		

[a] Computed as the absolute value of the difference between the size of the left and right elements.

[b] Paired sample t test (two-tailed) with resident males and their respective replacements as paired observations, based on square-root-transformed asymmetry values.

Table 3

Levels of character asymmetry[a] (mm) exhibited by males defending territories in high-quality marsh habitat and those defending territories in relatively marginal upland field habitat

| Character | Habitat | n | Asymmetry | | G[b] | p |
			Mean	SE		
Tarsus	Marsh	35	0.25	0.044	0.33	.565
	Upland	42	0.20	0.025		
Wing	Marsh	35	0.66	0.107	0.51	.475
	Upland	42	0.78	0.088		
Tail	Marsh	31	1.31	0.250	0.00	.976
	Upland	40	1.18	0.271		
Epaulet, red	Marsh	35	1.28	0.177	0.22	.637
	Upland	42	1.23	0.133		
Epaulet, total	Marsh	35	1.08	0.147	2.48	.115
	Upland	42	1.50	0.174		

[a] Computed as the absolute value of the difference between the size of the left and right elements.

[b] Likelihood ratio test of the effect of character asymmetry (square root transformed) on the probability of holding a territory in marsh habitat [binary logistic regression with asymmetry and condition (i.e., residual body mass, see text) as predictors; SAS Institute, 1994].

characters, residents were no more symmetrical overall (paired-sample t test based on composite asymmetry scores: $t = 0.61$, df $= 19$, $p = .55$). Thus, we found little evidence to suggest that asymmetry and success in competition for a territory are associated in male red-winged blackbirds.

Territory quality

We predicted that, among males that establish territories, those characterized by low levels of asymmetry would more often be found defending territories in high-quality marsh habitat. To test this prediction, we compared the morphology of males that held territories in the lowland study area (i.e., marsh habitat) with that of the original territory owners involved in the removal experiment (i.e., upland habitat). For males from marsh habitat, we included only individuals that held territories in 1994 ($n = 35$) because that was the year we sampled males from the upland study area. The upland sample included all 41 residents from the removal study, as well as one additional territory owner that had been captured opportunistically. Habitat status (i.e., marsh versus upland) was unrelated to male size (simple logistic regression: $G = 0.59$, df $= 1$, $p = .44$), but the probability of holding a territory in marsh habitat was higher for males in superior condition ($G = 10.79$, df $= 1$, $p = .001$).

To assess the relationship between habitat status and asymmetry while simultaneously controlling effects of individual condition, we developed multiple logistic regression models, specifying habitat as the response variable and treating character asymmetry and residual body mass as predictors. In each of the five models (developed separately by character), the effect of asymmetry on the probability of holding a territory in marsh habitat was nonsignificant (Table 3). Similarly, analysis based on composite asymmetry scores ($n = 71$ males) revealed no relationship between habitat status and asymmetry overall (logistic regression with asymmetry and residual body mass as predictors, asymmetry effect: $G = 1.20$, df $= 1$, $p = .27$). Thus, we found no evidence to support the prediction that males characterized by low levels of asymmetry more often establish territories in high-quality habitat.

Success among territory owners in high-quality habitat

Of 40 males that held territories in the lowland study area in 1993, 35 (88%) were ultimately captured and included in the study. Eighteen of these individuals returned to defend the same territories in 1994. Of 22 previously unbanded males that also held territories in 1994 (presumed to be first-time breeders), 17 were ultimately captured and processed. Thus, morphological and breeding data were assembled for 52 individual males. Because some males were present during both years, all analyses were conducted separately by year. Data from the four focal marshes were combined for analysis because preliminary tests indicated no between-site differences in measures of morphology or breeding performance in either 1993 or 1994.

Recruitment of mates

In 1993, harem size varied from zero (for males that failed to recruit any social mates) to five (mean $= 2.1 \pm 0.22$, $n = 35$). Harem sizes were somewhat smaller in 1994 (mean $= 1.4 \pm 0.16$, $n = 35$), but still showed appreciable variation among males (range: 0–4). Contrary to the results of a long-term study of the same population (Weatherhead and Boag, 1995), larger males did not attract more social mates during the 2 years of the present investigation (1993, $r = -.06$, $n = 35$, $p = .72$; 1994, $r = -.26$, $n = 35$, $p = .13$). However, harem size did increase with increasing breeding experience, albeit in only 1 of the 2 years of study (1993, $r = .35$, $n = 35$, $p = .04$; 1994, $r = .23$, $n = 35$, $p = .19$). Harem size was not related to male condition in either 1993 ($r = .21$, $n = 35$, $p = .22$) or 1994 ($r = .13$, $n = 35$, $p = .45$).

