

significant difference in weighted effect size among mating system types ($Q_b = 6.26$, $df = 2$, $P = 0.043$), but none of the pairwise comparisons were significant. Effect sizes and associated statistics are summarized in Table 3b.

Weighted two-way ANOVA on effect size indicated that there were significant interactions between taxa and mating system ($Q = 16.53$, $df = 1$, $P < 0.001$), taxa and survival estimate type ($Q = 6.10$, $df = 1$, $P = 0.014$), and taxa and monitoring technique ($Q = 4.51$, $df = 1$, $P = 0.034$). Thus the individual effects of these factors could not be examined. There was no significant interaction between taxa and trait type or exclusion category. Taxa was a significant moderator variable when controlling for trait type ($Q = 16.24$, $df = 1$, $P < 0.001$) and exclusion category ($Q = 13.60$, $df = 1$, $P < 0.001$). Controlling for taxa, trait type ($Q = 14.18$, $df = 2$, $P < 0.001$) and exclusion category ($Q = 11.37$, $df = 1$, $P < 0.001$) also had significant effects.

SPECIES AS UNITS OF ANALYSIS

At the species level the weighted average effect size was $r = 0.13$ (95% confidence interval: 0.10–0.15), which is significantly greater than zero ($z = 8.94$, $P < 0.00001$). The mean effect size was significantly smaller for secondary sexual traits than for ordinary traits or "mating rate" ($Q_b = 15.85$, $df = 2$, $P < 0.001$). The latter did not differ significantly from each other. It was also significantly greater for behavioral than morphological secondary sexual traits ($Q_b = 20.51$, $df = 1$, $P < 0.001$). There was no difference in the effect size for species with free-ranging males compared to those with captive or radiotelemetry marked males ($Q_b = 1.99$, $df = 1$, $P = 0.15$). The effect size was significantly larger for species where the estimate was based on life span rather than a comparison of live and dead individuals ($Q_b = 15.32$, $df = 1$, $P < 0.001$), and for "strongly excluded" species compared to "included" or "weakly excluded" species ($Q_b = 18.08$, $df = 2$, $P < 0.001$). The mean effect size was significantly greater for insects/spiders than it was for birds ($Q_b = 25.65$, $df = 1$, $P < 0.001$). There was no significant difference in weighted effect size among mating system types ($Q_b = 4.46$, $df = 2$, $P = 0.15$). However, when we looked only at birds, effect size differed be-

tween mating system types ($Q_b = 13.70$, $df = 2$, $P = 0.001$). It was significantly lower for polygynous species ($r = 0.05$) than for socially monogamous ($r = 0.14$) or lekking species ($r = 0.28$; both pairwise comparisons, $P < 0.05$). The latter did not differ from each other. Effect sizes and associated statistics are summarized in Table 3c.

Weighted two-way ANOVA on effect size indicated that there was a significant interaction between taxa and mating system ($Q = 11.36$, $df = 1$, $P < 0.001$) and taxa and monitoring technique ($Q = 28.80$, $df = 1$, $P < 0.001$). Thus the individual effects of these factors could not be examined. There was no significant interaction between taxa and trait type, survival estimate type, or exclusion category. Taxa was a significant moderator variable when controlling for trait type ($Q = 10.28$, $df = 1$, $P < 0.001$), survival estimate type ($Q = 16.17$, $df = 1$, $P < 0.001$), and exclusion category ($Q = 6.09$, $df = 1$, $P = 0.014$). Controlling for taxa, only exclusion category ($Q = 6.09$, $df = 1$, $P = 0.014$) had a significant effect (trait type: $Q = 4.62$, $df = 2$, $P = 0.10$; survival estimate type: $Q = 0.49$, $df = 1$, $P > 0.50$). Considering the results of the weighted two-way ANOVAs at the study and species level, it therefore appears that most of the variation in effect size is determined by whether the animal is a bird or an insect/spider, rather than monitoring or survival estimation techniques, mating system, or trait type. Inclusion criteria may, however, have some influence on effect size.

ALTERNATIVE APPROACHES: MIXED-EFFECT MODELS AND UNWEIGHTED EFFECT SIZES

When mixed-effect models were used, the estimate of the weighted mean effect size was larger. It varied slightly depending on the moderator variable. The mean weighted effects at the sample, study, and species level were $r = 0.15$, 0.16 , and 0.21 ($z = 6.75$, 5.67 , and 5.31 ; all $P < 0.0001$). When examined at the species level, there was significant between-group heterogeneity for the moderator variables: morphological versus behavioral secondary sexual traits ($Q_b = 11.28$, $df = 1$, $P < 0.001$), survival estimate type ($Q_b = 7.17$, $df = 1$, $P = 0.007$), and taxon (bird versus insect/spider; $Q_b = 6.83$, $df = 1$, $P = 0.009$). There was no significant heterogeneity for trait type

($Q_b = 0.31$, $df = 2$, $P = 0.31$), mating system type ($Q_b = 1.07$, $df = 2$, $P = 0.59$), monitoring method ($Q_b = 0.21$, $df = 1$, $P = 0.65$), or exclusion/inclusion type ($Q_b = 0.64$, $df = 2$, $P = 0.73$). These findings broadly agree with those from the fixed-effect models. The only exceptions being that trait type and exclusion/inclusion type were significant moderator variables in fixed-effect models (Table 3c).

