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REVIEW ARTICLE

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How important are direct fitness benefits of sexual selection?

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Abstract Females may choose mates based on the expression of secondary sexual characters that signal direct, material fitness benefits or indirect, genetic fitness benefits. Genetic benefits are acquired in the generation subsequent to that in which mate choice is performed, and the maintenance of genetic variation in viability has been considered a theoretical problem. Consequently, the magnitude of indirect benefits has traditionally been considered to be small. Direct fitness benefits can be maintained without consideration of mechanisms sustaining genetic variability, and they have thus been equated with the default benefits acquired by choosy females. There is, however, still debate as to whether or not males should honestly advertise direct benefits such as their willingness to invest in parental care. We use meta-analysis to estimate the magnitude of direct fitness benefits in terms of fertility, fecundity and two measures of paternal care (feeding rate in birds, hatching rate in male guarding ectotherms) based on an extensive literature survey. The mean coefficients of determination weighted by sample size were 6.3%, 2.3%, 1.3% and 23.6%, respectively. This compares to a mean weighted coefficient of determination of 1.5% for genetic viability benefits in studies of sexual selection. Thus, for several fitness components, direct benefits are only slightly more important than indirect ones arising from female choice. Hatching rate in male guarding ectotherms was by far the most important direct fitness component, explaining almost a quarter of the variance. Our analysis also shows that male sexual advertisements do not always reliably signal direct fitness benefits.

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Introduction

Sexual selection arises from variance in mating success due to female choice and/or male–male competition (Darwin 1871). Females often agree to a high degree upon the ranking of potential mates with respect to their attractiveness, and these preferences generally have a significant genetic component (Bakker and Pomiankowski 1995). This consistency in mating preferences has provided an obstacle to functional explanations for the evolution and the maintenance of directional mate preferences, particularly when males do not interact with females after copulation (Taylor and Williams 1982).

Females may benefit from being choosy through direct, material benefits obtained in the present generation, or from indirect, genetic benefits for their offspring in the subsequent generation (Andersson 1994; Møller 1994a). Direct benefits may derive from enhanced fertility, fecundity or paternal care obtained from mating with preferred males, enhanced courtship feeding, higher quality of a breeding territory, anti-predator behaviour of a mate, or simply the absence of directly transmitted diseases (Hoelzer 1989; Hamilton 1990; Andersson 1994; Møller 1994a). Indirect, genetic benefits may derive from enhanced viability of offspring because of genetically based viability or parasite resistance, or from enhanced attractiveness of sons to females in the following generation (Fisher 1930; Hamilton and Zuk 1982; Heywood 1989). Genetic benefits have the inherent problem that strong directional selection will tend to drive all alleles affecting preferred traits to fixation. This creates the 'lek paradox', which contrasts strong and unanimous mate preferences with no apparent reason for such unanimity (Taylor and Williams 1982). Hamilton and Zuk (1982) suggested that host–parasite interactions might help maintain genetic variance in viability traits, on which females could continuously base their mate choice, and other mechanisms have also been proposed (see review in Charlesworth 1987; Andersson 1994). Fitness per se has a small but significant additive genetic component (Burt 1995).

Direct fitness benefits have traditionally been assumed to be of overriding importance because their effects are immediate, and do not require mechanisms that maintain genetic variance. Thus, mate choice for direct, material benefits has almost been considered a trivial case by theoreticians because this is bound to be widespread and of major importance (Møller 1994a). It is therefore unsurprising that theoretical models of direct benefit mechanisms are few and scattered (Heywood 1989; Grafen 1990; Price et al. 1993; Kirkpatrick 1996). Mate choice for direct benefits may, however, be less straightforward than once thought because the relationship between the magnitude of direct benefits and the expression of secondary sexual characters is not always positive as predicted (Møller 1994a). Burley (1986), in a classical experiment, showed that females mated to the most attractive males in fact obtained fewer direct benefits in terms of paternal care than females mated to less attractive males. Interspecific differences in this pattern have recently been attributed to mechanisms of sexual selection. Møller and Thornhill (1998) argued that species with indirect benefits show differential parental investment by females, while females mated to the more extravagantly ornamented males provide less parental care in species with direct fitness benefits. Thus, mate choice for direct fitness benefits is not clear-cut and needs assessment.

Based on our current knowledge, we can state with some confidence that both direct and indirect fitness benefits are probably at work. The remaining question is then: What is their relative magnitude? Here we attempt to estimate the magnitude of direct benefits from female choice of preferred males in terms of three fitness components: fertility, fecundity and paternal care. We then compare these estimates with that obtained for indirect, viability effects estimated in a previous study (Møller and Alatalo 1999).

Recent theoretical models have also asked whether males should reliably signal the direct benefits they offer to females (Kokko 1998). Depending on the background assumptions, signals may or may not be reliable. For example, male signals are more likely to be honest if the opportunities for polygyny are low. An empirical survey of the strength of the relationship between signalling and different direct benefits is therefore required. It can provide an indication of which assumptions are most likely to be correct; and whether this is constant or varies across taxa and types of signals.

Materials and methods

We determined the relationship between the expression of male secondary sexual characters (or other characters associated with male mating success that appear to influence female choice decisions) and four components of direct fitness for females. The relationship between the expression of secondary sexual characters and indirect components of fitness have been dealt with extensively elsewhere (Møller and Alatalo 1999). Such effects are either genetic benefits or maternal effects due to differential investment by females [the latter may also have evolved because of the presence of genetic effects (Sheldon 2000)]. First, fertility was determined as either (1) the proportion of eggs fertilised among females mated to a given male; (2) the probability that copulation led to offspring production; or (3) the proportion of eggs that hatched in species without paternal care. Since multiple mating is common among females of many species and sperm storage may occur, we can be sure that this effect is larger than estimated here. Second, we determined fecundity as (1) clutch size; (2) the number of eggs laid over a specified time interval; or (3) litter size in live-bearing species. Third, we determined male investment in parental care in birds as (1) the proportion of feeding visits to offspring relative to the total number of feeds by both male and female, or (2) the absolute feeding rate of the male. Where possible we used the latter measure because differential allocation by females may lead to an underestimate of the absolute amount a male invests in offspring. Four, we also included measures of hatching success for fish, amphibians and insects where there is paternal care but males do not feed offspring. In all these species it is clear that male parental behaviour is a major factor in the hatching success (e.g. due to fanning of eggs or attacking predators). We excluded data on fledgling production or the number of young reared to independence by birds and mammals because we did not feel we could adequately cover the huge literature that this entails. However, we are unaware of any study relating the expression of secondary sexual characters to the quality of male parental care and subsequently to offspring viability (recruitment into the following reproducing population). In addition, variation in territory quality is likely to play a major role in offspring survival because it will influence the rate at which offspring are fed. Thus, we would need to partition reproductive success into effects related to the expression of male secondary sexual characters and effects due to territory quality per se. We are unaware of any studies that have done so. We treated eggs in the nest as a sexually selected character in fish. Exclusive male parental care in insects (and fish) appears to be a sexually rather than naturally selected trait, because females should use the number of clutches or eggs a male cares for as a reliable signal of paternal intent and quality (Tallamy 2000).

We searched the literature extensively by systematically consulting the content pages (and then examining candidate papers) for each issue of *Animal Behaviour* (1993–October 2000), *Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, *Behaviour* and *Ethology* up until November 2000. For papers up to 1992 we mainly relied on the review by Andersson (1994), and for studies of paternal care the review by Møller and Thornhill (1998). We also consulted papers cited by Johnstone (1995) as studies where a correlation between a signal and either fecundity or reproductive success was examined (irrespective of whether or not a significant relationship was found). We also used three key references to 'forward search' using an electronic database (*Web of Science*). We obtained a list of all papers that had cited Knapp and Kovach (1991), Robertson (1990) and Hoelzer (1989). We then examined these for relevant data. We also examined the reference lists of these papers and identified additional candidate studies. We did not exclude any studies from the present analyses that fit our criteria, with the exception of studies that did not report a test statistic that could be used in the meta-analysis (e.g. Jones et al. 1986). Finally, we asked scientists for unpublished studies on the relationship between expression of male secondary sexual characters and direct fitness benefits. Obviously, we make no claim to have identified all relevant studies. Obtaining every possible study is an almost impossible task (Cooper and Hedges 1994). We do not believe our search method was strongly biased towards certain effect sizes. Any bias that it may have produced can be taken into future consideration, however, because our search method is clearly outlined.

We used Pearson's correlation coefficient r as a measure of effect size for the relationship between the expression of secondary sexual characters and direct fitness. If the original sources did not provide a correlation coefficient, we transformed the statistics into a correlation coefficient using the formulae for transformation given by Rosenthal (1991, p. 19). These Pearson correlation coefficients were subsequently transformed by means of Fisher's transformation to Z_r values on which all subsequent analyses were performed.

The weighting factor in a meta-analysis is the inverse of the effect size variance. Hence studies where the effect size is known with greater certainty receive a larger weighting. The asymptotic variance in Fisher's transformation of r is $V=1/(n-3)$. We therefore adjusted the mean weighted effect size at the study level using $n-3$ as the adjustment factor (Rosenthal 1991, pp. 27–28). Although fixed-effect models have been used more often in biology, mixed or random-effect models are preferable (Gurevitch and Hedges 1999). A fixed-effect model assumes that all studies share a common true effect size and that the observed variation is only due to sampling error. This is obviously a false assumption for behavioural ecology. Studies employ different techniques (e.g. experimental and observational approaches) and various measures of outcome. There is also likely to be variation due to genuine differences in effect size among taxa (Arnqvist and Nilsson 2000). We cannot fully control for these sources of variation so we ran mixed-effect models using the software package MetaWin 2.0 (Rosenberg et al. 2000).

The mean weighted effect size is $Z_r=\Sigma\ (n_j-3)Z_{rj}\ /\Sigma\ (n_j-3)$, where Z_{rj} is the z-transformed effect size for analysis unit j. We consider each reference given in the tables to represent a separate study. Where there were several samples per study, we first calculated the weighted mean effect size per study, and the mean sample size for that study. We then analysed the results at the study level. For the analysis of effect size at the species level we used the Z_r values directly if only one study was available. If several studies were available, we first calculated the mean weighted effect size Z_r for that species. We then used the arithmetic mean sample size for studies of that species to determine the appropriate adjustment factor at the species level. For each level of analysis the mean weighted Z_r values was tested against the null hypothesis that it did not differ significantly from zero (Rosenthal 1991). To do this we determined whether the 95% confidence intervals for the mean weighted Z_r value overlapped zero using resampling methods that do not require that the data fit parametric assumptions. Confidence intervals were generated via a bias-corrected bootstrapping approach with 999 iterations (Rosenberg et al. 2000).

We subsequently calculated an estimate of heterogeneity in effect sizes among analysis units using the formula provided by Rosenthal (1991, pp. 73–74): $Q_T=\sqrt{(n_j-3)(Z_{rj}-\text{mean } Z_r)^2}$, which has a χ^2 distribution with $K-1$ degrees of freedom, where K is the number of analysis units (e. g. studies, species). If there was significant heterogeneity, we then tested for variation among groups of studies (e.g. taxa) by examining the significance of the Q_M statistic. This tests whether effect size differs significantly between groups. There were seven species where studies with effect sizes involving both grouping factors were recorded. In these cases, we used the weighted mean effect for each grouping factor per species when analysing the influence of grouping factors. When calculating the overall weighted mean effect, however, only one data point per species was used.

