

Asymmetry and Mating Success in a Periodical Cicada, *Magicicada septendecim* (Hemiptera: Cicadidae)

John R. Cooley

*Department of Ecology and Evolutionary Biology, University of Connecticut, CT,
USA*


Abstract

Phenotypic symmetry results from both a genetic predisposition and the influence of the developmental environment. Although most studies of mate choice and phenotypic asymmetry are couched in terms of active choice for ‘good genes’, an alternative viewpoint is to consider incidental mating biases that arise from the functional effects of asymmetrical phenotypes. This paper (i) discusses the specific situations in which symmetry-based mate choice may be likely, and (ii) presents research on female mate choice and symmetry in the periodical cicada, *Magicicada septendecim* (L.). Male mating aggregations and lack of mating gifts or parental care make this species an ideal target for studying female choice for superior mates, and thus for a relationship between male symmetry and male mating success.

Corresponding author: John R. Cooley, Department of Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, U-43, Storrs CT 06269, USA. E-mail: jcooley@sp.uconn.edu

Introduction

For bilaterally symmetric organisms, deviations from symmetry result from (i) genetic influences (because genotypes susceptible to perturbation or with poorly interacting constituents lead to asymmetries), (ii) environmental influences (because conditions during development influence production of a symmetrical phenotype), or (iii) interactions between these two factors. In any population, zero-centered, normally distributed deviations from perfect bilateral symmetry are termed ‘fluctuating asymmetry’, a term that refers to normally-distributed, non-adaptive asymmetries with a mean value of zero (FA; Van Valen 1962). Although fluctuating asymmetry is a population index, if a population exhibits FA, then the asymmetries of its members are individual manifestations of deviations from normal development; the asymmetries of individuals are often referred to as FA although the term itself was defined as a measure of population characteristics (Møller 1993c; Møller & Swaddle 1997).

	E	T	H	9	9	3	B	Dispatch: 4.6.04	Journal: ETH	CE: Hema
	Journal Name			Manuscript No.				Author Received:	No. of pages: 17	PE: K.S. Kavitha

It is not a gross exaggeration to state that for nearly every paper finding an effect or correlate of FA, there is another dismissing the same relationship. At their core, some of the most recent and hotly debated exchanges in symmetry theory (see Møller 1993a; Palmer 1996; Houle 1997; Leamy 1997; Markow & Clarke 1997; Møller & Thornhill 1997a,b; Palmer & Strobeck 1997; Pomiankowski 1997; Swaddle 1997; Whitlock & Fowler 1997; Clarke 1998; Houle 1998; Bjorksten et al. 2000a,b; Chapman & Goulson 2000; Swaddle 2003) are disputes over causation. Although symmetry has been used to address diverse topics, from mate choice to environmental degradation (Clarke 1993; Møller & Swaddle 1997), attributing measurable patterns of asymmetry to any one of several potential causes is a task made difficult by the tendency of FA data to be correlative. Meta-analyses (Thornhill & Møller 1998; Vøllestad et al. 1999; Gates 2002; Møller & Jennions 2002) have been suggested as a means for attaching some statistical power to collections of such correlative data, but the meta-analysis approach itself has spurred almost as many controversies as fluctuating asymmetry itself (Clarke 1998; Simmons et al. 1999; Palmer 2000; Jennions & Møller 2001; Kotiaho & Tomkins 2002).

Symmetry and Mate Choice

Controversies aside, the possibility that fluctuating asymmetry correlates with some aspect of individual quality makes symmetry a possible target of mate choice evolution. Although most examples in the literature discuss female mate discrimination, most or all of the conclusions of the fluctuating asymmetry literature apply no matter which sex is choosy. As examples, symmetry has been linked to male dominance in fallow deer (Malyon & Healy 1994), attractiveness in humans (Gangstead et al. 1994; Møller 1995), and mating success in barn swallows (Møller 1993b, 1994) and zebra finches (Swaddle 1996). Symmetrical male Japanese scorpionflies generally tend to win both inter- and intra-specific fights for control of mating gifts (Thornhill 1992a,b), the most symmetrical male dung flies and houseflies are also the most successful breeders (Liggett et al. 1993; Møller 1996), and the most symmetrical dragonflies (*Coenagrion puella*) have the highest lifetime mating success (Harvey & Walsh 1993). Although not all studies show a relationship between symmetry and mating success (see Oakes & Barnard 1994; Tomkins & Simmons 1998), at least some mate choice mechanisms appear to favor symmetry or its correlates.

Mate Choice and Symmetry in Periodical Cicadas

North American periodical cicada (*Magicicada*) mating aggregations and complex courtship suggest a long history of sexual selection. Detailed descriptions of *Magicicada* life cycles, species, populations, biology, and behavior may be found in Williams & Simon (1995); Marshall & Cooley (2000), and Cooley & Marshall (2001). In brief, *Magicicada* are highly mobile insects; males form dense aggregations in which they make loud species-specific calls and search for females,

while females enter male singing aggregations and produce timed visual and acoustical receptivity signals in response to the calls of a nearby male. A male participating in such a signaling 'duet' begins a complex, multi-part courtship sequence directed at the signaling female (Cooley 1999; Cooley & Marshall 2001). The dense, multi-species male choruses, male-female duets, and complex courtship provide ample opportunities for sexual selection, manifested through mate choice, forcing behavior, intrasexual mating competition, and other such interactions. Alexander (1975) proposed that *Magicicada* male choruses are non-resource based leks, in which females have the opportunities to compare and discriminate among potential mates. Yet within-species mate choice and mate choice criteria remain largely unexplored in *Magicicada* (but see, Cooley & Marshall 2004); thus a logical starting point is to search for a correlation between mating success and a general choice criterion or correlate such as FA. I chose to assess the relationships of wing, leg, and tymbal asymmetries to male mating success in *Magicicada* using simple experiments in which females were provided an excess of males captured from a natural chorus.

