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SEXUALLY SELECTED TRAITS AND ADULT SURVIVAL: A META-ANALYSIS

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ABSTRACT

Traits correlated with male mating success are likely to be subject to sexual selection. Sexually selected characters are thought to be costly to develop and maintain. If males do not vary their investment in sexual traits in relation to their ability to bear the costs, there should be a negative relationship between male longevity or survival and the expression of sexual traits. In particular, a negative relationship is predicted by pure Fisherian models for the evolution of sexual ornaments. The same should also be true for traits that evolve via pleiotropy (e.g., due to sensory exploitation or bias) with no subsequent evolution of condition dependent modification. We collected information on the relationship between traits correlated with male mating rate and estimates of adult male survivorship or life span. In total we obtained 122 samples from 69 studies of 40 species of bird, spider, insect, and fish. In a meta-analysis we calculated the average sample size weighted correlation between trait expression and adult survival. Analyses at the level of samples, studies,

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and species revealed significant positive relationships (r = 0.08, 0.10, and 0.13, respectively; all P < 0.001). The unweighted correlation at the species level was r = 0.24. In general, males with larger ornaments or weapons, greater body size, or higher rates of courtship showed greater survivorship or longevity. This finding is inconsistent with pure Fisherian models or other models that do not incorporate condition or quality dependent trait expression. It suggests that male investment in sexually selected traits is not fixed but varies in relation to the ability to pay the underlying costs of expressing these characters. Hence, many secondary sexual characters are likely to be condition dependent in their expression.

INTRODUCTION

SEXUAL SELECTION on traits arises when certain phenotypic characters lead to differences in reproductive success among individuals that compete for access to mates and, ultimately, gametes (Andersson 1994). Comparative evidence suggests that sexually selected traits are costly to produce or maintain (Clutton-Brock et al. 1985; Promislow 1992; Promislow et al. 1992, 1994; but see Owens and Bennett 1994). There are at least three explanations for variation among males in the phenotypic expression of sexually selected characters. First, there may be a direct trade-off between sexual and natural selection (Selander 1965). For example, investing in traits that increase mating success by influencing female choice may be exactly balanced by decreased survivorship and reduced male longevity. Male longevity may decline due to greater attraction of predators and parasites (e.g., Gray and Cade 1999; review: Zuk and Kolluru 1998), or the high energetic costs of sexual displays (e.g., Vehrencamp et al. 1989). This attractiveness-mortality balance is exemplified by the line of equilibrium in models of Fisherian runaway (Lande 1981), and it is an example of antagonistic pleiotropy (e.g., Bertran et al. 1998; Brooks 2000). For pure Fisherian traits that are attractive for entirely arbitrary reasons, males with larger traits pay greater costs and should live for shorter periods of time.

The second explanation for phenotypic variation among males that express sexually selected traits may be that these traits are condition dependent, with males varying their investment in relation to their ability to bear the costs of producing or maintaining the trait (Zahavi 1975, 1977; Andersson 1986; Iwasa and Pomiankowski 1991). Variation in the ability to bear costs may be purely environmental in origin, or may reflect underlying differences in male genetic quality. The convention is to speak of "condition" as the factor that moderates the costs of signaling. A range of subsidiary models can then be invoked to explain the maintenance of heritable variation in male condition (review: Jennions and Petrie 2000). Models where males signal their "genetic viability" assume that, on average, males of higher quality are more likely to be in better condition. In handicap models in which quality is signaled, the marginal costs of an increase in investment at a given level of signaling must be greater for lower quality males (Grafen 1990). Consequently, individual optimization of trait expression leads to higher quality males investing more heavily in sexual traits (Figure 1).

Males with larger sexual traits need not pay higher absolute costs because the expression of these traits is correlated with their ability to bear costs (van Noordwijk and de Jong 1986; Zeh and Zeh 1988; Figure 1). Researchers often assume that there will be a positive relationship between trait expression and male longevity when the trait is an honest advertisement of male quality (reviews: Price et al. 1993; Johnstone 1995; Höglund and Sheldon 1998). This is not necessarily the case; positive, negative, or neutral relationships are all possible (Grafen 1990). Empirically, however, these relationships are not equally plausible, as negative relationships may require extreme life histories (Kokko 1998). Several authors have argued that a positive relationship is most likely to occur when sexual traits are condition dependent (e.g., Zeh and Zeh 1988).

The third explanation for phenotypic variation in sexually selected traits is that the benefit of any single sexual trait may vary in relation to the expression of other sexually selected traits, leading to either positive or negative relationships between these traits and therefore generating among-male variation for any given trait (e.g., Reynolds 1993; Jennions and Backwell 1998). Møller and Pomiankowski (1993) have argued that multiple sexual signals can
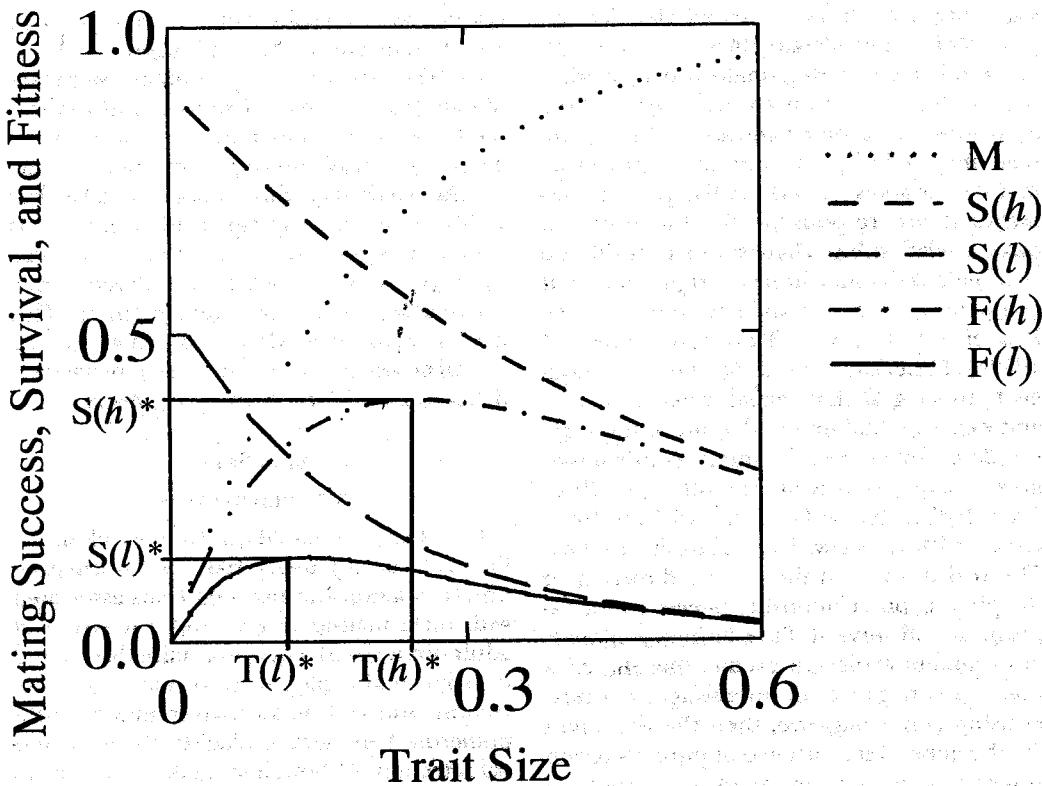
FIGURE 1. MALE QUALITY, SEXUAL TRAIT SIZE, AND SURVIVORSHIP

The following graph is redrawn from Zeh and Zeh (1988). The terms h and l in parentheses designate high and low quality individuals. The mating rate curve (M) is the same regardless of quality. It depends only on level of investment in the sexually selected trait (T). The cost of the trait is expressed in terms of survival (S): higher quality individuals pay a smaller absolute cost and show a smaller marginal decrease in survivorship for a given change in trait investment. The fitness curves (F) for the two male types are shown and the optimal investment indicated by asterisks. At the optima, high quality males have larger sexual traits (T(h) > T(l)), as well as higher survivorship (S(h) > S(l)), than low quality males. Details of the equations for the curves can be found in Zeh and Zeh (1988). Graphs that show life histories where S(h) < S(l) are presented in Kokko (1998).

provide multiple messages, be redundant to a certain extent, or act as unreliable signals that are no longer functional. If multiple signals are condition dependent expressions of the same underlying quality, then we should expect a positive relationship between their variation. Hence, this third explanation only applies when there are multiple messages, unreliable signals, and/or females have multiple preferences for sexual traits (e.g., Brooks and Couldridge 1999). Apparent exceptions to this conclusion could arise if data are pooled when female preference functions or the efficacies

of different signals vary temporally or spatially (review: Jennions and Petrie 1997). Males identical in quality should invest disproportionately in those signals with the greatest efficacy in the contingent circumstances.