The samples included in a meta-analysis may represent a biased sample if the probability of publication is influenced by a specific result (Hunter and Schmidt 1990), such as a statistically non-significant result. We attempted to test for any bias in the published literature by: (1) inspection of the funnel graph relating effect size to sample size (Light and Pillemer 1984); (2) determining the correlation between sample size and effect size (Begg and Mazumdar 1994); (3) using the 'trim and fill' method of Duvall and Tweedie (2000) to estimate the number of 'missing studies' that could be due to publication bias. We then tested the robustness of our findings by recalculating weighted mean effects sizes after including hypothetical 'missing studies'; (4) determining the relationship between effect size and year of publication (Gontard-Danek and Møller 1999; Palmer 1999; Vøllestad et al. 1999); (5) testing for a difference in effect size between published and unpublished studies; and (6) calculating the fail-safe number of studies, X, needed to nullify an effect at the 5% level, following Rosenthal (1991, p. 104) as:

$$X = (\sum Zj)^2/2.706 - K \quad \text{(a)}$$

where $Z_j=Z_{rj}\ \sqrt{(n_j-3)}$ and K is the number of analysis units. The fail-safe number estimates the number of studies that are unknown to us as a result either of journals rejecting papers with null results or scientists not writing up papers on null results. A different way of viewing the fail-safe number is that it provides an estimate of the number of future studies needed to change a significant effect to a non-significant one. Further details concerning publication bias testing can be found in Møller and Jennions (2001). Unless otherwise stated, all tests are two-tailed with the α level of significance set at 5%.

Results

Fertility

Effect sizes for the relationship between fertility and the expression of a sexually selected trait were collected from 26 studies of 24 species (Table 1). Of these studies, 21 of 26 were positive (binomial test, $P<0.0001$). The weighted average effect size was $r=0.237$ (95% CI: 0.083–0.436). There was significant heterogeneity in effect size ($Q_T=50.11$, $df=25$, $P=0.002$), but the mean effect size did not differ significantly between frogs, insects and birds ($Q_M=3.24$, $df=2$, $P=0.408$). At the species level, 21 of 24 effects were positive (binomial test, $P<0.0001$). The weighted average effect size was $r=0.251$ (95% CI: 0.066–0.448). Again, there was significant heterogeneity in effect size ($Q_T=41.86$, $df=23$, $P=0.009$), but the mean effect size did not differ significantly between frogs, insects and birds ($Q_M=2.60$, $df=2$, $P=0.459$). The unweighted study and species mean effect sizes were $r=0.198$ (95% CI: 0.060–0.336) and 0.205 (95% CI: 0.059–0.351), respectively.

Fecundity

Effect sizes for the relationship between fecundity and the expression of a sexually selected trait were collected from 76 studies of 51 species (Table 2). Of these studies, 62 of 76 were positive (binomial test, $P<0.001$). The weighted average effect size was $r=0.164$ (95% CI: 0.108–0.220). There was significant heterogeneity in effect size ($Q_T=102.2$, $df=75$, $P=0.020$), but the mean effect size did not differ significantly between birds and insects ($Q_M=0.001$, $df=1$, $P=0.984$). For insects, the mean effect size did not differ between studies where the trait was a nuptial gift versus an aspect of the male's phenotype ($Q_M=0.380$, $df=1$, $P=0.563$). At the species level, 39 of 51 effects were positive (binomial test, $P<0.001$). The weighted average effect size was $r=0.151$ (95% CI: 0.080–0.223). Again, there was significant heterogeneity in effect size ($Q_T=70.17$, $df=50$, $P=0.030$), but the mean effect size did not differ significantly between birds and insects ($Q_M=0.004$, $df=1$, $P=0.957$). For insects, the mean effect size did not differ between species where the trait was a nuptial gift versus an aspect of the male's phenotype ($Q_M=0.604$, $df=1$, $P=0.491$). The unweighted study and species mean effect sizes were 0.186 (95% CI: 0.125–0.247) and 0.172 (95% CI: 0.097–0.246).

Table 1 Effect sizes found for fertility in studies of sexual selection. Taxa are amphibians (*A*), birds (*B*), fish (*F*), insects (*I*) and mammals (*M*). The *test statistic* is the test statistic used in the original source for calculating effect size. *r* is Pearson's product–moment correlation coefficient used as an estimate of the effect size. *n* is sample size

Species	Taxa	Character	Test statistic	*r*	*n*	Reference
Bufo americanus	A	Body size (Ratio)	r_s=–0.29	–0.169	19	Kruse (1981)
Bufo bufo	A	Body size (Ratio)	*r*=0.379	0.379	41	Davies and Halliday (1977)
Bufo bufo	A	Body size (Ratio)	*r*=–0.17	–0.17	76	Höglund and Robertson (1987)
Bufo cognatus	A	Body size (Ratio)	*F*=0.51	–0.125	34	Krupa (1988)
Clethrionomys glareolus	M	Urine marking	χ^2=1.77	0.172	60	Horne (1998)
Coelopa frigida	I	Body size	χ^2=11.8	0.176	379	Crocker and Day (1987)
Danaus plexippus	I	Spermatophore size	*t*=1.79	0.364	23	Oberhauser (1989)
Falco sparverius	B	Colour	r_s=0.225	0.225	52	Wiehn (1997)
Galerucella nymphaeae	I	Body size	*Z*=0.06	0.008	61	Parri et al. (1997)
Geospiza fortis	B	Plumage colour	r_s=0.14	0.14	44	Price (1984)
Gryllus bimaculatus	I	Chosen vs small male	contrast *F*=0.66	–0.138	35	Simmons (1987)
Hirundo rustica	B	Tail length	*r*=0.028	0.028	800	Møller (1994a)
Hirundo rustica	B	Song	*r*=0.048	0.048	291	A.P. Møller (unpublished)
Hyperolius marmoratus	A	Paired vs unpaired	Hedge's *g*	0.374	26	Grafe (1997)
Hyphessobrycon pulchripinnis	F	No of matings (1 vs 10)	*P*<0.01	0.505	26	Nakatsuru and Kramer (1982)
Mus musculus	M	Preferred	χ^2=7.60	0.291	90	Drickamer et al. (2000)
Nezara viridula	I	Inexperienced vs rejected	*P*<0.001	0.264	155	McLain (1998)
Nezara viridula	I	Accepted vs rejected	*P*<0.001	0.222	220	McLain (1998)
Oenanthe leucura	B	Stones carried	*r*=0.021	0.021	51	A.P. Møller et al. (unpublished)
Ololygon rubra	A	Body size (Ratio)	*P*<0.0001	0.95	62	Bourne (1993)
Ololygon rubra	A	Body size (Ratio)	*P*<0.0001	0.95	20	Bourne (1993)
Papilio machaon	I	Spermatophore size	*t*=1.525	0.529	7	Svärd and Wicklund (1991)
Pavo cristatus	B	Train length	*r*=0.28	0.28	8	Petrie and Williams (1993)
Physalaemus pustulosus	A	Body size	*F*=1.4	0.147	68	Ryan (1983)
Rana temporaria	A	Body size (Ratio)	*r*=0.202	0.202	116	Gibbons and McCarthy (1986)
Taeniopygia guttata	B	Leg bands	*P*<0.1	0.359	21	Burley (1986)
Taeniopygia guttata	B	Leg bands	*U*=83.5	0.562	21	Burley (1986)
Thalassoma bifasciatum	F	Mating success	*r*=–0.718	–0.718	33	Warner et al. (1995)
Uperolia laevigata	A	Body size difference	$P=6\times10^{-8}$	0.916	35	Robertson (1990)

Paternal care: feeding in birds

Effect sizes for the relationship between feeding effort and the expression of a sexually selected trait were collected from 39 studies of 26 bird species (Table 3). Of these studies, 29 of 39 were positive (binomial test, $P<0.001$). The weighted average effect size was $r=0.099$ (95% CI: –0.055–0.238), which does not differ significantly from zero. There was no significant heterogeneity in effect size ($Q_T=41.84$, $df=38$, $P=0.310$), and the mean effect size did not differ significantly between measures based on the proportion of visits by males, or the absolute feeding rate of males ($Q_M=0.109$, $df=1$, $P=0.765$). At the species level, 18 of 26 effects were positive (binomial test, $P<0.001$). The weighted average effect size was $r=0.112$ (95% CI: –0.080–0.293), which does not differ significantly from zero. Again there was no significant heterogeneity in effect size ($Q_T=25.35$, $df=25$, $P=0.440$), and the mean effect size did not differ significantly between measures based on the proportion of visits by males, or the absolute feeding rate of males ($Q_M=0.037$, $df=1$, $P=0.852$). The unweighted study and species mean effect sizes were 0.125 (95% CI: –0.011–0.263) and 0.136 (95% CI: –0.045–0.317). Again, neither unweighted effect is significantly greater than zero.

Paternal care: hatching success in ectotherms with male guarding

Effect sizes for the relationship between hatching success and the expression of a sexually selected trait were collected from 26 studies of 20 species (Table 4). Of these studies, 25 of 26 were positive (binomial test, $P<0.0001$). The weighted average effect size was $r=0.477$ (95% CI: 0.373–0.584). Overall, there was no significant heterogeneity in effect sizes ($Q_T=26.76$, $df=25$, $P=0.368$). For fish, the mean effect size did not differ significantly between studies where the preferred trait was eggs in the nest or some aspect of male phenotype (display or morphology) ($Q_M=0.166$, $df=1$, $P=0.692$). At the species level, all 20 effects were positive (binomial test, $P<0.0001$). The weighted average effect size was $r=0.468$ (95% CI: 0.368–0.556). Again there was no overall significant heterogeneity in effect sizes ($Q_T=15.77$, $df=19$, $P=0.673$). For fish, the mean effect size did not differ significantly between species where the preferred trait was eggs in the nest or some aspect of male phenotype (display or morphology) ($Q_M=0.06$, $df=1$, $P=0.811$). The unweighted study and species mean effect sizes were 0.467 (95% CI: 0.159–0.368) and 0.480 (95% CI: 0.367–0.593).

Mean effect sizes and 95% confidence intervals for the various sub-divisions of the data-set are presented in Table 5.