Methods and Results

Brood II *Magicicada septendecim* emerged in a large open field near Horsepen Lake State Wildlife Management Area, Buckingham County, VA, in May 1996 (see Williams & Simon 1995 for discussion of brood terminology). Vegetation in the field consisted primarily of oak, maple, and tulip tree stump sprouts from logging approx. 2 yr prior; the surrounding forest contained primarily oaks and maples, interspersed with patches of planted pines. The morning after their final ecdysis, newly emerged cicadas ('teneral' cicadas) are readily identifiable by their dull color, soft bodies, and by their low positions in the vegetation; the teneral period lasts five or more days, after which the adult cicada is fully mature and sexually receptive (Maier 1982; Cooley 1999; Marshall 2000). Because female *Magicicada* generally mate only once (Cooley 1999; Marshall 2000; Cooley & Marshall 2004), to ensure that only unmated females were used in this study, teneral females were collected early in the mornings several days before beginning experiments and allowed to mature in single-sex storage cages made by enclosing living vegetation in 200 l hardware cloth cages. Males were collected from among those actively chorusing immediately before the start of the experiments.

All experiments took place in two large, cylindrical, approx. 3000-l white nylon tulle cages placed over stump sprouts, with vegetation trimmed so that all parts of the cages could be reached and observed with minimum disturbance. To start each experimental trial, I placed 10 mature females and 20 recently captured males into each cage; the densities in these cages were comparable with natural densities (Cooley 1999). Each cage was examined for matings at least once per hour, a conservative sampling interval as normal matings last longer than 2 h (Cooley 1999). This experimental design, in which females are given free access to an excess number of males, probably tends to encourage male-male scramble

competition and accentuate quality differences among males, because sexually receptive females signal to calling males (Cooley 1999; Cooley & Marshall 2001), causing all nearby males to intensify their efforts to find the signaling female. I removed all mating pairs upon first observation and immediately preserved them in 70% ethanol. When all females had been removed, or at the end of the day, the remaining, unpaired males were preserved in a separately marked jar. The experiment was repeated the following day using different cicadas. I collected a total of 27 mating pairs; three unmated male cicadas were lost, and all other cicadas were accounted for. Each preserved male was given a numerical code that, without a key, provided no information about mating status. I investigated three classes of asymmetries and their relationships to mating success: (i) left-right character size asymmetries, (ii) asymmetries in tymbal rib number, and (iii) presence or absence of anomalous wing vein characters.

Left-Right Size Asymmetries

Methods and results

A trained technician, unaware of the design or purpose of the study (see Houle 1998), made measurements of the right and left sides of three forewing characters, two hindwing characters, and two leg characters (Fig. 1). For measurements, the technician used a calibrated ocular micrometer mounted in the eyepiece of a Zeiss binocular dissecting microscope and clamped each wing or leg flat between two pieces of microscope slide glass using a homemade holding jig. All measurements on each cicada were repeated four times on separate occasions, and between each measurement session, the specimens were recoded so that the technician was unaware she was remeasuring the same specimens. The technician skipped measurements on damaged cicadas. The numbers of specimens used in the analysis for each character are noted in Table 1.

For each character, individuals for which there were not at least three measurements were eliminated from consideration. The repeated measurements were analyzed using an ANOVA design to ensure that variation came from actual asymmetry differences, not from measurement repetitions (see Palmer & Strobeck 1986, 1992; Palmer 1994; Swaddle et al. 1994). Mixed-model ANOVAs had the following structure: factors were repetition (1–4) and side (left/right), and the dependent variables were the seven characters. Characters F27, H40, FFEM, and HFEM failed this test, and character F15 was close to failing, indicating that measurement error accounted for a significant amount of the variability in the full data set. To reduce this error, for each side of each character, the most extreme value of the four repetitions was excluded; the removal of extreme measurements has the added advantage of making the measurements more conservative estimates of asymmetry. For each character, individuals for which there were not three remaining measurements were eliminated from consideration. The data were again examined using a mixed-model ANOVA; in only one case (hindwing character H40) did repetition continue to explain a significant amount of the

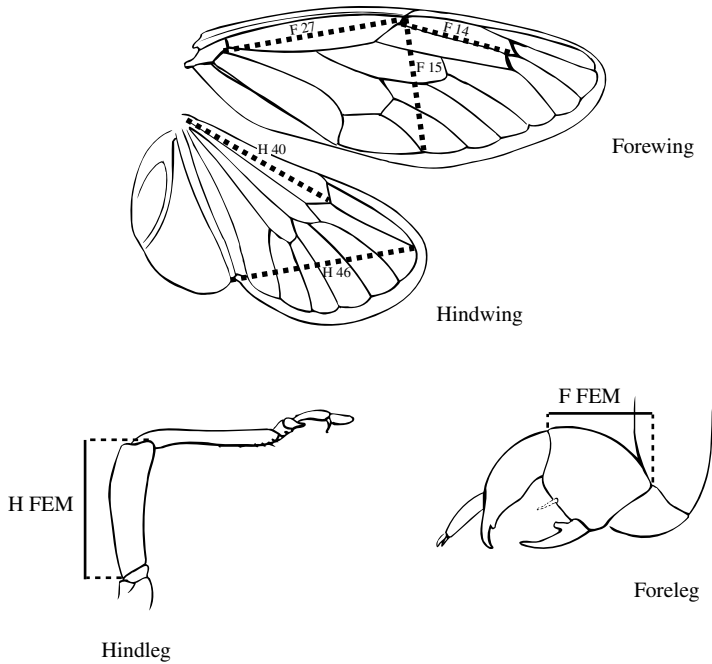


Fig. 1: Characters used in analysis of phenotypic symmetry. F14: Forewing character no. 14 from Simon 1983. F15: Forewing character no.15 from Simon 1983. F27: forewing character no. 27 from Simon 1983. H40: Hindwing character no. 40 from Simon 1983. H46: Hindwing character no. 46 from Simon 1983. FFEM: Fore-femur length. HFEM: hind femur length. Wing diagram adapted from Simon 1983, leg structure diagrams adapted from White 1973 and Borror et al. 1989

Table 1: Numbers of cicadas used in analysis of symmetry and mating success, after damaged individuals were eliminated from consideration

Character	Mated males	Unmated males
F14	25	43
F15	23	47
F27	22	43
H40	26	40
H46	24	42
FFEM	24	45
HFEM	24	40
Cumulative	22	40

variation in the data. Kolmogorov–Smirnov tests confirmed this relationship, so this character was discarded (Table 2).

