Forum

Testing the sexy son hypothesis—a research framework for empirical approaches

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Sexual selection by direct and/or indirect benefits as well as sexual conflict determines the evolution of animal mating systems (e.g., Andersson and Simmons 2006). In polygynous mating systems, the female preference of apparently useless or deleterious male characteristics can be understood if a correlation between preferred male characteristics and direct benefits for the female exists (see polygyny threshold model, e.g., Orians 1969), such as improved paternal care or territorial quality (e.g., Price et al. 1993; Iwasa and Pomiankowski 1999). This issue is particularly interesting in facultative polygynous mating systems with biparental care because the female's choice of a polygynous male as a mate is most often accompanied by a reduction in paternal care by this mate (for a review, see Ligon 1999). Several studies (e.g., Johnson et al. 1994; Pribil and Searcy 2001; Moreno et al. 2002; but see Both 2002) have observed a reduction in offspring number and/or offspring performance in females mated with a polygynous male, thus raising doubt in the relevancy of the polygyny threshold model (see, e.g., Orians 1969) in these instances. More generally, females of most species do not seem to take any appreciable direct benefits of their mate choice (Kirkpatrick and Ryan 1991; Andersson 1994).

Since the 1970s, indirect benefits are discussed as a possibility to explain female choice (Kirkpatrick and Ryan 1991; Andersson and Simmons 2006). Weatherhead and Robertson (1979) proposed the sexy son hypothesis (SSH) as an additional explanation for the establishment of polygyny. According to this hypothesis, females are assumed to compensate for their direct inferior breeding success by the increased number of descendents produced by their sexy—and therefore polygynous—sons (see Table 1). The idea of focusing on fitness advantages as a result of male attractiveness is similar to the "Fisherian runaway selection process" (see, e.g., Andersson and Simmons 2006). The "good genes" model (see Table 1), that is, the idea of an indirect benefit due to the male's genetic quality, is a second, complementary hypothesis that is discussed as a possibility to explain female choice by indirect benefits (Andersson and Simmons 2006; Charmantier and Sheldon 2006). Both hypothesized mechanisms, SSH and good genes, belong to the same continuum of indirect selection (Kokko et al. 2002; Radwan 2002). SSH as well as good genes postulate that indirect benefits due to male characteristics in a specific species will be similar for all females of this species (see also Table 1). Compatible genes, on the other hand, try to explain intraspecific differences in female mate choice (see Table 1). According to this theory, each individual female tries to enhance its fitness by choosing a male with a genetic pattern that is compatible with its own genetic configuration (e.g., Neff and Pitcher 2005).

Another approach to understand mating behavior that results in deleterious female reproductive success, such as off-spring number or performance, is the idea of sexual conflict (see Table 1; Gavrilets et al. 2001; Cameron et al. 2003; Arnqvist and Rowe 2005; Andersson and Simmons 2006; Lessells 2006; Parker 2006; Rice et al. 2006). Sexual conflict is driven by the opposed reproductive interests in females and males that result in sexually antagonistic behavior and coevolving adaptations. Whereas the traditional hypotheses of sexual selection, such as the polygyny threshold model and SSH, discuss the importance of direct versus indirect benefits, sexual conflict considers the possibility that polygynous males are not beneficial to females, neither directly nor indirectly. For example, Arnqvist and Kirkpatrick (2005) demonstrated that extrapair copulations, which do not lead to any direct advantages such as additional food resources or shelter, in socially monogamous birds are in line with sexual conflict assumptions as indirect benefits are much smaller than the direct negative selection caused by depressed paternal investment by social males.

The present study will focus on SSH because SSH as well as the good genes assumption are based on the relative magnitude of direct and indirect effects of mate choice and thus have become relevant to the recent debate of whether sexual conflict can result in sexually antagonistic selection. SSH developed by Weatherhead and Robertson (1979), further called "narrow-sense SSH," refers to mating systems with biparental care. In these mating systems, females mated with a polygynous male normally receive less assistance than females mated with a monogamous male (see, e.g., Ligon 1999) and thus suffer from direct fitness consequences that have to be (over)compensated by their sexy sons. On the other hand, "broad-sense SSH" encompasses polygyny and promiscuous mating systems with and without biparental care. Alatalo (1998) argues that the costs of any additional choice may be so minor that female choice for honestly signaling males, that is good genes, may evolve even if the indirect benefits on offspring quality are small. A similar argument can be given for SSH if mates of attractive males do not suffer any direct fitness consequences.