Table 2 Effect sizes found for fecundity in studies of sexual selection. Taxa are amphibians (*A*), birds (*B*), fish (*F*), insects (*I*) and mammals (*M*). Nuptial gift was present (*Y*) or not (*N*). The *test statistic* is the test statistic used in the original source for calculating effect size. *r* is Pearson's product-moment correlation coefficient used as an estimate of the effect size. *n* is sample size

Species	Taxa	Nuptial gift	Character	Test statistic	*r*	*n*	Reference
Aleochara curtula	I	N	Mating status =pheromone	$P<0.05$	0.318	38	Peschke (1987)
Aleochara curtula	I	N	Mating status =pheromone	$P<0.05$	0.476	17	Peschke (1987)
Ceratitis capitata	I	N	Pheromone	$F=9.7$	–0.316	83	Whittier and Kaneshiro (1995)
Clethrionomys glareolus	M	–	Pheromone	$r=0.069$	0.069	37	Horne (1998)
Clethrionomys glareolus	M	–	Mating rank	$P=0.099$	–0.206	73	Oksanen et al. (1999)
Coelopa frigida	I	N	Choice vs no choice	Hedge's *g*	0.15	38	Crocker and Day (1987)
Coelopa frigida	I	N	Choice vs no choice	Hedge's *g*	0.015	19	Crocker and Day (1987)
Coelopa frigida	I	N	Body size	$r=0.022$	0.022	59	A. Gilburn (personal communication)
Coelopa vanduzeei	I	N	Body size	$r=–0.209$	–0.209	53	A. Gilburn (personal communication)
Coelopa nebularum	I	N	Body size	$r=0.136$	0.136	60	A. Gilburn (personal communication)
Cyrtodiopsis dalmanni	I	N	Eye width	$r_s=0.22$	0.22	31	Wilkinson and Reillo (1994)
Danaus plexippus	I	Y	Spermatophore size	$P=0.386$	–0.185	22	Oberhauser (1989)
Dectitus verrucivorus	I	Y	Spermatophore weight	Partial $r= –0.019$	–0.019	46	Wedell and Arak (1989)
Dectitus verrucivorus	I	Y	Spermatophore weight	Partial $r= –0.170$	–0.17	28	Wedell and Arak (1989)
Diapreps abbreviatus	I	N	Body size	$t=0.257$	0.048	30	Harari et al. (1999)
Drosophila grimshawi	I	N	High vs Low protein diet	$t=2.03$	0.252	63	Droney (1996)
Drosophila melanogaster	I	N	Body size	$t=2.52$	–0.37	42	Pitnick (1991)
Drosophila melanogaster	I	N	Body size	$F=4.24$	–0.246	68	Pitnick (1991)
Drosophila melanogaster	I	N	Body size	$F=0.09$	–0.033	87	Pitnick (1991)
Drosophila montana	I	N	Song frequency	$t=0.039/0.061$	0.064	100	Hoikkala et al. (1998)
Drosophila subobscura	I	Y	Feeding drop	$\chi^2=6.06$	0.301	67	Steele (1986)
Drosophila subobscura	I	Y	Feeding drop	$\chi^2=0.06$	0.03	67	Steele (1986)
Emberiza citrinella	B	–	Colour intensity	$r=0.050$	0.05	32	Sundberg (1995)
Emberiza citrinella	B	–	Colour	$r=–0.050$	–0.05	61	Sundberg (1995)
Ephestia elutella	I	N	Body size	$F=6.7$	0.312	64	Phelan and Baker (1986)
Falco sparverius	B	–	Colour	$r_s=0.190$	0.19	57	Wiehn (1997)
Falco tinnunculus	B	–	Tail	$r_s=–0.03$	–0.03	66	Palokangas et al. (1992)
Falco tinnunculus	B	–	Brightness score	$P=0.001$	0.349	89	Tolonen and Korpimäki (1994)
Falco tinnunculus	B	–	Brightness score	$r_s=0.54$	0.54	25	Palokangas et al. (1994)
Ficedula albicollis	B	–	Patch size	$F=3.7$	0.043	2018	Qvarnström et al. (2000)
Ficedula hypoleuca	B	–	Colour	Hedge's *g*	0.056	10	Røskaft and Järvi (1983)
Galerucella nymphaeae	I	N	Body size	$t=1.13$	–0.144	61	Parri et al. (1997)
Gryllus bimaculatus	I	N	Chosen vs small male	contrast $F=4.96$	0.357	35	Simmons (1987)
Harpobittacus nigriceps	I	N	Body size	$P=0.035$	0.47	20	Thornhill (1983)
Harpobittacus nigriceps	I	N	Body size	$P=0.02$	0.52	20	Thornhill (1983)
Hirundo rustica	B	–	Tail length	$F=8.03$	0.442	36	Møller (1992)
Hirundo rustica	B	–	Tail asymmetry	$r=0.061$	0.061	261	Møller (1992)
Hirundo rustica	B	–	Tail asymmetry	$F=0.04$	0.037	35	Møller (1993)
Hirundo rustica	B	–	Tail length	$r=0.40$	0.4	55	de Lope and Møller (1993)
Hirundo rustica	B	–	Tail spot	Contrast $F=0.98$	0.136	54	Kose and Møller (1999)
Hirundo rustica	B	–	Tail spot	Contrast $F=7.44$	0.363	51	Kose et al. (1999)
Hirundo rustica	B	–	Tail asymmetry	$r=0.115$	0.115	108	Møller and Cadée (2000)
Hirundo rustica	B	–	UV	$r_s=–0.298, –0.168$	–0.234	83	Perrier (2000)
Hirundo rustica	B	–	Tail length	$r=0.05$	0.05	710	A.P. Møller (unpublished)
Hirundo rustica	B	–	Song	$r=0.074$	0.074	291	A.P. Møller (unpublished)
Ips pini	I	N	Body size	$F=0.56$	0.087	75	Robertson and Roitberg (1998)
Ips pini	I	N	Body size	$F=4.07$	0.238	70	Robertson (1998)
Kawanaphila nartee	I	Y	Spermatophore (yes/no)	$F=14.48$	0.525	40	Simmons (1990a)
Luscinia svecica	B	–	Colour rings	$P=0.18$	–0.23	34	Rohde et al. (1999)
Lutzomyia longipalpis	I	N	Preferred	r=0.10	0.1	186	Jones et al. (1998)
Nauphoeta cinerea	I	N	Dominance	$r=0.067$	0.067	164	Moore (1994)
Nezara viridula	I	N	Antenna length	$t=3.0$	0.469	37	McLain (1998)
Nezara viridula	I	N	Antenna length	$t=0.28$	0.041	49	McLain (1998)
Nezara viridula	I	N	Inexperienced vs rejected	$P=0.762$	0.024	157	McLain (1998)

Table 2 (continued)

Species	Taxa	Nuptial gift	Character	Test statistic	*r*	*n*	Reference
Nezara viridula	I	N	Accepted vs rejected	P=0.847	0.013	232	McLain (1998)
Nezara viridula	I	N	Mating success	r=0.38	0.38	26	McLain and Marsh (1990)
Nezara viridula	I	N	Mating success	r=0.52	0.52	28	McLain and Marsh (1990)
Nezara viridula	I	N	Body size (difference)	r=0.31	0.31	44	McLain et al. (1990)
Nezara viridula	I	N	Body size (difference)	r=–0.15	–0.15	44	McLain et al. (1990)
Nezara viridula	I	N	Body size	r=0.28	0.28	165	McLain et al. (1990)
Nymphicus hollandicus	B	–	Natural vs forced pair	Hedge's *g*	0.226	15	Yamamoto et al. (1989)
Oecanthus nigricornis	I	Y	Attractiveness	r=0.37	0.37	34	Brown (1997)
Oenanthe leucura	B	–	Stones carried	r=0.300	0.3	37	Moreno et al. (1994)
Oenanthe leucura	B	–	Stones carried	F=0.19, t=0.00	0.042	31	Soler et al. (1996)
Oenanthe leucura	B	–	Stones carried	r=–0.031	–0.031	51	A.P. Møller et al. (unpublished)
Ophioblennius atlanticus	F	–	Body size	r=0.35	0.35	41	Côte and Hunte (1989)
Papilio machaon	I	Y	Spermatophore size	t=0.306	0.088	13	Svärd and Wicklund (1991)
Parus major	B	–	Colour	r=0.264	0.264	36	Norris (1993)
Parus major	B	–	Colour	r=–0.110	–0.11	606	Lemel (1993)
Parus montanus	B	–	Song rate	r_s=0.05	0.05	53	Welling et al. (1997)
Passer domesticus	B	–	Colour	r= –0.13, –0.48	–0.305	41	Møller (1989)
Passer domesticus	B	–	Colour	Hedge's g	0.075	58	Veiga (1993)
Passer domesticus	B	–	Colour	r=0.35	0.35	14	Kimball (1995)
Passer domesticus	B	–	Smaller badge	R^2=0.02	0.141	28	Griffith et al. (1999)
Pavo cristatus	B	–	Train length	r=0.832	0.832	8	Petrie and Williams (1993)
Phasianus colchicus	B	–	Spur length	r=0.36	0.36	45	von Schantz et al. (1989)
Phasianus colchicus	B	–	Spur length	r=0.76	0.76	18	Göransson et al. (1990)
Pieris napi	I	Y	Spermatophore size	contrast F=47.96	0.853	21	Karlsson (1998)
Poecilimon veluchianus	I	Y	Spermatophore (yes/no)	F=3.78	–0.334	34	Reinhold and Heller (1993)
Polygona c-album	I	N	Plant type	F=0.518	0.148	28	Wedell (1996)
Requena verticalis	I	Y	Spermatophore size	Contrast F=1.48	0.241	31	Gwynne (1988)
Sepsis cynipsea	I	N	Body size	r=0.15, 0.32	0.235	38	Blanckenhorn et al. (1998)
Stator limbatus	I	N	Body size	r=0.5	0.5	38	Fox et al. (1995)
Stator limbatus	I	N	Body size	r=0.632	0.632	30	Fox et al. (1995)
Stator limbatus	I	N	Body size	P<0.001	0.444	55	Savalli and Fox (1998)
Stator limbatus	I	N	Body size	P=0.001	0.378	76	Savalli and Fox (1998)
Taeniopygia guttata	B	–	Leg bands	Contrast F=0.375	0.167	14	Burley (1986)
Taeniopygia guttata	B	–	Leg bands	Z=3.11	0.372	70	Zann (1994)
Taeniopygia guttata	B	–	Leg bands	Contrast F=6.92	0.64	18	Swaddle (1996)
Taeniopygia guttata	B	–	Attractiveness	t=1.98	0.397	22	Balzer and Williams (1998)
Tenebrio molitor	I	N	Infection intensity	F=12.74	0.54	32	Worden et al. (2000)
Tetrao tetrix	B	–	Copulatory success rank	P<0.01	0.463	31	Rintamäki et al. (1998)
Upupa epops	B	–	Strophe length	P<0.05	0.462	18	Martín-Vivaldi et al. (1999)
Valenciennea longipinnis	F	–	Body size	Partial r=0.23	0.23	9	Takegaki and Nakazono (1999)

Publication bias

First, we plotted the relationship between effect size and sample size (Light and Pillemer 1984). Inspection of plots suggested funnel-shaped relationships (Fig. 1). The variance in effect size for cases with a sample size below the median was larger than the variance for cases with a sample size above the median for all four fitness components at the study level (Variance ratio tests: fertility: $F_{12,12}$=31.14, P<0.0001; fecundity: $F_{37,37}$=2.82, P=0.001; parental care in birds: $F_{18,19}$=2.09, P=0.06; hatching success in guarding ectotherms: $F_{12,12}$=2.64, P=0.053). At the species level the same was true (fertility: $F_{11,11}$=56.54, P<0.0001; fecundity: $F_{24,25}$=3.21, P=0.0026; hatching success in guarding ectotherms: $F_{9,9}$=5.25, P=0.011), except for parental care in birds ($F_{12,12}$=1.14, P=0.412). The distribution of effect sizes did not differ significantly from normality at the study and species level for fecundity and parental care in birds or hatching success in guarding ectotherms at the