The debate as to whether a sexually selected trait is Fisherian, the pleiotropic effect of sensory biases or species recognition, or an honest advertisement of male parental ability or genetic viability is rarely resolved. A recent meta-analysis supports the claim that sexual traits indicate genetic variation in male viability because the offspring sired by males with more

elaborate traits show increased viability (review: Møller and Alatalo 1999). The strength of the effect is, however, small on an ecological time scale, but not on an evolutionary time scale. Few studies have been able to fully eliminate the possibility that confounding environmental variables or differential parental investment are responsible for the observed positive relationship. There is also new evidence that male traits may honestly signal parental competence (e.g., Östlund and Ahnesjö 1998; Rasa et al. 1998; review: Møller and Thornhill 1998b). Fisherian and viability indicator models both suggest that sexual traits are costly, and experimental manipulations of the magnitude of sexual traits generally confirm that greater expression is more costly (e.g., Ryan 1985; Møller 1989a; Grether and Grey 1996; Grether 1997; review: Zuk and Kolluru 1998). The real distinction then is the direction of the phenotypic relationship between trait expression and survival. Pure Fisherian models of ornament evolution predict that the relationship is negative. If, on average, the relationship is not negative, then the argument for the general importance of pure Fisherian runaway is greatly weakened. Conversely, if the average relationship is positive, this argues that more viable males (be this due to genetic or environmental variation) invest more in sexual advertisement, but the reproductive rewards of greater investment do not increase sufficiently rapidly to create "overinvestment," nor do they show increased mortality of more viable males (e.g., Møller and de Lope 1994). This raises the question for theoreticians as to why this should be the case (Grether 1997). The answer may be found in the fact that longevity is generally the best predictor of lifetime reproductive success (Clutton-Brock 1988). Mating rates of more attractive males may only rarely be sufficiently high to compensate for a shorter life span.

Several individual studies have reported that sexually selected ornaments show a significant positive correlation with male longevity (e.g., Grether 1997), while others have reported a significant negative relationship (e.g., Macias Garcia et al. 1994). Single studies cannot resolve the issue of general patterns in nature. Here we use meta-analysis to determine the wider pattern. Meta-analysis is an increasingly popular way to resolve issues in ecological and evolutionary studies (review: Arnqvist and Wooster 1995). It provides a quantitative summary of data from a range of sources and reduces the biases that can emerge from simple vote-counting procedures or purely descriptive accounts of a field of study (Cooper and Hedges 1994). Vote counting may lead to erroneous conclusions because rejection of the alternative hypothesis is generally considered to represent acceptance of the null hypothesis. This is a very weak claim when studies have low statistical power, as is often the case in behavioral fields (Cohen 1988; Murphy and Myors 1998).

DATA SETS

INCLUDED STUDIES

Our data set is based on: (i) a search of the literature until January 1999 for information on the relationship between traits associated with male mating success and a measure of adult survival; (ii) a questionnaire distributed to behavioral ecologists who study sexual selection; and (iii) email correspondence with numerous behavioral ecologists who study sexual selection. Although we make no claims to have included all relevant studies, we believe that there was no bias in our method of data collection and that we made reasonable attempts to locate unpublished work.

For 99 of 122 samples, the male trait has been shown to be significantly correlated with male mating success ($P < 0.05$), and/or has been experimentally manipulated to show a direct effect on mating success or attractiveness in at least one study (Table 1). This does not mean that all the studies have found a significant effect of the trait on mating success (e.g., spur length in *Phasianus colchinus*, see Mateos and Carranza 1996). We also included 5 samples that examined spur length in *Meleagris gallopavo* or wattles in *P. colchicus*; these are dimorphic, secondary sexual characters that have probably evolved via sexual selection, even if there is currently weak selection on them. Finally, we included measures of "attractiveness," "mating rate" (e.g., matings/year or courtship), and "reproductive rate" (e.g., offspring/year) as a substitute measure of trait expression for 13 species (18 samples). Short-term variation in mating rate is likely to reflect a difference in access to mates due to sexual

selection; chance events can also generate variation in mating rates, however (Sutherland 1985). We assumed that males with higher mating or reproductive rates possessed traits that increased their sexual attractiveness or access to higher quality females. We excluded one species of damselfly where the distribution of daily mating rate did not differ from that expected by chance (Fincke 1986, 1988). In five of the 13 species, variation in mating rate has been clearly documented to occur via female choice or male-male competition (*Phasianus colchinus, Tetrao tetrix, Cervus elaphus, Mirounga anguistora, Poecilia reticulata*). In six species, biased adult sex-ratios (*Anthus pratensis*), the presence of floater males but not females (*Melospiza melodia*), a correlation between within-nest paternity and male phenotype (*Parus caeruleus*), the repeatability of male mating success across sites (*Erythemis simplicicollis*), a correlation between male traits and fighting success (*Tetraopes tetraopthalmus*), and a correlation between male traits and daily mating rate (*Sympetrum danae*) all suggest that sexual selection has a likely role in mating success. In two species, *Alcedo atthis* and *Passerina cyanea*, there is no direct evidence for sexual selection on male traits; however, high levels of extra-pair paternity in *P. cyanea* (Westneat 1990) are suggestive of female choice. On average, within-nest paternity in birds is positively related to the size of the resident male's secondary sexual traits (Møller and Ninni 1998). We tested the outcome of meta-analysis based on different traits in an analysis of heterogeneity with inclusion criteria as a moderator variable.

The estimates of adult survival rates varied among studies. In some cases they were estimates of reproductive life span or "days alive" as an adult. In others, they were simply information on whether or not an individual survived between two samples (e.g., to the next breeding season) or was alive at the end of the study/experiment. A comparison of trait size in live and dead males cannot be used to estimate the intensity of selection on the trait, unless the sample sizes for the two classes represent the natural frequency of these discrete fitness states (review: Blanckenhorn et al. 1999). Whenever possible we used estimates of survival that were corrected for variation in age among individuals; uncorrected initial age

could obscure the relationship between trait expression and survival. In particular, because trait expression and age are usually positively correlated and females tend to prefer older males (review: Kokko 1998), this might generate a spurious negative correlation between trait expression/mating success and survival. This should make our tests less likely to detect a statistically significant positive relationship.

EXCLUDED STUDIES

We did not include data on survival rates for discrete alternative reproductive phenotypes because we are interested in traits that are subject to directional sexual selection. Alternate phenotypes may be maintained by frequency dependent selection. In addition, despite theoretical interest in determining whether the phenotypes have equal fitness, there is very little data on adult mortality in these systems (review: Gross 1996). For example, Ryan et al. (1992) noted the dearth of data on mortality rates of different morphs of poeciliid fish; they therefore estimated adult mortality *assuming* equal fitness of morphs to see whether the mortality parameters obtained were biologically plausible. It might be assumed that males that pursue the subordinate tactic (e.g., satellites, sneakers) generally have lower mortality, thereby generating a negative relationship between expression of the "dominant" sexual trait and survival. Several available studies suggest otherwise. For example, Clifton and Robertson (1993) and Allen (1995) found that male morphs less preferred by females were equally likely to be depredated or parasitized, while Zuk et al. (1995) found higher rates of parasitism among noncalling crickets. A separate meta-analysis of the difference in longevity between alternate morphs may be warranted once sufficient data are available.

We have also excluded some well-known artificial selection experiments because data on individual mortality in relation to phenotype are not presented. The mechanism of selection is therefore unclear. For example, guppy (*Poecilia reticulata*) coloration evolves in response to the presence of predators (review: Houde 1997), but this is probably due to the combined effects of differential male survival *and* mating success. In general, artificial selection over several generations for larger or more

TABLE 1

Evidence that the traits we have used in the meta-analysis are sexually selected

Species	Character	Evidence	Remarks	Reference
Acrocephalus arundinaceus	Song	C	Correlated with male extra-pair paternity	1
Agelaius phoeniceus	Size	C	Correlated with harem size, dominance	2
Alcedo atthis	Annual reproduction	MS+	Not related to body size; no strong evidence for sexual selection	3
Anthus pratensis	Annual reproduction	MS	Not all males mated, so opportunities for female-choice or male-male competition	4
Carpodacus mexicanus	Plumage	E	Field manipulation of color	5
C. mexicanus	Plumage	CT	Laboratory mate-choice experiments with naturally colored males	6
C. mexicanus	Body size	C	Correlated with pairing/reproductive success	7
C. mexicanus	Wing length	C	Correlated with pairing/reproductive success	7
Delichon urbica	Mass	C	Correlated with seasonal reproductive success	8
Ficedula albicollis	Color patch	C	Correlated with mating order	9
F. albicollis	Color patch	CT/E	Laboratory mate choice experiments where forehead patch size was manipulated	10
F. hypoleuca	Plumage	CT	Laboratory mate-choice experiments with naturally colored males	11
F. hypoleuca	Plumage	CT/E	Laboratory mate-choice experiments where plumage was experimentally manipulated	12
F. hypoleuca	Plumage	C	Mating order	13
Gallus domesticus	Comb size/spur length	CT	Laboratory mate-choice experiments on males differing in comb size after artificial selection	14
Geospiza fortis	Body size	C	Beak measures and wing size are correlated with reproductive success	15
Hirundo rustica	Tail length	E	Numerous field studies experimentally manipulating tail length	16
Meleagris gallopavo	Spur length	D	No direct evidence	–
Melospiza melodia	First year success	MS	Floater males, but not females	17
Oenanthe leucura	Stone carrying	C	Correlated with reproductive success	18
Parus caeruleus	Paternity	MS	Female less likely to engage in EPC; paternity correlates with phenotype*	19
P. major	Song	C	Correlated with the number of young fledged	20
Passer domesticus	Badge size	C	Correlated with pairing success	21
P. domesticus	Badge size	C	Negatively correlated with number of offspring fledged	22
Passerina cyanea	Successful status	MS+	13.6–17.9% of males accounted for 50% of fledglings	23
Pavo cristatus	Train length	E	Field study with manipulation of train length	24
P. cristatus	Eye spots	E	Field study with manipulation of eye spot number	24
P. cristatus	Eye spots	C	Correlated with number of mates	25
Phasianus colchicus	Mating success	MS	Mating success is related to male morphology	26
P. colchicus	Weight	C	Correlated with number of offspring	27
P. colchicus	Wing length	C	Correlated with number of chicks and females	27
P. colchicus	Tail length	C	Correlated with number of females	27
P. colchicus	Spur length	C	Correlated with number of chicks and females	28
P. colchicus	Spur length	C	Correlated with number of chicks and females	29
P. colchicus	Spur length	E	Field study; spur length experimentally manipulated	29
P. colchicus	Wattle size	D	No direct evidence	–
P. colchicus	Wattle color	D	No direct evidence	–
Ptilonorhynchus violaceus	Bower quality	C	Correlated with mating success	30
Tetrao tetrix	Mating success	MS	Related to dominance, lack of tail damage	31

