

Bilateral Symmetry and Sexual Selection: A Meta-Analysis

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ABSTRACT: A considerable body of primary research has accumulated over the last 10 yr testing the relationship between developmental instability in the form of fluctuating asymmetry and performance of individuals in mating success itself or sexual attractiveness. This research comprises 146 samples from 65 studies of 42 species of four major taxa. We present the results of a meta-analysis of these studies, which demonstrates that there is indeed an overall significant, moderate negative relationship: for studies, the overall mean Pearson's r or effect size = $-.42$, $P < .0005$; for species, the overall mean $r = -.34$, $.01 < P < .025$. Based on calculated fail-safe numbers, the effect-size estimates are highly robust against any publication or reporting bias that may exist. There is considerable evidence that the magnitude of the negative correlation between fluctuating asymmetry and success related to sexual selection is greater for males than for females, when a secondary sexual trait rather than an ordinary trait is studied, with experimentation compared with observation, and for traits not involved with mobility compared with traits affecting mobility. There is also limited evidence that higher taxa may differ in effect size and that intensity of sexual selection negatively correlates with effect size.

Keywords: developmental instability, fluctuating asymmetry, mate choice, meta-analysis, secondary sexual characters, sexual selection.

Developmental stability reflects the ability of individuals to undergo stable development under given environmental conditions (review in Møller and Swaddle 1997). Measures of developmental instability include fluctuating asymmetry, the frequency of phenodeviants, and a number of other measures (reviews in Palmer and Strobeck 1986; Parsons 1990; Graham et al. 1993a, 1993b; Møller

1997b). Developmental instability is caused by a range of different environmental (e.g., temperature, food quality and quantity, pollutants, parasitism) and genetic factors (e.g., inbreeding, hybridization, homozygosity, mutations, chromosomal anomalies; reviews in Møller and Swaddle 1997; Thornhill and Møller 1997), and the magnitude of developmental stability of an individual thus may become a reliable reflection of the phenotypic or genotypic quality of an individual in its environment (Møller 1990; Thornhill and Sauer 1992). Developmental instability often appears to have a significant additive genetic component (Møller and Thornhill 1997a, 1997b), and offspring will therefore resemble their parents with respect to asymmetry and phenodeviance. This heritability and the potential reliable signal of quality by developmental stability suggests that individual fluctuating asymmetry or phenodeviance may play an important role in sexual selection.

Sexual selection arises from the reproductive advantages that certain individuals have over others of the same sex and species due to mate choice or competition among individuals of the chosen sex (Darwin 1871; Andersson 1994). Models of sexual selection posit that choosy individuals benefit from their mate choice in terms of direct benefits such as parental care or in terms of indirect benefits via their attractive sons or their offspring of higher than average viability (review in Andersson 1994). Choosy individuals that mate with symmetric partners may benefit in terms of direct or indirect fitness advantages (Møller 1990, 1993a; Thornhill and Sauer 1992; Thornhill and Gangestad 1993; Watson and Thornhill 1994), or mate choice may simply reflect a pre-existing bias for symmetrical phenotypes (Møller 1992b). It has been predicted that, in general across species, there will exist a biologically significant negative correlation between asymmetry and success of individuals in sexual competition (Møller 1990; Thornhill 1992b).

Many studies have addressed the question of whether sexual selection is related to fluctuating asymmetry. This research has been reported over the period from 1987 to present, and results are variable. Some studies have reported negative relationships between female mate preferences and fluctuating asymmetry (e.g., Møller 1992a,

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1993*b*; Thornhill 1992*a*; Swaddle and Cuthill 1994*a*, 1994*b*; Thornhill and Gangestad 1994), and similar results have been reported for measures of sexual selection such as mating success (e.g., Harvey and Walsh 1993; Liggett et al. 1993; Arcese 1994; Córdoba-Aguilar 1995; Hasegawa 1995; McLachlan and Cant 1995). Other studies, however, have reported an absence of any effect (e.g., Markow and Ricker 1992; Fiske et al. 1994; Ueno 1994; J. Deutsch, unpublished manuscript; K. Omland, unpublished manuscript). The conclusions from the various studies therefore differ considerably (partial reviews in Møller 1993*a*; Leung and Forbes 1996).

In this article we meta-analytically review sexual selection in relation to the level of individual fluctuating asymmetry in morphological characters using published and unpublished investigations. Meta-analysis is an appropriate tool for synthesizing the disparate results on symmetry and sexual competitiveness across investigations. Meta-analytic procedure is discussed in detail in Hedges and Olkin (1985), Rosenthal (1991), and Cooper and Hedges (1994). Arnqvist and Wooster (1995) discuss some recent applications of meta-analysis to questions in ecology and evolution. Meta-analysis allows determination of the generality of a relationship between the two variables sexual competition and bilateral symmetry across investigations. Moreover, meta-analysis allows statistical analysis of the variance in effects (i.e., the magnitude and direction of the relationship) across investigations of asymmetry and sexual competition (e.g., investigations of the relationship in males vs. females).

We analyze the variation across studies and species in the relationship between bilateral asymmetry and sexual selection by investigating whether the magnitude of the relationship between fluctuating asymmetry and sexual selection (i.e., the effect size) is moderated by the sex studied; the kind of trait studied (secondary sexual character vs. an ordinary morphological trait); the study method (experimental or observational); higher taxonomic grouping; direct effects of the character studied on the mobility of the organism; and the intensity of sexual selection. The general pattern of sexual selection among animals is greater sexual selection in males than in females. Accordingly, females are choosier, and males are more ornamented and engage more in contests for the opposite sex (Darwin 1871; Thornhill and Alcock 1983; Andersson 1994). Fluctuating asymmetry thus may be implied to play a more prominent role in sexual selection among males as compared with females. We predict that effect sizes will be greater in studies of sexual selection in males than in studies of sexual selection in females.

We predict that there will be larger negative correlations between asymmetry and performance in sexual competition for studies involving secondary sexual traits

than studies involving ordinary traits. Some studies have indicated that the level of fluctuating asymmetry in secondary sexual characters is larger than in ordinary morphological characters (Møller 1990, 1992*c*, 1993*c*, 1994; Møller and Höglund 1991; Manning and Chamberlain 1993; Radesäter and Halldórsdóttir 1993; Møller et al. 1995; but see Balmford et al. 1993). If this pattern proves to be general, we would expect that choosy females would be able to discriminate more easily among males differing in asymmetry of secondary sexual character as compared with ordinary morphological traits, and if symmetry reflects direct or indirect benefits to be gained by its preference, then females are expected to assess it. If symmetry reflects fighting ability or resource-holding power, symmetry may become a determinant of the outcome of male-male agonistic or scramble competitions for females.

Observational studies of sexual selection and bilateral asymmetry often lack controls of variables that may affect sexual attractiveness and mating success such as body size, vigor, and related variables. Thus, we predict that experimental manipulation of asymmetry in a study will be more likely to yield an effect if asymmetry plays a role in sexual selection.

It is of interest to know if effect sizes differ among major taxa. However, there are no strong a priori expectations (i.e., predictions) of which we are aware.

Fluctuating asymmetry may have important effects on the mobility of organisms, particularly if the trait in question is directly involved in locomotion (Møller 1991; Evans et al. 1994; Manning and Ockenden 1994; Swaddle et al. 1997). We would then predict that choosy females would be better able to discriminate among males differing in asymmetry of traits directly involved in locomotion as compared with other traits; the same prediction holds for males assessing other males during agonistic sexual competition.

Finally, the intensity of sexual selection may directly affect the degree of fluctuating asymmetry. The additive genetic variance present, and hence the intensity of directional mate preferences, will depend on mutation-selection balance. The genetic variance of traits subjected to directional selection may initially increase because of selection against genetic modifiers that hide the variance (Møller and Pomiankowski 1993). However, the additive genetic variance is likely to decrease after a long period of intense sexual selection that brings alleles to fixation. In turn, this may result in a decrease in the intensity of directional sexual selection. Comparative studies of phenotypic variation in extravagant feather ornaments in birds have revealed that indeed there is an initial increase in relative asymmetry during evolution from an absence of a secondary sexual character to the presence of such

a character (J. J. Cuervo and A. P. Møller, unpublished manuscript). However, this initial increase in asymmetry depends strongly on the mating system, with a marked reduction in asymmetry when going from monogamy over polygyny to lek breeding. Therefore, we might expect a negative relationship between effect size and the intensity of sexual selection.

Material and Methods

Data Acquisition

Data acquisition involved a combination of literature and Internet searches and correspondence with colleagues working on symmetry and sexual selection. Table 1 lists all samples ($N = 146$) from a total of 65 studies of 42 species used in our analysis. Data acquisition was terminated on January 1, 1997. Full discussion of the data acquisition procedures can be obtained from either author.

A study met eligibility for inclusion if it was possible to estimate one or more effect sizes for the relationship between asymmetry and mating success or mate preference for one or both sexes. Preferences include opposite-sex judgments of attractiveness of facial or other body traits by humans. It is established that such judgments reflect sexual and romantic interest in the person judged (Singh 1995; Quinsey et al. 1996).