Table 3 Effect sizes found for feeding by male birds in studies of sexual selection. Taxa are amphibians (*A*), birds (*B*), fish (*F*), insects (*I*) and mammals (*M*). Feeding rate was either absolute male feeding rate (*A*) or proportion of male feeds (*P*). The *test statistic* is the test statistic used in the original source for calculating effect size. *r* is Pearson's product-moment correlation coefficient used as an estimate of the effect size. *n* is sample size

Species	Feeding measure	Character	Test statistic	*r*	*n*	Reference
Acrocephalus schoenobaenus	A	Song flights	r=0.019	0.019	21	Buchanan and Catchpole (2000)
Acrocephalus schoenobaenus	A	Song repertoire	F=5.63	0.488	20	Buchanan and Catchpole (2000)
Agelaius phoeniceus	A	Display	r_s=0.69	0.69	39	Searcy and Yasukawa (1981)
Agelaius phoeniceus	–	Display	P=0.04	0.53	15	Eckert and Weatherhead (1987)
Agelaius phoeniceus	–	Display	P=0.40	0.266	10	Eckert and Weatherhead (1987)
Cardinalis cardinalis	A	Plumage colour	P=0.12	0.377	17	Linville et al. (1998)
Cardinalis cardinalis	A	Colour	P=0.12	0.377	17	Linville et al. (1998)
Carpodacus mexicanus	P	Colour	r_s=0.42	0.42	32	Hill (1991)
Dendroica petechia	A	Colour	r_s=–0.54	–0.54	11	Studd and Robertson (1985)
Dendroica petechia	A	Colour	r_s=–0.60	–0.6	27	Studd and Robertson (1985)
Dendroica petechia	A	Colour	r_s=0.01	0.01	16	Lozano and Lemon (1996)
Emberiza citrinella	A	Colour	r=–0.65	–0.65	18	Sundberg and Larsson (1994)
Falco sparverius	A	Colour	r_s=0.42	0.42	20	Wiehn (1997)
Falco tinnunculus	A	Tail	r_s=–0.10	–0.1	38	Palokangas et al. (1992)
Falco tinnunculus	A	Brightness score	r=0.16	0.16	33	Tolonen and Korpimäki (1994)
Falco tinnunculus	A	Colour	r_s=0.46	0.46	23	Palokangas et al. (1994)
Ficedula albicollis	P	Colour	F=2.02	–0.214	47	Qvarnström (1997)
Ficedula hypoleuca	P	Colour	t=1.17	0.14	70	Lundberg and Alatalo (1992)
Ficedula hypoleuca	A	Colour	Hedge's *g*	0.15	22	Sætre et al. (1995)
Ficedula hypoleuca	A	Colour	Hedge's *g*	–0.057	22	Sætre et al. (1995)
Ficedula hypoleuca	A	Song repertoire	r=–0.02, 0.09	0.027	27	Rinden et al. (2000)
Ficedula hypoleuca	A	Colour	r=0.07	0.087	36	Rinden et al. (2000)
Ficedula hypoleuca	A	Song repertoire	r=0.09	0.027	21	Rinden et al. (2000)
Ficedula hypoleuca	A	Colour	r=0.11	0.087	27	Rinden et al. (2000)
Ficedula hypoleuca	A	Colour	F=5.326	0.27	74	Sanz (2001)
Geospiza fortis	–	Colour	r=0.35	0.35	20	Price (1984)
Guiraca caerulea	A	Colour	Mean r=0.115	0.115	15	Keyser and Hill (2000)
Guiraca caerulea	A	Colour	Mean r=0.49	0.49	9	Keyser and Hill (2000)
Hirundo rustica	P	Tail length	r=0.12	0.12	16	Smith and Montgomerie (1992)
Hirundo rustica	A	Tail length	r=0.048	0.048	167	Møller (1992)
Hirundo rustica	A	Tail length	P<0.05	–0.358	30	de Lope and Møller (1993)
Hirundo rustica	A	Tail asymmetry	F=17.88	–0.481	69	Møller (1994b)
Hirundo rustica	A	Tail length	F=30.94	–0.536	69	Møller (1994b)
Hirundo rustica	A	UV	r_s=0.246, –0.105	0.073	23	Perrier (2000)
Larus argentatus	A	Courtship feeding	r=0.735	0.735	6	Niebuhr (1981)
Luscinia svecica	P	Colour	r=0.12	0.12	21	Reinsborg (1995)
Luscinia svecica	A	Leg bands	P=0.36	0.245	14	Rohde et al. (1999)
Luscinia svecica	A	Leg bands	P=0.72	0.092	15	Rohde et al. (1999)
Oenanthe leucura	A	Stones carried	r=0.56	0.56	13	Moreno et al. (1994)
Panurus biarmicus	A	Beard	r=–0.73	–0.73	48	Hoi and Hoi-Leitner (1997)
Parus major	A	Colour	F=0.09	0.047	41	Norris (1990)
Parus montanus	A	Song rate	r_s=0.59	0.59	16	Welling et al. (1997)
Passer domesticus	P	Colour	r=0.49	0.49	13	Kimball (1995)
Saxicola torquata	P	Song rate	r=0.59	0.59	13	Greig-Smith (1982)
Sterna hirundo	A	Courtship feeding	r=0.57	0.57	9	Nisbet (1973)
Sterna hirundo	A	Courtship feeding	r_s=0.92	0.92	7	Wiggins and Morris (1986)
Sturnus vulgaris	A	Repertoire size	r_s=–0.318	–0.318	15	Mountjoy and Lemon (1997)
Sylvia atricapilla	A	Song	r_s=–0.65	–0.65	12	Hoi-Leitner et al. (1993)
Taeniopygia guttata	P	Leg bands	g=–0.46	–0.46	31	Burley (1988)
Upupa epops	A	Strophe length	τ=0.56	0.56	9	Martín-Vivaldi et al. (1999)
Upupa epops	A	Strophe length	τ=0.26	–0.26	11	Martín-Vivaldi et al. (1999)

study level (Kolomogorov-Smirnov tests, Lilliefors, all P>0.08). Distributions did, however, differ from normality for hatching success in guarding ectotherms at the species level (D_{max}=0.196, P=0.042) and fertility at both the study and species level (D_{max}=0.201, P=0.008 and D_{max}=0.200, P=0.014). Overall, the distribution of effect sizes was slightly skewed towards more positive effect sizes at smaller sample sizes.

Second, we determined the correlation between sample size and effect size (Begg and Mazumdar 1994). The effect size decreased significantly with increasing sample size for hatching success in fish where the male trait was morphological or behavioural, and for fecundity (both P<0.05). More generally, 9 of 10 mutually exclusive sub-divisions of the data showed a decrease in effect size as sample size increased. This skew could be

Table 4 Effect sizes found for hatching success in male guarding ectotherms in studies of sexual selection. Taxa are amphibians (*A*), birds (*B*), fish (*F*), insects (*I*) and mammals (*M*). Eggs were in nest (*Y*) or not (*N*). The *test statistic* is the test statistic used in the original source for calculating effect size. *r* is Pearson's product–moment correlation coefficient used as an estimate of the effect size, *n* is sample size

Species	Taxa	Eggs in nest	Character	Test statistic	*r*	*n*	Reference
Aidablennius sphynx	F	Y	Eggs in nest	F=45.5	0.698	49	Kraak (1996)
Amblyglyphidodon leucogaster	F	Y	Eggs in nest	Contrast F=0.204	0.021	461	Goulet (1998)
Chrysiptera cyanea	F	Y	Eggs in nest	r=0.46	0.46	138	Gronell (1989)
Cichlasoma citrinellum	F	N	Body size	t=0.523	0.228	12	Rogers (1995)
Cottus bairdi	F	N	Body size	r_s=0.91	0.91	6	Downhower and Brown (1980)
Cottus gobio	F	Y	Partial brood lose	χ^2=7.98	0.399	50	Bisazza and Marconato (1988)
Etheostoma flabellare	F	Y	Eggs in nest	t=3.89	0.529	41	Lindström and Sargent (1997)
Etheostoma nigrum	F	N	Defensiveness	t=2.12	0.384	27	Grant and Colgan (1983)
Gasterosteus aculeatus	F	Y	Eggs in nest	χ^2=1.81	–0.196	41	Belles-Isles et al. (1990)
Gasterosteus aculeatus	F	N	Pectoral fin	r=0.34	0.34	18	Künzler and Bakker (2000)
Gasterosteus aculeatus	F	N	Redness (food-deprived)	F=0.10	0.087	14	Candolin (2000)
Gasterosteus aculeatus	F	N	Redness (fed)	F=14.3	0.724	14	Candolin (2000)
Gasterosteus aculeatus	F	N	Redness (difference)	r=0.141, 0.529	0.335	18	Candolin (2000)
Ips pini	I	–	Body size	r=0.522	0.522	32	Reid and Roitberg (1985)
Oxylebius pictus	F	Y	Eggs in nest	r_s=0.423	0.423	184	DeMartini (1987)
Parasitizopus armaticeps	I	–	Body size	Hedge's g	0.361	143	Rasa et al. (1998)
Pimephales promelas	F	Y	Eggs in nest	t=4.77	0.847	10	Sargent (1988)
Pimephales promelas	F	Y	Eggs in nest	t=3.34	0.763	9	Sargent (1988)
Pomatoschistus microps	F	Y	Eggs in nest	t=2.549	0.648	11	Lindström (1998)
Pomatoschistus microps	F	N	Small nest entrance	P>0.70	0.065	35	Jones and Reynolds (1999)
Pomatoschistus minutus	F	Y	Eggs in nest	r_s=0.62	0.62	46	Forsgren et al. (1996)
Pomatoschistus minutus	F	N	Preferred	P<0.01	0.341	57	Forsgren (1997)
Rana catesbeiana	A	-	Body size	r=0.61	0.61	26	Howard (1978)
Spinachia spinachia	F	N	Preferred	t=0.31	0.137	12	Östlund and Ahnesjö (1998)
Spinachia spinachia	F	N	Body shake frequency	r=0.566	0.566	17	Östlund and Ahnesjö (1998)
Stegastes partitus	F	N	Display	r=0.943	0.943	18	Knapp and Kovach (1991)
Stegastes partitus	F	N	Display	r=0.33	0.33	8	Knapp and Warner (1991)
Stegastes partitus	F	Y	Previous brood success	P=0.01	0.549	22	Knapp (1993)
Stegastes rectifraenum	F	Y	Eggs in nest	G=6.55	0.518	44	Petersen and Marchetti (1989)
Valenciennea longipinnis	F	N	Body size	Partial r=0.78	0.78	9	Takegaki and Nakazono (1999)

due to publication bias or reflect rational design of studies such as the difference in sample size between experimental and observational studies (Møller and Jennions 2001).