TABLE 1
Continued

Species	Character	Evidence	Remarks	Reference
T. tetrix	Mating success	MS	Experimentally damaging tail feathers decreases peripheral males' mating success	32
Bolitotherus cornutus	Horn size	C	Correlated with courtship/attendance and copulation/courtship	33
Chironomus plumosus	Body size	C	Negatively correlated with mating success	34
Coenagrion puella	Body size	C	Negatively correlated with mating success (life span corrected)	35
Drosophila melanogaster	Body size	C	Correlation of wing size with mating success	36
D. melanogaster	Body size	C	Correlated with mating success	37
D. melanogaster	Body size	C	Correlated with mating success	38
Erythemis simplicicollis	Daily success	MS	Related to male competitive ability; male success repeatable across sites (Experiment)	39
H. nigriceps	Body size	C	Correlated with mating success	40
Hetaerina americana	Wing spot	E	Field study; experimental manipulation of wing spots	41
H. americana	Body size	C	Correlated with mating success	42
Hygrolycosa rubrofasciata	Drumming	C	Correlated with mating success	43
H. rubrofasciata	Movement	C	Correlated with mating success	44
Jalmenus evagoras	Forewing length	C	Correlated with mating efficiency	45
Nezara viridula	Pronotum width	C	Correlated with mating success	46
Panorpa japonica	Pheromone (FA)	CT	Laboratory mate-choice experiments; females only had olfactory access to males; males with low FA were strongly preferred	47
Plathemis lydia	Aggression	C	Correlated with matings/hour	48
Sympetrum danae	Daily mating rate	C	Daily rate is not due to chance; behavior and size influence mating rate	49
Tetraopes tetraopthalmus	Mating efficiency	MS	Mating success is related to body size because larger males are better at displacing rivals; there is no evidence for active female choice	50
Cervus elaphus	Mating success	MS	Mating success related to harem size, days held and matings/hind/day; it is correlated with fighting success, which is correlated with male size	51
Mirounga angustirostris	Inseminations/year	MS	Related to social rank, which is related to size	52
Girardinichthys multiradiatus	Body depth	CT	Laboratory mate-choice experiments on naturally differing males	53
Poecilia reticulata	Attractiveness	CT	Laboratory mate-choice experiments on naturally differing males; attractiveness is strongly correlated with male phenotype	54

References: 1) Hasselquist et al. 1996. 2) Searcy 1979b; Eckert and Weatherhead 1987; Searcy and Yasukawa 1995 (Table 7.5). 3) Bunzel and Drüke 1989. 4) Hötker 1989. 5) Hill 1991. 6) Hill 1990. 7) Badyaev and Martin 2000. 8) Bryant 1988. 9) Gustafsson et al. 1995. 10) Sætre et al. 1997. 11) Slagsvold and Drevon 1999. 12) Sætre et al. 1994. 13) Järvi et al. 1987. 14) von Schantz et al. 1995. 15) Price 1984a. 16) Møller 1994 (review). 17) Smith 1988. 18) Moreno et al. 1994; Soler et al. 1996. 19) Kempenaers et al. 1997. 20) McGregor et al. 1981. 21) Møller 1989b. 22) Griffith et al. 1999. 23) Payne 1989. 24) Petrie and Halliday 1994. 25) Petrie et al. 1991; Yasmin and Yahya 1996. 26) Grahn 1993. 27) Witzell 1991. 28) Witzell 1991; Göransson et al. 1990. 29) von Schantz et al. 1994. 30) Borgia 1985. 31) Alatalo et al. 1991. 32) Höglund et al. 1994. 33) Conner 1988. 34) Neems et al. 1990. 35) Banks and Thompson 1985. 36) Wilkinson 1987. 37) Partridge et al. 1987a,b. 38) Partridge and Farquar 1983. 39) McVey 1988. 40) Thornhill 1983. 41) Grether 1996. 42) Grether 1996. 43) Kotiaho et al. 1996, 1998. 44) Kotiaho et al. 1998. 45) Elgar and Pierce 1988. 46) McLain 1987. 47) Thornhill 1992b. 48) Koenig and Albon 1987. 49) Michiels and Dhondt 1991. 50) McLain and Boromisa 1987; McCauley 1982. 51) Clutton-Brock et al. 1988; Rose 1995. 52) Le Boeuf and Reiter 1988. 53) Garcia et al. 1994. 54) Brooks (personal communication); Houde 1997.

Note: E — trait experimentally manipulated; C = trait correlated with a measure of mating/reproductive success ($P < 0.05$); CT — mate choice tests showed that females preferred males with greater expression of the trait; MS = mating/reproductive success is related to a male trait likely to have a causal effect; MS− = no clear evidence for sexual selection influencing mating/reproductive success; D = sexually dimorphic trait. *Møller and Ninni (1998) found that more attractive males generally have higher paternity in birds.

elaborate sexually selected traits tends to increase juvenile rather than adult mortality (e.g., Partridge and Fowler 1993). A weakness of artificial selection studies is that they leave open the question of the phenotypic relationship between sexual trait expression and adult survival when the population approaches a new equilibrium. Even so, we have included data from one study where individual mortality was reported in lines subject to artificial selection (von Schantz et al. 1995).

In compiling the data set we noticed that traits that function as long-distance mate attractants (usually acoustic or pheromone signals) are underrepresented. This is because data that relate individual mortality to phenotype are rarely presented. Most authors only show that artificially produced signals (e.g., acoustic playbacks or pheromone-baited traps) attract predators or parasites (review: Zuk and Kolluru 1998). These traits are assumed to show a strong negative relationship between expression and survival, but data that test whether more actively signaling males have greater parasite loads or die sooner are often lacking (for exceptions see Allen 1995; Kotiaho et al. 1999). Common sense might suggest, for example, that males that signal more often invariably suffer higher predation if their calls attract predators. This assumes, however, that males do not modify their behavior in a compensatory manner. In a recent study, Hedrick (2000) showed that sexually attractive crickets with long calling bouts are much "shyer" and more sensitive to the presence of predators. Thus the relationship between call-bout duration and mortality is unclear. Data on actual male mortality rates are required.

Some well-known studies that colleagues cited as evidence that, for example, brighter colored or larger males are more susceptible to predation, were unusable. This was because the comparison was between male and female survival (e.g., Haas 1976; Anholt 1997), the authors combined data from both sexes (e.g., Trexler et al. 1992; Grant and Grant 1995), or the evidence came from predator attraction to dummies or playbacks (e.g., Ryan 1985). For *Geospiza fortis*, selection on body size varies between climatic extremes (Gibbs and Grant 1987). Unfortunately, most of the published data combined the sexes. Even so, directional selection for large body size appears to be stronger than that for smaller body size (sample sizes are similar; see Table 1 in Grant and Grant 1995). The positive effect we report for *G. fortis* is based on the available data. Finally, we excluded data on the genetic correlation between sexual trait expression and adult longevity or mortality (e.g., Hughes 1995; Brooks 2000).

META-ANALYSIS

Meta-analysis involves calculating the magnitude of a general effect of interest to provide a quantitative summary of statistical tests from different studies, as well as analyzing sources of variation in effect size. Estimates of effect size from different sources are combined, taking sample size into consideration, to yield a weighted mean effect size. We calculated the effect size as the Pearson product-moment correlation coefficient (r) between trait expression and a measure of survival rate. Effect sizes were reported in the original publications in a variety of forms (e.g., t, F, χ^2, and P-values). When means and standard deviations were available, we used the software package *MetaWin* (Rosenberg et al. 1997) to calculate the effect size estimate, Hedge's d. All these effects were then converted to r using the formulae in Rosenthal (1994:237–240).

Effect size measures the strength of a relationship. An effect size of $r = 0.10$ is considered "small," 0.30 "medium," and 0.50 "large" (Cohen 1988). In our calculations we first transformed r to Z, using Fisher's transformation, $Z = \frac{1}{2} \ln_e [(1 + r)/(1 - r)]$ (Sokal and Rohlf 1995). We then calculated the mean weighted effect size at the sample level by entering the data as an "effect data file" in *MetaWin*. The variance in effect size (V_j) per analysis unit is $1/(N_j - 3)$, where N_j = sample size for analysis unit j. The inverse of the variance is used as the weighting factor, so that studies where the effect size is known with higher certainty (lower variance) are given greater weighting (Hedges 1994). In meta-analysis, fixed-effect models assume that samples within a class share a common true effect size, while mixed-effect models assume that samples within a class have a common mean effect but that there is also random variation in effect sizes within a class. Most workers have used fixed-effect models, although

mixed-effect models are probably more appropriate (Gurevitch and Hedges 1999). There is, as yet, no consensus among evolutionary biologists as to which model type to use, so we also use fixed-effect models. However, we also repeated all analyses using random-effect models and we present a brief summary of these results as well. Briefly, the two model types give very similar results, but effect sizes were greater and moderator variables less important in random-effect models.