Some studies investigated the relationship between fluctuating asymmetry and characters supposedly involved in sexual selection without investigating the actual relationship between trait asymmetry and mate preferences or mating success (Thornhill 1992c; Thornhill and Sauer 1992; Eggert and Sakaluk 1995; Ryan et al. 1995). Therefore, these studies had to be excluded from the analyses because we could not estimate the magnitude of the relationship between trait asymmetry and mate preference or mating success. Uetz et al.'s (1996) study of male courtship success in relation to symmetry in leg ornaments of male wolf spiders was excluded because asymmetry was generated, in part, by growth following natural amputation of legs rather than by developmental instability. Simmons and Ritchie's (1996) study was not included because it clearly deals with directional asymmetry and mating success, not fluctuating asymmetry. We restricted the analyses to studies of animals and thus excluded some recent studies of pollinator preferences for symmetrical flowers (Møller 1995, 1996a; Møller and Eriksson 1995).

Statistical Procedures

How to deal with dependence of data in meta-analysis is thoroughly described in Hedges and Olkin (1985), Ro-

senthal (1991), and Cooper and Hedges (1994). We followed their recommendations.

There were 146 samples from 65 studies of 42 species from which effect sizes were calculated (table 1). We calculated effect size for samples, but our analysis focused on the units of studies and species. The multiple sample effects in many of the multiple-sample studies were not independent, their dependence being due to multiple effect-size estimates from data from identical or partly overlapping groups of individuals. Analysis at the study level eliminated this kind of dependence of effect sizes in most cases. When possible dependence arises in our analysis across studies or species, it is discussed, and additional analyses are conducted to eliminate any dependence. A study's effect size is a sample-size weighted mean of the relevant samples in the study (Rosenthal 1991, pp. 27–28, and below). There were no cases where multiple, different studies of the same species report data on the same subjects. Thus, this form of dependence was not an issue.

Another type of dependence is relevant in this meta-analysis. It occurs when studies with similar or identical features show less variability in their mean effect sizes than does the entire sample of studies. In this meta-analysis, such intraclass correlation of study effects could arise from multiple studies of single species showing correlations. Thus, we combined studies in cases where there are multiple, different studies of a single species to achieve a single species' mean effect-size estimate (see below).

Meta-analysis consists of obtaining an estimate of the magnitude of the general effect of interest and treatment of the variation in effect sizes across the units of analysis. Various techniques are available for combining effect sizes across studies to determine the magnitude of the general effect. We used the effect size of Pearson's r , which estimates the correlation in the population of studies or species between the variables of fluctuating asymmetry and mating success or sexual attractiveness. The effect size as r is a common effect-size currency and is easily interpreted: it expresses a relationship between variables. Effect sizes were sometimes reported in the primary literature and in unpublished manuscripts we examined in forms other than r (t , F , χ^2 statistics, Mann-Whitney U -test, Spearman or Kendall rank-order correlation coefficients). The Pearson r effect size was calculated from each of the other statistics using standard conversion formulas (e.g., $\sqrt{t^2/(t^2 + df)}$; see Rosenthal 1991, p. 19, or any general treatment of meta-analysis for the formulas) in order to have all effect sizes in terms of r .

In meta-analysis of effect sizes based on r , computations are actually carried out on Fisher's transformation of r to Z , because it allows more valid combinations of

Table 1: The 146 samples from 65 studies of asymmetry and sexual competition

Species	Effect type	Taxon	Mobility	Sex	r	N	Sex trait	Sexual selection	Experiment	Trait	Reference
<i>Anas platyrhynchos</i>	Pairing	3	1	1	-.140	36	0	.5	0	Tarsus	K. Omland, unpublished manuscript
<i>A. platyrhynchos</i>	Pairing	3	1	1	.200	36	0	.5	0	Tarsus	K. Omland, unpublished manuscript
<i>Chironomus plumosus</i>	Mating	1	1	1	-.363	359	0	2.0	0	Wing	McLachlan and Cant 1995
<i>Coenagrion puella</i>	Mating	1	1	1	-.255	492	0	1.5	0	Wing	Harvey and Walsh 1993
<i>Copaichromis thinos</i>	Attrac./mating	2	0	1	-.052	41	1	2.0	0	Bower	M. Taylor, G. Tuner, R. Robinson, and J. Stauffer, Jr., unpublished manuscript
<i>Cyprinodon pecosensis</i>	Terr. hold	2	1	1	-.445	153	0	1.0	0	Skeleton	Kodric-Brown 1997
<i>C. pecosensis</i>	Terr. hold	2	1	1	.228	52	0	1.0	0	Skeleton	Kodric-Brown 1997
<i>Drosophila melanogaster</i>	Mating	1	0	1	-.549	49	0	1.5	1	Bristles	Markow 1987
<i>Drosophila mojavensis</i>	Mating	1	0	1	-.005	44	0	1.5	0	Bristles	Markow and Ricker 1992
<i>D. mojavensis</i>	Mating	1	1	1	.124	44	0	1.5	0	Wing	Markow and Ricker 1992
<i>Drosophila nigrospiracula</i>	Mating	1	0	1	-.023	368	0	2.0	0	Bristles	Polak 1997
<i>D. nigrospiracula</i>	Mating	1	0	1	.018	291	0	2.0	0	Bristles	Polak 1997
<i>Drosophila pseudoobscura</i>	Mating	1	1	1	-.171	100	0	1.5	0	Wing	Markow and Ricker 1992
<i>D. pseudoobscura</i>	Mating	1	0	1	-.017	100	0	1.5	0	Aristal branch	Markow and Ricker 1992
<i>D. pseudoobscura</i>	Mating	1	1	1	-.429	100	0	1.5	0	Wing	Markow and Ricker 1992
<i>D. pseudoobscura</i>	Mating	1	0	1	-.113	100	0	1.5	0	Bristles	Markow et al. 1996
<i>D. pseudoobscura</i>	Mating	1	0	1	-.038	100	1	1.5	0	Sex comb	Markow et al. 1996
<i>Drosophila simulans</i>	Mating	1	0	1	.048	100	0	1.5	0	Bristles	Markow and Ricker 1992
<i>D. simulans</i>	Mating	1	1	1	.395	100	0	1.5	0	Wing	Markow et al 1996
<i>D. simulans</i>	Mating	1	0	1	.176	100	0	1.5	0	Aristal branch	Markow and Ricker 1992
<i>D. simulans</i>	Mating	1	0	1	.099	100	0	1.5	0	Bristles	Markow and Ricker 1992
<i>D. simulans</i>	Mating	1	0	1	.084	100	0	1.5	0	Bristles	Markow et al. 1996
<i>D. simulans</i>	Mating	1	0	1	.036	100	1	1.5	0	Sex comb	Markow et al 1996
<i>D. simulans</i>	Mating	1	1	1	.158	100	0	1.5	0	Wing	Markow and Ricker 1992
<i>Eyprepocnemis plorans</i>	Mating	1	1	0	.010	216	0	1.5	0	Tibia	A. Castro and A. Martin-Alganza, unpublished manuscript
<i>E. plorans</i>	Mating	1	1	1	.050	230	0	1.5	0	Tibia	A. Castro and A. Martin-Alganza, unpublished manuscript
<i>Forficula auricularia</i>	Mating	1	0	1	-.876	13	1	1.5	0	Forceps	Radesäter and Halldórsdóttir 1993
<i>F. auricularia</i>	Mating	1	0	1	-.612	20	1	1.5	0	Forceps	Radesäter and Halldórsdóttir 1993
<i>Gallinago media</i>	Mating	3	0	1	.023	21	1	2.0	0	Feather color	Fiske et al. 1994
<i>G. media</i>	Mating	3	1	1	.189	22	0	2.0	0	Wing	Fiske et al. 1994
<i>G. media</i>	Mating	3	1	1	-.273	22	0	2.0	0	Tarsus	Fiske et al. 1994
<i>Gallus gallus</i>	F. choice	3	0	1	.231	10	1	1.0	1	Wattle	Ligon et al. 1997
<i>G. gallus</i>	F. choice	3	0	1	-.115	10	1	1.0	1	Ear lappet color	Ligon et al. 1997
<i>G. gallus</i>	F. choice	3	0	1	.115	10	1	1.0	1	Hackle	Ligon et al. 1997
<i>Gryllus campestris</i>	Phototaxis	1	1	1	-.458	39	0	1.5	0	Tibia	Simmons 1995
<i>Harmonia oxyridis</i>	Mating	1	1	1	-.079	166	0	1.5	0	Wing	Ueno 1994
<i>Hippodamia convergens</i>	Mating	1	0	0	.025	116	0	2.0	0	Color	K. Hughes, unpublished manuscript
<i>H. convergens</i>	Mating	1	0	1	.037	104	0	2.0	0	Color	K. Hughes, unpublished manuscript
<i>Hirundo rustica</i>	Mating	3	1	1	-.130	390	0	0.0	0	Wing	Møller 1994
<i>H. rustica</i>	Mating	3	1	1	-.445	61	1	0.0	1	Tail	Møller 1992a
<i>H. rustica</i>	Mating	3	1	1	-.927	33	1	0.0	1	Tail	Møller 1993b
<i>H. rustica</i>	Mating	3	1	1	-.150	367	1	0.0	0	Tail	Møller 1994
<i>Homo sapiens</i>	Mating	4	0	0	-.320	95	1	1.0	1	Breast	Singh 1995
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.250	95	1	1.0	0	Breast	Singh 1995
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.190	95	1	1.0	1	Breast	Singh 1995
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.043	91	0	1.0	0	Face	R. Thornhill and S. Gangestad, unpublished manuscript