To test the prediction that symmetrical males attract more social mates, we examined the relationship between harem size and asymmetry in each character, controlling for male breeding experience in each instance using multiple linear regression (MLR). In 1993, partial coefficients describing the relationship between harem size and asymmetry were significant ($p \le .05$) or marginally nonsignificant ($p \le .1$) for two of the five characters measured (Table 4). In both instances, however, the direction of the relationship was opposite to that predicted: for both wing length and red epaulet length, departures from perfect symmetry were positively related to suc-

Table 4

Multiple linear regression models evaluating effects of character asymmetry[a] (asym, in mm, square root transformed) and breeding experience (exp, in years) on the number of social mates recruited by individual males

Model Year	Character	n	R^2	Source	Coefficient[b]	F	p
1993	Tarsus	35	.17	Asym	−1.397	1.78	.191
				Exp	0.303	5.29	.028
	Wing	35	.20	Asym	0.973	3.17	.084
				Exp	0.264	4.20	.049
	Tail	32	.14	Asym	−0.197	0.18	.678
				Exp	0.298	4.41	.044
	Epaulet, red	34	.26	Asym	1.108	6.53	.016
				Exp	0.257	4.53	.041
	Epaulet, total	35	.13	Asym	−0.273	0.38	.543
				Exp	0.281	4.42	.044
1994	Tarsus	35	.10	Asym	0.907	1.54	.224
				Exp	0.121	1.52	.227
	Wing	35	.05	Asym	−0.076	0.03	.872
				Exp	0.137	1.77	.193
	Tail	31	.10	Asym	−0.364	1.25	.273
				Exp	0.148	2.03	.165
	Epaulet, red	35	.06	Asym	0.183	0.26	.613
				Exp	0.126	1.58	.218
	Epaulet, total	35	.12	Asym	−0.582	2.57	.118
				Exp	0.121	1.56	.220

[a] Computed as the absolute value of the difference between the size of the left and right elements.
[b] Partial regression coefficient.

Table 5

Multiple linear regression models evaluating effects of character asymmetry[a] (asym, in mm, square root transformed) and male size (measured as length of the tarsus, in mm) on the number of fledglings raised per female on the territory of a given male

Model Year	Character	n	R^2	Source	Coefficient[b]	F	p
1993	Tarsus	30	.16	Asym	−0.465	0.15	.701
				Size	0.961	4.11	.053
	Wing	30	.15	Asym	−0.223	0.12	.733
				Size	1.050	4.85	.036
	Tail	27	.15	Asym	−0.289	0.33	.571
				Size	1.075	4.18	.052
	Epaulet, red	30	.15	Asym	−0.187	0.10	.759
				Size	1.021	4.88	.036
	Epaulet, total	30	.18	Asym	0.431	0.83	.371
				Size	0.916	3.89	.059
1994	Tarsus	28	.06	Asym	−0.168	0.01	.916
				Size	0.596	1.66	.210
	Wing	28	.19	Asym	−1.389	3.96	.058
				Size	0.630	2.19	.152
	Tail	24	.11	Asym	−0.380	0.42	.524
				Size	0.757	2.48	.130
	Epaulet, red	28	.07	Asym	0.095	0.03	.875
				Size	0.603	1.73	.200
	Epaulet, total	28	.06	Asym	0.053	0.01	.931
				Size	0.592	1.56	.223

[a] Computed as the absolute value of the difference between the size of the left and right elements.
[b] Partial regression coefficient.

cess in attracting social mates (Table 4). Neither relationship was apparent among males that bred in 1994, nor were effects of other character asymmetries evident in that year (Table 4). Finally, harem size was not related to composite asymmetry in either 1993 (MLR with breeding experience and asymmetry as predictors, asymmetry effect: partial coefficient = 0.00, F = 0.02, df = 1,28, p = .89) or 1994 (partial coefficient = 0.00, F = 0.08, df = 1,28, p = .79). Thus, we found no evidence to suggest that males characterized by low levels of asymmetry attract disproportionately high numbers of social mates.