The weighted mean effect size is $Z_r = \Sigma W_j Z_{rj} / \Sigma W_j$, where Z_{rj} is the Fisher's Z-transformed effect size (r) for analysis unit j, and $W_j = 1/V_j = N_j - 3$. Samples within studies and multiple studies of a single species lack statistical independence (Felsenstein 1985). We therefore examined our results at three levels of analysis: samples, studies, and species. We computed weighted mean effect size at the study level using a similar approach. For each study k, we calculated the weighted mean effect Z_{rk} using the effect sizes and sample sizes for each sample within that study. We then calculated the average sample size per study $N_k = \Sigma N_j / S_k$, where S_k is the number of samples for study k. The mean weighted effect size across studies was then $\Sigma W_k Z_{rk} / \Sigma W_k$, where $W_k = N_k - 3$. Mean weighted effect size at the species level was carried out in an identical manner. The output of the MetaWin package presents the mean weighted effect size and 95% confidence intervals. We then back-calculated and expressed effect sizes in terms of r. The standard error of the mean weighted effect size was calculated directly from the confidence intervals. We tested the null hypothesis that the mean weighted effect size did not differ from zero by calculating the standard normal deviate (mean/standard error):

$$Z\text{-}score = |mean\ Z_r| / [1/\Sigma(N_j - 3)]^{1/2}$$
(Cooper and Hedges 1994:268).

To test the robustness of this result, we calculated the fail-safe number of analysis units X using the equation:

$$X = (\Sigma Z\text{-}score_j)^2 / 3.842 - K$$

where $Z\text{-}score_j$ = the standard normal deviate for each analysis unit = $Z_{rj} (N_j - 3)^{1/2}$.

The value 3.842 (=1.96^2) is based on a two-tailed alpha value of 0.05. The fail-safe number is an estimate of the number of unknown cases needed to eliminate the overall significance of the weighted mean effect size at the indicated level of significance when the mean effect size of the unknown cases is zero.

Previous meta-analyses have not clearly stated how samples are grouped into studies. Inevitably, some subjectivity is required in this regard. To ensure that readers can independently replicate our results, we have explicitly coded studies in Table 2. In general, each published paper represents a single study. In some cases, however, a single paper is treated as two studies. This occurred when data was presented for two or more study sites (e.g., Payne 1989), or experiments were conducted in two different habitats (e.g., Kotiaho et al. 1999). Separate laboratory experiments were not treated as independent studies (e.g., Partridge and Farquhar 1983), nor were data from the same population in different years (e.g., Searcy 1979a).

HETEROGENEITY AND MODERATOR VARIABLES

A measure of the heterogeneity in effect sizes among analysis units was calculated as Q defined by the equation:

$$Q = \Sigma(N_j - 3)(Z_{rj} - mean\ Z_r)^2.$$

This has approximately a χ^2 distribution with $K-1$ degrees of freedom, where K = number of analysis units. If there was significant overall heterogeneity, we then tested for the role of explanatory moderator variables that might account for variation in effect size. We scored samples with respect to:

a) whether the trait was an ordinary trait, a secondary sexual character, or a measure of attractiveness/mating rate/reproductive rate (listed as "mating rate" traits in Table 3). Secondary sexual traits were then scored as being morphological or behavioral characters. We made these comparisons because secondary sexual characters may display a higher degree of condition dependence than ordinary morphological traits. If so, they should be associated with more positive effect sizes. If behavioral secondary sexual characters are more responsive to recent changes in status or condition, they may also show a larger effect size than morphological traits.

TABLE 2

Effect size (Pearson's r) between male trait and a measure of survival for 122 samples from 69 studies of 40 species

Species	Character	N	r	Trait type	Sex trait type	Mating type	Monitoring type	Survival estimate	Inclusion/ Exclusion	Statistic	Reference
Acrocephalus arundinaceus	Song	56	0.157	2	1	1	1	1	1	$P = 0.24$	1
Alcedo atthis	Annual production	74	0.13	3	—	0	1	1	0	Spearman's r	2
Anthus pratensis	Annual production	49	0.11	3	—	0	1	1	0	r	3
Agelaius phoeniceus	Wing	42	−0.159	1	1	1	1	0	1	$t = 1.02$	4
A. phoeniceus	Wing	41	−0.113	1	1	1	1	0	1	$t = 0.709$	4
A. phoeniceus	Wing	35	0.108	1	1	1	1	0	1	$t = 0.625$	4
A. phoeniceus	Wing	303	0.078	1	1	1	1	0	1	$t = 1.358$	5
A. phoeniceus	Wing	214	0.024	1	1	1	1	0	1	$t = 0.347$	5
A. phoeniceus	Tarsus	303	0.174	1	1	1	1	0	1	$t = 3.06$	5
A. phoeniceus	Tarsus	214	0.115	1	1	1	1	0	1	$t = 1.68$	5
A. phoeniceus	Wing	194	0.103	1	1	1	1	0	1	Hedge's d (a)	6
A. phoeniceus	Wing	380	−0.034	1	1	1	1	0	1	Hedge's d	6
A. phoeniceus	Body size	66	0.126	1	1	1	1	0	1	Hedge's d	7
A. phoeniceus	Body size	196	0.065	1	1	1	1	0	1	Hedge's d	8
A. phoeniceus	Body size	293	−0.008	1	1	1	1	0	1	Hedge's d	8
A. phoeniceus	Wing	75	0.012	1	1	1	1	0	1	Hedge's d	7
A. phoeniceus	Wing	207	0.194	1	1	1	1	0	1	Hedge's d	8
A. phoeniceus	Wing	348	0.081	1	1	1	1	0	1	Hedge's d	8
A. phoeniceus	ulna/humerus	18	0.131	1	1	1	1	0	1	Hedge's d	9
A. phoeniceus	ulna/humerus	88	0.069	1	1	1	1	0	1	Hedge's d	9
A. phoeniceus	Body size	48	0.02	1	1	1	1	1	1	$P = 0.90$	10
A. phoeniceus	Wing	17	−0.274	1	1	1	1	1	1	$P = 0.083$	11
Carpodacus mexicanus	Plumage	150	0.135	2	2	0	1	0	1	$t = 1.66$	12
C. mexicanus	Plumage	212	0.167	2	2	0	1	0	1	$t = 2.45$	12
C. mexicanus	Plumage	304	0.168	2	2	0	1	0	1	$t = 2.94$	13
C. mexicanus	Plumage	348	0.014	2	2	0	1	0	1	$t = 0.26$	13
C. mexicanus	Body size	164	0.236	1	1	0	1	0	1	Hedge's d	14
C. mexicanus	Wing length	171	−0.099	1	1	0	1	0	1	Hedge's d	14
C. mexicanus	Wing length	247	−0.048	1	1	0	1	0	1	Hedge's d	15
C. mexicanus	Wing length	172	0.308	1	1	0	1	0	1	Hedge's d	16
Delichon urbica	Mass	99	0.24	1	—	0	1	1	1	r	17
Ficedula albicollis	Color patch	1424	0.076	2	2	1	1	0	1	B/sw $t = 2.89$	18
Ficedula hypoleuca	Plumage	41	−0.33	2	2	1	1	0	0	Partial r	19
F. hypoleuca	Plumage	74	0.259	2	2	1	1	0	0	$Z = 2.23$	20
F. hypoleuca	Plumage	86	0.187	2	2	1	1	0	0	$Z = 1.73$	20