Table 1 (Continued)

Species	Effect type	Taxon	Mobility	Sex	r	N	Sex trait	Sexual selection	Experiment	Trait	Reference
<i>H. sapiens</i>	Mating	4	0	0	-.040	104	0	1.0	0	Skeleton	Gangestad and Thornhill 1997
<i>H. sapiens</i>	M. choice	4	0	0	-.076	500	1	1.0	0	Breast	Manning et al. 1997
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	.609	16	0	1.0	1	Face	Swaddle and Cuthill 1995
<i>H. sapiens</i>	Mating	4	0	0	-.360	62	0	1.0	0	Skeleton	Thornhill and Gangestad 1994
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.541	13	0	1.0	0	Face	Grammer and Thornhill 1994
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.290	95	1	1.0	0	Breast	Singh 1995
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.170	35	0	1.0	0	Skeleton	Gangestad et al. 1994
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.540	13	0	1.0	0	Face	Grammer and Thornhill 1994
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.530	35	0	1.0	1	Face	R. Thornhill and W. Honilla, unpublished manuscript
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.208	93	0	1.0	0	Face	R. Thornhill and S. Gangestad, unpublished manuscript
<i>H. sapiens</i>	Mating	4	0	0	-.248	59	0	1.0	0	Skeleton	Baker 1997
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.531	35	0	1.0	1	Face	R. Thornhill and W. Honilla, unpublished manuscript
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.348	59	0	1.0	0	Skeleton	Baker 1997
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.541	64	0	1.0	1	Face	D. Perrett, D. Kurt, K. Lee, and D. Rowland, unpublished manuscript
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.900	17	0	1.0	1	Face	L. Mealey, R. Bridgestock, and G. Townsend, unpublished manuscript
<i>H. sapiens</i>	Attrac./M. choice	4	0	0	-.920	17	0	1.0	1	Face	L. Mealey, R. Bridgestock, and G. Townsend, unpublished manuscript
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	-.660	12	0	1.0	1	Face	L. Mealey, R. Bridgestock, and G. Townsend, unpublished manuscript
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	-.580	11	0	1.0	1	Face	L. Mealey, R. Bridgestock, and G. Townsend, unpublished manuscript
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	.693	16	0	1.0	1	Face	Swaddle and Cuthill 1995
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	-.330	37	0	1.0	0	Skeleton	Gangestad et al. 1994
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	-.600	13	0	1.0	0	Face	Grammer and Thornhill 1994
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	-.640	13	0	1.0	0	Face	Grammer and Thornhill 1994
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	-.228	82	0	1.0	0	Face	R. Thornhill and S. Gangestad, unpublished manuscript
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	.085	91	0	1.0	0	Face	R. Thornhill and S. Gangestad, unpublished manuscript
<i>H. sapiens</i>	Mating	4	0	1	-.270	60	0	1.0	0	Skeleton	S. Gangestad and R. Thornhill, unpublished manuscript
<i>H. sapiens</i>	F. choice	4	0	1	-.299	61	0	1.0	0	Skeleton	Thornhill et al. 1995
<i>H. sapiens</i>	Mating	4	0	1	-.240	68	0	1.0	0	Skeleton	Baker 1997
<i>H. sapiens</i>	Mating	4	0	1	-.380	99	0	1.0	0	Skeleton	Gangestad and Thornhill 1997
<i>H. sapiens</i>	Mating	4	0	1	-.290	104	0	1.0	0	Skeleton	Gangestad and Thornhill 1997

Table 1 (Continued)

Species	Effect type	Taxon	Mobility	Sex	r	N	Sex trait	Sexual selection	Experiment	Trait	Reference
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	-.541	64	0	1.0	1	Face	D. Perrett, D. Burt, K. Lee, and D. Rowland, unpublished manuscript
<i>H. sapiens</i>	Mating	4	0	1	-.320	60	0	1.0	0	Skeleton	Thornhill and Gangestad 1994
<i>H. sapiens</i>	Attrac./F. choice	4	0	1	-.272	68	0	1.0	0	Skeleton	Baker 1997
<i>H. sapiens</i>	Attractiveness	4	0	*	.630	49	0	1.0	1	Face	Langlois et al. 1994
<i>H. sapiens</i>	Attractiveness	4	0	*	.700	49	0	1.0	1	Face	Langlois et al. 1994
<i>H. sapiens</i>	Attractiveness	4	0	*	-.141	64	0	1.0	0	Face	Kowner 1996
<i>H. sapiens</i>	Attractiveness	4	0	*	-.066	64	0	1.0	1	Face	Kowner 1996
<i>Ischnura denticollis</i>	Mating	1	1	1	-.444	95	0	1.5	0	Forewing	Córdoba-Aguilar 1995
<i>I. denticollis</i>	Mating	1	1	1	-.425	95	0	1.5	0	Tibia	Córdoba-Aguilar 1995
<i>I. denticollis</i>	Mating	1	1	1	-.297	95	0	1.5	0	Hindwing	Córdoba-Aguilar 1995
<i>Kobus kob</i>	Mating	4	0	1	-.024	98	1	2.0	0	Horn	J. Deutsch, unpublished manuscript
<i>Luscinia svecica</i>	F. choice	3	0	1	-.485	22	1	0.0	1	Color bands	Fiske and Amundsen 1997
<i>L. svecica</i>	F. choice	3	0	1	-.594	22	1	0.0	1	Color bands	Fiske and Amundsen 1997
<i>Musca domestica</i>	Mating	1	1	0	-.119	50	0	2.0	0	Tibia	Møller 1996c
<i>M. domestica</i>	Mating	1	1	0	-.442	100	0	2.0	0	Wing	Møller 1996c
<i>M. domestica</i>	Mating	1	1	0	-.307	50	0	2.0	0	Wing	Møller 1996c
<i>M. domestica</i>	Mating	1	1	0	-.080	100	0	2.0	0	Tibia	Møller 1996c
<i>M. domestica</i>	Mating	1	1	1	-.643	50	0	2.0	0	Tibia	Møller 1996c
<i>M. domestica</i>	Mating	1	1	1	-.389	100	0	2.0	0	Wing	Møller 1996c
<i>M. domestica</i>	Mating	1	1	1	-.150	100	0	2.0	0	Tibia	Møller 1996c
<i>M. domestica</i>	Mating	1	1	1	-.542	50	0	2.0	0	Wing	Møller 1996c
<i>Myrmeleotettix maculatus</i>	Phonotaxis	1	0	1	-.860	30	1	1.5	1	Stridulator	A. Møller, unpublished manuscript
<i>M. maculatus</i>	Phonotaxis	1	0	1	-.630	30	1	1.5	1	Stridulator	A. Møller, unpublished manuscript
<i>Oryx gazella</i>	Terr. holder	4	0	1	-.176	99	0	1.0	0	Horn	Møller et al. 1997
<i>O. gazella</i>	Terr. holder	4	0	1	-.147	134	1	1.0	0	Horn	Møller et al. 1997
<i>Ourebia ouribi</i>	Mating	4	0	1	-.368	42	1	1.0	0	Horn	Arcese 1994
<i>Panorpa japonica</i>	Mating	1	1	0	-.098	22	0	1.0	0	Wing	Thornhill 1992a
<i>P. japonica</i>	F. choice	1	1	1	-.840	25	1	1.0	1	Pheromone	Thornhill 1992a
<i>P. japonica</i>	F. choice	1	1	1	-.600	15	0	1.0	1	Pheromone	Thornhill 1992a
<i>P. japonica</i>	F. choice	1	1	1	-.680	25	0	1.0	0	Wing	Thornhill 1992b
<i>P. japonica</i>	Mating	1	1	1	-.839	21	0	1.0	0	Wing	Thornhill 1992a
<i>P. japonica</i>	Mating	1	1	1	-.462	121	0	1.0	0	Wing	Thornhill 1992b
<i>Passer domesticus</i>	F. choice	3	0	1	-.530	14	1	0.0	0	Badge	Kimball 1995
<i>Pavo cristatus</i>	Mating	3	1	1	-.534	16	1	2.0	0	Train	Hasegawa 1995
<i>Platycypha caligata</i>	Mating	1	0	1	.030	55	1	2.0	1	Tibia color	M. Jennions, unpublished manuscript
<i>Poecilia reticulata</i>	F. choice	2	0	1	.625	16	1	1.5	0	Spot color/ predator+	Gong and Gibson 1996
<i>P. reticulata</i>	F. choice	2	0	1	-.707	22	1	1.5	0	Spot color	Gong and Gibson 1996
<i>P. reticulata</i>	F. choice	2	0	1	-1.000	31	1	1.5	0	Spot color	Gong and Gibson 1996
<i>P. reticulata</i>	F. choice	2	0	1	-1.000	31	1	1.5	0	Spot color	Gong and Gibson 1996
<i>P. reticulata</i>	F. choice	2	0	1	.069	56	1	1.5	0	Spot color	Brooks and Caithness 1995
<i>P. reticulata</i>	F. choice	2	0	1	.004	34	1	1.5	0	Spot color	Brooks and Caithness 1995
<i>P. reticulata</i>	F. choice	2	0	1	-.865	12	1	1.5	1	Spot pattern	Sheridan and Pomiankowski 1997
<i>P. reticulata</i>	F. choice	2	0	1	-.035	34	0	1.5	0	Spot color	Brooks and Caithness 1995
<i>P. reticulata</i>	F. choice	2	0	1	.000	34	0	1.5	0	Spot color	Brooks and Caithness 1995
<i>Polyblepharis opaca</i>	Mating	1	1	0	-.520	103	0	2.0	0	Wing	M. Poulsen, B. Myrthue, and L. Sand, unpublished manuscript
<i>P. opaca</i>	Mating	1	1	1	-.854	84	0	2.0	0	Wing	M. Poulsen, B. Myrthue, and L. Sand, unpublished manuscript
<i>Scatophaga stercoraria</i>	Mating	1	1	1	-.518	87	0	2.0	0	Tibia	Liggett et al. 1993
<i>S. stercoraria</i>	Mating	1	1	1	-.397	87	0	2.0	0	Wing	Liggett et al. 1993
<i>Sepsis cynipsea</i>	Mating	1	1	1	-.243	106	1	2.0	0	Tibia	Allens and Simmons 1996
<i>Sorex araneus</i>	Mating/RS	4	0	1	-.090	19	1	1.0	0	Scent gland	Stockley et al. 1996