Because the magnitude of asymmetry may scale allometrically with size, I used the average values calculated above to calculate a scaled asymmetry for each character in each individual according to the following formula:

Table 2: ANOVA tests for measurement error (significant differences among repetitions of the same measurement on the same individual) and handedness (significant differences between the right and left sides of an individual). Character H40 fails the measurement error test

Character	N	ANOVA		R ²
		p (repetition)	p (side)	
F14	68	0.312	0.944	0.013
F15	70	0.097	0.651	0.016
F27	65	0.413	0.598	0.011
H40	66	0.010	0.615	0.031
H46	66	0.186	0.186	0.020
FFEM	69	0.793	0.133	0.008
HFEM	64	0.496	0.391	0.009

$$2 \times \frac{|\text{Right} - \text{Left}|}{|\text{Right} + \text{Left}|} = \text{Scaled Asymmetry}$$

Because this index of asymmetry is scaled to the size of the character, it allows comparisons of the relative levels of asymmetry among individuals. I used scaled asymmetry values for all subsequent analyses and comparisons discussed below.

I calculated average sizes for the right and left sides of the six remaining characters for each specimen. To determine whether any asymmetry was truly FA or whether it represented species-typical right/left morphological asymmetry (e.g. the right side is typically different from the left), I used a Lilliefors' test of normality of scaled, signed asymmetries and Sokal and Rohlf's test of skew and kurtosis significance (Table 3). Only characters F15 and FFEM pass both these tests; H46 passes the kurtosis/skew test, but not the Lilliefors' test. These analyses indicate that some of the characters do not exhibit normal distributions typical of FA (Table 3). I also calculated sizes for each character by averaging all right/left values, to allow evaluation of any relationship between size and mating success.

I examined correlations among asymmetries of the different characters by constructing a Pearson pairwise correlation matrix with Bonferroni corrections (Table 4). Wing character asymmetries tend to be correlated, but correlation patterns do not consistently indicate uniformity of expressed asymmetry across all characters within an individual. Correlations among character sizes are stronger (i.e. there is some indication of allometric relationships among characters; Table 5), and there is a relationship between character size and degree of asymmetry (Table 6).

For each individual, I examined the relationship between both the symmetry and average size of each independent character and mating status, using Mann-Whitney U-tests (Table 7). Although the original experimental design was intended to be balanced, since not all males mated, there were approximately twice as many unmated cicadas as mated cicadas. Because of the unbalanced design, analyses were conducted using a nonparametric ANOVA equivalent, which

Table 3: Tests for normality of signed, scaled asymmetries. Measurements from only two characters, F15 and FFEM, appear normally distributed, and thus fit the definition of fluctuating asymmetry

Character	Lilliefors' p (normality)	Sokal G1 (skew)	Sokal G2 (kurtosis)	Conclusion
F14	0.001	Pass	Fail	Not normally distributed
F15	0.566	Pass	Pass	Normally distributed
F27	0.001	Fail	Fail	Not normally distributed
H46	0.010	Pass	Pass	Not normally distributed
FFEM	0.067	Pass	Pass	Normally distributed
HFEM	0.003	Fail	Pass	Not normally distributed

Table 4: Pearson pairwise correlation matrix for character asymmetry

	F14	F15	F27	(H40)	H46	FFEM	HFEM
F14	1.000						
F15	0.411*	1.000					
F27	0.180	0.483*	1.000				
(H40)	-0.068	-0.257	-0.121	1.000			
H46	0.258	-0.027	-0.114	-0.098	1.000		
FFEM	0.054	0.069	-0.042	-0.121	-0.255	1.000	
HFEM	0.016	0.205	0.211	-0.169	0.111	0.073	1.000

*Indicates Bonferroni corrected significance $p \leq 0.05$.

Table 5: Pearson pairwise correlation matrix for character size

	F14	F15	F27	(H40)	H46	FFEM	HFEM
F14	1.000						
F15	0.715	1.000					
F27	0.600	0.613	1.000				
(H40)	0.636	0.586	0.581	1.000			
H46	0.702	0.780	0.636	0.630	1.000		
FFEM	0.529	0.680	0.561	0.429	0.511	1.000	
HFEM	0.515	0.663	0.557	0.600	0.664	0.752	1.000

All values significant, Bonferroni corrected significance $p \leq 0.05$.

preserved the intuitive transparency of the data, but sacrificed statistical power. Mated males had significantly more symmetrical fore-femurs (character FFEM) than unmated males. There was no relationship between mating success and the size of any character.

For each individual, a cumulative asymmetry score was calculated by summing the unsigned (absolute-value) asymmetries of all characters (Leung [5](#) et al. 2000; Hewa-Kapugee & Hoffman 2001). Any individuals that lacked

Table 6: Pearson pairwise correlation matrix with Bonferroni probabilities for character sizes and asymmetry

Size	Symmetry						
	F14	F15	F27	(H40)	H46	FFEM	HFEM
F14	0.031*						
F15	-0.141	0.089*					
F27	-0.008	0.073	-0.021*				
(H40)	-0.069	0.092	0.078	0.045*			
H46	0.003	0.204	-0.064	0.055	-0.116*		
FFEM	-0.111	0.030	0.105	0.204	-0.108	-0.084*	
HFEM	-0.184	0.092	0.011	0.064	-0.045	-0.118	-0.106*

*Indicates Bonferroni corrected significance $p \leq 0.05$.