Third, we used the 'trim and fill' method of Duvall and Tweedie (2000) to estimate the number of 'missing studies' that could be due to publication bias. Using the *L* estimator, this identified 8, 13, 4 and 3 missing studies, respectively, at the species level for the fitness components fertility, fecundity, feeding in birds, and hatching success in guarding ectotherms. We therefore recalculated the weighted means including these 'missing' cases. The recalculated effect sizes were 0.441 (95% CI: 0.248–0.595) for fertility, 0.051 (95% CI: –0.027–0.136) for fecundity, 0.015 (95% CI: –0.184–0.211) for parental care in birds and 0.432 (0.321–0.534) for hatching success in guarding ectotherms. These values differed from the initially calculated mean effect sizes by +0.190, –0.100, –0.097 and –0.036, respectively.

Fourth, we determined the relationship between effect size and year of publication. There were no significant correlations between year of publication and effect size for each of the four fitness components (all P>0.05). This was true even when year effects were analysed separately as a moderator variable (explanatory variable) in the meta-analysis.

Fifth, we tested for a difference in effect size between unpublished and published studies. There was no significant difference for studies of feeding in birds or fertility effects (Mann-Whitney tests: n=36,3, P=0.460; U=35, n=24,2, P=0.290, respectively). Sample sizes for unpublished studies were very small so these tests have little statistical power. There was, however, a significantly smaller effect size for unpublished than published studies of fecundity (Mann-Whitney U=421.5, n=68,8, P=0.011).

Finally, we calculated the fail-safe number of studies needed to nullify an effect at the 5% level following Rosenthal (1991). By convention, a fail-safe number of $5n$+10 indicates a robust result. The fail-safe number was not robust for fertility effects in birds and insects, fecundity effects in insects with nuptial gifts, or feeding effects in birds (Table 5).

Table 5 Mean effect size, 95% confidence intervals, estimate of correlation between sample size and effect size (*R(Begg)*), fail-safe number, and correlation between effect size and year (*Year*) for different fitness components and levels of analysis, *n* is sample size

Fitness component	Taxa	*n*	Mean *r*	95% CI	*R*(Begg)	Fail-safe	Year number
Species level of analysis							
Fertility	All taxa	24	0.251	0.066–0.448	–0.168	601*	
	Birds	6	0.181	0.072–0.320	–0.543	8	
	Frogs	8	0.453	0.056–0.797	–0.167	208*	
	Insects	6	0.168	0.013–0.329	–0.029	23	
Fecundity	All taxa	51	0.151	0.080–0.223	–0.357 **	923*	
	Birds	17	0.15	0.052–0.259	–0.531 *	97*	
	Insects (All)	31	0.155	0.056–0.259	–0.330	344*	
	Insects (Nuptial gifts)	9	0.223	–0.013–0.498	–0.017	34	
	Insects (Other traits)	22	0.139	0.042–0.230	–0.486 *	141*	
Feeding rate	All	26	0.112	–0.080–0.293	–0.275	4	
	Feeding rate	20	0.099	–0.123–0.329	–0.247	0	
	Proportion of feeds	7	0.141	–0.155–0.389	–0.270	0	
Offspring survival	All taxa	20	0.468	0.368–0.556	–0.134	1,319*	
	Fish (All)	17	0.468	0.337–0.561	–0.093	877*	
	Fish (Eggs in nest)	12	0.455	0.293–0.574	0.081	569*	
	Fish (Other traits)	9	0.489	0.315–0.718	–0.717*	116*	
Study level of analysis							
Fertility	All taxa	26	0.237	0.083–0.436	–0.227	651*	–0.03
	Birds	6	0.154	0.061–0.288	–0.543	8	–0.61
	Frogs	9	0.424	0.062–0.744	–0.084	222*	0.32
	Insects	7	0.164	–0.001–0.318	–0.071	28	0.38
Fecundity	All taxa	76	0.164	0.108–0.220	–0.342**	2,510*	–0.13
	Birds	36	0.17	0.097–0.258	–0.323	599*	–0.11
	Insects (All)	36	0.168	0.081–0.257	–0.332*	577*	–0.11
	Insects (Nuptial gifts)	9	0.223	–0.035–0.484	0.017	34	0.49
	Insects (Other traits)	27	0.159	0.072–0.243	–0.453*	303*	–0.34
Feeding rate	All	39	0.101	–0.055–0.238	–0.244	30	–0.18
	Feeding rate	30	0.073	–0.099–0.255	–0.199	0	–0.03
	Proportion of feeds	7	0.136	–0.158–0.393	–0.270	0	–0.09
Offspring survival	All taxa	26	0.477	0.373–0.584	–0.063	1,977*	–0.33
	Fish (All)	23	0.479	0.350–0.598	0.006	1,427*	–0.31
	Fish (Eggs in nest)	12	0.458	0.285–0.583	0.081	569*	0.05
	Fish (Other traits)	11	0.512	0.314–0.737	–0.579	184*	–0.59

*$P<0.05$, **$P<0.01$

Discussion

In this paper we have attempted to determine the relative magnitude of four different kinds of direct, material benefits obtained by females during their mate choice. For fertility, fecundity, feeding in birds and paternal care in ectotherms we found mean effect sizes adjusted for sample size of 0.251, 0.151, 0.114 and 0.468, respectively (Fig. 2). This implies that 6.3%, 2.3%, 1.3% and 23.6% of the variance in these direct fitness components are associated with the expression of preferred male traits. A recent meta-analysis of the importance of indirect, viability effects in studies of sexual selection, measured as the correlation between expression of secondary sexual characters and survival of offspring, showed that the weighted mean effect was $r=0.122$. Thus about 1.5% of the variance in offspring viability could be explained by differences in the expression of chosen male sexual characters (Møller and Alatalo 1999; Fig. 2). Direct comparison of the magnitude of direct and indirect effects is obviously based on an assumption of similarity in the quality of the underlying data. The effect sizes of the present study and that of Møller and Alatalo (1999) are robust, as measured by the fail-safe number, and after controlling for a number of potentially confounding variables (this study; A.P. Møller and M.D. Jennions, unpublished data). Other measures of publication bias used in this study also suggest that the effect size estimates are robust.

While the effects of direct and indirect benefits may not be directly comparable because they are based on different fitness components, it seems unlikely that a very weak relationship can translate into a strong fitness relationship at a later stage in the life cycle. Aside from the direct benefits of greater hatching success in ectotherms, the direct benefits from female choice due to greater fecundity, fertility or male feeding of offspring are fairly small. Thus, there is strong evidence of taxon-specific differences in the relative importance of direct

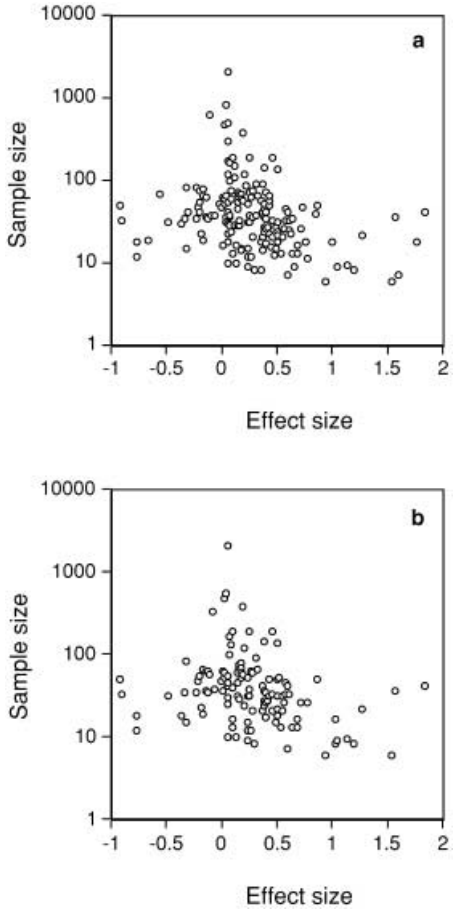

Fig. 1 Funnel plots at (a) the study level of analysis and (b) the species level of analysis. Effect size is the z-transformed Pearson product-moment correlation coefficient

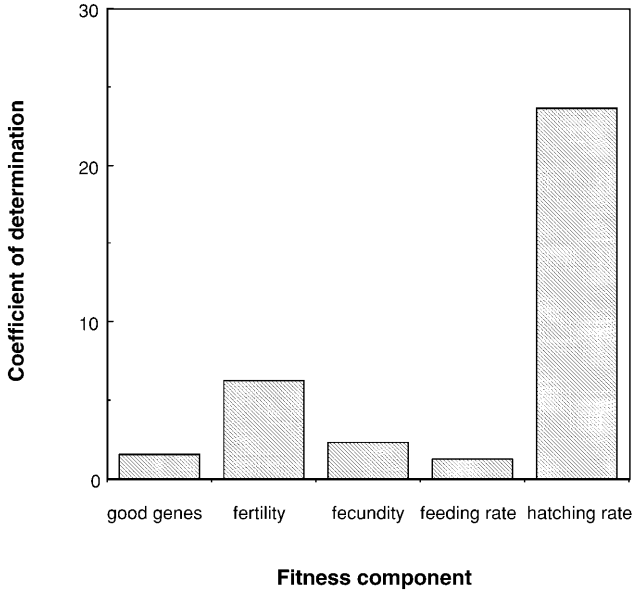

Fig. 2 Coefficient of determination (r^2) for indirect fitness benefits (from Møller and Alatalo 1999) and direct fitness benefits (from the present study) of sexual selection

fitness benefits. Male sexual traits only predict an extra 1–5% of the variation in these three fitness components relative to indirect fitness gains. Kirkpatrick and Barton (1997) developed a theoretical model which suggested that the absolute force of indirect selection on mating preferences is small. They noted, however, that the question of the relative strength of this force compared to that from direct selection on mating preferences is an unknown empirical question. Our findings suggest that many previous papers may have overestimated the difference in the relative strength of these two forces.

Here we have assumed throughout that any correlation between the expression of secondary sexual characters and fertility, fecundity or paternal care can be entirely attributed to non-genetic sire effects. This is obviously not the case. First, studies of infertility in humans have shown that only a fraction can be attributed to males, while a larger proportion can be attributed to women (Khatamee 1988; WHO 1990). Many clinical cases of infertility in humans are caused by infections and sexually transmitted diseases. However, multiple mating and sperm storage may lead to an underestimate of variation in male fertility.

Second, and perhaps most important, the magnitude of these direct effects can partly be attributed to the effects of assortative mating, where females of poor fertility, fecundity or parental care become mated to males with small secondary sexual characters. Maternal effects may therefore lead to the direct benefits provided by males being overestimated. In some cases, such as that of black grouse, *Tetrao tetrix*, reported by Rintamäki et al. (1998), it seems highly unlikely that the change in fecundity was due to a non-genetic male effect. There is no obvious mechanism whereby males can increase female fecundity. We cannot exclude these cases from the analysis, however, because subtle material benefits in species where males only transfer sperm (and females were experimentally assigned to males) have been detected (e.g. McLain 1998).