At present there is no method to perform meta-analysis in a phylogenetic framework. Some readers may be concerned that species with larger sample sizes, such as collared flycatchers (*F. albicollis*), contribute disproportionately to the weighted mean effect size. Each species can be given equal importance by simply calculating the average effect size without weighting for sample size per species. The unweighted average effect size is $r = 0.24$ (95% confidence interval: 0.19–0.29), which is significantly greater than zero ($z = 8.95$, $P < 0.0001$). If only species effect sizes based on "included" traits are used, the mean effect is $r = 0.21$ (95% confidence interval: 0.14–0.28), which is still significantly greater than zero ($z = 5.96$, $P < 0.0001$; Table 3d). The effect size was positive for 33 of the 40 species (Binomial test, $P < 0.001$) and 21 of 27 species using only the "included" trait criteria (Binomial test, $P < 0.01$). Thus, even with the highly statistically conservative approach of simply noting whether the mean relationship per species is positive or negative, there is still a statistically significant trend for a positive relationship between trait expression and survivorship.

MALE TRAIT-OFFSPRING VIABILITY VERSUS MALE TRAIT-OWN VIABILITY

Møller and Alatalo (1999) reported that the weighted average effect size for the relationship between the expression of preferred male traits and offspring viability was $r = 0.128$. The unweighted average effect size was $r = 0.218$. These values are very similar to those reported in the present study ($r = 0.125$ and 0.237 , respectively). Møller and Alatalo (1999) included seven species used in the present analysis. This allows us to test for differences in effect size using a paired approach. The difference (Cohen's q) was calculated as the effect size for male trait-offspring survival minus the effect size for male trait-own survival. Mean weighted

q was 0.022 (CI 95%: -0.040 – 0.022), which does not differ from zero ($z = 0.61$, $P = 0.27$). Giving equal weighting to each species (i.e., no weighting for sample size), the average effect sizes was $q = 0.161$ (CI 95%: 0.0070 – 0.315), which is significantly greater than zero ($z = 2.04$, $P = 0.02$). Thus the trend was for a greater effect size in the relationship between male trait and offspring viability than for the relationship between male trait size and his own adult viability. In five species the male trait-offspring viability effect size was greater, and in one case it was identical. There was also a strong trend towards a significant correlation between the two effect sizes ($r = 0.75$, $P = 0.075$), but the sample size is small and more data are need ($N = 7$ species).

PUBLICATION BIAS

There was no correlation between year of publication and effect size ($r = -0.011$, $N = 122$ samples, $P > 0.50$; $r = -0.135$, $N = 69$ studies, $P > 0.20$). This was true when birds and insects/spiders were analyzed separately at the study level (birds: $r = -0.06$, $N = 46$; insects: $r = -0.123$, $N = 19$). At the sample level, the mean weighted effect size did not differ significantly between unpublished ($r = 0.049$) and published samples ($r = 0.087$) ($Q_b = 1.99$, $df = 1$, $P = 0.158$; $N = 109$ published, 13 unpublished; Table 3d). At the study level of analysis, however, there was a difference in the mean weighted effect size for unpublished ($r = -0.03$) and published studies ($r = 0.118$) ($Q_b = 24.38$, $df = 1$, $P < 0.0001$; $N = 61$ published, 8 unpublished; Table 3d). In a mixed-effect model, however, the difference is far less significant ($Q_b = 4.41$, $df = 1$, $P = 0.04$).

The risk that publication or retrieval bias alters the conclusions from meta-analyses is perhaps best measured by calculating the fail-safe number. Rosenthal (1991) suggested that a fail-safe number five times larger than the sample size plus 10 indicates a robust result. Table 3 (a–d) shows that the fail-safe number is almost always robust. In particular, at the species level of analysis and using the most conservative trait inclusion criteria, the fail-safe number is 408 against a current sample of 27 species.

Inspection of the plots of sample sizes against effect sizes for samples, studies, and species all

suggest a funnel-shaped relationship (Figure 2). The variance in effect size for samples with a sample size below the median was significantly larger than the variance for samples with a sample size above the median (Variance ratio test: $F = 3.24$, $df = 60, 60$, $P < 0.001$). The same was true when analyzed at the level of studies ($F = 3.67$, $df = 34, 33$, $P < 0.001$) and at the level of species ($F = 6.06$, $df = 19, 19$, $P < 0.001$). There was also no evidence that the effect size was less normally distributed at smaller sample sizes (Figure 3).