Table 1 (Continued)

Species	Effect type	Taxon	Mobility	Sex	r	N	Sex trait	Sexual selection	Experiment	Trait	Reference
<i>Stenurella melanura</i>	Mating	1	1	0	-.119	33	0	1.5	0	Elytra	Møller and Zamora-Muñoz 1997
<i>S. melanura</i>	Mating/M. choice	1	0	0	-.621	26	1	1.5	1	Antenna	Møller and Zamora-Muñoz 1997
<i>S. melanura</i>	Mating/M. choice	1	1	0	-.221	26	0	1.5	1	Elytra	Møller and Zamora-Muñoz 1997
<i>S. melanura</i>	Mating	1	0	0	-.590	34	1	1.5	0	Antenna	Møller and Zamora-Muñoz 1997
<i>S. melanura</i>	Mating	1	0	1	-.358	69	1	1.5	0	Antenna	Møller and Zamora-Muñoz 1997
<i>S. melanura</i>	Mating/male comp.	1	0	1	-.584	38	1	1.5	1	Antenna	Møller and Zamora-Muñoz 1997
<i>S. melanura</i>	Mating	1	1	1	-.127	71	0	1.5	0	Elytra	Møller and Zamora-Muñoz 1997
<i>S. melanura</i>	Mating/male comp.	1	1	1	-.174	38	0	1.5	1	Elytra	Møller and Zamora-Muñoz 1997
<i>Tachycineta bicolor</i>	Mating/RS	3	1	1	.020	21	0	.0	0	Tail	Dunn et al. 1994
<i>Taeniopygia guttata</i>	F. choice	3	0	1	.200	10	1	.0	1	Color bands	Jennions 1997
<i>T. guttata</i>	F. choice	3	0	1	-.778	8	1	.0	1	Color bands	Bennett et al. 1996
<i>T. guttata</i>	F. choice	3	0	1	-.790	9	1	.0	1	Color bands	Swaddle and Cuthill 1994b
<i>T. guttata</i>	F. choice	3	0	1	-.718	9	1	.0	1	Color bands	Swaddle and Cuthill 1994b
<i>T. guttata</i>	F. choice	3	0	1	-.749	10	1	.0	1	Plumage	Swaddle and Cuthill 1994a
<i>Tetrao tetrix</i>	F. choice	3	0	1	-.150	42	1	2.0	0	Tail feather	Rintamaki et al. 1997
<i>T. tetrix</i>	F. choice	3	1	1	-.390	39	0	2.0	0	Tarsus	Rintamaki et al. 1997
<i>T. tetrix</i>	F. choice	3	0	1	-.070	46	1	2.0	0	Tail feather	Rintamaki et al. 1997
<i>T. tetrix</i>	F. choice	3	1	1	-.310	43	0	2.0	0	Tarsus	Rintamaki et al. 1997
<i>Vidua macroura</i>	Mating	3	1	1	.250	7	1	1.5	0	Tail	Savalli 1997
<i>Vidua paradisaea</i>	F. choice	3	1	1	.538	13	1	2.0	†	Tail	Oakes and Barnard 1994
<i>Xiphophorus cortezi</i>	F. choice	2	0	1	-.571	12	1	2.0	1	Body bar	Morris and Casey 1997

Note: Effect: Attract. = attractiveness rated; Terr. = territory; M. = male; F. = female; RS = reproductive success. Taxon: 1 = insect; 2 = fish; 3 = bird; 4 = mammal. Mobility: 1 = trait studied involved in mobility; 0 = trait not so involved. Sex: 1 = male, 0 = female, * = attractiveness, but sexes of attractiveness raters not separated. Sex trait: 1 = secondary sexual trait; 0 = ordinary trait. Sexual selection = mean rating of sexual selection intensity. Experiment: 1 = experimental; 0 = observational; † = experimental design confounded trait size and symmetry.

effects than combining the untransformed r 's (e.g., Rosenthal 1991, p. 21). Thus, a Fisher's Z_r value for each r effect size was calculated. Table 1 gives the untransformed r effect sizes only. They can be transformed to Z_r from tabulated values in any general statistics book or converted by $Z_r = 1/2 \log_e [(1 + r)/(1 - r)]$. For reporting of effect sizes, the meta-analytically derived results in terms of Z_r are transformed back to their corresponding r 's.

Computations

Average weighted Z_r was computed as an estimate of combined effect sizes (e.g., Rosenthal 1991; Shadish and Haddock 1994):

$$\text{Weighted } \bar{Z}_r = \frac{\sum w_j Z_{rj}}{\sum w_j}, \quad (1)$$

where w_j is the weight factor of analysis unit j (sample, study, or species, depending on the analysis). The Z_{rj} statistic is the Z -transformed r effect size of analysis unit j .

For analysis of the 146 samples, at the level of samples, mean weighted effect size, \bar{Z}_r , was computed with equation (1), with $w = Nj - 3$ (Rosenthal 1991, pp. 27–28). For analysis at the studies' level, in the case of studies with only one sample, the study's Z_r in the above equation (1) was that study's Z_r . In the case of studies with multiple samples, the Z_r for the study was a mean of the Z_r 's of the samples weighted by sample size ($N - 3$) because some multiple-sample studies had disparate N 's across samples. This procedure was the basis for the weighted \bar{Z}_r effect size calculated for all studies. The same procedure was followed for analysis at the species' level. In the case of species with only one study, that study's Z_r in the above equation (1) was that species' Z_r . In the case of species with multiple studies, the Z_r for the species was a mean of the Z_r 's of the studies weighted by the studies' mean sample size based on $N - 3$. This procedure of calculating study and species' mean weighted Z_r (i.e., \bar{Z}_r) appropriately puts emphasis on variation in N in computing effect size.

The calculated weighted \bar{Z}_r 's of interest were tested

against the null hypothesis of no effect by examining the statistical significance of their associated r 's. The \bar{Z}_r was converted to r and then r 's significance at the appropriate degree-of-freedom level was determined. Confidence intervals on these r 's are calculated following Hedges and Olkin (1985, pp. 230–232).

Statistical heterogeneity in effect sizes among analysis units was tested using the standard procedure of calculating a χ^2 statistic as follows (see Rosenthal 1991, pp. 73–74):

$$\chi^2 = \sum (N_j - 3)(Z_{rj} - \bar{Z}_r)^2, \quad (2)$$

where N_j is the sample size of the analysis unit, Z_{rj} is the Fisher-transformed effect size of analysis unit j , \bar{Z}_r is the weighted mean Z_r , calculated as described above. The χ^2 has $K - 1$ degrees of freedom, and K is the number of analysis units.