Third, females may differentially allocate resources to reproduction and invest more heavily when mated to an attractive male (for a review, see Sheldon 2000). This could increase both the rate of production and survival of offspring, again leading us to overestimate the direct benefits the male provides. In studies of feeding behaviour, however, differential allocation may increase the relative investment of the female to that of the male. This could lead to an underestimate of the direct benefits the male provides when the analysis is based on the proportion of feeding visits by males rather than on absolute feeding rate. In our analysis, however, we found no difference in effect size between cases based on proportional or absolute measures of offspring feeding by males.

Fourth, a male's genetic contribution, either due to general 'viability genes' or genetic complimentary with the female, may increase offspring viability (Zeh and Zeh 1996; Møller and Alatalo 1999). This may increase the number of offspring born or eggs laid if females reabsorb or abort inferior zygotes. If weak offspring disap-

pear shortly after birth then researchers may be less likely to count them. Misidentification of eggs as unfertilised may also arise when failure occurs prior to cell division, or within the first few mitotic divisions. Olsson and Shine (1997) discuss the difficulties of distinguishing infertility from other explanations. Again, hidden genetic benefits could lead to an overestimate of the direct benefits a male provides.

Fifth, in insects there is often a short-term increase in egg production immediately after mating due to males transferring chemicals that promote oviposition. These chemicals often act in a dose-dependent manner and larger males are likely to transfer greater amounts (Eberhard 1996). Although we treat this short-term change as an increase in fecundity, there may be no net effect on the lifetime reproductive output of a female (for a review, see Arnqvist and Nilsson 2000). Again, this is likely to lead to an overestimate of the net direct benefit of mating with a more attractive male. In at least some cases, larger doses of chemicals promoting oviposition may have negative effects on female longevity and no actual effect on the average rate of egg production.

For the five reasons outlined above we can therefore conclude that the direct fitness benefits of sexual selection are probably overestimated in the present study.

We have only considered four different kinds of direct fitness benefits. Fertility, fecundity and aspects of paternal care are, however, the direct fitness benefits most likely to be widespread and of general importance. Of course, there are potentially numerous other direct fitness benefits of mate choice including territory quality of males, courtship feeding (including nutrients or defensive chemicals transferred in spermatophores or seminal fluid) (e.g. Ivy et al. 1999; Heller et al. 2000), and the absence of directly transmitted parasites and diseases (e.g. Simmons 1990b). While these effects may be of importance in particular systems, the correlation between male sexual signals and these benefits remains unknown.

Arnqvist and Nilsson (2000) recently provided an interesting complementary meta-analysis. They examined the effect of multiple mating on female fecundity, fertility and lifespan by comparing singly versus multiply mated females. Females were randomly assigned to each group. The mean correlations (expressed as Pearson's *r*) were 0.218 (95% CI, 0.127, 0.431) for egg production, 0.450 (0.484, 0.390) for offspring production and 0.06 (–0.173, 0.172) for longevity. Clearly, females gained direct benefits from remating. These correspond to explaining 4.8%, 20.3% and 0.4% of the variation in the fitness components (correlations were generally lower for species without nuptial feeding, suggesting smaller benefits and even costs to remating). These beneficial effects are, however, due to mating with two or more and usually several males rather than a single male. For female choice *among* males during a single mating to have the same effect then the difference in resources provided by a chosen male would have to be more than twice that provided by a randomly selected male. Such extreme variation in male quality seems unlikely. Indeed, if that was the case, we would have expected to locate more studies where authors correlated fecundity gains with the size of male nuptial gifts. Most of the papers that we encountered, however, used the single versus multiple mating approach to assess the benefits of nuptial gifts (e.g. Butlin et al. 1987; Rutowski et al. 1987). This strongly suggests that most workers implictly assume that variation among males in the size of nuptial gifts will have effects on female fitness that are too small to be detected with standard sample sizes.

The present study also has important implications for power analyses and determination of necessary sample sizes for experiments. Empiricists will typically perform a study and then test the null hypothesis of no difference between treatments. A power analysis will be based on the presumed magnitude of the "true" effect. In the absence of information, most biologists present results for a medium-size effect of r=0.30 as defined by Cohen (1988). Given that the mean effect sizes estimated in the present study were r =0.114, 0.151, 0.251, and 0.468, this assumption is only justified for studies looking at direct benefits due to parental care in ectotherms. Whether effects of this magnitude are generally the case in ecological and evolutionary studies is not clear. In a survey of 36 published meta-analyses in biology, A.P. Møller and M.D. Jennions (unpublished data) found that the mean variance explained is about 5%. Thus, in the absence of information, an average effect size of r=0.2 is probably more appropriate. If this is the true effect size, a sample size of 200 is needed to detect a significant relationship with α set to 5% with 80% power. If the effect size is r=0.1, as in several of the studies presented in Tables 1 –4, then a sample of more than 800 individuals is required. Thus, empiricists will need to work very hard to safely conclude that there is "no small or intermediate effect" when examining the hypothesis that male secondary traits are honest signals of male parental quality.

Should male signals reveal their parenting ability? Models of the evolution of signals of parenting ability have reached conflicting conclusions (Price et al. 1993; Fitzpatrick et al. 1995; Kokko 1998). Fitzpatrick et al. (1995) suggested that signals should have no cost in terms of reducing parenting ability. However, this conclusion is at conflict with costs being implicit in the evolution of reliable signals (Grafen 1990). Price et al. (1993) concluded that signals might be so costly that they reduced the amount of care and hence the fecundity of females mated to ornamented males. Kokko (1998) considered that males either signal their parenting ability honestly or reduce their investment in parental care when attractive due to differential parental investment by their mates. The option adopted depends on the marginal gains from multiple mating. If opportunities for polygyny or extra-pair paternity are minimal, this should result in honest advertisement of male parental care. However, if opportunities for multiple mating are large, differential parental investment should evolve. Møller and Thornhill (1998) and Møller (2000) provided comparative, empiri-

cal support for these predictions. The present meta-analyses suggest that to obtain reliable information on male food provisioning of offspring, the expression of male secondary sexual characters is generally not very useful.

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References

Andersson M (1994) Sexual selection. Princeton University Press, Princeton, N.J.

Arnqvist G, Nilsson T (2000) The evolution of polyandry: multiple mating and female fitness in insects. Anim Behav 60:145–164

Bakker TCM, Pomiankowski A (1995) The genetic basis of female mate preferences. J Evol Biol 8:129–171

Balzer AL, Williams TD (1998) Do female zebra finches vary primary reproductive effort in relation to male attractiveness? Behaviour 135:297–309

Begg CB, Mazumdar M (1994) Operating characteristics of a rank correlation test for publication bias. Biometrics 50:1088–1101

Belles-Isles J-C, Cloutier D, FitzGerald GJ (1990) Female cannibalism and male courtship tactics in three-spined sticklebacks. Behav Ecol Sociobiol 26:363–368

Bisazza A, Marconato A (1988) Female mate choice, male–male competition and parental care in the river bullhead *Cottus gobio* L. (Pisces, Cottiidae). Anim Behav 36:1352–1360

Blanckenhorn WU, Reusch T, Mühlhäuser C (1998) Fluctuating asymmetry, body size and sexual selection in the dung fly *Sepsis cynipsea*: testing the good genes assumptions and predictions. J Evol Biol 11:735–753

Bourne GR (1993) Proximate costs and benefits of mate acquisition at leks of the frog *Ololygon rubra*. Anim Behav 45: 1051–1059

Brown WD (1997) Courtship feeding in tree crickets increases insemination and female reproductive life span. Anim Behav 54:1369–1382

Buchanan KL, Catchpole CK (2000) Song as an indicator of male parental effort in the sedge warbler. Proc R Soc Lond B 267:321–326

Burley N (1986) Sexual selection for aesthetic traits in species with biparental care. Am Nat 127:415–445

Burley N (1988) The differential-allocation hypothesis: an experimental test. Am Nat 132:611–628

Burt A (1995) The evolution of fitness. Evolution 49:1–8

Butlin RK, Woodhatch CW, Hewitt GM (1987) Male spermatophore investment increases female fecundity in a grasshopper. Evolution 41:221–225

Candolin U (2000) Increased signalling effort when survival prospects decrease: male–male competition ensures honesty. Anim Behav 60:417–422

Charlesworth B (1987) The heritability of fitness. In: Bradbury JW, Andersson MB (eds) Sexual selection: testing the alternatives. Wiley, New York, pp. 21–40

Cohen J (1988) Statistical power analysis for the behavioral sciences, 2nd edn. Erlbaum, Hillsdale, N.J.

Cooper H, Hedges LV (eds) (1994) The handbook of research synthesis. Russell Sage Foundation, New York

Côte IM, Hunte W (1989) Male and female mate choice in the redlipped blenny: why bigger is better. Anim Behav 38:78–88

Crocker G, Day T (1987) An advantage to mate choice in the seaweed fly *Coelopa frigida*. Behav Ecol Sociobiol 20:295–301

Darwin C (1871) The descent of man, and selection in relation to sex. Murray, London

Davies NB, Halliday TR (1977) Optimal mate selection in the toad *Bufo bufo*. Nature 269:56–58

DeMartini EE (1987) Paternal defence, cannibalism and polygamy: factors influencing the reproductive success of painted greenling (Pisces: Hexagrammidae). Anim Behav 35:1145–1158

Downhower JF, Brown L (1980) Mate preferences of female mottled sculpins, *Cottus bairdi*. Anim Behav 28:728–734

Drickamer LC, Gowaty PA, Holmes CM (2000) Free female mate choice affects reproductive success and offspring viability and performance. Anim Behav 59:371–378

Droney DC (1996) Environmental influences on male courtship and implications for female choice in a lekking Hawaiian *Drosophila*. Anim Behav 51:821–830

Duvall S, Tweedie R (2000) Trim and fill: a simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. Biometrics 56:455–463

Eberhard WG (1996) Female control: sexual selection by cryptic female choice. Princeton University Press, Princeton, N.J.