Overall, the distribution of effect sizes was skewed towards more positive values. The distribution differed from normality at the sample and study level, but not at the species level (Kolomogorov-Smirnov tests, Lilliefors; $D_{max} = 0.145, 0.124$, and 0.136 ; $P < 0.001$, $P = 0.01$, and $P = 0.06$). This skew was due to a consistent trend for the relationship between sample size and effect size (r_{obs}) to show a negative relationship (Table 3a-d). This does not appear to be a consequence of combining effect sizes from studies collected from different taxa or using different criteria because r_{obs} is negative irrespective of the subgroup examined. We carried out an ANCOVA with trait type, survival estimate type, monitoring type, mating system, taxon (bird or insect/spider), and exclusion type as factors and sample size as the covariate. There was a significant relationship between sample size and effect size at both the sample ($F = 7.025$, $df = 1, 107$, $P = 0.009$) and study level of analysis ($F = 5.903$, $df = 1, 54$, $P = 0.018$). The relationship was marginally significant at the species level ($F = 4.01$, $df = 1, 25$, $P = 0.056$). These data therefore indicate that studies with smaller sample sizes are more likely to report a positive effect size.

Differences in effect size between groups were not related to differences in r_{obs} (cf. Palmer 1999). The only contrasts for which the differ-

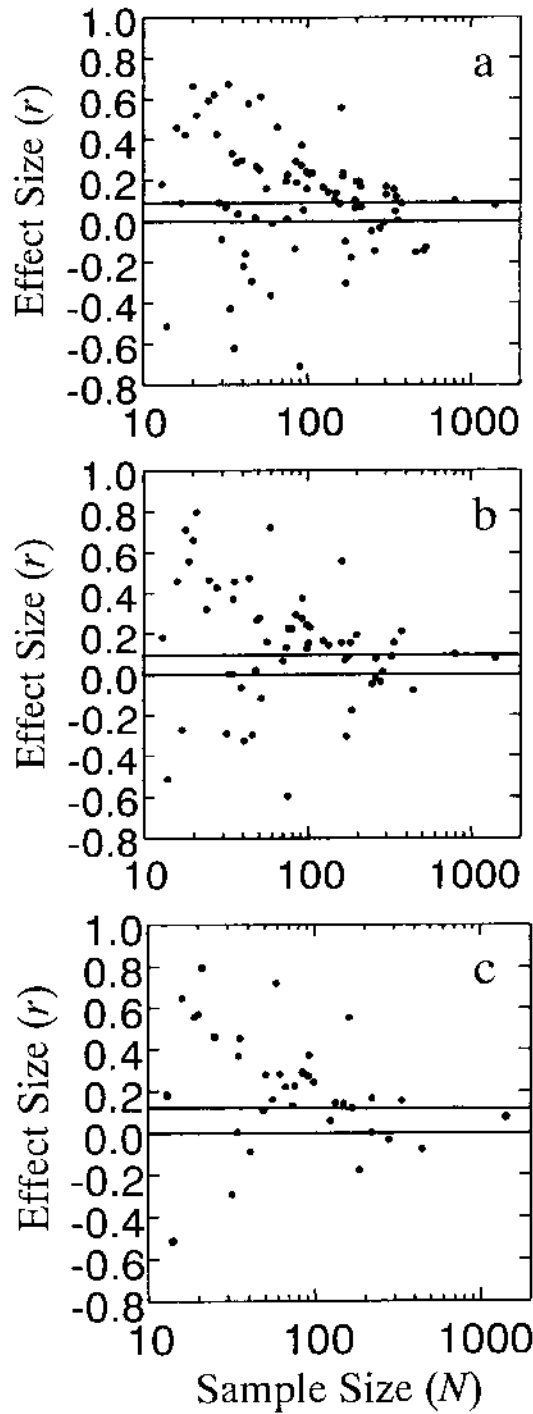


FIGURE 2. SAMPLE SIZE AND EFFECT SIZE.

The relationship between sample size (N) and effect size (r) for: (a) samples, (b) studies, and (c) species. The lower horizontal line is for a mean effect of zero. The upper line is for the observed weighted mean effect size.