TABLE 2
Continued

Species	Character	N	r	Trait type	Sex trait type	Mating type	Monitoring type	Survival estimate	Inclusion/ Exclusion	Statistic	Reference
F. hypoleuca	Plumage	259	−0.148	2	2	1	1	0	1	$t = 2.45$	21
Gallus domesticus	Comb size	163	−0.155	2	2	1	2	0	1	$\chi^2 = 11.14$	22
G. domesticus	Comb size	537	−0.131	2	2	1	2	0	1	$\chi^2 = 9.21$	22
G. domesticus	Comb size	521	−0.146	2	2	1	2	0	1	$\chi^2 = 11.13$	22
G. domesticus	Comb size	360	0.005	2	2	1	2	0	1	$\chi^2 = 0.01$	22
G. domesticus	Spur length	350	0.117	2	2	1	2	0	1	$t = 2.18$	22
Geospiza fortis	Body size	198	0.191	1	—	0	1	0	1	Hedge's d	23
G. fortis	Body size	100	0.034	2	—	0	1	0	1	$B/se\ t = 0.33$ (b)	24
Hirundo rustica	Tail length	20	0.749	2	2	0	1	0	1	$t = 4.80$	25
H. rustica	Tail length	85	0.293	2	2	0	?	0	?	$P = 0.007$	26
H. rustica	Tail length	28	0.576	2	2	0	1	0	?	$F = 9.92$	27
H. rustica	Tail length	16	0.265	2	2	0	1	0	1	$P = 0.29$	28
H. rustica	Tail length	804	0.099	2	2	0	1	0	1	$t = 2.83$	29
H. rustica	Tail length	380	0.208	2	2	0	1	0	1	Hedge's d	30
Meleagris gallopavo	Spur length	33	0.672	2	2	2	2	0	0	Hedge's d	31
M. gallopavo	Spur length	36	−0.626	2	2	2	2	0	0	Hedge's d	31
Melospiza melodia	First year production	92	0.27	3	—	0	1	1	0	r	32
Oenanthe leucura	Total stones carried	25	0.2	2	1	0	1	0	1	P (Fisher's)	33
Parus caeruleus	Paternity	32	0.601	3	—	0	1	0	0	P (Fisher's)	34
P. caeruleus	Paternity	40	0.297	3	—	0	1	0	0	P (Fisher's)	34
P. caeruleus	Paternity	85	0.475	3	—	0	1	1	0	P (Fisher's)	34
P. major	Song	85	0.288	2	—	0	1	1	1	$F = 7.5$	35
P. major	Song	21	0.125	2	1	0	1	0	1	$\chi^2 = 0.33$	36
P. major	Song	27	0.452	2	1	0	1	0	1	$t = 2.533$	36
Passer domesticus	Badge size	84	−0.138	2	2	0	1	0	1	Hedge's d	37
P. domesticus	Badge size	61	−0.013	2	2	0	1	0	1	Hedge's d	37
P. domesticus	Badge size	84	−0.409	2	2	0	1	0	—	Hedge's d	37
P. domesticus	Badge size	28	0.089	2	2	0	1	0	1	Hedge's d	37
P. domesticus	Badge size	46	−0.297	2	2	0	1	0	1	$t = 2.06$ (c)	38
Passerina cyanea	First year success	158	0.085	3	—	0	1	0	0	$\chi^2 = 1.16$	39
P. cyanea	Subsequent success	165	0.218	3	—	0	1	0	0	$\chi^2 = 7.87$	39
P. cyanea	First year success	147	0.105	3	—	0	1	0	0	$\chi^2 = 1.63$	40
P. cyanea	Subsequent success	202	0.072	3	—	0	1	0	0	$\chi^2 = 1.51$	40
Pavo cristatus	Train length	21	0.628	2	2	2	1	0	1	$t = 3.517$	41
P. cristatus	Eye spots	17	0.453	2	2	2	1	0	1	$t = 1.97$	41

TABLE 2
Continued

Species	Character	N	r	Trait type	Sex trait type	Mating type	Monitoring type	Survival estimate	Inclusion/ Exclusion	Statistic	Reference
Phasianus colchicus	Spur length	125	0.164	2	2	1	2	0	1	$F = 3.35$	42
P. colchicus	Mating success	82	−0.176	3	—	1	2	0	0	$t = 0.98$	42
P. colchicus	Weight	38	0.03	1	—	1	2	0	1	$i = 0.06$	43
P. colchicus	Weight	32	0.015	1	—	1	2	0	1	$i = 0.03$	43
P. colchicus	Weight	29	0.039	1	—	1	2	0	1	$i = 0.08$	43
P. colchicus	Wing length	38	0.015	1	—	1	2	0	1	$i = 0.03$	43
P. colchicus	Wing length	32	−0.05	1	—	1	2	0	1	$i = -0.10$	43
P. colchicus	Wing length	29	−0.05	1	—	1	2	0	1	$i = -0.10$	43
P. colchicus	Tail length	38	0.046	2	2	1	2	0	1	$i = 0.09$	43
P. colchicus	Tail length	32	0.091	2	2	1	2	0	1	$i = 0.18$	43
P. colchicus	Tail length	29	0.141	2	2	1	2	0	1	$i = 0.28$	43
P. colchicus	Spur length	38	0.02	2	2	1	2	0	1	$i = 0.04$	43
P. colchicus	Spur length	32	−0.064	2	2	1	2	0	1	$i = -0.13$	43
P. colchicus	Spur length	29	0.23	2	2	1	2	0	1	$i = 0.48$	43
P. colchicus	Spur length	44	0.416	2	2	1	2	0	1	$F = 8.79$	44
P. colchicus	Tail length	44	0.52	2	2	1	2	0	1	$F = 15.56$	44
P. colchicus	Vertical wattle size	44	0.79	2	2	1	2	0	1	$F = 69.69$	44
P. colchicus	Horizontal wattle size	27	0.787	2	2	1	2	0	1	$F = 40.76$	44
P. colchicus	Wattle color	37	0.285	2	2	1	2	0	0	$Z = 1.733$	44
Ptilonorhynchus violaceus	Bower quality	49	0.42	2	1	2	1	1	1	Partial $r=0.42$	45
Tetrao tetrix	Mating success	76	0.224	3	—	2	1	0	2	$t = 1.98$	46
Bolitotherus cornutus	Horn size	134	0.142	2	2	2	1	1	1	$B/se=0.164$	47
Chironomus plumosus	Body size	34	−0.45	1	—	2	2	1	1	r	48
Chironomus plumosus	Body size	30	−0.09	1	—	2	2	1	1	r	48
Coenagrion puella	Body size	186	−0.178	1	—	1	1	1	1	$P = 0.015$	49
Drosophila melanogaster	Body size	25	0.77	1	—	2	2	1	1	r	50
D. melanogaster	Body size	25	0.69	1	—	2	2	1	1	r	50
D. melanogaster	Body size	25	0.7	1	—	2	2	1	1	r	50
Erythemis simplicicollis	Daily success	161	0.554	3	—	1	1	1	0	r	51
Harpobittacus nigriceps	Body size	66	0.787	1	—	1	2	1	1	r	52
H. nigriceps	Body size	52	0.608	1	—	1	2	1	1	r	52
Hetaerina americana	Wing spot	51	0.275	2	2	1	1	1	1	$B/se=t=2.0$	53
H. americana	Body size	51	0.223	1	—	1	1	1	1	$B/se=t=1.6$	53
Hygrobyssa rubrofasciata	Drumming	18	0.71	2	2	2	2	1	1	Kendall T	54
H. rubrofasciata	Drumming	103	0.228	2	1	2	2	0	1	$P = 0.021$	55

TABLE 2
Continued

Species	Character	N	r	Trait type	Sex trait type	Mating type	Monitoring type	Survival estimate	Inclusion/ Exclusion	Statistic	Reference
H. rubrofasciata	Drumming	28	0.61	2	1	2	2	1	1	Spearman's r	56
H. rubrofasciata	Drumming	100	0.26	2	1	2	1	1	1	Spearman's r	57
H. rubrofasciata	Drumming	108	0.236	2	1	2	2	1	1	Spearman's r	58
H. rubrofasciata	Drumming	95	0.052	2	1	2	2	1	1	Spearman's r	58
H. rubrofasciata	Drumming	60	-0.365	2	1	2	2	0	1	$t = 1.71$	59
H. rubrofasciata	movement	90	0.713	2	1	2	2	0	1	$t = 5.47$	59
H. rubrofasciata	movement	100	0.17	2	1	2	1	1	1	Spearman's r	57
Jalmenus evagoras	Forewing length	35	0.414	1	—	2	1	0	1	$P = 0.014$	60
Nezara viridula	Pronotum width	93	0.37	1	—	2	2	0	1	(d)	61
Panorpa japonica	Pheromone (FA)	21	0.796	2	1	1	2	1	1	$P = 0.0002$	62
Plathemis lydia	Aggression	13	0.18	2	—	1	1	1	0	r	63
Symphtran deanae	Daily mating rate	20	0.57	3	—	2	—	1	0	r	64
Tetraopes tetraophthalmus	Mating efficiency	337	0.152	3	—	2	—	1	0	r	65
Cervus elaphus	Mating success	35	0.322	3	—	1	—	1	2	r	66
Mirounga angustirostris	Inseminations/year	16	0.647	3	—	2	—	1	2	P 0.005	67
Girardinichthys multiradiatus	Body depth	14	-0.516	2	2	2	2	0	1	Hedge's d	68
Poecilia reticulata	Attractiveness	279	-0.035	3	—	2	2	0	2	t 0.578	69

References: 1) Hasselquist 1998. 2) Bonrel and Drake 1989. 3) Holder 1989. 4) Searcy 1979a. 5) Johnson et al. 1989. 6) Weatherhead et al. 1987. 7) Weatherhead and Clark 1994. 8) Weatherhead and Clark 1994. 9) Weatherhead et al. 1984. 10) Weatherhead and Boag 1995. 11) Yasukawa 1987. 12) Hill 1991. 13) Nolan et al. 1988: Nolan (personal communication). 14) Badyaev and Martin 2000. 15) Badyaev (personal communication). 16) Badyaev (personal communication). 17) Bryant 1988. 18) Qvarnström et al. 1998. 19) Järvi et al. 1987. 20) Slagsvold and Lifjeld 1988. 21) Slagsvold et al. 1995. 22) von Schantz et al. 1995. 23) Boag and Grant 1981. 24) Price 1984b. 25) Møller 1988a. 26) Saino et al. 1997. 27) Møller and de Lope 1994. 28) Brown and Brown 1999. 29) Møller and Nielsen 1997. 30) Møller 1991. 31) Badyaev et al. 1998. 32) Smith 1988. 33) Møller (personal communication). 34) Kempenaers et al. 1997. 35) McGregor et al. 1981. 36) Lambrechts and Dhondt 1986. 37) Møller 1980b. 38) Griffith (personal communication). 39) Payne 1989. 40) Payne 1989. 41) Petrie 1992. 42) Gahn 1993. 43) Witzell 1991. 44) Papeschi 1998. 45) Borgia 1993. 46) Borgia 1993. 47) Connor 1988. 48) Neems et al. 1990. 49) Banks and Thompson 1985. 50) Partridge and Farquhar 1983. 51) McVey 1988. 52) Thornhill 1983. 53) Goether 1996. 54) Mappes et al. 1996. 55) Kotiaho et al. 1996. 56) Kotiaho et al. 1999. 57) Kotiaho et al. 1999. 58) Kotiaho (personal communication). 59) Kotiaho et al. 1998. 60) Elgar and Pierce 1988. 61) McLain 1987. 62) Thornhill 1992a. 63) Koenig and Albon 1987. 64) Michiels and Dhondt 1991. 65) McCauley 1983. 66) Clutton-Brock et al. 1988. 67) Le Boeuf and Reiter 1988. 68) Garcia et al. 1994. 69) Brooks (personal communication).