Since it was first proposed by Weatherhead and Robertson (1979), SSH has been discussed vividly. Several theoretical studies either support (Weatherhead 1994; Kokko et al. 2002; McNamara et al. 2003) or attempt to argue against SSH (e.g., Kirkpatrick 1985; Wagner 1994; Alatalo and Ratti 1995). Recent sophisticated empirical studies dealing with SSH have reached contrasting results (compare Gwinner and Schwabl 2005; Head et al. 2005; Orteiza et al. 2005; Gustafsson and Qvarnström 2006; Huk and Winkel 2006). However, these studies differ in terms of the explicit research questions they ask and thus highlight the importance of questioning precisely what factors should be measured. The aim of the present paper is to shed light on the contrasting empirical results by analyzing the appropriateness of various research questions in empirical tests of SSH and in so doing to differentiate between "critical predictions" and "compatible predictions" (see Table 2). Critical predictions should be studied in future work as they address topics that are at the core of the predictions of SSH. Critical predictions are therefore able to validate or invalidate SSH as a hypothesis explaining female choice. Compatible predictions are aspects that can be discussed in the light of this hypothesis without directly addressing the critical predictions. Thus, compatible predictions only test for "by-product" predictions that can neither validate nor invalidate SSH.

Table 1
Definitions of major concepts

Definitions

Sexual conflict: Sexual conflict refers to intersexual conflict. It describes the diverging interests in males and females to optimize their fitness. From the point of few of one sex, this is done best if the mate cares for the young thus freeing resources (e.g., time and energy) that can be invested in additional offspring. Regarding to polygynous mating systems, sexual conflict means the optimization of male reproductive success by having mated with multiple females although reproductive success of a polygynously mated female is reduced.

Good genes: Good genes refer to the assumption of an additive indirect genetic benefit that increases offspring quality. Offspring quality, that is, viability, leads to a compensation of any inferior direct reproductive success, that is, fewer offspring.

Fisherian runaway selection: Fisherian runaway selection assumes indirect genetic benefits in mating decisions. This process assumes that sexual selection for a specific trait was at first correlated with a small increase in viability. During evolution, the female preference for this trait becomes exaggerated while the good genes effect loses its importance. At the end, sexual selection is driven only by the attractiveness of this trait and not by any additive genetic effect that is relevant for natural selection.

Sexy son hypothesis: The sexy son hypothesis (SSH) is closely related to the good genes assumption and the fisherian runaway selection process. SSH, too, assumes indirect genetic benefits that are able to compensate any an inferior direct reproductive success, that is, fewer offspring. The main difference between good genes and SSH is that SSH assumes an indirect effect due to the attractiveness of the sons whereas good genes focus on viability in sons and daughters. However, attractiveness is not specified and can be every trait that increases a male's probability to become polygynous.

Compatible genes: Compatible genes also belong to indirect genetic benefits that increase the genetic quality of offspring. Whereas good genes generally lead to positive effects, compatible genes are beneficial only for specific individuals. That is, a positive effect depends on the interplay of the individual genetic architecture of both mates.

SSH: CRITICAL AND COMPATIBLE PREDICTIONS

A major reason for the different conclusions reached by empirical studies dealing with SSH is that they differ both in terms of the variables investigated and of the different treatment factors compared. How best to test SSH empirically? The major emerging critical prediction is that indirect effects, that is, genes delivered by the male, do increase lifetime reproductive success in sons. Therefore, females of attractive males, which in narrow-sense SSH suffer from inferior direct fitness estimates, in the long run achieve the same fitness as females mated with a monogamous male (Weatherhead and Robertson 1979). This prediction, however, occurs also in the good genes hypothesis (see Andersson and Simmons 2006; Charmantier and Sheldon 2006). According to SSH, it is its sexy sons who are assumed to be responsible for this compensation as they inherit their father's genes which in turn enable them to become polygynous themselves, thus increasing the number of grandchildren produced. SSH therefore predicts that females mated with a polygynous male rear sons that become polygynous themselves. More specifically, the number of polygynous breeding attempts should be higher in sons descending from females mated with a polygamous male than in sons descending from females mated with a monogamous male. Investigation of this prediction would clarify whether the un-

derlying assumption of SSH, that is heritability of attractiveness, is valid. This would be, however, no direct evidence for the compensation of any direct inferior fitness consequences. To test SSH, the aforementioned second critical prediction must also be investigated, that is, a fitness (over)compensation with respect to the number of F_{1+x} descendents.