Reproductive success of females

One component of male reproductive success in a polygynous species is the average success of females within the harem. To determine whether this component of male success was related to male symmetry, we first computed the number of fledglings raised per female on the territory of each male. The analysis was thus restricted to those males that had recruited at least one social mate, and each male was represented once in a given test. Average female success was unrelated to male breeding experience (1993, r = .04, n = 30, p = .81; 1994, r = −.02, n = 28, p = .91) or condition (1993, r = −.20, n = 30, p = .30; 1994, r = .10, n = 28, p = .60), but was positively related to male size (i.e., tarsus length), at least among males that bred in 1993 (r = .39, n = 30, p = .03; corresponding values for 1994: r = .25, n = 28, p = .19). To control the effects of male size in analyses of asymmetry variation, we again used an MLR approach (similar to that described above), with average female success as the response variable and male size and asymmetry as predictors. Of the 10 models developed (by character and year), only one was suggestive of a relationship between female success and male character asymmetry (Table 5), and in this instance (wing asymmetry in 1994) the relationship only approached statistical signifi-

cance (p = .06). Similarly, female success was not related to male composite asymmetry in either 1993 (partial coefficient = 0.00, F = 0.02, df = 1,24, p = .88) or 1994 (partial coefficient = 0.00, F = 0.00, df = 1,21, p = .95). Thus, we found little evidence that females nesting on the territories of symmetrical males realize higher annual reproductive success.

Within-pair paternity

To assess variation in within-pair paternity, we first computed the proportion of sampled nestlings that were legitimate for each male (e.g., Gibbs et al., 1990; Westneat, 1993). Although all 26 males resident on the two focal marshes were sampled and included in the parentage analysis, broods of only 19 males survived to an age at which blood samples could be obtained (mean number of nestlings sampled per male = 7.5 ± 0.81). Of these 19 males, 9 achieved full within-pair paternity, 8 achieved partial paternity (proportion of nestlings legitimate: 0.64–0.93), and 2 males suffered complete loss of paternity as a result of extrapair mating. Complete loss of paternity was not an artifact of there being few nestlings available for analysis: parentage for the 2 males was based on samples of 4 and 13 nestlings, from 1 and 4 complete broods, respectively.

Because almost half of all males suffered no loss of paternity, we analyzed these data by comparing males that achieved full paternity with those that suffered reduced paternity (either partial or complete) as a result of extrapair mating. Loss of paternity was unrelated to male breeding experience (simple logistic regression with paternity status as the response variable: G = 0.09, df = 1, p = .77), size (i.e., tarsus length; G = 0.18, df = 1, p = .67), or nutritional condition (i.e., residual body mass; G = 0.84, df = 1, p = .36). Males characterized by high levels of red epaulet asymmetry were more likely to suffer reduced paternity (Table 6), but the relationship only approached statistical significance (p = .07). Effects

Table 6

Levels of character asymmetry[a] (mm) exhibited by males that achieved full within-pair paternity and those that suffered reduced paternity as a result of extrapair mating

Character	Paternity	n	Asymmetry		G[b]	p
			Mean	SE		
Tarsus	Full	9	0.28	0.068	0.54	.461
	Reduced	10	0.20	0.042		
Wing	Full	9	0.65	0.152	0.06	.813
	Reduced	10	0.78	0.217		
Tail	Full	9	0.77	0.164	0.73	.392
	Reduced	9	1.38	0.579		
Epaulet, red	Full	9	1.23	0.188	3.23	.072
	Reduced	10	2.00	0.349		
Epaulet, total	Full	9	1.43	0.545	0.09	.769
	Reduced	10	1.56	0.238		

[a] Computed as the absolute value of the difference between the size of the left and right elements.

[b] Likelihood ratio test of the effect of character asymmetry (square root transformed) on the probability of achieving full paternity (binary logistic regression; SAS Institute, 1994).

Table 7

Levels of character asymmetry[a] (mm) exhibited by males known to have sired extrapair young and males that apparently did not sire extrapair young

Character	Status of male	n	Asymmetry		G[b]	p
			Mean	SE		
Tarsus	Successful	8	0.24	0.060	0.11	.742
	Unsuccessful	18	0.23	0.044		
Wing	Successful	8	0.69	0.208	0.19	.659
	Unsuccessful	18	0.65	0.125		
Tail	Successful	8	1.42	0.648	0.28	.599
	Unsuccessful	16	0.99	0.152		
Epaulet, red	Successful	8	1.95	0.431	3.34	.068
	Unsuccessful	17	1.27	0.234		
Epaulet, total	Successful	8	0.77	0.211	2.12	.145
	Unsuccessful	18	1.42	0.301		

[a] Computed as the absolute value of the difference between the size of the left and right elements.