Moderator Variables

Significant heterogeneity in effect sizes determined with the χ^2 test above does not provide information about the nature of the differences. The location of systematic differences across analysis units is determined by tests of contrast in focused tests (Rosenthal 1991, pp. 79–84). The statistical significance of the difference in two groups of r 's, based on Z_r , is obtained from a Z (the standard normal deviate) calculated as:

$$\frac{\sum \lambda_j Z_{rj}}{\sqrt{\sum \frac{\lambda_j^2}{w_j}}}, \quad (3)$$

where λ_j is the contrast weight determined by a hypothesis of the analysis unit (sample, study, or species), chosen such that the sum of λ_j 's will be zero. For example, a contrast based on sex would be λ_1 (male) = $-1/N_1$, where N_1 = number of male analysis units, and λ_2 (female) = $1/N_2$, where N_2 = number of female analysis units. The variable Z_{rj} is the Fisher Z_r for any analysis unit, and w_j is the inverse of the variance of the effect size for the analysis unit. For Fisher Z_r , $w_j = N_j - 3$.

By means of focused tests, we determined whether the six variables listed in the introduction to this article affected the magnitude of the relationship between fluctuating asymmetry and sexual selection among units of analysis. For contrasts involving studies and species, Z_{rj} in equation (3) was the N -weighted mean Z_r described above for cases of multiple-sample studies and multiple-study species. For example, to analyze the contrast of effect sizes in investigations of male versus female at the studies' level, the Z_r for males in (3) in each study involved multiple samples of males in the sample-size weighted $(N - 3)$ mean Z_r for males in the study.

In table 1, the data are indicated for the sex showing the effect, the major taxon of each species, the type of trait studied, and whether the trait is a secondary sex trait or not.

Samples were classified with respect to the intensity of sexual selection on a three-grade scale from 0 to 2, with 0 representing social monogamy, 1 resource-defense and female-defense polygyny, and 2 extreme polygyny such as lekking. We independently scored all species involved, and the consistency in the ranking was high as demonstrated by a strong positive correlation (Spearman rank order correlation r_s , $0 = .72$, $N = 42$ species, P (two-tailed) $< .0001$). We used the mean score in the meta-analysis (see table 1). The samples were also classified as representing characters that can affect mobility (such as wing asymmetry) or cannot affect mobility (such as asymmetry in a color pattern or sternopleural chaetae) (table 1).

Finally, the samples were classified as experimental or observational depending on whether they were based on the manipulation of the asymmetry of a character or whether they just reported a relationship between asymmetry and sexual selection without manipulation of asymmetry (table 1). One experimental study was excluded from the analyses (Oakes and Barnard 1994) because the experimental design does not allow discrimination between an effect of character size and character asymmetry (Brookes and Pomiankowski 1994).

The samples included may represent a biased sample of all studies if publication is influenced by a specific result (Hunter and Schmidt 1990), such as an effect size with $P \leq .05$. This problem seems unlikely because the literature on developmental stability and sexual selection is a mixture of studies demonstrating and not demonstrating an effect of developmental instability on mating success or attractiveness. Publishing bias is therefore not assumed to increase the probability of a Type I error in the meta-analysis. The fail-safe number of studies was calculated, following Rosenthal (1991, p. 104), as:

$$X = \frac{(\sum Z_j)^2}{2.706} - K, \quad (4)$$

where $Z_j (= Z_{rj} \times \sqrt{N_j - 3})$ is the standard normal deviate of analysis unit j , and K is the number of analysis units combined to calculate the effect size. The number 2.706 is based on P (one-tailed) = .05. The fail-safe number estimates the number of unknown additional studies that would be needed to eliminate an overall effect's significance at the 5% level when those studies showed an average null result ($\bar{Z} = 0.00$) (Rosenthal 1991, p. 104). Thus, it is an estimate of the number of studies that are unknown to us as a result of either journals' rejection of papers with null results or scientists not

reporting studies with null results. It also is an estimate of future studies with null results that would be needed to change a significant effect to an insignificant one.

Certain adjustments were made to improve the overall effect-size estimates based on our knowledge of methodological problems that make certain reported estimates irrelevant. The excluded experimental study by Oakes and Barnard (1994) was mentioned above. Two studies of human faces were also excluded because of experimental (i.e., manipulation) effects that make the results highly suspect. Langlois et al. (1994) and Swaddle and Cuthill (1995) made perfectly symmetrical faces using computer techniques by duplicating half-faces of subjects or by using mirror-images. These perfectly symmetrical faces were compared with normal, unaltered faces for attractiveness and were found to be much less attractive than normal faces. Thus, these studies gave large effect sizes in the direction of more asymmetrical being more attractive (table 1). Recent studies have shown that computer-generated symmetrical faces contain unnatural facial shape and feature size and texture (D. Perrett, D. Burt, K. Lee, and D. Rowland, unpublished manuscript; L. Mealey, R. Bridgestock, and G. Townsend, unpublished manuscript). Including these two studies would reduce the accuracy of estimates of effect size.

L. Mealey, R. Bridgestock, and G. Townsend (unpublished manuscript) also used hemi-faces but did not compare them with the normal, unaltered faces from which they were made. Instead, Mealey et al. compared the ratings of similarity of perfectly symmetrical faces made from left and right hemi-faces, and thus facial symmetry, with attractiveness ratings of the unaltered faces.

It should also be pointed out that Kowner (1996) used, in part, hemi-faces to make perfectly symmetrical faces that were then rated in comparison to the unaltered faces from which the symmetrical faces were made. However, the experimental effects involved very elderly and child subjects and thus are not relevant to the domain of our meta-analysis; that is, they are irrelevant in terms of sexual attractiveness. We did include, however, Kowner's (1996) reports of attractiveness ratings of normal, unmanipulated, young adult faces measured for facial symmetry using procedures developed elsewhere (Grammer and Thornhill 1994).

One sample of a total of four reported by Gong and Gibson (1996) was also excluded. They reported three effects showing strong negative relationships between asymmetry and sexual attractiveness of male guppies and one effect showing a strong positive effect. The positive effect was created by the experimental protocol that examined the influence of a predator's presence on female choice of decorated males. The predator's presence apparently caused females to devalue decoration in males,

and thus females could not be assessing symmetry in that sample. Note that although Gong and Gibson's (1996) study was experimental, involving a predator's effect on female preference, it is not listed as an experiment in table 1 because asymmetry of spots was measured but not manipulated. Using the focused test approach described above, we test for a statistically significant difference between the excluded samples and studies mentioned above and the remainder of the effect sizes.

As recommended typically by statisticians, all statistical tests reported are one-tailed when the direction of a relationship is predicted; otherwise, tests are two-tailed. The arbitrary $P = .05$ is used to designate statistical significance. We make no adjustments (e.g., Bonferroni adjustments) for Type I error rates. Given that the number of tests conducted in this article is not extremely high, any adjustment for Type I error rate would increase the Type II error rate, which is widely recognized as the most problematic inferential error (Cohen 1988). Of course, in the end, readers will evaluate statistical significance in terms of tailness and magnitude of probability based on their own preferences.

Results

Fluctuating asymmetry and mating success or attractiveness measures exist for 146 samples from 65 studies of 42 species (table 1). Six of these samples were excluded, which eliminated three studies: two samples each in Langlois et al. (1994) and Swaddle and Cuthill (1995), which eliminated these two studies altogether; Oakes and Barnard (1994) (only one sample in this study); and one of four samples of Gong and Gibson (1996). These excluded samples gave an overall weighted effect size of $r = 0.651$ ($-0.54 \leq r \leq -0.78$, one-tailed confidence interval [CI]), $.05 < P$ (one-tailed) $< .1$, compared to an overall weighted effect size for the remaining 140 samples of $r = -0.42$ ($-0.38 \leq r \leq -0.46$, one-tail CI), P (one-tailed) $< .0005$. A contrast or focused test revealed that excluded and included groups are statistically significantly different with $Z = 11.86$, $P < .0001$ (table 2). In this contrast, each included sample was weighted (λ) as $-1/140$ and each excluded sample as $1/6$. Clearly, the included samples showed much higher negative correlations between asymmetry and mating success measures than did the excluded samples. The excluded samples leave a total of 62 studies and 41 species, which are analyzed below.