SSH as well as the good genes hypothesis predict that the number of grand-offspring is similar or higher in females mated with a polygynous male than in females mated with a monogamous male. Whereas a greater number of grand-offspring would be in line with SSH, a lower number would be an argument against this hypothesis. In case of a similar reproductive success, it is rather difficult to distinguish between 1) instances that observed no significant differences in fitness due to the fact that there really were no differences—as proposed by SSH—and 2) empirical studies that failed to detect a difference in the number of grandchildren, although females mated with a polygynous male in fact could not compensate direct inferior reproductive success. In long-lived species with several subsequent breeding events, another important parameter is the consequence of mating behavior for any further breeding success in the future, that is, the risk to suffer from sexually transmitted diseases especially in females mating with polygynous males (see Thrall et al. 2000). SSH studies on long-lived species, therefore, have to investigate not only the number of grandchildren of the actual breeding event but also possible subsequent differences in female longevity or offspring performance in any further breeding attempts (for the possibility of an increase in longevity in polygynously mated females, see also Garamszegi et al. 2004).

However, only few empirical studies have to date focused on these critical predictions. In particular, lifetime reproductive success, measured in terms of the number of grand-offspring produced, has rarely been investigated (see Hunt et al. 2004).

In addition to these critical predictions, further research predictions that encompass the theoretical concept of SSH can be made. These compatible predictions deal with topics that rely on the validity of the critical predictions mentioned above. Females have to be able to detect males that will pass on genes that increase the probability of rearing sons that will become polygynous during their own reproductive phase. Various studies demonstrate that females are able to detect "attractive" males by secondary sexual characteristics such as ornamentation (e.g., Gustafsson et al. 1995; Sheldon et al. 1999; Siitari et al. 2002). As a second compatible prediction, one should expect that females trade mate choice between male attractiveness and pairing status in species with biparental care as pairing status is an indicator of male assistance in these species. Third, if a female mated with a polygynous male rears sexy sons that are able to compensate any direct inferior reproductive success, one might argue that such females could be expected to shift their brood sex ratio toward producing more males than females (Burley 1981). Similarly, one should expect that sons of polygynous (thus attractive) males should exhibit behavior that increases their probability to become polygynous themselves.

SSH IN POLYGYNOUS MATING SYSTEMS WITH BIPARENTAL CARE

Especially interesting are female decision opportunities in species with short-term pair-bond, that is, species in which females and males choose their partner at the beginning of the actual reproduction period, in which fitness is mainly attributed to habitat quality, male assistance during the rearing of offspring, and heritable male attractiveness. For convenience, a facultative bigynous mating system is assumed to make female mate choice decisions more explicit. At the

Table 2

Empirical studies dealing with compatible or critical predictions

Critical predictions (exhaustive) supportive of SSH	No support of SSH
Narrow-sense SSH, that is, (over)compensation of inferior reproductive success via sexy sons in biparental mating systems	
Huk and Winkel (2006): Correlational study in pied flycatcher (*Ficedula. hypoleuca*); polygynous pairing in primary females resulted in sons with a higher probability of becoming polygynous. Moreover, a small but significant inferior direct reproductive success was compensated in terms of the number of grandchildren	Huk and Winkel (2006): Correlational study in pied flycatcher (*F. hypoleuca*); polygynous pairing did not increase attractiveness in sons of secondary females, that is, the number of sons becoming polygynous. Moreover, females without male assistance were not able to compensate inferior direct reproductive success in terms of the number of grandchildren
	Gustafsson and Qvarnström (2006): Correlational study in the collared flycatcher (*Ficedula albicollis*); polygynous pairing, that is, primary and secondary females with male assistance, resulted in less attractive sons and fewer grandchildren as compared with females mated with a monogamous male
Broad sense SSH, that is, a sexy son effect in polygynous and promiscuous mating systems with and without biparental care	
Rundle et al. (2007): Experimental study in *Drosophila melanogaster*; male descendents of attractive males were 30% more successful on average at securing mates than male descendents of unattractive males	Rundle et al. (2007): Experimental study in *D. melanogaster*; male descendents of attractive and unattractive fathers did not differ in productivity
Head et al. (2005): Experimental study in the house cricket (*Acheta domesticus*); females mated to attractive males incur a substantial survival cost that is predominantly outweighed by their attractive sons	Orteiza et al. (2005): Experimental study in *D. melanogaster*; a multigeneration fitness assay found that indirect effects through sexy sons could not recoup the direct costs
Pai and Yan (2002): Experimental study in red flour beetles (*T. castaneum*); females mating with multiple males (2–16 males) enhanced the relative fitness of F1 males in comparison with singly mated females. F1 males from mothers with 16 different males inseminated more females than F1 males from mothers with a single partner. Thus, polyandry enhances the chance to get a mate with superior genes, that is, genes that increase the attractiveness of their sons	Whittier and Kaneshiro (1995): Experimental study in the Mediterranean fruit fly (*Ceratitis capitata*); father/son correlation and sibling analysis showed no heritable component to male copulatory success
	Simmons (2003): Quantitative genetics in the field cricket (*Teleogryllus oceanicus*); no positive genetic correlation between paternity in sons and polyandry in daughters as predicted by the "sexy sperm" hypothesis