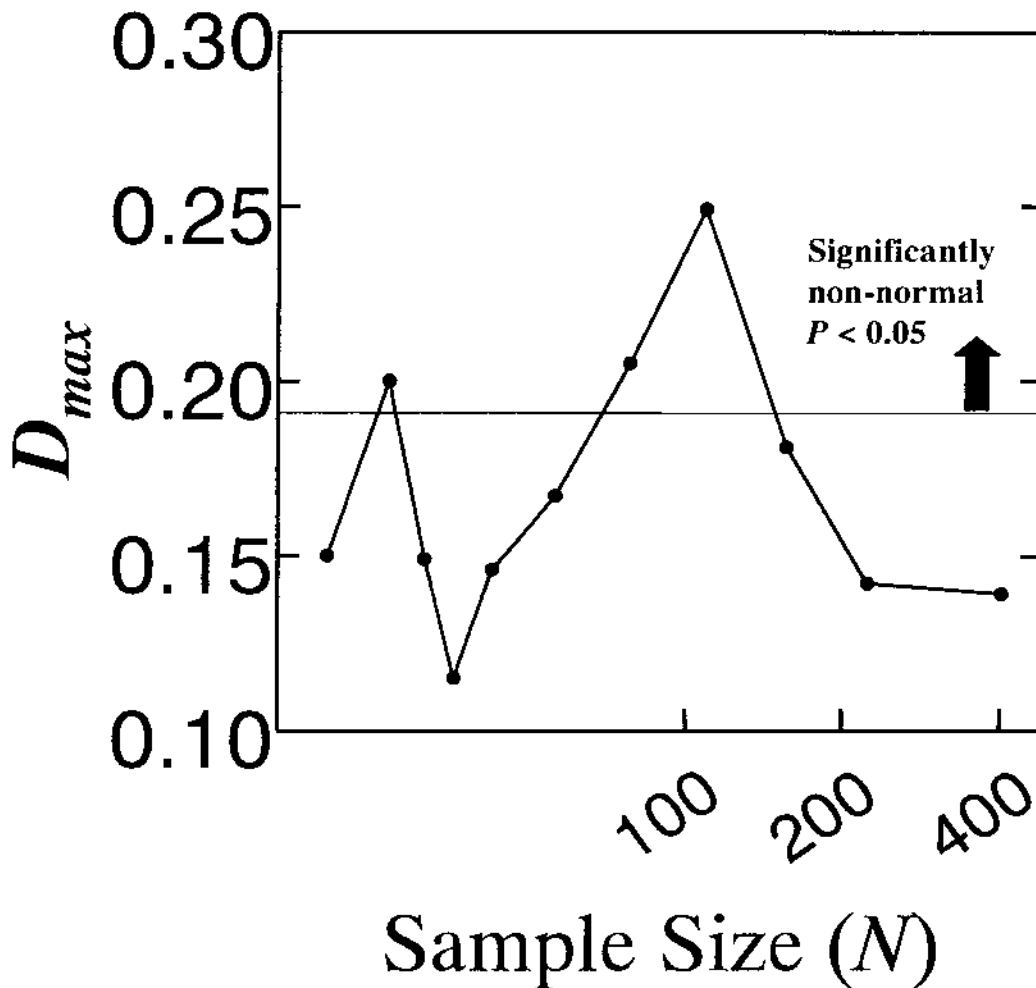


FIGURE 3. NORMALITY AND SAMPLE SIZE.

Departures from normality as a function of sample size for the 122 samples. D_{max} is from a Kolomogorov-Smirnov test where $N = 20$.

ence in r_{obs} , approached significance were between "mating rate" as a trait and ordinary or secondary sexual traits at the sample and study level (both $z = 1.89$, $P = 0.06$). There was no difference in r_{obs} for any other contrasts between groups with significantly different effect sizes (all $P > 0.12$). It is also worth noting that r_{obs} did not differ between published and unpublished work at the study or sample level of analysis. In fact the trend was towards more negative r_{obs} for unpublished work (samples: $r_{obs} = -0.657$; studies: $r_{obs} = -0.429$). This suggests that negative values of r_{obs} for published

studies may not reflect the failure of authors to publish negative effect sizes when sample sizes are small.

What effect do sample size, trait inclusion criteria, and level of analysis have on our main conclusion that there is a positive effect size? To test this we looked *only* at the species level of analysis, excluded species with sample sizes smaller than the median ($N_{average} > 61$ males), and used the conservative approach of only examining the direction of the effect. The effect size was positive for 17 of 20 species, and for 11 of 13 species when the effect size was

TABLE 4

Additional studies with data on adult mortality that were not included in the meta-analysis