Table 7: Kruskal–Wallis one-way ANOVA analysis of mating status and signed, scaled asymmetry (left columns) and average character size (right columns). Mated and unmated males differed only in levels of asymmetry for character FFEM

	Symmetry		Size	
	U-value	p-value	U-value	p-value
FA characters (Table 3)				
F15	479	≤ 0.685	514	≤ 0.367
FFEM	880	$\leq 0.028^*$	673	≤ 0.979
H46	266	≤ 0.531	287	≤ 0.838
F14	613	≤ 0.508	747	≤ 0.442
F27	733	≤ 0.539	674	≤ 0.991
HFEM	495	≤ 0.112	613	≤ 0.789

symmetry measurements for all of the characters were not used in this analysis. I calculated a cumulative fluctuating asymmetry score by summing only the unsigned asymmetries of the two characters exhibiting fluctuating asymmetry, F15 and FFEM. Both of these cumulative measures should tend to (i) expose genomic effects by allowing repeated measures of developmental stability; and (ii) maximize any overall asymmetry differences among individuals. Thus, they should be sensitive assays for whether asymmetries of any combinations of characters influence mating ability (cf. Møller & Swaddle 1997). Using Kruskal–Wallis one-way ANOVAS, I found no relationship between cumulative asymmetry and mating status (Fig. 2). Cumulative fluctuating asymmetry scores for mated males were significantly lower than for unmated males (Fig. 2); however, as the cumulative FA score is the sum of F15 and FFEM asymmetries, this result can be attributed to the influence of character FFEM, since character F15 alone was not significantly different between mated and unmated males.

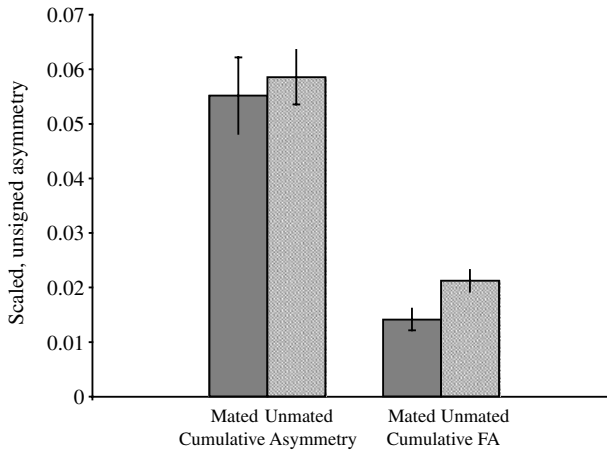


Fig. 2: Comparisons of cumulative asymmetry scores for mated and unmated males. Left columns: Cumulative asymmetry (sum of unsigned asymmetries for each character); No significant difference between mated and unmated males (Kruskal-Wallis one-way ANOVA; $U = 198$, $p \leq 0.655$). Right columns: cumulative fluctuating asymmetry (sum of unsigned asymmetries for characters F15 and FFEM); mated males have significantly smaller cumulative FA scores than unmated males (Kruskal-Wallis one-way ANOVA; $U = 667$, $p \leq 0.022$). Bars are standard errors

Tymbal Rib Asymmetries

Methods and results

The number of tymbal ribs in *M. septendecim* varies from 11 to 13, and rarely, the right and left tymbals have different numbers of ribs. On each numerically coded specimen, the number of ribs on both tymbals was counted twice. Because tymbal ribs sometimes branch and merge, only sclerotizations that remained separate from any other structures for more than 3/4 of their total length, and only structures that formed an acute angle with the nearest sclerotization were counted as ribs. Two of 27 mated males had an asymmetrical number of tymbal ribs, while 5/45 unmated males had differing numbers of tymbal ribs on each side of their bodies; this proportion did not differ statistically (two-tail Fisher exact test $p < 1.000$), although the overall number of asymmetrical males is so low that this test has little statistical power.

Wing Venation Asymmetries

Methods and results

Because wing venation in *M. septendecim* can be highly variable, the technician scored each cicada for the presence/absence of extra wing veins and whether the anomalies were bilaterally symmetrical. These venation anomalies are distinct from 'wing crumpling', or incomplete expansion of the wings at the final molt, noted in some crowded populations (White et al. 1979). None of the cicadas

used in this study had crumpled wings. Sixteen of the 77 males used in this study had asymmetrical wings; each individual had at least one non-symmetrical instance of atypical wing venation, either in the form of extra or missing wing veins. Four of the 16 mated, while 12 did not. To determine whether mated males were underrepresented in the group of abnormal-winged males, I used a chi-square test of independence to uncover any relationship between mating success and wing type. No such association is apparent ($\chi^2 = 0.899$, $p > 0.1$, $df = 1$). As an alternative test, and to address concerns of statistical power from the small sample size, I used a computer algorithm to generate a null expectation for the association between wing abnormalities and mating success. For 10 000 iterations, the algorithm randomly selected a 16 male sample from the 27 mated and 50 unmated males in the study and then tabulated the number of mated males in the sample. After 10 000 iterations, the algorithm constructed percentiles, which describe the probability of finding only four mated males in any 16-member random sample from the original data. Details of the algorithm are published in Cooley (1999), and percentiles are shown in Fig. 3. The number of mated and unmated males among the atypically-veined males was not significantly different from that expected by chance.