Note: Trait type: 1 = ordinary trait, 2 = secondary sexual character, 3 = mating rate/attractiveness; Sex trait type: 1 = behavioral, 2 = morphological; Mating type: 0 = monogamous, 1 = polygynous/territorial, 2 = lekking/active male searching; Monitoring type: 1 = free-ranging, 2 = laboratory/telemetry; Survival estimate: 0 = dead/alive, 1 = life span/"days alive"; Inclusion/Exclusion: 0 = Strongly excluded, 1 = Included, 2 = Weakly excluded. "Statistic" refers to the data in the original paper used to calculate the effect size. Hedge's d indicates that means and standard deviations were used to calculate effect size. Standardized selection intensity i was used as an approximate measure of Hedge's d (it differs in that the "before sample" includes the dead individuals, and it therefore underestimates the value of Hedge's d). (a) Standard deviation was incorrectly presented in the original paper (see Weatherhead and Clark 1994). (b) Mean of 4 values of variables associated with body size. (c) Negative, because females prefer smaller badged males in this population (Griffith et al. 1999). (d) Recalculated as small versus large comparison so $df = 1$.

TABLE 3

Summary statistics for the relationship between male traits and survival for different moderator variables

(a) Samples

Class	Weighted Effect size (r)	95% CI Lower	95% CI Upper	N	z	Q_w	Fail-safe	r_{bias}
All samples	0.084	0.068	0.099	122	10.331***	780.4***	5583 +	−0.294***
Ordinary traits	0.079 a	0.051	0.107	43	5.572***	229.7***	438 +	−0.02 ns
Secondary sexual traits	0.064 a	0.042	0.085	61	5.834***	453***	1125 +	−0.382**
"Mating rate"	0.182 b	0.138	0.225	18	8.014***	75.2***	349 +	−0.545*
Behavioral sex traits	0.126 a	0.063	0.188	17	3.905***	154.5***	101 +	−0.302 ns
Morphological sex traits	0.056 b	0.033	0.078	44	4.809***	294.2***	512 +	−0.307*
Monogamous	0.109 a	0.081	0.137	36	7.590***	133.8***	561 +	−0.367*
Polygynous/territorial	0.059 b	0.037	0.080	58	5.367***	367.6***	923 +	−0.135 ns
Lekking/Active male search	0.130 a	0.086	0.174	28	5.748***	266.3***	364 +	−0.481*
Free-ranging	0.102 a	0.083	0.120	78	10.748***	281.2***	2614 +	−0.353**
Captive or telemetry	0.035 b	0.004	0.065	44	2.215*	485.7***	515 +	−0.271 ns
Survivor/Nonsurvivor	0.050 a	0.032	0.068	87	5.385***	487.4***	1070 +	−0.239*
Life span/days alive	0.188 b	0.157	0.219	35	11.518***	238.2***	1688 +	−0.369*
Strongly Excluded	0.244 a	0.197	0.288	18	10.063***	136.9***	544 +	−0.579*
Included	0.064 b	0.047	0.081	99	7.382***	578.7***	2324 +	−0.25*
Weakly Excluded	0.053 b	−0.042	0.147	5	1.088 ns	15.1**	2	−
Birds	0.066 a	0.049	0.084	91	7.523***	400.3***	2020 +	−0.23*
Insects/Spiders	0.206 b	0.163	0.248	27	9.284***	328.5***	784 +	−0.471*
Mammals	0.430	0.166	0.637	2	3.085**	1.8 ns	4	−
Fish	−0.055	−0.169	0.060	2	−0.942 ns	3 ns	0	−

continued

Conversely, if early life experiences affect both adult mortality and the ontogeny of traits, then morphological traits may show stronger effect sizes.

b) the mating system. We scored species as socially monogamous, polygynous/territorial, or lekking/active male searching. Birds were scored following Gontard-Danek and Møller (1999), and other species following descriptions in the papers used to calculate the effect size. We made these comparisons on the assumption that effect size will vary in relation to the intensity of sexual selection on a trait. Also, previous studies have shown that the mating system influences reported effect sizes (Gontard-Danek and Møller 1999; Thornhill et al. 1999).

c) the certainty with which the fate of individuals was known. We distinguished between studies where the individuals were free-ranging and studies where they were captive or radiotelemetry was used. We made this comparison because the latter studies are more likely to determine the actual fate of individuals. However, one caveat is that laboratory studies with predators may overestimate the intensity of predation (e.g., Kotiaho et al. 1998 vs. Kotiaho et al. 1999).

d) whether the estimate of survival was based on a comparison between living and dead individuals or an estimate of adult life span/"days alive." Different estimation techniques may systematically under or overestimate the true effect size.

e) the criteria for inclusion of the trait. We scored traits as: (0) "excluded" because the trait was only included on the basis of sexual dimorphism or the trait was "mating rate" in a species with weaker evidence

TABLE 3
Continued

(b) Studies

Class	Weighted Effect size (r)	95% CI Lower	Upper	N	z	Q_w	Fail-safe	r_{bias}
All studies	0.101	0.081	0.122	69	9.683***	390.5***	2288 +	−0.352**
Ordinary traits	0.062 a	0.023	0.102	22	3.086**	124.6***	75	−0.06 ns
Secondary sexual traits	0.094 a	0.067	0.121	34	6.777***	190.7***	526 +	−0.409*
"Mating rate"	0.190 b	0.140	0.239	13	7.387***	59.1***	216 +	0.676*
Behavioral sex traits	0.190 a	0.115	0.262	13	4.942***	89.3***	109 +	−0.434 ns
Morphological sex traits	0.080 b	0.051	0.109	21	5.352***	94.2***	138 +	−0.217 ns
Monogamous	0.111 a	0.078	0.143	25	6.651***	90.7***	305 +	−0.485*
Polygynous/territorial	0.074 a	0.043	0.105	24	4.665***	169.5***	191 +	−0.155 ns
Lekking/Active male search	0.145 a	0.096	0.194	20	5.720***	127.7***	228 +	−0.436 ns
Free-ranging	0.104 a	0.082	0.127	52	9.121***	211.4***	1279 +	−0.405**
Captive or telemetry	0.082 a	0.031	0.134	17	3.119**	182.3***	129 +	−0.301ns
Survivor/Nonsurvivor	0.060 a	0.035	0.086	41	4.578***	198.5***	238 +	−0.242 ns
Life span/days alive	0.171 b	0.137	0.204	28	9.875***	169.7***	986 ·	0.369 ns
Strongly Excluded	0.226 a	0.170	0.281	10	7.670***	39.3***	136 +	−0.164 ns
Included	0.084 b	0.062	0.107	55	7.361***	316.8***	1067 +	−0.309*
Weakly Excluded	0.070 b	−0.028	0.167	4	1.393 ns	13.5**	5	−
Birds	0.080 a	0.057	0.103	46	6.801***	157.3***	625 +	−0.258 ns
Insects/Spiders	0.213 b	0.165	0.260	19	8.479***	195.9***	444 +	−0.505*
Mammals	0.430	0.166	0.636	2	3.085**	1.8 ns***	4	−
Fish	−0.056	−0.170	0.060	2	−0.942 ns	3 ns***	0	−

continued

that this varies due to sexual selection; (1) always "included" because the trait was significantly correlated with "mating rate"; (2) "weakly excluded" because the trait was "mating rate," but there is well-documented evidence for strong sexual selection in the study species. We made this comparison because the criteria for inclusion may influence the effect size (Englund et al. 1999). Furthermore, "mating rate" may be a better predictor of the attractiveness/dominance of a male than a single, sexually selected trait if sexual selection acts on several traits and/or most variation in mating rate is due to sexual selection.

f) the taxa of the study animal. We scored this as bird, mammal, fish, and insect/spider. We made this comparison because previous studies have shown that the taxonomic status can sometimes explain variation in effect size (e.g., Thornhill et al. 1999).