Eckert CG, Weatherhead PJ (1987) Male characteristics, parental quality and the study of mate choice in the red-winged blackbird (*Agelaius phoeniceus*). Behav Ecol Sociobiol 20:35–42

Fisher RA (1930) The genetical theory of natural selection. Clarendon, Oxford

Fitzpatrick S, Berglund A, Rosenqvist G (1995) Ornaments or offspring – costs to reproductive success restrict sexual selection processes. Biol J Linn Soc 55:521–526

Forsgren E (1997) Female sand gobies prefer good fathers over dominant males. Proc R Soc Lond B 264:1283–1286

Forsgren E, Karlsson A, Kvarnemo C (1996) Female sandgobies gain direct benefits by choosing males with eggs in their nests. Behav Ecol Sociobiol 39:91–96

Fox CW, McLennan LA, Mousseau TA (1995) Male body size affects female lifetime reproductive success in a seed beetle. Anim Behav 50:281–284

Gibbons MM, McCarthy TK (1986) The reproductive output of frogs *Rana temporaria* (L.) with particular reference to body size and age. J Zool (Lond) 209:579–593

Gontard-Danek M-C, Møller AP (1999) The strength of sexual selection: a meta-analysis of bird studies. Behav Ecol 10:476–486

Göransson GT, Schantz T von, Fröberg I, Helgée A, Witzell H (1990) Male characteristics, viability and harem size in the pheasant, *Phasianus colchicus*. Anim Behav 40:89–104

Goulet D (1998) Spawning success in the damselfish *Amblyglyphidodon leucogaster*: the influence of eggs in the nest. Anim Behav 55:651–664

Grafe TU (1997) Costs and benefits of mate choice in the lek-breeding reed frog, *Hyperolius marmoratus*. Anim Behav 53:1103–1117

Grafen A (1990) Sexual selection unhandicapped by the Fisher process. J Theor Biol 144:475–416

Grant JWA, Colgan PW (1983) Reproductive success and mate choice in the johnny darter *Etheostoma nigrum* (Pisces: Percidae). Can J Zool 61:437–446

Greig-Smith PW (1982) Song rates and parental care by individual male stonechats (*Saxicola torquata*). Anim Behav 30:245–252

Griffith SC, Owens IPF, Burke T (1999) Female choice and annual reproductive success favour less-ornamented male house sparrows. Proc R Soc Lond B 266:765–770

Gronell AM (1989) Visiting behaviour by females of the sexually dichromatic damselfish, *Chrysiptera cyanea* (Teleostei, Pomacentridae): a probable method of assessing male quality. Ethology 81:89–122

Gurevitch J, Hedges LV (1999) Statistical issues in ecological meta-analyses. Ecology 80:1142–1149

Gwynne DT (1988) Courtship feeding and the fitness of female katydids (Orthoptera: Tettigoniidae). Evolution 42:545–555

Hamilton WD (1990) Mate choice near and far. Am Zool 30:341–352

Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? Science 218:384–387

Harari AR, Handler AM, Landolt PJ (1999) Size-assortative mating, male choice and female choice in the curculoinid beetle *Diapreps abbreviatus*. Anim Behav 58:1191–1200

Heller K-G, Fleischmann P, Lutz-Röder A (2000) Carotenoids in the spermatophores of bushcrickets (Orthoptera: Ephippigerinae) Proc R Soc Lond B 267:1905–1908
Heywood JS (1989) Sexual selection by the handicap mechanism. Evolution 43:1387–1397
Hill GE (1991) Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339
Hoelzer GA (1989) The good parent process of sexual selection. Anim Behav 38:1067–1078
Höglund J, Robertson JGM (1987) Random mating by size in a population of common toads (*Bufo bufo*). Amphibia-Reptilia 8:321–330
Hoi H, Hoi-Leitner M (1997) An alternative route to coloniality in the bearded tit: females pursue extra-pair fertilizations. Behav Ecol 8:113–119
Hoikkala A, Aspi J, Suvanto L (1998) Male courtship song frequency as an indicator of male genetic quality in an insect species, *Drosophila montana*. Proc R Soc Lond B 265:503–508
Hoi-Leitner M, Nechtelberger H, Dittami J (1993) The relationship between individual differences in male song frequency and parental care in blackcaps. Behaviour 126:1–12
Horne TJ (1998) Evolution of female choice in the bank vole. PhD thesis, Department of Biological and Environmental Science, University of Jyväskylä, Finland
Howard RD (1978) The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32:850–871
Hunter JE, Schmidt FL (1990) Methods of meta-analysis: Correcting error and bias in research findings. Russell Sage, Beverly Hills
Ivy TM, Johnson JC, Sakaluk SK (1999) Hydration benefits to courtship feeding in crickets. Proc R Soc Lond B 266: 1523–1527
Johnstone RA (1995) Sexual selection, honest advertising and the handicap principle: reviewing the evidence. Biol Rev Camb Philos Soc 70:1–65
Jones JC, Reynolds JD (1999) Influence of oxygen stress on female choice for male nest structure in the common goby. Anim Behav 57:189–196
Jones KN, Odendaal FJ, Ehrlich PR (1986) Evidence against the spermatophore as paternal investment in checkerspot butterflies (Euphydras: Nymphalidae). Am Midl Nat 116:1–6
Jones TM, Balmford A, Quinnell RJ (1998) Fisherian flies: the benefits of female choice in a lekking sandfly. Proc R Soc Lond B 264:1651–1657
Karlsson B (1998) Nuptial gifts, resource budgets and reproductive output in a polyandrous butterfly. Ecology 79:2931–2940
Keyser AJ, Hill GE (2000) Structurally based plumage coloration is an honest signal of male quality in male blue grosbeaks. Behav Ecol 11:202–209
Khatamee MA (1988) Infertility: a preventable epidemic. Int J Fertil 33:246–250
Kimball R (1995) Sexual selection in house sparrows, *Passer domesticus*. PhD thesis, University of New Mexico, Albuquerque, N.M.
Kirkpatrick M (1996) Good genes and direct selection in the evolution of mating preferences. Evolution 50:2125–2140
Kirkpatrick M, Barton NH (1997) The strength of indirect selection on female mating preferences. Proc Natl Acad Sci USA 94:1282–1286
Knapp RA (1993) The influence of egg survival on the subsequent nest fidelity of female bicolor damselfish, *Stegastes partitus*. Anim Behav 46:111–121
Knapp RA, Kovach JT (1991) Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes partitus*. Behav Ecol 2:295–300
Knapp RA, Warner R (1991) Male parental care and female choice in the bicolored damselfish, *Stegastes partitus*: bigger is not always better. Anim Behav 41:747–756
Kokko H (1998) Should advertising parental care be honest? Proc R Soc Lond B 265:1871–1878
Kose M, Møller AP (1999) Sexual selection, feather breakage and parasites: The importance of white spots in the tail of the barn swallow. Behav Ecol Sociobiol 45:430–436
Kose M, Mänd R, Møller AP (1999) Sexual selection for white tail spots in the barn swallow in relation to habitat choice by feather lice. Anim Behav 58:1201–1205
Kraak SBM (1996) Female preferences and filial cannibalism in *Aidablennius sphynx* (Teleostei, Blenniidae): a combined field and laboratory study. Behav Process 36:85–98
Krupa JJ (1988) Fertilization efficiency in the Great Plains toad (*Bufo cognatus*). Copeia 1988:800–802
Kruse KC (1981) Mating success, fertilization potential, and male body size in the American toad (*Bufo americanus*). Herpetologica 37:228–233
Künzler R, Bakker TCM (2000) Pectoral fins and paternal quality in sticklebacks. Proc R Soc Lond B 267:999–1004
Lemel J (1993) Evolutionary and ecological perspectives of status signalling in the great tit (*Parus major* L.). PhD thesis, Department of Zoology, University of Gothenburg, Gothenburg, Sweden
Light RJ, Pillemer DB (1984) Summing up: the science of reviewing research. Harvard University Press, Cambridge, Mass.
Lindström K (1998) Effects of costs and benefits of brood care on filial cannibalism in the sand goby. Behav Ecol Sociobiol 42:101–106
Lindström K, Sargent RC (1997) Food access, brood size and filial cannibalism in the fantailed darter, *Etheostoma flabellare*. Behav Ecol Sociobiol 40:107–110
Linville SU, Breitwisch R, Schilling AJ (1998) Plumage brightness as an indicator of parental care in northern cardinals. Anim Behav 55:119–127
Lope F de, Møller AP (1993) Female reproductive effort depends on the degree of ornamentation of their mates. Evolution 47:1152–1160
Lozano GA, Lemon RE (1996) Male plumage, paternal care and reproductive success in yellow warblers, *Dendroica petechia*. Anim Behav 51:265–272
Lundberg A, Alatalo RV (1992) The pied flycatcher. Poyser, London
Martín-Vivaldi M, Palomino JJ, Soler M, Soler JJ (1999) Song strophe-length and reproductive success in a non-passerine bird, the hoopoe *Upupa epops*. Ibis 141:670–679
McLain DK (1998) Non-genetic benefits of mate choice: fecundity enhancement and sexy sons. Anim Behav 55:1191–1201
McLain DK, Marsh NB (1990) Male copulatory success: heritability and relationship to mate fecundity in the southern green stinkbug, *Nezara viridula* (Hemiptera: Pentamidae). Heredity 64:161–167
McLain DK, Lanier DL, Marsh NB (1990) Effects of female size, mate size and number of copulations on fecundity, fertility and longevity of *Nezara viridula*. Ann Entomol Soc Am 83:1130–1136
Møller AP (1989) Natural and sexual selection on a plumage signal of status and on morphology in house sparrows, *Passer domesticus*. J Evol Biol 2:125–140
Møller AP (1992) Sexual selection in the monogamous barn swallow (*Hirundo rustica*). II. Mechanisms of sexual selection. J Evol Biol 5:603–624
Møller AP (1993) Female preference for apparently symmetrical male sexual ornaments in the barn swallow *Hirundo rustica*. Behav Ecol Sociobiol 32:371–376
Møller AP (1994a) Sexual selection and the barn swallow. Oxford University Press, Oxford
Møller AP (1994b) Symmetrical male sexual ornaments, paternal care, and offspring quality. Behav Ecol 5:188–194
Møller AP (2000) Male parental care, female reproductive success, and extrapair paternity. Behav Ecol 11:161–168
Møller AP, Alatalo RV (1999) Good genes effects in sexual selection. Proc R Soc Lond B 266:85–91
Møller AP, Cadée N (2000) Within-individual variation in asymmetry and performance of the barn swallow *Hirundo rustica*. In: Cadée N, Aspets écologiques de la résistance contre le stress chez l'hirondelle de cheminée *Hirundo rustica*. PhD thesis, Laboratoire d'Ecologie, Université Pierre et Marie Curie, Paris, France