Compatible predictions (not exhaustive) supportive of SSH	No support of SSH
Females choose attractive males	
Siitari et al. (2002): Experimental study in the pied flycatcher (*F. hypoleuca*); females preferred males with increased UV plumage coloration when the effect of territory quality is controlled for	Wiehn (1997): Correlational study in the American kestrel (*Falco sparverius*); no male trait was clearly related to the time males had to wait before obtaining females
Females trade mate choice between male attractiveness and pairing status	
Slagsvold and Drevon (1999): Experimental study in the pied flycatcher (*F. hypoleuca*); females trade between male mating status and male attractiveness	
Females mated with attractive males produce more sons than daughters	
Sheldon et al. (1999): Experimental study in the blue tit (*Parus caeruleus*); positive relationship between the proportion of sons in a male's brood and measures of ultraviolet plumage coloration	Dreiss et al. (2006): Correlational study in the blue tit (*P. caeruleus*); no relationship between male color ornamentation and brood sex ratio
Griffith et al. 2003: Correlational study in the blue tit (*P. caeruleus*); males with relatively brighter UV coloration produced a greater proportion of sons in their broods	Olsson et al. 2005: Experimental study in the sand lizard (*Lacerta agilis*); negative relationship between proportion of sons in a male's brood and male coloration
Dreiss et al. (2006): Correlational study in the blue tit (*P. caeruleus*); positive relationship between the length of the strophe bout and the proportion of sons in their broods	Parker (2005): Experimental study in the red junglefowl (*Gallus gallus*); no evidence for a female bias in the sex ratio of their brood in response to either their own condition or the attractiveness of the males with whom they copulate
Pike and Petrie (2005): Experimental study in the peafowl (*Pavo cristatus*); females control the primary sex ratio of their offspring in response to paternal attractiveness	Nishiumi (1998) and Westerdahl et al. (2000): Correlational study in the great reed warbler (*Acrocephalus arundinaceus*); primary females had a higher proportion of sons in their broods than secondary females. According to SSH, primary and secondary females should adjust their sex ratio in favor of sons
Leitner et al. (2006): Experimental study with captive canaries (*Serinus canarina*); females exposed to playback of more attractive songs produced larger eggs that are normally more likely to hatch male offspring	
Sons of attractive males exhibit morphological traits and/or behavior that increases their probability to become polygynous	
Bakker (1993) showed heritability of male attractiveness in stickleback	Hadfield et al. (2006): Experimental study in the blue tit (*P. caeruleus*); variation in plumage coloration is only weakly heritable, and a positive genetic covariation between parental color and offspring fitness was not observed
Houtman (1992): Correlational study in zebra finches (*Taeniopygia guttata*); sons of attractive males have higher song rates	
Gwinner and Schwabl (2005): Correlational/experimental study in the European starling (*Sturnus vulgaris*); sons of polygynous fathers defended more nest-boxes and produced more courtship songs	
Norris (1993): Experimental study in the great tit (*Parus major*): plumage trait associated with attractiveness in males was heritable	

beginning of the reproduction period, all males are unmated. Females should therefore select males on the basis of habitat quality and attractiveness; they should primarily select attractive males occupying a superior habitat in order to increase their reproductive success. In the subsequent breeding season, unpaired females have ideally to decide whether 1) to mate with these superior (but already mated) males, thus becoming a secondary female sharing their male with the already existing primary female, or to mate with a still unmated male that is either 2) less attractive or 3) one which occupies a territory of lower quality (but see, e.g., Searcy and Yasukawa 1989 for alternative no-compensation models). In the latter case, these females do not have to share their monogamous mate. In order to test SSH, only females of the categories 1) and 2) should be compared with test SSH. A comparison between 1) and 3), on the other hand, is not appropriate for testing SSH as fitness differences are due to differences in territorial differences. A good system may be, therefore, a facultative polygynous species that does not defend feeding territories, thus making territorial differences less important.