Focused contrast tests to detect the source of heterogeneity were not generally required (Rosenthal 1991) because there were only two groups per analysis of variance. The output of *MetaWin* presents Q for both within and between-group heterogeneity (Rosenberg et al. 1997). The associated level of significance of Q_B is thus the probability that the difference in mean effect size between two groups occurred by chance. When there were three groups we followed the contrast methods of Cooper and Hedges (1994:292–293), using the Bonferroni correction procedure. We calculated the χ^2 value for the contrast, which was then compared to the critical value at the 98.3

TABLE 3
Continued

(c) Species

Class	Weighted Effect size (r)	95% CI Lower	95% CI Upper	N	z	Q_c	Fail-safe	r_{bias}
All species	0.125	0.098	0.152	40	8.944***	216.7***	1200 +	−0.349*
Ordinary traits	0.172 a	0.105	0.237	10	4.976***	80.8***	93 +	−0.491 ns
Secondary sexual traits	0.078 b	0.042	0.114	18	4.256***	62.3***	97	−0.17 ns
"Mating rate"	0.199 a	0.146	0.250	12	7.279***	37.7***	194 +	−0.629*
Behavioral sex traits	0.319 a	0.213	0.419	7	5.636***	13.3*	53 +	0.036 ns
Morphological sex traits	0.051 b	0.013	0.089	11	2.606**	28.5**	0	0.191 ns
Monogamous	0.141 a	0.086	0.195	12	4.991***	18.8 ns	69	−0.196 ns
Polygynous/territorial	0.099 a	0.061	0.136	13	5.088***	60.4***	156 +	−0.434 ns
Lekking/Active male search	0.168 a	0.112	0.222	15	5.825***	133***	160 +	−0.311 ns
Free-ranging	0.135 a	0.105	0.166	29	8.556***	106.6***	659 +	−0.51**
Captive or telemetry	0.088 a	0.029	0.146	11	2.922**	108.1***	70 +	−0.127 ns
Survivor/Nonsurvivor	0.058 a	0.014	0.101	17	2.601**	49.7***	34	−0.157 ns
Life span/days alive	0.169 b	0.134	0.203	23	9.414***	151.7***	766 +	−0.473*
Strongly Excluded	0.244 a	0.183	0.303	9	7.662***	36.5***	118 +	−0.067 ns
Included	0.100 b	0.068	0.132	27	6.099***	148.6***	408 −	−0.283 ns
Weakly Excluded	0.070 b	−0.028	0.167	4	1.393 ns	13.5**	5	−
Birds	0.091 a	0.058	0.123	22	5.399***	50***	202 +	−0.266 ns
Insects/Spiders	0.255 b	0.201	0.307	14	8.984***	121.4***	352 −	−0.402 ns
Mammals	0.430	0.166	0.636	2	3.085**	1.8 ns	4	−
Fish	−0.056	−0.170	0.060	2	−0.942 ns	3 ns	0	−

continued

percentage point of the chi-square distribution ($df = 1$) because a total of three pairwise contrasts are possible when there are three groups ($0.983 = 1 - 0.05/3$). There were only two species of fish and mammal respectively. We therefore limited pairwise comparisons for taxa to that between birds and insects/spiders. In a few cases, the scores for a moderator variable differed for samples within a study (4 cases) or studies within a species (5 cases). When we moved to a higher level of analysis, the study or species effect size for the variable of interest was only calculated from lower level units of analysis with the same score for that variable. We used the variable with the largest number of samples, largest sample size, or least well represented at the next level of analysis.

Different moderator variables may be correlated with each other, and this could obscure trends in the data. We therefore used two-way ANOVA models, following the procedure given by Hedges (1994:293–295). Briefly, we ran weighted ANOVAs in *Systat 8.0*, with effect size as the dependent variable. The weight was the reciprocal of the sampling variance. The weighted sum of squares for each factor and the interaction equals the Q statistics for each moderator variable and the interaction. Omnibus tests (using the Q statistics) were then carried out to see whether the moderator variables were significant and whether they interacted. Each model contained the factor taxa (bird and insect/spider) and one of five moderator variables. We excluded data from mammals and fish because there were too few cases to examine interaction terms. For mating sys-

TABLE 3
Continued

(d) Other

Class	Weighted Effect size (r)	95% CI Lower	95% CI Upper	N	z	Q_w	Fail-safe	r_{bias}
Unpublished samples	0.049 a	−0.002	0.100	13	1.879 ns	124.6***	62	−0.657*
Published samples	0.087 a	0.071	0.104	109	10.281***	654.1***	4358 +	−0.255**
Unpublished studies	−0.032 a	−0.088	0.023	8	−1.135 ns	40.3***	0	−0.429 ns
Published studies	0.118 b	0.096	0.140	61	10.506***	332.1***	2268 +	−0.322*
Unweighted Effect sizes								
All species	0.237	0.187	0.287	40	8.949***	–	–	−0.349*
Included + Weakly Excluded	0.226 a	0.164	0.287	31	6.935***	–	–	−0.364*
Included only	0.213 a	0.144	0.279	27	5.963***	–	–	−0.238 ns

Note: "Mating rate" includes measures of attractiveness, mating rate, and reproduction rate. The effect size is Pearson's correlation r, with upper and lower limits to the 95% Confidence Intervals (CI). For effect sizes, values with different subscripts for a given moderator variable have a pairwise difference with $P < 0.05$ (Bonferroni corrected). N is the number of analysis units. z is the standard normal deviate for the mean effect size. Q_w is the within-class heterogeneity in effect sizes. The fail-safe number is the number of hypothetical null results needed to reduced the mean effect size to a value not significantly greater than zero. A " + " indicates a robust fail-safe number, being greater than $5N-10$ (Rosenthal 1991). r_{bias} is the Spearman correlation between sample size and effect size per analysis unit. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ns = nonsignificant.

tem type and exclusion/inclusion type we reduced the number of levels per factor from three to two so that both levels were represented in both taxa. To do this we removed data on monogamous species (none coded for insects/spiders) and traits that were "weakly excluded" (none coded for insects/spiders). We carried out weighted two-way ANOVAs at the study and species levels of analysis.

We compared effect sizes between this analysis and that of Møller and Alatalo (1999). We were able to pair effect sizes for seven species and therefore calculate the difference in effect size (Cohen's q), which is defined as $Z_{r1} - Z_{r2}$. This has an estimated variance of $1/(N_1 - 3) + 1/(N_2 - 3)$ (Rosenthal 1994). The weighting factor is the inverse of the variance. We then calculated the weighted mean Cohen's q and tested the null hypothesis that it did not differ significantly from zero by calculating the standard normal deviate.

PUBLICATION BIAS

We tested for a publication bias following standard protocols. First, we examined a plot of sample size versus effect size. If there is no publication bias, this graph is funnel-shaped and centered on the weighted mean effect size with reduced variance in the estimate as sample size increases (Light and Pillemer 1984; Begg 1994). We used variance ratio F-tests to determine whether there was lower variance in effect size estimates for samples above the median sample size. Second, we tested whether departures from normality of the effect size distribution depended on sample size by conducting one-sample Kolmogorov-Smirnov (K-S) tests for normality (Lilliefors test) on overlapping groups of 20 samples (e.g., 1–20, 11–30, 21–40; see Palmer 1999). Third, we tested whether the overall distribution of effect sizes around the mean value was symmetrical (i.e., normally distributed).

We calculated the Spearman's r_s correlation between effect size and sample size to determine whether studies with smaller sample sizes produced either a more positive or negative effect size than studies with larger sample sizes. This is the so-called r_{bias} of Palmer (1999). Meta-analysts do not recommend the promotion of the term r_{bias} (Gurevitch and Hedges 1999), in part because of the confounding role of mod-

erator variables (e.g., Thornhill et al. 1999). Even so, due to strong claims by Palmer (1999) that differences in sample sizes can systematically bias comparisons between classes of effect sizes, we calculated r_{bias} for each subset of moderator variables. When there was a significant effect of a moderator variable, we compared r_{bias} between classes using $Z_{diff} = (Z_1 - Z_2)/[1.06/(N_1 - 3) + 1.06/(N_2 - 3)]^{1/2}$—which is distributed as t for ∞ df (Zar 1984). This tests whether reported differences in effect size between groups are due to differences in sample sizes combined with significant r_{bias} (Palmer 1999). We also examined the significance of the covariate "sample size" in an ANCOVA where moderator variables were included as fixed factors and effect size was the dependent variable. There was no slope heterogeneity (all $P > 0.15$) and interactions between sample size and factors were removed from the final model (*Systat 8.0* 1998). We did not include interactions between factors in the model as there were too many interactions represented by only one or two cases. We excluded data on mammals and fish as there were only two samples per taxon.

We tested whether there was a correlation between year of publication and effect size (unpublished studies were treated as 2000 publications). We compared mean weighted effect sizes and r_{bias} between published and unpublished studies.

In general, our statistical procedures follow the standard procedures outlined in Hedges and Olkin (1985) and Cooper and Hedges (1994) (e.g., Møller and Thornhill 1998a; Palmer 1999). Unless otherwise stated, all statistical tests are two-tailed with alpha set at 0.05.

RESULTS

SAMPLES AS UNITS OF ANALYSIS

Measures of the relationship between survival and the expression of a trait positively correlated with male mating success were collected from 69 studies of 40 species for a total of 122 samples (Table 2). Of these relationships, 29 were negative and 93 were positive. The weighted average effect size was $r = 0.08$ (95% confidence interval: 0.07–0.10), which is significantly greater than zero ($z = 10.31$, $P < 0.00001$). The mean effect size did not differ significantly between ordinary and sec-

ondary sexual traits, but it was significantly greater for "mating rate" ($Q_B = 22.5$, $df = 2$, $P < 0.001$). It was also significantly greater for behavioral than morphological secondary sexual traits ($Q_B = 4.27$, $df = 1$, $P = 0.04$). The effect size was significantly larger for samples that involved free-ranging males than those with captive or radiotelemetry marked males ($Q_B = 13.49$, $df = 1$, $P < 0.001$). It was larger when the estimate was based on life span rather than a comparison of live and dead individuals ($Q_B = 54.79$, $df = 1$, $P < 0.001$), and for "strongly excluded" than "included" or "weakly excluded" traits ($Q_B = 49.70$, $df = 2$, $P < 0.001$). The mean effect size was significantly greater for insects/spiders than it was for birds ($Q_B = 34.83$, $df = 1$, $P < 0.001$). There was also a significant difference in weighted effect size among the three groups classified on the basis of mating type ($Q_B = 12.73$, $df = 2$, $P = 0.002$). Monogamous and lekking/active male search systems did not differ significantly, but both had significantly larger effect sizes than those for polygynous systems (both $P < 0.05$). Effect sizes and associated statistics are summarized in Table 3a.