Studies as Units of Analysis

The magnitude of the overall weighted effect size for the 62 studies is $r = -0.42$ ($-0.40 \leq r \leq -0.44$, one-tailed

Table 2: Summary of major meta-analytic effects

Data	Weighted effect size (r)	N	Analysis unit	Probability of r
1. Excluded samples	.65	6	samples ^a	.05 < P < .1
2. Remaining samples	-.42	140	samples ^b	P < .0005
Study-level analysis:				
Studies excluding samples in row 1	-.42	62	studies	P < .0005
Studies including samples in row 1	-.36	65	studies	P < .0025
3. Male success	-.44	59	studies ^a	P < .0005
4. Female success	-.34	17	studies ^b	P < .10
5. Sex trait	-.52	33	studies ^a	P < .001
6. Ordinary trait	-.29	37	studies ^b	P < .05
7. Sex trait, face included	-.59	39	studies ^a	P < .0005
8. Ordinary trait, face excluded	-.23	32	studies ^b	P = .10
9. Experiment	-.57	20	studies ^a	P = .005
10. Observation	-.35	46	studies ^b	P = .003
11. Mobility trait	-.34	24	studies ^a	P = .055
12. Nonmobility trait	-.45	42	studies ^b	P = .002
Sexual selection intensity	studies ^c	...
Higher taxon	studies ^c	...
Species-level analysis:				
Species excluding samples in row 1	-.34	41	species	P < .025
Species including samples in row 1	-.31	42	species	P = .025
13. Male success	-.35	41	species ^a	P = .016
14. Female success	-.25	7	species ^b	P = .30
15. Sex trait	-.42	25	species ^a	P = .015
16. Ordinary trait	-.23	25	species ^b	P = .15
17. Sex trait, face included	-.59	25	species ^a	P = .001
18. Ordinary trait, face excluded	-.23	25	species ^b	P = .15
19. Experiment	-.59	12	species ^a	P = .02
20. Observation	-.29	34	species ^b	P = .05
21. Mobility trait	-.25	23	species ^a	P = .25
22. Nonmobility trait	-.35	24	species ^b	P = .05
Sexual selection intensity	species ^d	...
Higher taxon	species ^c	...

Note: Data: Sequential paired numbers refer to two contrasts tested by focused tests. Analysis unit: Paired analysis units with different superscript letters are significantly different by focused tests at $P \leq .05$. Analysis units with a superscript c or d refer to contrasts with four groups; c connotes a statistically significant ($P \leq .05$) contrast and d an insignificant one. See the "Results" section.

CI), and P (one-tailed) < .0005 (table 2). This study effect is weighted by sample size as described in the "Material and Methods" section. The pattern is virtually identical when the mean effect is weighted by both sample size and sample number per study: $r = -0.42$ ($-0.39 \leq r \leq -0.43$, one-tailed CI), P (one-tailed) < .0005. The two-factor (sample size and number) weighting procedure follows that outlined by Rosenthal (1991, pp. 79–84). Even if the three excluded studies and the excluded sample from Gong and Gibson (1996) are included, the overall weighted effect size is statistically significantly different from zero ($N = 65$ studies, $r = -0.36$ [$-0.33 \leq r \leq -0.38$, one-tailed CI], $.001 < P$ (one-tailed) < .0025)

(table 2). The fail-safe number for the overall effect from the 62 studies ($r = -0.42$) is 9,618.

The studies show significant heterogeneity ($N = 62$ included studies) in effect sizes: $\chi^2 = 1,062$, $df = 61$, $P < .001$. Thus, even with the six excluded samples removed, there is significant heterogeneity in effect sizes among the 62 studies. Focused tests to examine moderator variables that could be important in explaining the variation in effect sizes across the 62 studies revealed the following.

For male versus female mating success or sexual attractiveness, $Z = 2.35$, P (one-tailed) = .009. The male effect size is significantly larger than the female effect size, as we predicted. That is, the r 's of the relationship

between asymmetry and sexual selection in males are significantly more negative than the r 's for the same relationship in females. Some studies reported effect sizes for both sexes, but there is no problem of dependence here because individuals of different sex were involved. The weighted mean r for males is -0.44 ($-0.42 \leq r \leq -0.47$, one-tailed CI), $P < .0005$ (59 studies represented) and for females is -0.34 ($-0.28 \leq r \leq -0.37$, one-tailed CI), $.05 < P < .1$ (17 studies) (table 2).

For secondary sexual trait or ordinary trait, $Z = 5.35$, P (one-tailed) $< .001$. As predicted, studies of secondary sexual trait show significantly stronger negative associations between asymmetry and sexual selection than studies of ordinary traits. Some studies reported effect sizes for both types of traits. The weighted mean r for secondary sexual trait is -0.52 ($-0.49 \leq r \leq -0.54$, one-tailed CI), P (one-tailed) $< .001$ (33 studies represented) and -0.29 ($-0.27 \leq r \leq -0.31$), $.025 < P$ (one-tailed) $< .05$ (37 studies) for ordinary traits (table 2). Reanalysis of this pattern with the human face included as a secondary sexual trait as is appropriate (Thornhill and Gangestad 1993) yields a similar and highly significant difference in effect sizes: weighted mean r for secondary sexual trait is -0.59 ($-0.57 \leq r \leq -0.62$, one-tailed CI), P (one-tailed) $< .0005$ (39 studies represented) and -0.23 ($-0.20 \leq r \leq -0.25$, one-tailed CI), P (one-tailed) = $.10$ (32 studies) for ordinary traits (P [one-tailed] $< .0001$ for Z) (table 2).

These analyses comparing secondary sexual and ordinary trait effect sizes are not independent because in some studies secondary sexual trait and ordinary traits were measured on the same individual. Taking this into account by excluding those studies reporting effect sizes for both sex traits and ordinary traits yields statistically significant differences in effect sizes with larger negative correlations between secondary sexual trait and asymmetry than between ordinary traits and asymmetry. The comparison including face as an ordinary trait yielded the following: secondary sexual trait, $r = -0.59$ ($-0.57 \leq r \leq -0.61$, one-tailed CI), P (one-tailed) = $.001$, $N = 25$ studies; ordinary trait, $r = -0.32$ ($-0.30 \leq r \leq -0.35$, one-tailed CI), P (one-tailed) = $.05$, $N = 29$ studies; P (one-tailed) $< .0001$ for Z . The comparison including face as a secondary sexual trait yielded the following: secondary sexual trait, $r = -0.64$ ($-0.61 \leq r \leq -0.67$, one-tailed CI), P (one-tailed) = $.0005$, $N = 23$ studies; ordinary trait, $r = -0.25$ ($-0.023 \leq r \leq 0.27$, one-tailed CI), P (one-tailed) = $.10$, $N = 27$ studies; P (one-tailed) $< .0001$ for Z .

For experimental versus observational effects, $Z = 15.54$, P (one-tailed) $< .0001$. Experimental studies yield larger negative correlations between asymmetry and performance related to sexual selection than observation

studies, as we predicted. Some studies reported effect sizes for both types of studies. The weighted mean r for experiments is -0.57 ($-0.55 \leq r \leq -0.60$, one-tailed CI), P (one-tailed) = $.005$ (20 studies represented) and -0.35 ($-0.33 \leq r \leq -0.37$, one-tailed CI), P (one-tailed) = $.003$ (46 studies) for observational studies (table 2). In no case was observation and experiment done on the same individuals in a single study.

For traits involved versus not involved in mobility, $Z = 2.67$, P (one-tailed) = $.0038$. Contrary to our prediction, studies of traits involved in mobility did not yield larger negative correlations between asymmetry and sexual selection than traits not so involved. Indeed, the effect difference is statistically significant in the opposite direction of prediction. Some studies contribute to both aspects of this comparison (e.g., tarsus asymmetry and tail asymmetry in black grouse). The r for not involved in mobility is -0.45 ($-0.043 \leq r \leq -0.48$, one-tailed CI), P (one-tailed) = $.0015$ (42 studies represented) and for involved is -0.34 ($-0.031 \leq r \leq -0.37$, one-tailed CI), P (one-tailed) = $.055$ (24 studies) (table 2).

Reanalysis was done to eliminate independence in the four studies in which the two types of traits were measured on the same individuals. Again, contrary to our prediction, studies of traits not involved with mobility have significantly larger negative correlations than studies of traits involved in mobility: $Z = 2.99$, P (one-tailed) = $.0014$ (r , involved, -0.37 [$-0.34 \leq r \leq -0.41$, one-tailed CI], P [one-tailed] = $.055$, 20 studies; r , not involved, -0.48 [$-0.46 \leq r \leq -0.50$, one-tailed CI], P [one-tailed] = $.0015$, 38 studies).

For intensity of sexual selection, $Z = 1.82$, P (one-tailed) = $.034$ (table 2). The weights (λ) in this analysis were for a linear contrast involving four groups with a sum of zero (λ 's = $-1, -3, 1, 3$) (see Rosenthal 1991, p. 80). The four effects tend to increase in size as the intensity of sexual selection declines, as we predicted. In this analysis, there were four categories of sexual selection intensity (0, 1, 1.5, 2) based on mean ratings by ourselves. The weighted average effect sizes for the four categories were as follows: $r = -0.51$, 11 studies, category 0; $r = -0.35$, 21 studies, category 1; $r = -0.57$, 16 studies, category 1.5; $r = -0.27$, 14 studies, category 2. There is no problem with dependence across studies because each species had only one sexual selection intensity score. There is no a priori rationale for examining the statistical significance of the effect in each of the four categories of selection. Thus, probabilities and confidence intervals are not provided.