Species	Trait	N	r	Remarks	Reference
<i>Sepsis cynipsea</i>	Size	34 (a)	0.094	Genetic correlation with adult longevity	1
<i>Scathophaga stercoraria</i>	Size	997	-0.12	Size vs. age as determined by wing damage	2
<i>Drosophila buzzatii</i>	Size	230	0.249	Size vs. age as determined by testes stage	3
<i>D. buzzatii</i>	Size	151	0.138	Size vs. age as determined by testes stage	3
<i>D. buzzatii</i>	Size	281	0.069	Size vs. age as determined by testes stage	3
<i>D. buzzatii</i>	Size	82	-0.048	Size vs. age as determined by testes stage	3
<i>Drosophila melanogaster</i>	Size	160 (b)	0.075	Phenotypic correlation with longevity	4
<i>D. melanogaster</i>	Size	160 (b)	0.234	Genetic correlation with longevity	4
<i>Pica pica</i>	Quality	53	Positive	Short vs. long-lived. Former have lower quality territories, but there is a "male effect" on breeding success independent of territory	5
<i>Geospiza fortis</i>	Size	634 (c)	Positive	1976-1977 ($I = 0.43$ to 0.74) (d)	6
<i>G. fortis</i>	Size	556 (c)	Negative	1984-1986 ($I = -0.08$ to -0.17) (d)	6

References: 1) Mühlhäuser 1998. 2) Burkhardt 1999. 3) Santos et al. 1992. 4) Hughes 1995. 5) Birkhead and Goodburn 1989 (Table 11.2); Goodburn 1989. 6) Grant and Grant 1995.

Note: Effect size is the product-moment correlation r . Unless otherwise stated, sample size refers to the number of males measured. (a) full-sib families; (b) genotype-crosses; (c) males and females combined; (d) I = intensity of selection.

only based on "included" traits (Binomial tests, both $P < 0.05$; see Figure 3c). Our main conclusion therefore seems to be very robust.

GENERAL DISCUSSION

There has long been debate as to the relative importance of Fisherian and viability indicator ("good gene") processes in the evolution of elaborate male traits. There is general evidence that sexually attractive traits are costly due to increased predation risk, higher rates of parasitism, and greater physiological costs (reviews: Andersson 1994; Zuk and Kolluru 1998). Surprisingly, the very simple prediction of pure Fisherian models—males with more elaborate traits will show reduced longevity—has rarely been directly tested (e.g., Kotiaho et al. 1996). Most evidence comes from acoustic playback experiments but, as already noted, these studies do not control for other modifications in male behavior or condition that may alter the cost of being more attractive (e.g., Hedrick 2000). Here we show that the average relationship between traits correlated with male mating success and traits correlated with male survivorship is positive. The mean effect was significantly positive, and has similar values at all three levels of analyses. For individual samples the mean weighted effect (r) was 0.08, for studies 0.10, and for species it was 0.13. The estimate was even higher when mixed-effect

models or unweighted effect size was calculated at the species level ($r = 0.21$ and 0.24 , respectively). If the traits we studied are generally costly, then their expression *must* be correlated with a hidden third variable that increases viability (e.g., van Noordwijk and de Jong 1986; Zeh and Zeh 1988).

Since purely attractive Fisherian traits are predicted to be relatively more important in species with highly polygamous mating systems, we compared effect sizes among monogamous, weakly polygynous, and lekking species. For birds, the effect size was most positive for lekking species, less so for socially monogamous species, and significantly weaker for polygynous species. Thus the expected linear trend was not observed. This may be due to large amounts of "hidden" sexual selection in socially monogamous species. Extra-pair copulations can greatly increase the actual variance in reproductive success among males and may lead to strong selection for secondary sexual characters (review: Møller and Ninni 1998). Because the correlation between trait size and survival was strongest for lekking species, this argues against purely attractive Fisherian traits predominating, even when male care is absent. Interestingly, Gontard-Danek and Møller (1999) reported that sexual selection on male secondary sexual traits is signifi-

cantly weaker in polygynous birds compared to socially monogamous or lekking birds.

There are several reasons to be cautious before discounting the prevalence of pure Fisherian traits in nature. First, we have only examined adult survival. The survival costs of sexual traits may mainly arise during earlier stages of a male's life (Owens and Bennett 1994). Juveniles that died before they developed the trait were excluded from our analysis. This could lead to an overestimate of the positive nature of the relationship between trait size and total viability, if males that died during trait development were more likely to have developed larger ornaments. There are, to our knowledge, only a few studies that show this effect (but see Brooks 2000). Most evidence comes from artificial selection or examination of genetic correlations in insects, where larger individuals suffer greater mortality due to prolonged larval development time (e.g., Wilkinson 1987; Partridge and Fowler 1993; Hughes 1995; Bertran et al. 1998; see Arnqvist 1994 for an unusual example). Price and Grant (1984) argued that selection favoring large body size in adult Darwin's finches *Geospiza fortis* due to natural and sexual selection is countered by selection for small body size during the juvenile stage. Unfortunately, they were unable to sex juveniles, so the importance of this effect for males cannot be determined. There seems to be a contradiction between the positive effect of sire trait size on offspring viability reported by Møller and Alatalo (1999) (assuming sexual trait size is heritable) and evidence from artificial selection studies that selection for larger traits increases juvenile mortality (e.g., Partridge and Fowler 1993). Clearly, more research is needed on mortality costs associated with the development of preferred sexual traits, as this may reveal the opposite relationship to that documented for adults (e.g., Clutton-Brock et al. 1985).