When testing SSH, it is important to analyze the reason for a mate choice decision in favor of a polygamous male. Is the choice based on the attractiveness of the male or is it based on the quality of the male's territory? It should be stressed that in the case of a positive correlation between territorial quality and male attractiveness, it is quite difficult to investigate SSH as it is not possible to distinguish fitness consequences between these 2 confounding factors in the field, that is territorial quality and male attractiveness. In this case, only experimental approaches can solve this problem by controlling territorial quality in the laboratory or by cross fostering of whole or partial broods (see, e.g., Hadfield et al. 2006). If habitat quality and male attractiveness are independent, that is, female choice in the sense of runaway selection, females should select an already mated male for 2 reasons: the already mated male occupies a superior habitat or is more attractive than the unpaired male. As one cannot rule out in most cases that territorial quality and male attractiveness are at least partially correlated, studies focusing on SSH experimental approaches, for example, cross fostering of whole or partial broods between females with different mating status and in territories of different quality, have to be preferred over correlational studies as they allow to break down correlations between territorial quality and male attractiveness.

As regards female perspective in mate choice, 3 categories can, therefore, be distinguished for females breeding in territories of similar quality: females mated with a monogamous male, primary females, and secondary females. As primary females, as a rule, receive more male assistance (Ligon 1999), their direct reproductive success is less affected than that of secondary females. Primary females therefore combine a pattern of relatively high direct male assistance with the supposed indirect benefits due to the genetic constitution of their attractive males (however, it is important not to consider primary females mated with a less attractive male occupying a superior habitat, see above). According to this combination, a comparison of primary females and females mated with a monogamous male should exhibit not only more polygynous sons in primary females but also a significantly higher number of grand-offspring as differences in direct reproductive success should be of minor importance.

REVIEW OF EMPIRICAL STUDIES

What have we learned from existing empirical studies? Different empirical studies demonstrated that female mating decisions may be explained by the good genes model of sexual selection. It was demonstrated that attractive males confer disease resistance to their offspring (Barber et al. 2001) or increase offspring viability (Hasselquist 1998; Byers and Waits 2006; Forsman and Hagman 2006). Whereas good genes may support fitness of sons and/or daughters, SSH predicts fitness advantages in sons only. According to Alatalo and Lundberg (1986), SSH should not apply in the model species *Ficedula hypoleuca* due to poor phenotypic quality of nestlings of secondary females. In their study, they supported their assumption by estimation of lifetime reproductive success. Contrary, Johnson et al. (1994) concluded that secondary females in the house wren (*Troglodytes aedon*) may recoup fitness losses in the next generation if male mating success is at least moderately heritable. However, both studies did not measure critical predictions of SSH directly.

A review of empirical studies revealed that compatible predictions of SSH were investigated by a rather large variety of studies. The majority of these studies have not been intended to look especially at SSH because compatible predictions of SSH do play a role in other theoretical concepts as well. Although each compatible prediction was supported by empirical results, the pattern is not unequivocal because several studies observed pattern that contradict compatible SSH predictions (see Table 2).

Empirical studies dealing with critical predictions of SSH are rare. These empirical approaches used either birds or insects as model species, whereas studies on other taxa are missing (see, e.g., Barbosa and Magurran 2006). Two correlational studies in the closely related collared flycatcher (*Ficedula albicollis*) and pied flycatcher (*F. hypoleuca*) revealed no support for narrow-sense SSH, that is, no compensation of inferior reproductive success via sexy sons (see Table 2; Gustafsson and Qvarnström 2006; Huk and Winkel 2006). However, in the pied flycatcher, this result held true for secondary females, whereas in primary females, that is, females with a relatively weak inferior direct reproductive success, the pattern was compatible with SSH (see Table 2). Recent studies, however, that did not look at the number of grand-offspring came to contrasting results (Both 2002; Garamszegi et al. 2004).