For the higher taxonomic groupings of insects, fishes, birds, and mammals, $Z = 7.69$, P (two-tailed) $< .0002$. Thus, there is statistically significant variation in effect sizes among the four taxonomic groupings (table 2). The

62 studies showed the following breakdown in mean weighted effect sizes: insects, $r = -0.35$ ($-0.30 \leq r \leq -0.38$, two-tailed CI), P (two-tailed) = .10, 22 studies; fishes, $r = -0.84$ ($-0.69 \leq r \leq -0.99$, two-tailed CI), P (two-tailed) = .02, six studies; birds, $r = -0.40$ ($-0.34 \leq r \leq -0.45$, two-tailed CI), P (two-tailed) = .08, 16 studies; mammals, $r = -0.32$ ($-0.27 \leq r \leq -0.36$, two-tailed CI), P (two-tailed) = .10, 18 studies. Contrast weights (λ) were 1, 2, -1, -2, respectively. The fish samples show the largest mean effect size, while the other three higher taxa exhibit mean effect sizes somewhat similar to the mean for all the studies.

Species as Units of Analysis

The mean weighted magnitude of the relationship between asymmetry and sexual competitiveness for the 41 species is $r = -0.34$ ($-0.31 \leq r \leq -0.37$, one-tailed CI), $.01 < P$ (one-tailed) $< .025$ (table 2). When the excluded samples are included in a reanalysis (adding Langlois et al. 1994; Oakes and Barnard 1994; Swaddle and Cuthill 1995; and Gong and Gibson's 1996 excluded sample), there is still a statistically significant relationship in the same direction as above: $r = -0.31$ ($-0.28 \leq r \leq -0.33$, one-tailed CI), P (one-tailed) = .025, $N = 42$ species (table 2). The fail-safe number for the overall effect size of the 41 species (i.e., $r = -0.34$) is 3,605.

The effect sizes of the 41 species exhibit significant heterogeneity: $\chi^2 = 341$, $df = 40$, $P < .001$. Thus, even with the methodologically questionable species, study, and samples out of the heterogeneity analysis, there is significant variation to be explained. Examination of the same six moderators as looked at in analysis of studies above revealed the following.

For male versus female performance related to sexual selection, $Z = 1.69$, P (one-tailed) = .046. As predicted, across species, in males, there are significantly larger negative correlations between asymmetry and sexual selection than in females. The weighted mean r for males is -0.35 ($-0.33 \leq r \leq -0.38$, one-tailed CI), P (one-tailed) = .016 (41 species represented) and -0.25 for females ($-0.21 \leq r \leq -0.29$, one-tailed CI), P (one-tailed) = .3 (seven species) (table 2).

For secondary sexual trait or ordinary trait, $Z = 4.02$, P (one-tailed) $< .0001$. As predicted, asymmetry in species' secondary sexual traits show significantly stronger negative relationships with sexual selection than species' ordinary traits. The weighted mean r for secondary sexual trait is -0.42 ($-0.39 \leq r \leq -0.45$, one-tailed CI), P (one-tailed) = .015 (25 species represented) and -0.23 ($-0.20 \leq r \leq -0.26$, one-tailed CI), P (one-tailed) = .15 (25 species) for ordinary traits. A stronger result is seen when the human face is included as a secondary

sexual character: $Z = 4.40$, P (one-tailed) $< .0001$ (r , secondary sexual trait, -0.59 [$-0.56 \leq r \leq -0.64$, one-tailed CI], P [one-tailed] = .001, 25 species; r , ordinary trait, -0.23 [$-0.20 \leq r \leq -0.26$, one-tailed CI], P [one-tailed] = .15, 25 species) (table 2).

In studies of certain species, secondary sexual traits and ordinary traits were measured on the same individuals, which generates dependence in the effect sizes of the two types of traits. Reanalysis excluding these cases yields the following: when face is considered an ordinary trait, $Z = 2.05$, P (one-tailed) = .020 (r , secondary sexual trait, -0.35 [$-0.32 \leq r \leq -0.38$, one-tailed CI], P [one-tailed] = .08, 16 species; r , ordinary trait, -0.25 [$-0.22 \leq r \leq -0.28$, one-tailed CI], P [one-tailed] = .15, 20 species). When the face is considered a secondary sexual trait, $Z = 1.43$, P (one-tailed) = .075 (r , secondary sexual trait, -0.34 [$-0.31 \leq r \leq -0.38$, one-tailed CI], P [one-tailed] = .08, 17 species; r , ordinary trait, -0.25 [$-0.21 \leq r \leq -0.29$, one-tailed CI], P [one-tailed] = .15, 16 species). Thus, in this reanalysis to correct potential dependence of data due to measures of both types of traits taken on the same individual, the significant effect found without the correction is also found when the face is considered an ordinary trait, but the effect just misses significance (i.e., $P = .05$) when the face is considered a secondary sexual trait.

For experimental versus observational effects, $Z = 4.58$, P (one-tailed) $< .0001$. As predicted, when species are studied experimentally, larger negative correlations between asymmetry and mating success or attractiveness are found than when species are studied observationally. The weighted mean effect size for experiments is $r = -0.59$ ($-0.56 \leq r \leq -0.63$, one-tailed CI), P (one-tailed) = .02 (12 species represented) and -0.29 ($-0.26 \leq r \leq -0.31$, one-tailed CI), P (one-tailed) = .05 (34 species) for observations (table 2).

For some species, both experimental and nonmanipulative studies were done on the same species. When those were removed from the analysis, the difference between experiments and observations is still statistically significant: $Z = 4.11$, P (one-tailed) $< .0001$. In this reanalysis, the weighted mean effect size for experiments $r = -0.47$ ($-0.44 \leq r \leq -0.50$, one-tailed CI), P (one-tailed) = .16 (seven species) and -0.23 ($-0.20 \leq r \leq -0.26$, one-tailed CI), P (one-tailed) = .12 (29 species) for observations.

For traits involved or not involved in mobility, $Z = 2.01$, P (one-tailed) = .023. The effect is statistically significant in the opposite direction of prediction. That is, across species, larger negative correlations between trait asymmetry and sexual selection occur for traits not involved with movement than for traits so involved. Weighted mean r for movement involved is -0.25

($-0.21 \leq r \leq -0.28$, one-tailed CI), P (one-tailed) = .05 (23 species) and -0.35 ($-0.32 \leq r \leq -0.38$, one-tailed CI), P (one-tailed) = .25 (24 species) for not involved (table 2). The same significant pattern is seen when species are removed from the analysis that contained effects for both mobility involved and not involved: $Z = 1.979$, P (one-tailed) = .024; weighted mean r is -0.31 ($-0.28 \leq r \leq -0.34$, one-tailed CI), P (one-tailed) = .13 (17 species) for mobility involved and -0.43 ($-0.40 \leq r \leq -0.45$, one-tailed CI), P (one-tailed) = .03 (18 species) for mobility not involved.

For intensity of sexual selection, $Z = 0.68$, P (one-tailed) = .248, not significant (table 2). This result is contrary to our prediction. In this analysis of effect-size variation among species, weights for a linear contrast involving four categories were as in the same analysis across studies. Average effect sizes for the four categories of selection intensity were as follows: $r = -0.40$, six species, category 0; $r = -0.26$, seven species, category 1; $r = -0.41$, 14 species, category 1.5; $r = -0.27$, 14 species, category 2.

For the higher taxonomic groupings of insects, fishes, birds, and mammals, $Z = 4.04$, P (two-tailed) < .0002 (table 2). The 41 species showed the following mean effect sizes: insects, $r = -0.34$ ($-0.32 \leq r \leq -0.36$, two-tailed CI), P (two-tailed) = .15, 21 species; fishes $r = -0.62$ ($-0.58 \leq r \leq -0.66$, two-tailed CI), P (two-tailed) = .40, four species; birds, $r = -0.27$ ($-0.24 \leq r \leq -0.30$, two-tailed CI), P (two-tailed) = .40, 11 species; mammals, $r = -0.22$ ($-0.18 \leq r \leq -0.25$, two-tailed CI), P (two-tailed) > .5, five species. Contrast weights were as in the analysis of higher taxonomic groups at the level of studies. The largest mean effect size is for the species of fish; the other three higher taxa exhibit much smaller effect sizes.

Discussion

Some of the studies reviewed show large effects in the opposite direction of the prediction that there will be a statistically significant negative relationship between asymmetry and performance in sexual competition (Langlois et al. 1994; Oakes and Barnard 1994; Swaddle and Cuthill 1995; one sample of Gong and Gibson 1996). These data were eliminated from our estimate of effect size on methodological grounds. These studies appear to be outliers that are not relevant to the effect of theoretical interest. Oakes and Barnard's (1994) experiment confounds trait symmetry and size. The other outliers predictably generated their large effects that are opposite to prediction because of the manipulation effects inherent in them. This is not to cast criticism on any of these studies. The excluded sample in Gong and Gibson (1996)

was designed to examine if a predator's presence eliminates mate choice for decoration, including symmetry; it did. The studies by Langlois et al. (1994) and Swaddle and Cuthill (1995) were valuable. It is clear that their procedures for studying facial symmetry are problematic. This could not have been known at the time they did their studies. Only with the accumulation of many studies and meta-analytic comparisons were the outliers identified and the problems with them revealed.