Second, survival estimates are not easy to obtain under field conditions because recapture probability and survival may be confounded (Lebreton et al. 1992). It is possible that recapture probabilities are directly related to male condition. If so, we should expect that our mean estimates of effect sizes represent underestimates of the true underlying effects. We can address this potential for bias in two

different ways. First, there will be no bias of this kind under laboratory conditions. Hence studies such as Mappes et al. (1996) are unbiased estimates. Similarly, studies of individuals with radiotransmitters provide unbiased estimates (e.g., Grahn 1993). We found no difference in weighted effect size between telemetry or laboratory studies and those of free-ranging animals. Second, the relationship between the expression of secondary sexual characters and survival has usually been determined using survival estimated as recapture probability rather than survival based on more sophisticated capture-mark-recapture models (review: Lebreton et al. 1992). For example, Møller (1991) estimated the relationship between tail length and survival in male barn swallows *Hirundo rustica* based on recaptures; however, a subsequent investigation based on mark-capture-recapture analyses according to modern techniques gave very similar results (Møller and Szep, unpublished data). This particular study may not be representative though, because the capture probability exceeded 95% in any given year. Third, another methodological problem could arise if researchers are more likely to examine patterns of mortality following extreme climatic events (e.g., Brown and Brown 1998, 1999) that yield results that differ significantly from the median effect. Longer-term studies suggest that the direction of selection on a trait may fluctuate through time (Gibbs and Grant 1987). Alternatively, one could argue that extreme events have important evolutionary effects because high mortality creates population bottlenecks.

Third, there was little data on conspicuous acoustic and chemical signals that are known to attract predators and parasites (review: Zuk and Kolluru 1998). These long-range attractant traits may be more likely to show the negative relationship predicted for Fisherian traits between attractiveness and mortality. On the other hand, no sexually selected traits associated with copulatory and postcopulatory courtship are included. It seems unlikely that expression of these sexually selected traits is strongly associated with increased mortality (Eberhard 1996; Jennions and Petrie 2000).

The observed positive relationship we report is consistent with sexual traits acting as honest advertisements of male genetic quality

as predicted by good-gene models of sexual selection. It is equally consistent with secondary sexual traits acting solely as advertisements of male phenotypic quality or parental ability as predicted by direct benefit models (Andersson 1994). Verbal models have predicted that older males will be of higher quality and should thus be preferred by females (Trivers 1972; Manning 1989; review: Jones et al. 2000). Kokko (1998), while confirming this is possible, has also shown that counterexamples can be constructed in which lower quality males live longer because they invest more in survival. If we start from the assumption that males with larger sexual traits are of better quality (at least in terms of condition), then these verbal models are supported. This suggests that the conditions under which higher quality males invest disproportionately more into mating than survival are limited. This is simply a restatement of Grether's 1997 observation that higher quality males do not "overinvest" in mating that leads to reduced survivorship.

Alternative explanations for the positive relationship must also be considered. First, the inclusion of individuals that differ in age may tend to generate a positive relationship if trait expression increases with age and the likelihood of survival increases with age. In general, survival prospects do not appear to differ appreciably among younger adults (e.g., similar mortality rates for one versus two-year old passerines: see chapters in Clutton-Brock 1988). In fact, studies of age dependent expression of secondary sexual characters suggest that there is an effect of senescence, with older males with larger sized secondary sexual characters having lower survival prospects (e.g., Clutton-Brock et al. 1982; Møller and de Lope 1999). There is a trend for survival probability to decrease with increasing age (e.g., Brown and Brown 1998). Failing to correct for variation in age is a source of variation that may therefore reduce (rather than increase) any overall positive trend between trait expression and survival prospects.

Second, the source of the underlying variation in male viability is usually unknown. It could be purely environmental in origin, although studies usually show a heritable component to life-history traits (Houle 1992, 1998). Males with greater access to resources may de-

velop larger sexual traits. The positive effect of food availability on male courtship and ornament size has been shown in many different studies (e.g., Jennions and Backwell 1998; Wagner and Hoback 1999). As such, the positive relationship we report, while consistent with, should not be interpreted as strong evidence for the importance of "good viability genes" processes in sexual selection. Even so, it leads us to conclude that males do not invest a fixed amount into sexually selected traits irrespective of their underlying viability. Differential investment in relation to male quality is the first requirement of any handicap model of signaling, be it an advert of direct or genetic benefits (Grafen 1990). Third, we have not distinguished between traits that influence mating success because they are beneficial during male-male competition versus female choice. Traits that evolve through female choice may show a different effect size to those that evolve through male-male combat. There is currently no consensus as to whether male-male competition and female choice usually act in the same or opposite directions (e.g., Moore and Moore 1999; reviews: Berglund et al. 1996; Qvarnström and Forsgren 1998).