[b] Likelihood ratio test of the effect of character asymmetry (square root transformed) on the. probability of extrapair fertilization success (binary logistic regression with asymmetry and breeding experience as predictors; SAS Institute, 1994).

of other character asymmetries were nonsignificant (Table 6), as was the effect of asymmetry overall (simple logistic regression based on composite asymmetry score: $G = 0.95$, df $= 1$, $p = .33$). Thus, we found little evidence to suggest that asymmetry and loss of paternity are associated in male red-winged blackbirds. However, limited sample sizes for this analysis require that conclusions here be viewed as somewhat tentative.

Extrapair mating success
Resident males varied considerably in the extent to which they achieved EPFs. Although more than half of sampled residents (18 of 26) sired no extrapair young, some males realized substantial gains through extrapair reproduction (number of extrapair nestlings sired per successful male $= 3.6 \pm 1.66$, $n = 8$ extrapair sires). Indeed, one male sired 15 extrapair nestlings, distributed among 6 broods reared on the territories of 4 different males (notably, this male also achieved full paternity in both broods reared on his own territory). Despite the variable success of extrapair sires, however, small samples precluded relating this variation to male morphology. Instead, we simply compared males classified according to whether or not they were known to have sired extrapair young.

The probability of EPF success was unrelated to male size (simple logistic regression with extrapair status as the response variable: $G = 0.11$, df $= 1$, $p = .74$) or nutritional condition ($G = 0.02$, df $= 1$, $p = .88$). However, consistent with previous work (Weatherhead and Boag, 1995), experienced males were far more likely to succeed in this regard. Extrapair sires had, on average, 2.1 years of breeding experience, whereas unsuccessful males had only 0.4 (i.e., most were first-time breeders). Simple logistic regression revealed that the effect of experience on the probability of EPF success was highly significant ($G = 6.91$, df $= 1$, $p = .009$). Accordingly, to control for experience in analyses of success relative to asymmetry, we developed multiple logistic regression models (with extrapair status as the response variable) and entered both breeding experience and asymmetry as predictors. Of the five models developed (by character), only one suggested a possible asymmetry effect ($p = .07$), and in this instance the direction was opposite to that predicted: males characterized by low levels of red epaulet asymmetry were less rather than more likely to achieve one or more EPFs (Table 7). Similarly, the probability of EPF success was unrelated to asymmetry

overall (logistic regression with breeding experience and composite asymmetry as predictors, asymmetry effect $G = 0.00$, df $= 1$, $p = .99$). Also noteworthy is the observation that the exceptionally successful extrapair sire (identified above) was not exceptionally symmetrical: of 22 other males assessed for both parentage and composite asymmetry, 5 (23%) had lower composite asymmetry scores than the exceptional extrapair sire. Moreover, none of these five comparatively symmetrical males sired any extrapair young. Overall, then, we found little evidence to suggest that symmetrical males are more likely to realize EPF success.

Annual reproductive success
The consistent lack of association between asymmetry and specific components of male success suggested that asymmetry was unlikely to be an important determinant of male success overall. To address this issue directly, we calculated true annual reproductive success (annual RS) for each of the 26 males included in the parentage analysis. Annual RS was computed as the total number of fledglings sired by a given male, either on his own territory or through extrapair mating. Simple linear correlation revealed a highly significant positive relationship between annual RS and breeding experience ($r = .59$, $n = 26$, $p = .001$), reflecting the influence of experience on both recruitment of social mates and EPF success (see above). On the other hand, annual RS was unrelated to male size ($r = .18$, $n = 26$, $p = .39$) or nutritional condition ($r = .07$, $n = 26$, $p = .75$).

To assess variation in annual RS relative to asymmetry, we developed separate regression models for each character (with annual RS as the response variable), in each instance controlling the effects of male breeding experience by including experience as a predictor. As expected, annual RS was not related to asymmetry in any of the characters examined (Table 8). Similarly, annual RS was unrelated to asymmetry overall (MLR with breeding experience and composite asymmetry as predictors, asymmetry effect: partial coefficient $= 0.00$, $F = 0.05$, df $= 1,20$, $p = .83$). Thus, using a comprehensive measure of reproductive success, we found no evidence that asymmetry influences reproductive performance among individual male red-winged blackbirds.