Discussion

The sizes of individual characters, which are correlated within an individual and thus are an index of overall size, were not correlated with mating success. This result contrasts the findings of Karban (1983), who found that larger males of the related species *Magisicada cassini* were more likely to be found *in copula* than smaller males. These different results could be the results of behavioral differences between the species used or the results of differences in experimental design (see also Cooley & Marshall 2004). The asymmetries of most characters in this study were also not correlated with mating success, with one exception: foreleg asymmetry did correlate with male mating success. This result carries with it a strong caveat: the statistical power of the tests used increases the odds of type II error, and only a strong effect of symmetry on experimental mating success could have been detected by this experimental and statistical design. Given the small magnitude of the asymmetries involved, this is a conservative approach, and it increases the believability of the correlation between foreleg asymmetries and mating success. How can this correlation be understood in light of what is known about the *Magisicada* mating system?

As a mate choice criterion, phenotypic symmetry is subject to a paradox: if only a small subset of genes have a predominant influence on phenotypic symmetry, then population-wide variation will tend to be homogenized by successive generations of selection – either by the elimination of variants prone to producing asymmetrical phenotypes, or by the spread of modifier genes that tend to enforce strict symmetry and reduce the contribution of individual genes to overall phenotypic symmetry. But as the number of genes involved in affecting symmetry increases (in the extreme, if its expression comes to reflect qualities of

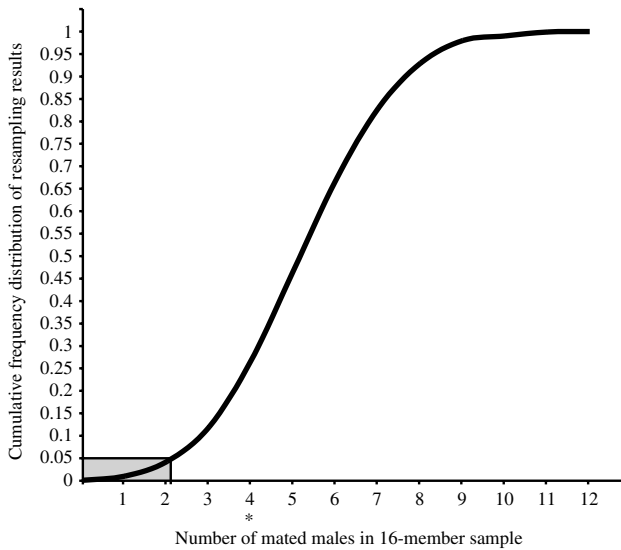


Fig 3: Results of resampling algorithm to evaluate whether mating frequency among males with wing venation anomalies differed from mating frequency of normal males. The algorithm draws a pseudorandom sample of 16 ‘abnormal’ males from a population similar to the study population (27 mated, 50 unmated males) and determines whether the mating frequency in the sample matches the mating frequency (4 of 16) in the actual sample of 16 males with asymmetrical wing venation. The algorithm repeats this process 10 000 times to generate a frequency histogram of results. The observed mating frequency among males with atypical wing venation falls well within the 95% frequency distribution of the resampling algorithm, so mating frequency is indistinguishable between males with normal and atypical wing venation

the overall genome), the less accurately symmetry identifies individual mates able to provide inheritable genetic benefits, because meiosis and independent segregation ensure that large, coadapted pieces of the genome are not passed on intact. Given either of these alternatives, how do correlations between symmetry and mating success arise?

Much of the fluctuating asymmetry literature stresses the role of intersexual selection in shaping mating systems and adopts the perspective that symmetry per se is a target of mate choice selection. Yet an alternative is to consider the role of FA in mating systems from an intrasexual selection perspective. In the absence of direct female choice for symmetrical mates, correlations between symmetry and male mating success could arise if symmetry and male condition or performance covaried, and differential male success resulted from functional variation in male phenotypic performance (Liggett et al. 1993; Møller & Pomiankowski 1994; Møller 1997; Møller & Swaddle 1997; Bateman 2000; Kruuk et al. 2003). Unlike variation in an individual trait that is the target of mate choice (for which heritable variation would quickly be exhausted), variation in male quality is virtually inexhaustible as long as variation in male mating success results from relative performance differences among males (this hypothesis is similar to some solutions of the ‘lek paradox’; see Hill 1994; Pomiankowski & Møller 1995). This

functional perspective concentrates on male performance outcomes, rather than the details of how males achieve those outcomes.

Japanese scorpionflies (*Panorpa japonica*) provide an example that can be analyzed from a functional perspective. In scorpionflies, male pheromonal attractiveness correlates with wing symmetry (Thornhill 1992c), which suggests that some males have both more symmetrical wings and more attractive pheromones and that females have mechanisms for detecting these differences. Yet there is an alternative, functional understanding of this correlation that does not directly invoke mate choice: as these insects must fly to scavenge dead arthropods for food, and as dietary substances may be included in pheromones, there is a functional link between wing symmetry, foraging success, and sexual attractiveness. Thus, females could 'choose' not on the basis of a single trait or a small suite of traits (such as symmetry or pheromone quality), but on the basis of the performance of the entire male organism.

Magicicada mating aggregations, complex courtship, and male-male competitive behaviors suggest a history of sexual selection in which females discriminate against some potential mates, although specific mate choice criteria, if any, remain unknown. Male-male scramble competition appears to play an important role in the *Magicicada* mating system (Cooley & Marshall 2004) because under typical chorus conditions, multiple males are able to perceive a signaling female, and the first male to find such a female has the greatest odds of mating success. Because mate rapprochement behaviors in *Magicicada* require males to fly, walk, and fend off competitors, the *Magicicada* mating system places a premium on locomotory capabilities, and defects in leg or wing characters may result in mating biases. Conditions in these experiments probably accentuated male-male scramble competition: several males could simultaneously perceive a female's signals. A functional hypothesis to explain why there was at least some correlation between symmetry and mating success in this study is that slight foreleg asymmetries affect mobility or maneuverability enough that males with the most symmetrical forelegs outcompete less symmetrical cicadas as they race to make contact with signaling females. Further examination of how leg asymmetries affect mobility and how cicadas use their different pairs of legs to search for mates are needed to test this hypothesis. If the association between symmetry and mating success uncovered in this study is relevant under natural conditions, then male-female rapprochement duets and male-male competition create conditions leading to differential male mating success without requiring females to have mechanisms specifically evolved for favoring symmetrical males.