CONCLUSIONS

To sum up, it can be concluded that empirical studies dealing with critical predictions to date only partially support SSH; that is, only studies with rather small direct fitness consequences are compatible with critical SSH predictions. Contrary, the demonstration of compensation of considerable lower direct reproductive success via a heritable genetic effect of male attractiveness, and hence male mating status in sons, is not demonstrated until now. Thus, facultative polygyny in biparental species seems to be best explained by sexual conflict. Approaches derived from quantitative genetic models of mate choice came to similar results (Kirkpatrick and Barton 1997; Charmantier and Sheldon 2006; Hadfield et al. 2006; Qvarnström et al. 2006). Recent studies therefore support the position that inferior direct reproductive success cannot be overcompensated by a "sexy son" effect (e.g., Kirkpatrick 1985). Thus, attractiveness of sexy sons and its resulting fitness advantages seem to be of minor biological effect.

The deception hypothesis, that is, the assumption that males hide their mating status and deceive females into polygyny in polyterritorial species (Alatalo et al. 1982; Temrin and Arak 1989; Ligon 1999), is an alternative no-compensation explanation that fits into sexual conflict assumptions. Slagsvold and Dale (1994) found little support for deception hypothesis while observing pied flycatcher behavior. They instead suggest that female pied flycatchers are able to detect male mating status but sometimes settle with mated males

because of cost of searching thus doing "the best of a bad job."

The impact of extrapair copulations for female choice decisions in the light of SSH has already been discussed by Wagner (1994) and Weatherhead (1984). As extrapair copulations allow females to benefit from "sexy genes" of attractive males even if they are not the primary or secondary female, differences between females mated with a monogamous male and primary or secondary females can be assumed to be mitigated. Thus, differences in territorial quality will become more important in these cases, highlighting the importance of comparing only females breeding in habitats of similar quality. A more precise approach would be to genetically detect male paternity (see Andersson and Simmons 2006).

As empirical studies focusing on critical SSH predictions are rare, future research is needed: ideally, the comparison of future fitness consequences between females that choose to be secondary females with the success they would have had if they had been paired with a monogamous male. As this is principally not possible, future research should therefore focus on a comparison of total fitness, that is, number of grand-offspring, between females mated with a monogamous male and primary females as well as between females mated with a monogamous male and secondary females while controlling for possible confounding variables such as timing of reproduction, habitat quality, and frequency of interactions with males. This total fitness measure should also incorporate female and offspring survival. Furthermore, these studies should use genetic proof of paternity as social matings are generally only rather poor measures of the numbers of offspring produced (e.g., Griffith et al. 2002). A fruitful avenue would be experimental approaches such as cross fostering of whole or partial broods (see, e.g., Hadfield et al. 2006) between females with different mating status.

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REFERENCES

Alatalo RV. 1998. Mate choice for offspring performance: major benefits or minor costs? Proc R Soc Lond B Biol Sci. 265:2297–2297.

Alatalo RV, Lundberg A. 1986. The sexy son hypothesis: data from the pied flycatcher Ficedula-Hypoleuca. Anim Behav. 34:1454–1462.

Alatalo RV, Lundberg A, Stahlbrandt K. 1982. Why do pied flycatcher females mate with already-mated males? Anim Behav. 30:585–593.

Alatalo RV, Ratti O. 1995. Sexy son hypothesis—controversial once more. Trends Ecol Evol. 10:52–53.

Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.

Andersson S, Simmons LW. 2006. Sexual selection and mate choice. Trends Ecol Evol. 21:296–302.

Arnqvist G, Kirkpatrick M. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. Am Nat. 165: S26–S37.

Arnqvist G, Rowe L. 2005. Sexual conflict. Princeton (NJ): Princeton University Press.

Bakker TCM. 1993. Positive genetic correlation between female preference and preferred male ornaments in sticklebacks. Nature. 363:255–257.

Barber I, Arnott SA, Braithwaite VA, Andrew J, Huntingford FA. 2001. Indirect fitness consequences of mate choice in sticklebacks: offspring of brighter males grow slowly but resist parasitic infections. Proc R Soc Lond B Biol Sci. 268:71–76.

Barbosa M, Magurran AE. 2006. Female mating decisions: maximizing fitness? J Fish Biol. 68:1636–1661.

Both C. 2002. Fitness costs of polygyny in female pied flycatchers Ficedula hypoleuca. Ardea. 90:129–138.

Burley N. 1981. Sex ratio manipulation and selection for attractiveness. Science. 211:721–722.

Byers JA, Waits L. 2006. Good genes sexual selection in nature. Proc Natl Acad Sci USA. 103:16343–16345.

Cameron E, Day T, Rowe L. 2003. Sexual conflict and indirect benefits. J Evol Biol. 16:1055–1060.