MAGNITUDE OF THE EFFECT

The mean effect size for the relationship between the expression of traits associated with male mating rate and survival for analysis at the species level was $r = 0.13$, accounting for 1.7% of variance in survival. In a single study, to detect a significant relationship between trait expression and adult survival at the 0.05 level with 80% probability, a sample size of over 800 males is required ($r = 0.10$, Cohen 1988). Most future studies will therefore fail to detect a significant relationship (only 2 of 122 samples in the current analysis had $N > 800$). Failure to reject the null hypothesis should therefore be viewed through the lens of statistical power analysis. We urge authors to interpret nonsignificant results with far greater caution.

Our estimates of the weighted effect size were almost always highly significant but, by definition, the effect strength was small (Murphy and Myers 1998). But what is the biological importance of our finding? First, in evolutionary studies, unlike social studies or medicine, it

is rarely important whether or not an effect is sufficiently strong to have major predictive powers. A trait that only has a very small selective advantage can, over evolutionary time scales, greatly increase in frequency due to the slow but steady cumulative effect of directional selection in each successive generation. Second, as noted, measurement error of survivorship is high and many of our measures of survival were over fairly short time periods. Given the high degree of statistical noise this introduces to the relationship, the true effect size may be larger than the estimated one. Third, measured effect sizes in evolutionary behavioral studies are usually small. At the species level of analysis, the weighted mean effect sizes (r) were: -0.24 for asymmetry versus mating success (Thornhill et al. 1999); -0.22 for asymmetry versus measures of sexual selection (Thornhill and Møller 1998); 0.14 for size versus measures of sexual selection (Thornhill and Møller 1998); 0.31 for size of secondary sexual characters versus mating success (Gontard-Danck and Møller 1999); 0.12 for male traits and offspring survival (Møller and Alatalo 1999); and 0.16 , -0.34 , -0.24 for the relationships between asymmetry and growth, fecundity, and survival, respectively (Møller 1999). At the study level of analysis, the average weighted mean effect sizes (direction removed) was 0.24 for relationships between mating success and eight behavioral or morphological traits in lekking males (Fiske et al. 1998). The maximum effect reported in a meta-analysis of correlates of paternity in birds was 0.34 (Møller and Ninni 1998). Effect sizes larger than a "medium strength" of $r = 0.30$ are therefore rare in behavioral ecology, even for widely accepted relationships like that between sexually selected traits and mating success. The reasons for such relatively low values may be related to the high degree of noise and random variation in biological relationships. For example, even though females may have strong mate preferences, these may not be realized because preferred males are unavailable in that particular site or year, or because other females have already attached themselves to these males. The considerable heterogeneity in effect sizes, even when moderator variables are used to partition the data, may partially reflect stochastic events as well as underlying

differences among species or be due to data being collected using different techniques.

Two direct comparisons of the effect size we obtained can be made. The effect size for the relationship between asymmetry and survival was -0.25 (Møller 1999). Thus, trait asymmetry is a stronger predictor of survival than the size or display rate of the traits in the present study. This translates to explaining 4.5% more of the variance in survival (6.2 vs. 1.7%). Surprisingly, there was no difference in the mean effect size for the relationship between male trait size and adult survival (this study) and that between the same male traits and offspring survival (Møller and Alatalo 1999). If anything, the latter was larger. We had expected that the former would be greater. The difference between the two should reflect the positive effect of environmentally induced variation in condition dependence on both survival and trait expression. The positive correlation of $r = 0.12$ reported by Møller and Alatalo (1999) may therefore be an overestimate of the genetic contribution of males to offspring viability. Maternal effects, including positive assortative mating with regards to genetic quality, nongenetic parental effects such as differential investment, and common environmental effects for fathers and offspring may have contributed to the net positive relationship. However, the magnitude of the good gene effect on offspring survival can also be estimated if we assume a relationship between the heritability of fitness and secondary sexual characters, and the magnitude of direct fitness benefits as suggested by Kirkpatrick and Barton (1997). Using estimates of the heritability of fitness from Burt (1995), of secondary sexual characters from Pomiankowski and Møller (1995), and the magnitude of direct fitness benefits from Kirkpatrick and Møller (unpublished study), the "good genes effect" estimate is very close to that obtained by Møller and Alatalo (1999). This suggests that there is no serious bias in the available data, or that the biases act in ways that cancel out. If the value of $r = 0.12$ is approximately correct, then the estimated effect in the present study is probably smaller than the true effect.