Table 8
Multiple linear regression models evaluating effects of character asymmetry[a] (asym, in mm, square root transformed) and breeding experience (exp, in years) on the annual reproductive success[b] of individual males

Model				Coef-		
Character	n	R^2	Source	ficient[c]	F	p
Tarsus	26	.36	Asym	−2.488	0.37	.549
			Exp	1.766	12.85	.002
Wing	26	.36	Asym	−0.961	0.17	.683
			Exp	1.786	12.74	.002
Tail	24	.37	Asym	1.270	0.47	.502
			Exp	1.789	12.11	.002
Epaulet, red	25	.36	Asym	1.180	0.46	.503
			Exp	1.710	11.62	.003
Epaulet, total	26	.39	Asym	−1.873	1.42	.246
			Exp	1.700	12.35	.002

[a] Computed as the absolute value of the difference between the size of the left and right elements.
[b] Total number of fledglings sired, both on and off the territory.
[c] Partial regression coefficient.

DISCUSSION

Despite the recent interest in hypotheses that propose that bilateral symmetry could underlie variation in individual male reproductive performance, there have been few comprehensive empirical investigations of the reproductive consequences of asymmetry for individual males under natural conditions. We attempted to provide as complete an analysis as was logistically possible for the system under study by evaluating each of several components of male reproductive success in relation to asymmetry measures for a variety of characters. To broaden the scope of analysis, we included characters that have an obvious signaling function (i.e., epaulet measures), those that might be expected to influence aerodynamic performance (i.e., wing and tail), and a composite asymmetry measure that should better reflect overall developmental competence. Significantly, perhaps the most salient result to emerge from our analyses relates not to any one component of male success or individual character, but rather becomes evident upon inspection of the results overall: our results consistently failed to support the prediction that males characterized by low levels of asymmetry realize a reproductive advantage. Results of a male removal experiment provided no evidence that asymmetry influences territory acquisition among male red-winged blackbirds. Similarly, we found no evidence that territory owners characterized by low levels of asymmetry were more likely to establish territories in high-quality habitat. Finally, intensive monitoring of breeding activity in high-quality habitat revealed that variable male reproductive success due to differences in harem size, average success of females within the harem, within-pair paternity, and extrapair fertilization success was generally unrelated to asymmetry levels exhibited by resident males. Thus, contrary to prediction, bilateral symmetry (and, by inference, developmental stability) appears not to be an important determinant of reproductive success among individual male red-winged blackbirds.

A potential limitation of some aspects of the present study is that, for certain reproductive components, the number of males included in the analyses was limited and hence some tests had low statistical power. This was particularly true of analyses related to within-pair paternity and extrapair mating success, where logistic constraints required that we include data from only a subsample of available males. However, given that the effects of individual character asymmetries on these

components of success rarely even approached statistical significance, and because there was no suggestion whatsoever that within-pair paternity or extrapair mating success might be associated with multicharacter asymmetry (arguably the most informative measure of asymmetry used here; see Palmer, 1994), it appears unlikely that additional data from our study population would alter our conclusions regarding the importance of asymmetry in this regard. Moreover, because asymmetry was not predictive of other components of success among territorial males, any subtle (i.e., undetected) effects of asymmetry on within-pair or extrapair mating success apparently would have had little substantive impact on male success overall.

Given that symmetry and reproductive success appear genuinely unrelated in male red-winged blackbirds, it is of interest to compare this result with those of similar studies of other avian species. The most extensive data come from Møller's (1994) work on natural populations of barn swallows. Møller found that males with relatively symmetrical wings and outer tail feathers were more likely to obtain a mate, a result he attributed to female preference for symmetrical males (see also Møller, 1992, 1993). While we can only speculate as to why Møller's findings differ from ours, it is possible that, contrary to Møller's interpretation, the advantages accrued to symmetrical male barn swallows are realized, not through female preferences, but through aerodynamic advantages of symmetry (Balmford and Thomas, 1992). Under this scenario, asymmetry may well influence the reproductive performance of aerial insectivores such as barn swallows more so than species that rely less heavily on aerial agility, i.e., red-winged blackbirds (see also Balmford et al., 1993). However, Møller (1993) also demonstrated that the mere appearance of an asymmetrical tail (created via experimental color manipulation) can influence the reproductive performance of male barn swallows. Thus, available evidence supports the interpretation that the mating advantage realized by symmetrical male barn swallows is mediated by female choice and occurs independently of any mechanical effects of asymmetry on aerial agility (see also Swaddle and Cuthill, 1994a,b). Aerodynamic considerations, therefore, are unlikely to account for the differences between Møller's (1994) results and those reported here.