What are the relationships among symmetry, mating success, and mating system evolution? The qualities for which symmetry is a proxy may lead to predictable gains for choosy individuals. These predictions lead to testable hypotheses addressing how females might, actively or incidentally, create or participate in situations favoring symmetrical males:

- 1 Unless females have specially evolved mechanisms for directly assessing symmetry, females' apparent choosiness likely results from functional correlates of symmetry.

2 For those species without male-donated resources, male parental care, or other phenotypic benefits available from differential mating, females can benefit only from choosing among males whose asymmetry differences have some genetic basis.

3 For those species where males provide access to resources, females can benefit from choosing if there is a genetic basis to symmetry or a functional link between symmetry and male performance (which may have heritable components), measured as ability to gather and contribute resources.

These testable hypotheses underscore the importance of explicitly considering the possible selective advantages of choosiness and the applicability of specific patterns of asymmetry to hypothetical evolved mechanisms for mate choice in the basis of symmetry.

Acknowledgements

I thank R. D. Alexander, L. Krueger, D. C. Marshall, and C. Simon for helpful discussion. Thanks also to the Horsepen Lake State Wildlife Management Area, Buckingham County, VA. Funding was provided by the Frank W. Ammermann Endowment of the UMMZ Insect Division, Japan Television Workshop Co., LTD, and by NSF DEB 98-07113 and DEB 99-74369 to Chris Simon.

This work contains portions of a doctoral thesis submitted by the author in partial fulfillment for a doctoral degree from the Horace Rackham School of Graduate Studies, The University of Michigan.

For background information on periodical cicadas and general brood distribution maps see the *Magicicada* website at http://www.insects.ummz.lsa.umich.edu/fauna/Michigan_cicadas/

Literature Cited

- Alexander, R. D. 1975: Natural selection and specialized chorusing behavior in chorusing insects. In: *Insects, Science, and Society* (Pimentel, D., ed.). Academic Press, New York, pp. 35–77.
- Bateman, P. W. 2000: The influence of weapon asymmetry on male-male competition success in a sexually dimorphic insect, the African King Cricket *Libanaisidus vittatus* (Orthoptera: Anostomatidae). *J. Ins. Behav.* **13**, 157–163.
- Bjorksten, T., David, P., Pomiankowski, A. & Fowler, K. 2000a: Fluctuating asymmetry of sexual and nonsexual traits in stalk-eyed flies: a poor indicator of developmental stress and genetic quality. *J. Evol. Biol.* **13**, 89–97.
- Bjorksten, T. A., Fowler, K. & Pomiankowski, A. 2000b: What does sexual trait FA tell us about stress? *TREE* **15**, 163–166.
- Chapman, J. W. & Goulson, D. 2000: Environmental versus genetic influences on fluctuating asymmetry in the house fly, *Musca domestica*. *Biol. J. Linn. Soc.* **70**, 4.
- Clarke, G. M. 1993: Fluctuating asymmetry of invertebrate populations as a biological indicator of environmental quality. *Environ. Pollut.* **82**, 207–211.
- Clarke, G. M. 1998: Developmental stability and fitness: the evidence is not quite so clear. *Amer. Nat.* **152**, 762–766.
- Cooley, J. R. 1999: Sexual behavior in North American cicadas of the genera *Magicicada* and *Okanagana*. PhD Thesis, The Univ. of Michigan, Ann Arbor MI USA.
- Cooley, J. R. & Marshall, D. C. 2001: Sexual signaling in periodical cicadas, *Magicicada* spp. (Hemiptera: Cicadidae). *Behaviour* **138**, 827–855.
- Cooley, J. R. & Marshall, D. C. 2004: Thresholds or comparisons: mate choice criteria and sexual selection in a periodical cicada, *Magicicada septendecim* (Hemiptera: Cicadidae). *Behaviour* **??**, ???–???
- 7 Gangstead, S. W., Thornhill, R. & Yeo, R. A. 1994: Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethol. Sociobiol.* **15**, 73–85.