STUDIES AS UNITS OF ANALYSIS

The effect size was positive for 55 of the 69 studies. The weighted average effect size was $r = 0.10$ (95% confidence interval: 0.08–0.12), which is significantly greater than zero ($z = 9.68$, $P < 0.00001$). The mean effect size did not differ significantly between ordinary and secondary sexual traits, but it was significantly greater for "mating rate" ($Q_B = 16.07$, $df = 2$, $P < 0.001$). It was also significantly greater for behavioral than morphological secondary sexual traits ($Q_B = 7.25$, $df = 1$, $P = 0.007$). There was no difference in the effect size for studies that involved free-ranging males compared to those with captive or radiotelemetry marked males ($Q_B = 0.59$, $df = 1$, $P = 0.44$). The effect size was significantly larger for studies where the estimate was based on life span rather than a comparison of live and dead individuals ($Q_B = 26.08$, $df = 1$, $P < 0.001$), and for "strongly excluded" compared to "included" or "weakly excluded" studies ($Q_B = 20.92$, $df = 2$, $P < 0.001$). The mean effect size was significantly greater for insects/spiders than it was for birds ($Q_B = 23.31$, $df = 1$, $P < 0.001$). There was a

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 between 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_s = 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_s = −0.011, N = 122 samples, P > 0.50; r_s = −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_s = −0.06, N = 46; insects: r_s = −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, Lillefors; $D_{max} = 0.145, 0.124,$ 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_{bias}) 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_{bias} 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_{bias} (cf. Palmer 1999). The only contrasts for which the differ-
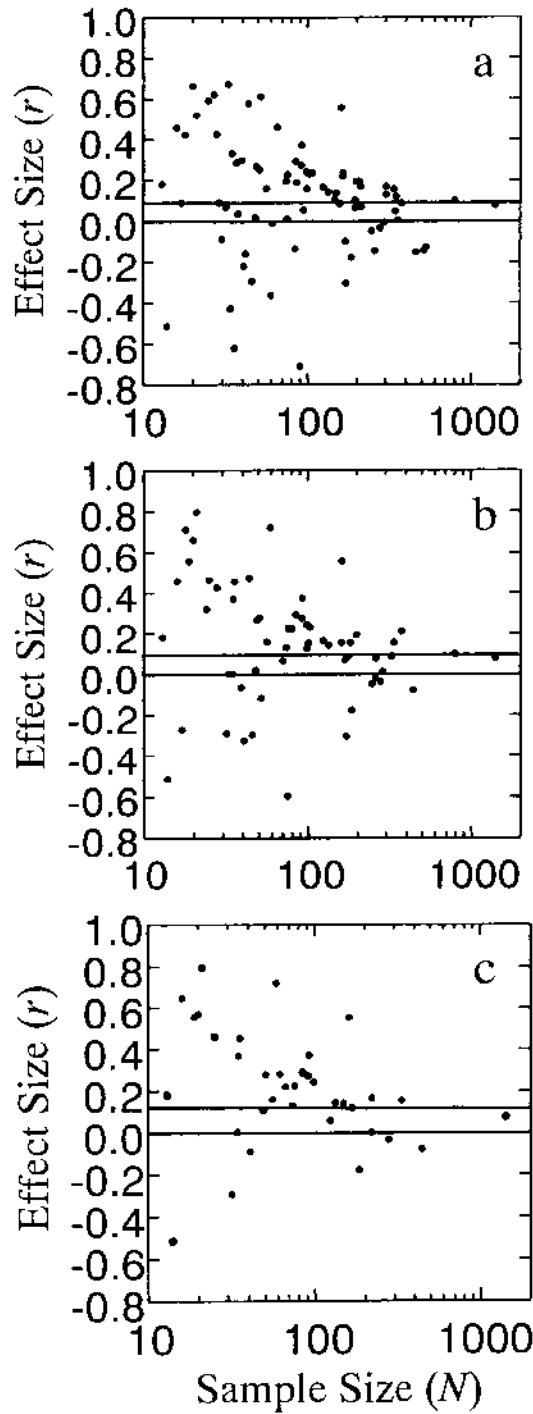
FIGURE 2.   SAMPLE SIZE AND EFFECT SIZE.

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.
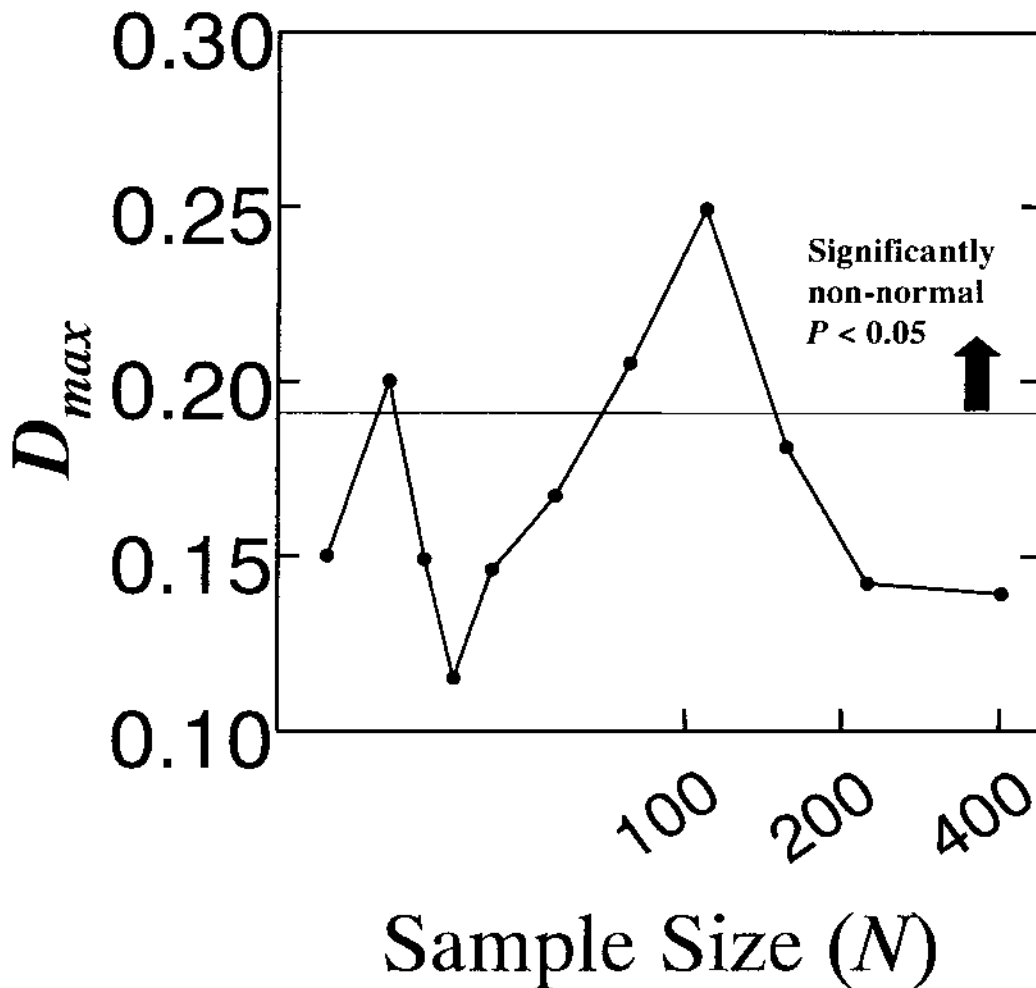
FIGURE 3. NORMALITY AND SAMPLE SIZE.

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_{bia} 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_{bia} for any other contrasts between groups with significantly different effect sizes (all $P > 0.12$). It is also worth noting that r_{bia} 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_{bia} for unpublished work (samples: $r_{bia} = -0.657$; studies: $r_{bia} = -0.429$). This suggests that negative values of r_{bia} 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
Sepsis cynipsea	Size	34 (a)	0.094	Genetic correlation with adult longevity	1
Scathophaga stercoraria	Size	997	−0.12	Size vs. age as determined by wing damage	2
Drosophila buzzatii	Size	230	0.249	Size vs. age as determined by testes stage	3
D. buzzatii	Size	151	0.138	Size vs. age as determined by testes stage	3
D. buzzatii	Size	281	0.069	Size vs. age as determined by testes stage	3
D. buzzatii	Size	82	−0.048	Size vs. age as determined by testes stage	3
Drosophila melanogaster	Size	160 (b)	0.075	Phenotypic correlation with longevity	4
D. melanogaster	Size	160 (b)	0.234	Genetic correlation with longevity	4
Pica pica	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
Geospiza fortis	Size	634 (c)	Positive	1976–1977 ($I = 0.43$ to 0.74) (d)	6
G. fortis	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 Myors 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-Danek 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 $\pm2\%$ 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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