If female barn swallows prefer symmetrical males, why do female red-winged blackbirds not show similar preferences? Conceivably, species might differ in the extent to which asymmetry conveys information regarding the quality of potential mates. Elsewhere we have shown that character asymmetries exhibited by male red-winged blackbirds are generally unrelated to measures of health, viability, or parental effort (Dufour and Weatherhead, 1998). Because these results are inconsistent with the premise that asymmetry indicates individual phenotypic or genotypic quality, it is perhaps not surprising that female red-winged blackbirds do not appear to use symmetry as a criterion for mate selection. At the same time, however, the nature of the benefits accrued to discriminating female barn swallows have not yet been identified, nor is it clear why symmetry should be indicative of male quality in some species and not in others (see, for instance, Leung and Forbes, 1996). Both of these issues will require closer scrutiny before predictions regarding the reproductive consequences of asymmetry are likely to be accurate.

To our knowledge, only two other avian studies have examined the reproductive consequences of asymmetry for individual males under natural conditions. Consistent with the results presented here, Yezerinac (1995) found that male yellow warblers (*Dendroica petechia*) characterized by low levels of tarsal or wing asymmetry were no more likely than other males to maintain full within-pair paternity, achieve extrapair

mating success, or realize higher reproductive success overall. Similarly, Lanctot (1996) reported that in the lek-breeding buff-breasted sandpiper (*Tryngites subruficollis*), male mating success (inferred from behavioral observations and/or genetic analysis of parentage) was apparently unrelated to asymmetry measures made on several traits. These recent studies, in combination with the results of the present investigation, suggest that the influence of asymmetry on male success may be considerably less ubiquitous than initially suggested, at least among natural populations of birds.

The prediction that symmetry should be associated with male reproductive success has received broader support from studies of invertebrates (Harvey and Walsh, 1993; Liggett et al., 1993; Markow and Ricker, 1992; McLachlan and Cant, 1995; Møller, 1996; Radesater and Halldorsdottir, 1993; Simmons, 1995; Thornhill, 1992a,b). Although these results are consistent with Møller's (1990) male quality/female choice hypothesis, several authors have noted that there are difficulties with this interpretation (Eggert and Sakaluk, 1994; Palmer, 1994; Ryan et al., 1995). Specifically, although virtually all of the studies cited above were based on asymmetry measures made on one or two individual characters, it is becoming increasingly apparent that single character asymmetries are likely to be poor predictors of overall developmental competence. This suggestion stems from the recognition that asymmetry measures made on different characters are at best only weakly correlated at the individual level (e.g., Dufour and Weatherhead, 1996; Ryan et al., 1995; see also Palmer and Strobeck, 1986, and references therein). Thus, unless the authors cited above fortuitously measured characters particularly revealing of underlying individual quality, it is unclear how Møller's (1990) hypothesis might account for these results. An alternative possibility, and that clearly favored by some authors (e.g., McLachlan and Cant, 1995), is that asymmetry has a direct mechanical impact on the functioning of certain traits, leading to a reduction in male competitive ability. Suggestively, most of these studies assessed asymmetry of wings or other functional appendages. However, explanations based on mechanical considerations clearly cannot account for all of the observed associations. For instance, Thornhill (1992a) demonstrated directly that female Japanese scorpionflies (*Panorpa japonica*) actively discriminate against males with high levels of forewing asymmetry. Again, whether discriminating females in this system actually receive either material or genetic benefits remains to be determined.

In conclusion, our results generally fail to support the prediction that male red-winged blackbirds characterized by low levels of asymmetry realize a reproductive advantage. Although this finding obviously does not negate such associations in other species, it does add to the growing suggestion (e.g., Eggert and Sakaluk, 1994; Ryan et al., 1995) that asymmetry-related reproductive consequences may be considerably less ubiquitous than initially supposed. Future studies should seek to identify the specific mechanisms underlying established associations between asymmetry and male mating success. Only with such information will it become possible to determine why developmental stability and bilateral symmetry appear to have individual-level fitness consequences in some species and not in others.

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