Møller AP, Jennions MD (2001) Testing and adjusting for publication bias. Trends Ecol Evol 16:580–586
Møller AP, Thornhill R (1998) Male parental care, differential parental investment by females, and sexual selection. Anim Behav 55:1507–1515
Moore AJ (1994) Genetic evidence for the 'good genes' process of sexual selection. Behav Ecol Sociobiol 35:235–241
Moreno J, Soler M, Møller AP, Lindén M (1994) The function of stone carrying in the black wheatear, *Oenanthe leucura*. Anim Behav 47:1297–1309
Mountjoy DJ, Lemon RE (1997) Male song complexity and parental care in the European starling. Behaviour 134:661–675
Nakatsuru K, Kramer DL (1982) Is sperm cheap? Limited male fertility and female choice in the lemon tetra (Pisces, Characidae). Science 216:753–755
Niebuhr V (1981) An investigation of courtship feeding in herring gulls, *Larus argentatus*. Ibis 123:218–223
Nisbet ICT (1973) Courtship feeding, egg-size and breeding success in common terns. Nature 241:141–142
Norris KJ (1990) Female choice and the quality of parental care in the great tit *Parus major*. Behav Ecol Sociobiol 27:275–281
Norris KJ (1993) Heritable variation in a plumage indicator of viability in male great tits *Parus major*. Nature 362:537–539
Oberhauser KS (1989) Effects of spermatophores on male and female monarch butterfly reproductive success. Behav Ecol Sociobiol 25:237–246
Oksanen TA, Alatalo RV, Horne TJ, Koskela E, Mappes J, Mappes T (1999) Maternal effort and male quality in the bank vole, *Clethrionomys glareolus*. Proc R Soc Lond B 266:1495–1499
Olsson M, Shine R (1997) Advantages of multiple mating to females: a test of the infertility hypothesis using lizards. Evolution 51:1684–1688
Östlund S, Ahnesjö I (1998) Female fifteen-spined sticklebacks prefer better fathers. Anim Behav 56:1177–1183
Palmer AR (1999) Detecting publication bias in meta-analyses: a case study of fluctuating asymmetry and sexual selection. Am Nat 154:220–233
Palokangas P, Alatalo RV, Korpimäki E (1992) Female choice in the kestrel under different availability of mating options. Anim Behav 43:659–665
Palokangas P, Korpimäki E, Hakkarainen H, Huhta E, Tolonen P, Alatalo RV (1994) Female kestrels gain reproductive success by choosing brightly ornamented males. Anim Behav 47:443–448
Parri S, Alatalo RV, Mappes J (1997) Do female leaf beetles *Galerucella nymphaeae* choose their mates and does it matter? Oecologia 114:127–132
Perrier C (2000) Réflectance du plumage dans les ultraviolets et sélection sexuelle chez l'Hirondelle des cheminées (*Hirundo rustica*). MSc thesis, Laboratoire d'Ecologie, Université Pierre et Marie Curie, Paris
Peschke K (1987) Male aggression, female mimicry and female choice in the rove beetle *Aleochara curtula* (Coleoptera, Staphylinidae). Ethology 75:265–284
Petersen CW, Marchetti K (1989) Filial cannibalism in the Cortez damselfish *Stegastes rectifraenum*. Evolution 43:158–168
Petrie M, Williams A (1993) Peahens lay more eggs for peacocks with larger trains. Proc R Soc Lond B 251:127–131
Phelan PL, Baker TC (1986) Male-size-related courtship success and intersexual selection in the tobacco moth, *Ephestia elutella*. Experientia 42:1291–1293
Pitnick S (1991) Male size influences mate fecundity and remating interval in *Drosophila melanogaster*. Anim Behav 41:735–746
Price T, Schluter D, Heckman NE (1993) Sexual selection when the female directly benefits. Biol J Linn Soc 48:187–211
Price TD (1984) Sexual selection on body size, territory and plumage variables in a population of Darwin's finches. Evolution 38:327–341
Qvarnström A (1997) Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. Proc R Soc Lond B 264:1225–1231
Qvarnström A, Forsgren E (1998) Should females prefer dominant males? Trends Ecol Evol 13:498–501
Qvarnström A, Pärt T, Sheldon BC (2000) Adaptive plasticity in mate preference linked to differences in reproductive effort. Nature 405:344–347
Rasa OAE, Bisch S, Teicher T (1998) Female mate choice in a subsocial beetle: male phenotype correlates with helping potential and offspring survival. Anim Behav 56:1213–1220
Reid ML, Roitberg BD (1985) Effects of body size on investment in individual broods by male pine engravers (Coleoptera: Scolytidae). Can J Zool 73:1396–1401
Reinhold K, Heller K-G (1993) The ultimate function of nuptial feeding in the bushcricket *Poecilimon veluchianus* (Orthoptera, Tettigoniidae: Phaneropterinae). Behav Ecol Sociobiol 32:55–60
Reinsborg T (1995) Feeding rate and reproductive success in the bluethroat *Luscinia s. svecica*. MSc thesis, University of Trondheim, Trondheim, Norway
Rinden H, Lampe HM, Slagsvold T, Espmark YO (2000) Song quality does not indicate male parental abilities in the pied flycatcher *Ficedula hypoleuca*. Behaviour 137:809–823
Rintamäki PT, Lundberg A, Alatalo RV, Höglund J (1998) Assortative mating and female clutch investment in black grouse. Anim Behav 56:1399–1403
Robertson IC (1998) Paternal care enhances male reproductive success in pine engraver beetles. Anim Behav 56:595–602
Robertson IC, Roitberg BD (1998) Duration of parental care in pine engraver beetles: why do larger males care less? Behav Ecol Sociobiol 43:379–386
Robertson JGM (1990) Female choice increases fertilization success in the Australian frog, *Uperolia laevigata*. Anim Behav 39:639–645
Rogers W (1995) Female choice predicts the best father in a biparental fish, the midas cichlid (*Cichlasoma citrinellum*). Ethology 100:230–241
Rohde PA, Johnsen A, Lifjeld JT (1999) Parental care and sexual selection in the bluethroat, *Luscinia s. svecica*: A field-experimental test of the differential allocation hypothesis. Ethology 105:651–663
Rosenberg MS, Adams DC, Gurevitch J (2000) Metawin: statistical software for meta-analysis, version 2.0. Sinauer, Sunderland, Mass.
Rosenthal R (1991) Meta-analytic procedures for social research. Sage, New York
Røskaft E, Järvi T (1983) Male plumage colour and mate choice of female pied flycatchers *Ficedula hypoleuca*. Ibis 125:396–400
Rutowski RL, Gilchrist GW, Terkanian B (1987) Female butterflies mated with recently mated males show reduced reproductive output. Behav Ecol Sociobiol 20:319–322
Ryan MJ (1983) Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. Evolution 39:261–272
Sætre G-P, Forsnes T, Slagsvold T (1995) Food provisioning in the pied flycatcher: do females gain direct benefits from choosing bright-coloured males? J Anim Ecol 64:21–30
Sanz JJ (2001) Experimentally reduced male attractiveness increases parental care in the pied flycatcher *Ficedula hypoleuca*. Behav Ecol 12:171–176
Sargent RC (1988) Paternal care and egg survival both increase with clutch size in the fathead minnow *Pimephales promelas*. Behav Ecol Sociobiol 23:33–37
Savalli UM, Fox CW (1998) Sexual selection and the fitness consequences of male body size in the seed beetle *Strator limbatus*. Anim Behav 55:473–483
Schantz T von, Göransson G, Andersson G, Fröberg I, Grahn M, Helgée A, Wittzell H (1989) Female choice selects for a viability-based male trait in pheasants. Nature 337:166–168
Searcy WA, Yasukawa K (1981) Does the 'sexy son' hypothesis apply to mate choice in red-winged blackbirds? Am Nat 117:343–348
Sheldon BC (2000) Differential allocation: tests, mechanisms and implications. Trends Ecol Evol 15:397–402

Simmons LW (1987) Female choice contributes to offspring fitness in the field cricket, *Gryllus bimaculatus* (De Geer). Behav Ecol Sociobiol 21:313–321

Simmons LW (1990a) Nuptial feeding in tettigonids: male costs and the rates of fecundity increase. Behav Ecol Sociobiol 27:43–47

Simmons LW (1990b) Post-copulatory guarding, female choice and the levels of gregarine infections in the field cricket, *Gryllus bimaculatus*. Behav Ecol Sociobiol 26:403–407

Smith HG, Montgomerie R (1992) Male incubation in barn swallows: the influence of nest temperature and sexual selection. Condor 94:750–759

Soler M, Soler JJ, Møller AP, Moreno J, Lindén M (1996) The functional significance of sexual display: stone-carrying in the black wheatear. Anim Behav 51:247–254

Steele RH (1986) Courtship feeding in *Drosophila subobscura*. I. The nutritional significance of courtship feeding. Anim Behav 34:1087–1098

Studd MV, Robertson RJ (1985) Sexual selection and variation in reproductive strategy in yellow warblers (*Dendroica petechia*). Behav Ecol Sociobiol 17:101–109

Sundberg J (1995) Parasites, plumage coloration and reproductive success in the yellowhammer *Emberiza citrinella*. Oikos 74: 331–339

Sundberg J, Larsson C (1994) Male coloration as an indicator of parental quality in the yellowhammer, *Emberiza citrinella*. Anim Behav 48:885–892

Svärd L, Wiklund C (1991) The effect of ejaculate output on female reproductive output in the European swallowtailed butterfly, *Papilio machaon* (L.) (Lepidoptera: Papilionidae). J Insect Behav 4:33–41

Swaddle JP (1996) Reproductive success and symmetry in zebra finches. Anim Behav 51:203–210

Takegaki T, Nakazono A (1999) Reproductive behavior and mate fidelity in the monogamous goby, *Valenciennea longipinnis*. Icthyol Res 46:115–123

Tallamy DW (2000) Sexual selection and the evolution of exclusive paternal care in arthropods. Anim Behav 60:559–567

Taylor PD, Williams GC (1982) The lek paradox is not resolved. Theor Popul Biol 22:392–409

Thornhill R (1983) Cryptic female choice and its implications in the scorpionfly, *Harpobittacus nigriceps*. Am Nat 122:765–788

Tolonen P, Korpimäki E (1994) Determinants of parental effort: a behavioural study in the Eurasian kestrel, *Falco tinnunculus*. Behav Ecol Sociobiol 35:355–362

Veiga JP (1993) Badge size, phenotypic quality, and reproductive success in the house sparrow: a study of honest advertisement. Evolution 47:1161–1170

Vøllestad LA, Hindar K, Møller AP (1999) A meta-analysis of fluctuating asymmetry in relation to heterozygosity. Heredity 83:206–218

Warner RR, Shapiro DY, Marcanato A, Petersen CW (1995) Sexual conflict: males with highest mating success convey the lowest fertilization benefits to females. Proc R Soc Lond B 262:135–139

Wedell N (1996) Male quality affects reproductive success in a paternally investing species. Am Nat 148:1075–1088

Wedell N, Arak A (1989) The wartbiter spermatophore and its effect on female reproductive output (Orthoptera: Tettigoniidae, *Dedictus verrucivorus*). Behav Ecol Sociobiol 24:117–125

Welling PP, Rytkönen SO, Koivula KT, Orell MI (1997) Song rate correlates with paternal care and survival in willow tits: advertisement of male quality? Behaviour 134:891–904

Whittier TS, Kaneshiro KY (1995) Intersexual selection in the Mediterranean fruit fly: does female choice enhance fitness? Evolution 49:990–996

WHO (1990) Global estimates for health situation assessment and projections. WHO, Geneva

Wiehn J (1997) Plumage characteristics as an indicator of male parental quality in the American kestrel. J Avian Biol 28: 47–55

Wiggins DA, Morris RD (1986) Criteria for female choice of mates, courtship feeding and paternal care in the common tern (*Sterna hirundo*). Am Nat 128:126–129

Wilkinson GS, Reillo PR (1994) Female choice response to artificial selection on an exaggerated male trait in a stalk-eye fly. Proc R Soc Lond B 255:1–6

Worden B, Parker PG, Pappas PW (2000) Parasites reduce attractiveness and reproductive success in male grain beetles. Anim Behav 59:543–550

Yamamoto JT, Shields KM, Millam JR, Roudybush TE, Grau CR (1989) Reproductive activity of force-paired cockatiels (*Nymphicus hollandicus*). Auk 106:86–93

Zann R (1994) Effects of band color on survivorship, body condition and reproductive effort of free-living Australian zebra finches. Auk 111:131–142

Zeh JA, Zeh DW (1996) The evolution of polyandry. 1. Intragenomic conflict and genetic incompatability. Proc R Soc Lond B 263:1711–1717