- Gates, S. 2002: Review of methodology of quantitative reviews using meta-analysis in ecology. *J. Anim. Ecol.* **71**, 547—557.
- Harvey, I. F. & Walsh, K. J. 1993. Fluctuating asymmetry and lifetime mating success are correlated in males of the damselfly *Coenagrion puella* (Odonata: Coenagrionidae). *Ecol. Entomol.* **18**, 198—202.
- Hewa-Kapugee, S. & Hoffman, A. A. 2001: Composite asymmetry as an indicator of quality in the beneficial wasp *Trichogramma nr. brassicae* (Hymenoptera: Trichogrammatidae). *J. Econ. Entomol.* **94**, 826—830.
- Hill, G. E. 1994: Trait elaboration via adaptive mate choice: sexual conflict in the evolution of signals of male quality. *Ethol. Ecol. Evol.* **6**, 351—370.
- Houle, D. 1997: Comment on “A meta-analysis of the heritability of developmental stability” by Møller and Thornhill. *J. Evol. Biol.* **10**, 17—20.
- Houle, D. 1998: High enthusiasm and low R-squared. *Evolution* **52**, 1872—1876.
- Jennions, M. D. & Møller, A. P. 2001: Relationships fade with time: a meta-analysis of temporal trends in publication in ecology and evolution. *Proc. Roy. Soc. Lond. B.* **269**, 43—48.
- Karban, R. 1983: Sexual selection, body size and sex-related mortality in the cicada *Magicicada cassini*. *Am. Midl. Nat.* **109**, 324—330.
- Kotiaho, J. A. & Tomkins, J. L. 2002: Meta-analysis: can it ever fail? *Oikos* **96**, 551—553.
- Kruuk, L. E. B., Slate, J., Pemberton, J. M. & Clutton-Brock, T. H. 2003: Fluctuating asymmetry in a secondary sexual trait: no associations with individual fitness, environmental stress or inbreeding, and no heritability. *J. Evol. Biol.* **16**, 101—113.
- Leamy, L. 1997: Is developmental stability heritable? *J. Evol. Biol.* **10**, 21—29.
- Leung, B., Forbes, M. R. & Houle, D. 2000: Fluctuating asymmetry as a bioindicator of stress: comparing efficacy of analyses involving multiple traits. *Amer. Nat.* **155**, 101—115.
- Liggett, A. C., Harvey, I. F. & Manning, J. T. 1993: Fluctuating asymmetry in *Scatophaga stercoraria* L.: successful males are more symmetrical. *Anim. Behav.* **45**, 1041—1043.
- Møller, A. P. 1993a: Fluctuating asymmetry. *Nature (London)* **363**, 217.
- Møller, A. P. 1993b: Female preference for apparently symmetrical male sexual ornaments in the barn swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.* **32**, 371—376.
- Møller, A. P. 1993c: Developmental stability, sexual selection and speciation. *J. Evol. Biol.* **6**, 493—509.
- Møller, A. P. 1994: Sexual selection in the barn swallow (*Hirundo rustica*). IV. Patterns of fluctuating asymmetry and selection against asymmetry. *Evolution* **48**, 658—670.
- Møller, A. P. 1995: Patterns of fluctuating asymmetry in sexual ornaments of birds from marginal and central populations. *Amer. Nat.* **145**, 316—327.
- Møller, A. P. 1996: Sexual selection, viability selection, and developmental stability in the domestic fly, *Musca domestica*. *Evolution* **50**, 746—752.
- Møller, A. P. 1997: Developmental stability and fitness: a review. *Amer. Nat.* **149**, 916—932.
- Møller, A. P. & Jennions, M. D. 2002: How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* **132**, 492—500.
- Møller, A. P. & Pomiankowski, A. 1994: Fluctuating asymmetry and sexual selection. In: *Developmental Instability: its origins and Evolutionary Implications* (Markow, T. A., ed.). Kluwer, The Netherlands, pp. 269—281.
- Møller, A. P. & Swaddle, J. P. 1997: *Asymmetry, Developmental stability, and Evolution*. Oxford Univ. Press, ?????.
- Møller, A. P. & Thornhill, R. 1997a: A meta-analysis of the heritability of developmental stability. *J. Evol. Biol.* **10**, 1—16.
- Møller, A. P. & Thornhill, R. 1997b: Developmental instability is heritable. *J. Evol. Biol.* **10**, 69—76.
- Maier, C. T. 1982. Observations on the seventeen-year periodical cicada, *Magicicada septendecim* (Hemiptera: Homoptera: Cicadidae). *Ann. Entomol. Soc. Am.* **75**, 14—23.
- Malyon, C. & Healy, S. 1994: Fluctuating asymmetry in antlers of fallow deer, *Dama dama*, indicates dominance. *Anim. Behav.* **48**, 248—250.
- Markow, T. A. & Clarke, G. M. 1997: Meta-analysis of the heritability of developmental stability: a giant step backward. *J. Evol. Biol.* **10**, 31—37.
- Marshall, D. C. 2000. Behavior and evolution of periodical cicadas (*Magicicada* spp.). PhD Dissertation, The Univ. of Michigan, Michigan.