Charmantier A, Sheldon BC. 2006. Testing genetic models of mate choice evolution in the wild. Trends Ecol Evol. 21:417–419.

Dreiss A, Richard M, Moyen F, White J, Møller AP, Danchin E. 2006. Sex ratio and male sexual characters in a population of blue tits, Parus caeruleus. Behav Ecol. 17:13–19.

Forsman A, Hagman M. 2006. Calling is an honest indicator of paternal genetic quality in poison frogs. Evolution. 60:2148–2157.

Garamszegi LZ, Török J, Michl G, Møller AP. 2004. Female survival, lifetime reproductive success and mating status in a passerine bird. Oecologia. 138:48–56.

Gavrilets S, Arnqvist G, Friberg U. 2001. The evolution of female mate choice by sexual conflict. Proc R Soc Lond B Biol Sci. 268:531–539.

Griffith SC, Ornborg J, Russell AF, Andersson S, Sheldon BC. 2003. Correlations between ultraviolet coloration, overwinter survival and offspring sex ratio in the blue tit. J Evol Biol. 16:1045–1054.

Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol. 11:2195–2212.

Gustafsson L, Qvarnström A. 2006. A test of the "sexy son" hypothesis: sons of polygynous collared flycatchers do not inherit their fathers' mating status. Am Nat. 167:297–302.

Gustafsson L, Qvarnström A, Sheldon BC. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. Nature. 375:311–313.

Gwinner H, Schwabl H. 2005. Evidence for sexy sons in European starlings (Sturnus vulgaris). Behav Ecol Sociobiol. 58:375–382.

Hadfield JD, Burgess MD, Lord A, Phillimre AB, Clegg SM, Owens IP. 2006. Direct versus indirect sexual selection: genetic basis of colour, size and recruitment in a wild bird. Proc R Soc Lond B Biol Sci. 273:1347–1353.

Hasselquist D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. Ecology. 79:2376–2390.

Head ML, Hunt J, Jennions MD, Brooks R. 2005. The indirect benefits of mating with attractive males outweigh the direct costs. PLoS Biol. 3:289–294.

Houtman AM. 1992. Female zebra finches choose extra-pair copulations with genetically attractive males. Proc R Soc Lond B Biol Sci. 249:3–6.

Huk T, Winkel W. 2006. Polygyny and its fitness consequences for primary and secondary female pied flycatchers. Proc R Soc Lond B Biol Sci. 273:1681–1688.

Hunt J, Bussière LF, Jennions MD, Brooks R. 2004. What is genetic quality? Trends Ecol Evol. 19:329–333.

Iwasa Y, Pomiankowski A. 1999. Good parent and good genes models of handicap evolution. J Theor Biol. 200:97–109.

Johnson IS, Kermott LH, Lein MR. 1994. Territorial polygyny in house wrens—are females sufficiently compensated for the cost of mate sharing? Behav Ecol. 5:98–104.

Kirkpatrick M. 1985. Evolution of female choice and male parental investment in polygynous species—the demise of the sexy son. Am Nat. 125:788–810.

Kirkpatrick M, Barton NH. 1997. The strength of indirect selection on female mating preferences. Proc Natl Acad Sci USA. 94:1282–1286.

Kirkpatrick M, Ryan MJ. 1991. The evolution of mating preferences and the paradox of the lek. Nature. 350:33–38.

Kokko H, Brooks R, McNamara JM, Houston AI. 2002. The sexual selection continuum. Proc R Soc Lond B Biol Sci. 269:1331–1340.

Leitner S, Marshall RC, Leisler B, Catchpole CK. 2006. Male song quality, egg size and offspring sex in captive canaries (Serinus canaria). Ethology. 112:554–563.

Lessells CM. 2006. The evolutionary outcome of sexual conflict. Philos Trans R Soc Lond B. 361:301–317.

Ligon JD. 1999. The evolution of avian breeding systems. New York: Oxford University Press.

McNamara JM, Houston AI, dos Santos MM, Kokko H, Brooks R. 2003. Quantifying male attractiveness. Proc R Soc Lond B Biol Sci. 270:1925–1932.

Moreno J, Veiga JP, Romasanta M, Sánchez S. 2002. Effects of maternal quality and mating status on female reproductive success in the polygynous spotless starling. Anim Behav. 64:197–206.

Neff BD, Pitcher TE. 2005. Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. Mol Ecol. 14:19–38.

Nishiumi I. 1998. Brood sex ratio is dependent on female mating status in polygynous great reed warblers. Behav Ecol Sociobiol. 44:9–14.