One general finding across levels of analysis and controlling for moderator variables was that effect size was larger for insects and spi-

ders than for birds. Zeh and Zeh (personal communication) have suggested one explanation: coefficients of variation in sexually selected traits are usually lower in birds than they are in arthropods. It is more difficult to detect a relationship between traits when variation is low.

Finally, the positive relationship between trait size and survival has implications for those studying life-history evolution. Schluter et al. (1991) noted that conflicting selection pressures on major life-history traits (antagonistic pleiotropy) are common. As such, studies of opposing selection provide information about the underlying mechanisms responsible. In this case, possible differences in the relationship between adult and juvenile mortality and trait expression warrant further investigation. These studies also noted that the identification of opposing forces of selection can be complicated by confounding variables, in particular differences in nutrition among individuals. Our findings confirm that this may generally be the case across a range of taxa and traits, emphasizing the importance of experimental manipulation to accurately determine the direct effect of selection on a trait of interest (e.g., Møller and de Lope 1994). Indeed, sexual display can be treated as just another life-history trait (Höglund and Sheldon 1998). While vigorously debated, there is clearly great value in experimental manipulation of life-history traits (in addition to calculation of genetic correlation between traits or artificial selection experiments) to promote understanding of the mechanistic bases of the trade-offs that determine life-history evolution (Sinervo and Svensson 1998).

PUBLICATION BIAS

Our conclusions could be erroneous if the observed studies are a biased sample of those conducted. We assessed this problem in several ways. First, we determined fail-safe numbers, which are the standard way of analyzing publication bias (Rosenthal 1991; Gurevitch and Hedges 1999). This represents the number of studies with a mean effect of zero needed to nullify the reported effect (Rosenthal 1991). We found large fail-safe numbers for analysis at the study and species level of 2,288 and 1,200. The fail-safe number was gen-

erally very robust, no matter how the data were divided up or which studies were included or excluded. Second, the variance in effect size estimates decreased as sample size increased. Third, there was no decrease in the normality of the distribution of effect size as sample size decreased. Fourth, we found a significant negative relationship between sample size and effect size. Thus studies with smaller sample sizes yielded larger, more positive effect sizes. There is a general trend in recent evolutionary meta-analyses that r_{bias} is in the direction of smaller studies that produce more extreme values in the same direction as the sign of the weighted mean effect size (e.g., Møller and Thornhill 1997 [sample: $r_{bias} = -0.146$, $N = 34$, $P > 0.50$]; Møller 1999 [samples for growth: $r_{bias} = 0.600$, $N = 11$, $P < 0.10$; fecundity: $r_{bias} = 0.405$, $N = 21$, $P < 0.10$; survival: $r_{bias} = 0.301$, $N = 29$, $P < 0.20$; Palmer 1999 [$P < 0.001$]; Gontard-Danek and Møller 1999 [$P = 0.007$]; Møller et al. 1999 [$r_{bias} = 0.308$, $N = 69$, $P = 0.01$]). In several cases this may be due to uncontrolled moderator variables that influence effect size, in particular whether the work was observational or experimental (compare Palmer 1999 with Thornhill et al. 1999). In the present study, however, the bias remained even when we controlled for six moderator variables. We do not know why this trend was observed. Gurevitch and Hedges (1999:1147–1148) concluded that a correlation between sample and effect size may reflect rational experimental design rather than publication bias. They recommend the fail-safe number as a more appropriate test than using r_{bias} .

There is no obvious theoretical or sociological reason for a publication bias. Data on survival is generally scarce and of interest whatever the finding. Furthermore, within sexual selection studies, there are theoretical reasons to expect either a negative or a positive relationship, depending on whether a trait evolves by Fisherian or honest indicator processes. Findings should be equally publishable regardless of the direction of the effect. Also, several studies were conducted with the main intention of describing how different components of fitness contribute to lifetime reproductive success (Clutton-Brock 1988; Newton 1989). It is hard to see why some descriptions would be less publishable than others. It is also

relevant to note that r_{bias} was negative for unpublished work, suggesting that publication bias alone cannot explain this particular result. Another potential problem is that studies that show a positive relationship may have been more frequently cited of late, and we were more likely to retrieve them for this meta-analysis. Other researchers have reported a year effect (e.g., Gontard-Danek and Møller 1999; Simmons et al. 1999), although temporal changes in research techniques or sampling effort should always be considered (Møller, unpublished data). There was, however, no evidence of a chronological change in effect size estimates, even when data were analyzed separately for birds and insects.

In conclusion, we found a small but highly significant positive relationship (accounting for $\pm 2\%$ of the variance) between the expression of sexually selected traits and male survival. Variation in this relationship was mainly due to differences between birds and insects/spiders.

There was also a significant influence of sample size. As Gontard-Danek and Møller (1999) pointed out, however, it is only through meta-analysis and the examination of publication bias that we can establish the true nature of the relationship between variables in nature.

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