The overall conclusion from the meta-analysis of the relationship between fluctuating asymmetry and mating success or attractiveness is that there is a significant negative relationship. This is seen at the level both of studies and of species. For the 62 included studies, the effect is $r = -0.42$, $P < .0005$, with a fail-safe number of more than 9,000. For the 41 species included in the analysis, the effect averages -0.34 , $.01 < P < .025$, with a fail-safe number of more than 3,000. Thus, it is highly unlikely that publication or reporting biases or future research could generate enough studies with zero results to render either of these effects statistically nonsignificant. When the excluded studies and sample are included in an analysis, the average effect sizes for both studies and species remain negative in sign, similar in magnitude to the effects with the exclusions, and significantly different from zero.

Because the species included vary considerably in the number of studies on asymmetry and sexual competition they have received, the analysis at the study level may be biased. That the analysis at the species' level also provides a significant mean effect provides confidence that, at least at this taxonomic level, there is no bias preventing the conclusion of a significant mean effect.

Fluctuating asymmetry is a measure that is prone to measurement error, and measurement error can elevate estimates of fluctuating asymmetry (Palmer and Strobeck 1986; Palmer 1994). Measurement error may create effect sizes of asymmetry and sexual competitiveness that hide real relationships between the two variables in some individual studies. This makes meta-analysis highly relevant in any conclusions about the biological significance of asymmetry.

Leung and Forbes (1996) examined by meta-analysis the relationship between asymmetry and fitness-related traits across many published studies. Their result of a mean negative effect for the relationship between asymmetry and the fitness measures in 61 species is consistent with our finding that such a relationship exists for asymmetry and the fitness component of mating success. Their overall effect size of $r = -0.26$, however, is not comparable to our overall effects because ours is based on mating success and theirs reflects many fitness components (growth, dominance, body mass, etc.). Leung

and Forbes examined fewer species (10) in terms of mating success than we did and did not give a separate mating success effect-size estimate, only an overall fitness effect size.

A meta-analysis is only as good as the system used to retrieve the relevant data from the literature and unpublished sources. All major methods for comprehensive retrieval of studies recommended by meta-analysts (Cooper and Hedges 1994) were used: extensive network of colleagues studying asymmetry and performance, literature search, and World Wide Web. Our retrieval approach coupled with the recency of the development of the research domain of symmetry and sexual selection (the last 10 yr and primarily the last 5 yr) leads us to conclude that our data are representative of studies to date.

The existence of the overall negative relationship between fluctuating asymmetry and sexual competitiveness indicates that sexual selection may often act to favor genes that improve offspring viability. Fluctuating asymmetry has been shown in other literature reviews of multiple studies to have an overall negative relationship with viability and female fecundity and a positive relationship with parasitism (Leung and Forbes 1996; Møller 1996*b*, 1997*a*; Møller and Swaddle 1997; Thornhill and Møller 1997). Also, fluctuating asymmetry apparently has a significant heritability, according to meta-analysis (Møller and Thornhill 1997*a*, 1997*b*). It should be mentioned that the reviews, other than Leung and Forbes (1996), of the relationship between fluctuating asymmetry and viability, female fecundity, and parasitism cited immediately above are, in essence, a form of meta-analysis: they examine overall direction of effects but do not measure average effect sizes.

One important and unique feature of meta-analysis is its utility for examining whether there is systematic variation in effect sizes across data from multiple studies. Even with the outliers mentioned above removed, there is statistically significant heterogeneity in effect sizes. We tested whether six variables could account for this effect-size variation; five were predicted moderators and the remaining one was exploratory. Meta-analysts warn that variables should be chosen on theoretical grounds sparingly (e.g., Rosenthal 1991). There are many other moderators that can be envisioned post hoc, but we chose not to test them. Our use of six seems a reasonable approach.

Meta-analysts also emphasize that caution must be used in interpreting the influence of moderators because of potential confounds. This is no different than in a traditional *t*-test or other comparison in which any significant difference found may be confounded by another overlooked variable. In traditional statistics, multiple regression can control one independent variable while the relation between another independent variable and a de-

pendent variable is examined. There has been some discussion of meta-analytic techniques that are analogous to multiple regression (Hedges 1994), but we chose not to apply them. At the species level, sample size is only 41, and with six moderator variables with some intercorrelation, effect-size estimates and statistical inference would be questionable in multiple regression. As the literature dealing with asymmetry and sexual selection grows, it will eventually be informative to exploit the meta-analytic analogue of multiple regression.

Thus, at this time, with the focused tests of contrasting mean effect sizes for each of the six moderator variables, the following are reasonable conclusions from our analysis. At both the study and species levels, there is evidence that three moderators account for significant variance in effect size. These are sex of study animal, whether the trait studied is a secondary sexual trait or ordinary trait, and whether the study experimentally manipulates the symmetry of a trait or not. As we predicted, there are greater negative correlations between asymmetry and performance in sexual competition when males rather than females are competing, when secondary sexual trait rather than ordinary traits are studied, and when the study involves experimental manipulation of a trait. The sex difference in effect size is predicted because in the species studied, sexual selection is stronger in males than in females. Secondary sex traits are predicted to show larger effects than ordinary traits because the former are the focus of sexual selection and there is some evidence (see the introduction to this article) that sex traits show greater asymmetry. This magnification of asymmetry could provide the basis for mate choice and intrasexual contests based on asymmetry. Experimental studies of symmetry's relation to sexual competitiveness are expected to show larger effects if symmetry is causally related to mating success and attractiveness to the opposite sex. Observational studies are often confounded by variables other than symmetry that influence sexual competitiveness. These moderator variables are significant despite any diluting influence of nonsystematic variance in effect size generated by error in measurement of fluctuating asymmetry. One reason that experimental studies yield larger effects than observational ones may be that observational studies contain error in measuring fluctuating asymmetry.

Leung and Forbes's (1996) meta-analysis did not show any difference in effect size between sexually selected traits ($r = -0.27$) and ordinary traits ($r = -0.26$). However, this comparison in their analysis is not comparable to our comparison of sexually selected and ordinary traits because they looked at many fitness components (see above), whereas we examined only success pertaining to sexual selection.

We also predicted that the intensity of sexual selection in a species would relate to the effect size, with larger effects seen with smaller selection intensities. This was predicted under the reasoning that strong sexual selection will often eliminate the variation in asymmetry in the trait involved and also exhaust genetic variation on which sexual selection is based. Across studies, the prediction was statistically satisfied, but it did not hold across species. Results are, therefore, mixed at the two levels of analysis. The analysis across species is problematic because of small sample sizes in the groups compared in the test of a linear trend in effect size. The two lowest categories of sexual selection intensities have only six and seven species, respectively. Studies of additional species when available would allow further testing of the relationship between asymmetry and sexual selection intensity. Future work could potentially improve on our crude categorization of species by sexual selection intensity.

There is no evidence that our reasoning leading to the prediction that traits affecting mobility would show stronger effects than traits not affecting mobility was valid. Indeed, there is considerable evidence that the pattern is statistically significant in the direction opposite to that predicted at the analysis levels of both studies and species.

We had no prediction about whether higher taxonomic grouping would moderate effect size. The analysis of both studies and species revealed that the four higher taxa that have been studied differ significantly in effect size. Fish showed the larger effect sizes in the analyses of both studies and species, but this should be interpreted with caution because only six studies of four species of fish were available. Insects with 21 species may be the only reliable taxonomic group estimate. Birds were represented by 11 species and mammals by only five. It has been hypothesized that poikilotherms will show a stronger negative relationship between asymmetry and fitness than homeotherms (for a discussion, see Leung and Forbes 1996). However, a meta-analysis revealed essentially identical effect sizes for species of both groups (Leung and Forbes 1996). Our study supports the hypotheses that poikilotherms will show larger effects, but this is probably the result of sample size variation across taxa. The hypothesis that poikilotherms will show greater effects assumes that poikilotherms' developmental stability will be more sensitive to stresses than homeotherms'. This is apparently not the case (Leung and Forbes 1996).

Meta-analysis is a relatively new method in behavioral ecology, and there is some controversy surrounding it (Møller and Thornhill 1997*b*). The main criticisms raised against its use in behavioral ecology are the same ones

raised much earlier when meta-analysis was introduced in the human social and behavioral sciences. The criticisms appear to reflect misunderstanding of the assumptions and goals of meta-analysis (Rosenthal 1991; Cooper and Hedges 1994; Arnqvist and Wooster 1995; Møller and Thornhill 1997*b*). Meta-analysis is not a panacea. It is, however, the most objective way to summarize, in statistically meaningful ways, a body of research. As aptly put by Hunt (1997, p. 1), meta-analysis is "how science takes stock." It is likely that meta-analysis will sweep through behavioral ecology after the brief period of initial resistance that characterizes all new and important ideas or methods.

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