- Marshall, D. C. & Cooley, J. R. 2000: Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. *Evolution* **54**, 1313—1325.
- Oakes, E. J. & Barnard, P. 1994: Fluctuating asymmetry and mate choice in paradise whydahs, *Vidua paradisaea*: an experimental manipulation. *Anim. Behav.* **48**, 937—943.
- Palmer, A. R. 1994: Fluctuating asymmetry analyses: a primer. In: *Developmental Instability: its origins and Evolutionary Implications* (Markow, T. A., ed.). Kluwer, The Netherlands, pp. 335—364.
- Palmer, A. R. 1996: Waltzing with asymmetry. *BioScience* **46**, 518—531.
- Palmer, A. R., 2000: Quasireplication and the contract of error: lessons from sex ratios, heritabilities, and fluctuating asymmetry. *Annu. Rev. Ecol. Syst.* **31**, 441—480.
- Palmer, A. R. & Strobeck, C. 1986: Fluctuating asymmetry: measurement, analysis, patterns. *Annu. Rev. Ecol. Syst.* **17**, 391—421.
- Palmer, A. R. & Strobeck, C. 1992. Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and the power of statistical tests. *Acta Zoologica Fennica* **191**, 57—72.
- Palmer, A. R. & Strobeck, C. 1997. Fluctuating asymmetry and developmental stability: heritability of observable variation vs. heritability of inferred cause. *J. Evol. Biol.* **10**, 39—49.
- Pomiankowski, A. 1997: Genetic variation in fluctuating asymmetry. *J. Evol. Biol.* **10**, 51—55.
- Pomiankowski, A. & Møller, A. P. 1995: A resolution of the lek paradox. *Proc. Roy. Soc. Lond. B.* **260**, 21—29.
- Simmons, L. W., Tomkins, J. L., Kotiaho, J. S. & Hunt, J. 1999: Fluctuating Paradigm. *Proc. Roy. Soc. Lond. B.* **266**, 593—595.
- Swaddle, J. P. 1996: Reproductive success and symmetry in zebra finches. *Anim. Behav.* **51**, 203—210.
- Swaddle, J. P. 1997: On the heritability of developmental stability. *J. Evol. Biol.* **10**, 57—61.
- Swaddle, J. P. 2003: Fluctuating asymmetry, animal behavior, and evolution. *Advan. Study Behav.* **32**, 169—205.
- Swaddle, J. P., Witter, M. S. & Cuthill, I. C. 1994: The analysis of fluctuating asymmetry. *Anim. Behav.* **48**, 986—989.
- Thornhill, R. 1992a: Fluctuating asymmetry and the mating system of the Japanese scorpionfly, *Panorpa japonica*. *Anim. Behav.* **44**, 867—879.
- Thornhill, R. 1992b: Fluctuating asymmetry, interspecific aggression, and male mating tactics in two species of Japanese scorpionflies. *Behav. Ecol. Sociobiol.* **30**, 357—363.
- Thornhill, R. 1992c: 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 & Møller, A. P. 1998: The relative importance of size and asymmetry in sexual selection. *Behavioral Ecology* **9**, 546—551.
- Tomkins, J. L. & Simmons, L. W. 1998: Female choice and manipulations of forceps size and symmetry in the earwig *Forficula auricularia* L. *Anim. Behav.* **56**, 347—356.
- Vøllestad, L. A., Hindar, K. & Møller, A. P. 1999: A meta-analysis of fluctuating asymmetry in relations to heterozygosity. *Heredity*. **83**, 206—218.
- Van Valen, L. 1962: A study of fluctuating asymmetry. *Evolution* **16**, 125—142.
- White, J., Lloyd, M. & Zar, J. H. 1979: Faulty eclosion in crowded suburban periodical cicadas: populations out of control. *Ecology* **60**, 305—315.
- Whitlock, M. C. & Fowler, K. 1997. The instability of studies of instability. *J. Evol. Biol.* **10**, 63—67.
- Williams, K. S. & Simon, C. 1995: The ecology, behavior, and evolution of periodical cicadas. *Annu. Rev. Entomol.* **40**, 269—295.

Received: xxxx xx, 200x

Initial acceptance: xxxx xx, 200x

9 Final acceptance: xxxx xx, 200x (*X. Xxxxxx*)

Author Query Form

Journal: ETH

Article: 993

Dear Author,

During the copy-editing of your paper, the following queries arose. Please respond to these by marking up your proofs with the necessary changes/additions. Please write your answers on the query sheet if there is insufficient space on the page proofs. Please write clearly and follow the conventions shown on the attached corrections sheet. If returning the proof by fax do not write too close to the paper's edge. Please remember that illegible mark-ups may delay publication.

Many thanks for your assistance.

Query reference	Query	Remarks
1	Au: Bjorksten, David, Pomiankowski & Fowler 2000 and Bjorksten, Fowler, & Pomiankowski 2000 has been changed to Bjorksten et al. 2000a,b so that this citation matches the list	
2	Au: Vollestad et al. 1999 has been changed to Vøllestad et al. 1999 so that this citation matches the list	
3	Au: Møller et al. 1995 has been changed to Møller 1995 so that this citation matches the list	
4	Au: Palmer and Strobeck 1982 has been changed to Palmer & Strobeck 1992 so that this citation matches the list	
5	Au: Hewa-Kapuge and Hoffman 2001 has been changed to Hewa-Kapugee & Hoffman 2001 so that this citation matches the list	
6	Au: Pomiankowski and Møller 1995 has been changed to Pomiankowski & Møller 1995 so that this citation matches the list	

7	Au: While searching in internet, we found that this title has been accepted by the journal 'Behaviour'. With this information we included the year of publication and journal name in this reference. Please update this with volume number and page range.	
8	Au: Please provide the place of publication.	
9	Production Editor: please supply dates.	
10	Au: Simon 1983 has not been included in the list, please supply publication details.	
11	Au: White 1973 has not been included in the list, please supply publication details.	
12	Au: Borrer et al. 1989 has not been included in the list, please supply publication details.	

MARKED PROOF

Please correct and return this set

Please use the proof correction marks shown below for all alterations and corrections. If you wish to return your proof by fax you should ensure that all amendments are written clearly in dark ink and are made well within the page margins.

<i>Instruction to printer</i>	<i>Textual mark</i>	<i>Marginal mark</i>
Leave unchanged	... under matter to remain	Stet
Insert in text the matter indicated in the margin	⤴	New matter followed by ⤴
Delete	⤵ through matter to be deleted	⤵
Delete and close up	⤵ through matter to be deleted	⤵
Substitute character or substitute part of one or more word(s)	/ through letter or ⤵ through word	New letter or new word
Change to italics	— under matter to be changed	≡
Change to capitals	≡ under matter to be changed	≡
Change to small capitals	≡ under matter to be changed	≡
Change to bold type	⤵ under matter to be changed	⤵
Change to bold italic	⤵ under matter to be changed	⤵
Change to lower case	Encircle matter to be changed	⊖
Change italic to upright type	(As above)	⤴
Insert 'superior' character	/ through character or ⤴ where required	⤴ under character e.g. ⤴
Insert 'inferior' character	(As above)	⤵ over character e.g. ⤵
Insert full stop	(As above)	⦿
Insert comma	(As above)	,
Insert single quotation marks	(As above)	⤴ and/or ⤵
Insert double quotation marks	(As above)	⤴ and/or ⤵
Insert hyphen	(As above)	Ⓜ
Start new paragraph	⤴	⤴
No new paragraph	⤵	⤵
Transpose	⤴	⤴
Close up	linking ⦿ letters	⦿
Insert space between letters	⤴ between letters affected	#
Insert space between words	⤴ between words affected	#
Reduce space between letters	⤴ between letters affected	⤴
Reduce space between words	⤴ between words affected	⤴