Norris K. 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. Nature. 362:537–539.

Olsson M, Wapstra E, Uller T. 2005. Differential sex allocation in sand lizards: bright males induce daughter production in a species with heteromorphic sex chromosomes. Biol Lett. 1:378–380.

Orians GH. 1969. On the evolution of mating systems in birds and mammals. Am Nat. 103:589–602.

Orteiza N, Linder JE, Rice WR. 2005. Sexy sons from re-mating do not recoup the direct costs of harmful male interactions in the *Drosophila melanogaster* laboratory model system. J Evol Biol. 18:1315–1323.

Pai AT, Yan GY. 2002. Polyandry produces sexy sons at the cost of daughters in red flour beetles. Proc R Soc Lond B Biol Sci. 269:361–368.

Parker GA. 2006. Sexual conflict over mating and fertilization: an overview. Philos Trans R Soc Lond B. 361:235–259.

Parker TH. 2005. No evidence for adaptive differential sex allocation in red junglefowl (*Gallus Gallus*). Auk. 122:1161–1168.

Pike TW, Petrie M. 2005. Offspring sex ratio is related to paternal train elaboration and yolk corticosterone in peafowl. Biol Lett. 1:204–207.

Pribil S, Searcy WA. 2001. Experimental confirmation of the polygyny threshold model for red-winged blackbirds. Proc R Soc Lond B Biol Sci. 268:1643–1646.

Price T, Schluter D, Heckman NE. 1993. Sexual selection when the female directly benefits. Biol J Linn Soc. 48:187–211.

Qvarnström A, Brommer JE, Gustafsson L. 2006. Testing the genetics underlying the co-evolution of mate choice and ornament in the wild. Nature. 441:84–86.

Radwan J. 2002. Good genes go fisherian. Trends Ecol Evol. 17:539–539.

Rice WR, Stewart AD, Morrow EH, Linder JE, Orteiza N, Byrne PG. 2006. Assessing sexual conflict in the *Drosophila melanogaster* laboratory model system. Philos Trans R Soc Lond B. 361:287–299.

Rundle HD, Odeen A, Mooers AO. 2007. An experimental test for indirect benefits in *Drosophila melanogaster*. BMC Evol Biol. 7:36.

Searcy WA, Yasukawa K. 1989. Alternative models of territorial polygyny in birds. Am Nat. 134:323–343.

Sheldon BC, Andersson S, Griffith SC, Örnberg J, Sendecka J. 1999. Ultraviolet colour variation influences blue tit sex ratios. Nature. 402:874–877.

Siitari H, Honkavaara J, Huhta E, Viitala J. 2002. Ultraviolet reflection and female mate choice in the pied flycatcher, *Ficedula hypoleuca*. Anim Behav. 63:97–102.

Simmons LW. 2003. The evolution of polyandry: patterns of genotypic variation in female mating frequency, male fertilization success and a test of the sexy-sperm hypothesis. J Evol Biol. 16:624–634.

Slagsvold T, Dale S. 1994. Why do female pied flycatchers mate with already mated males—deception or restricted mate sampling. Behav Ecol Sociobiol. 34:239–250.

Slagsvold T, Drevon T. 1999. Female pied flycatchers trade between male quality and mating status in mate choice. Proc R Soc Lond B Biol Sci. 266:917–921.

Temrin H, Arak A. 1989. Polyterritoriality and deception in passerine birds. Trends Ecol Evol. 4:106–109.

Thrall PH, Antonovics J, Dobson AP. 2000. Sexually transmitted diseases in polygynous mating systems: prevalence and impact on reproductive success. Proc R Soc Lond B Biol Sci. 267:1555–1563.

Wagner RH. 1994. Mixed mating strategies by females weaken the sexy son hypothesis. Anim Behav. 47:1207–1209.

Weatherhead PJ. 1984. Mate choice in avian polygyny. Am Nat. 123:873–875.

Weatherhead PJ. 1994. Mixed mating strategies by females may strengthen the sexy son hypothesis. Anim Behav. 47:1210–1211.

Weatherhead PJ, Robertson RJ. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis." Am Nat. 113:201–208.

Westerdahl H, Bensch S, Hansson B, Hasselquist D, von Schantz T. 2000. Brood sex ratios, female harem status and resources for nestling provisioning in the great reed warbler (*Acrocephalus arundinaceus*). Behav Ecol Sociobiol. 47:312–318.

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

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