1-3 Extra-Pair Paternity and Sexual Selection

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Abstract In socially monogamous species a male and a female form a pair bond, sometimes for life, in order to raise offspring. Despite their exclusive social association, both partners may copulate with additional individuals outside the pair bond. Such extra-pair copulations are common in many socially monogamous species and they often lead to mixed paternity among a brood or litter. How does a male's success at obtaining a social mate and safeguarding paternity in his own brood relate to his extra-pair success? Answering this question is important to understand the effect of extra-pair paternity on the strength of sexual selection among males. Several scenarios can be envisioned. The first is that extra-pair young are sired by unpaired males at the cost of paired males. If this is the case, male reproductive skew is reduced, the effect of competition among males to enter the pool of breeders is lessened and the strength of sexual selection decreases with the rate of extra-pair paternity. Nevertheless, in such systems extra-pair paternity may still be a major route to male reproductive success and hence an important arena for sexual selection. Under a second scenario, extra-pair paternity will leave male reproductive success relatively unaffected. This is when unfaithful males tend to gain and lose paternity to the same extent. The third scenario is that the same males that are successful at pairing with a social mate and securing paternity in their brood, are also successful at siring extra-pair young. In this case, the strength of sexual selection on males is clearly increased. Thus, although social monogamy seems to restrict sex differences in the strength of sexual selection, extra-pair paternity may create opportunities for sexual selection, particularly among males. The occurrence of extra-pair paternity may therefore explain the evolution of exaggerated primary and secondary male sex traits, ultimately resulting in sexual dimorphism even in socially monogamous species. We review studies that implement paternity analyses in wild populations to examine the role of extra-pair paternity for the strength of sexual selection. In most studies variation among males in their reproductive success increased due to extra-pair fertilizations, and much of the variation was caused by differential success in securing extra-pair mates and in avoiding losing paternity with the social mate. Most studies also

found a positive covariance between extra- and within-pair success, a further indication that extra-pair paternity intensifies sexual selection. However, the reported estimates of the strength of sexual selection may be biased due to systematic influences of random mating and to limitations of sampling. The effect of extra-pair paternity on the strength of sexual selection and the best way to estimate it, remain debatable. Nevertheless, multiple mating appears to drive sexual selection in several monogamous species by providing an important path to male reproductive success.

1-3.1 How does Extra-Pair Paternity influence Sexual Selection?

Parentage analyses can reveal hidden reproductive interactions between individuals that are not social partners. Extra-pair matings are a special case of promiscuity where social pair bonds exist and persist despite copulations with multiple partners by one or both pair members. The relevance of extra-pair interactions in re-shaping social mating systems varies between species. In some species or populations, extra-pair matings are no more than exceptional events (e.g. Dearborn et al. 2001; Egger et al. 2006), whereas in others extra-pair paternity is a phenomenon that cannot be ignored when describing mating patterns because of a substantial discrepancy between the observable apparent mating system and the actually realized mating system (e.g. Double and Cockburn 2003; Sefc et al. 2008). Extra-pair copulations (EPCs) are of special interest in socially monogamous species where promiscuity is otherwise absent. Pair bonding and social monogamy are relatively rare – except in birds (Lack 1968, p.148) – yet occur in a wide range of animal taxa (e.g. Caldwell 1997; Kvarnemo et al. 2000; Baeza 2008; Steinauer 2009). However, social monogamy frequently goes hand in hand with multiple mating (e.g. Chapple 2003; Lodé and Lesbarrères 2004; Cohas and Allainé 2009; Griffith et al. 2002).

1-3.1.1 Extra-Pair Paternity

Because social monogamy usually coincides with biparental care (e.g. Caldwell 1997; DeWoody et al. 2000; Runcie 2000; Bennett and Owens 2002, p.79; Tallamy 2009; Wright et al. 2009), EPCs can be seen as reproductive parasitism of some males at the cost of others. Due to anisogamy, a male can fertilize many more ova than those produced by its mate and in most species male reproductive success is limited by access to fertile females. Thus, male benefits of EPCs appear straightforward: gaining additional offspring cared for by other males. Indeed, strong selection on male EPC behavior may be all that is needed to explain patterns of extra-pair paternity. However, such male behavior has several implications which make the situation more complicated (Westneat and Stewart 2003).

First, if some males gain extra-pair young (EPY) other males must lose fertilizations. Male pursuit of EPCs should thus increase male-male competition, and this not only before copulation, at the social level, but also in the form of sperm competition after copulation. Increased competition for access to fertilizations should also lead to the evolution of paternity protection behavior, such as mate guarding or frequent copulation (Birkhead and Møller 1992, ch.7-9), which may trade off with the pursuit of EPCs.

Second, there is a connection between the occurrence of paternal care and sexual selection via EPCs because extra-pair success may come at a cost when males have to trade off the pursuit of extra-pair mates with offspring care (Westneat et al. 1990). When extra-pair fertilizations are successful, the payoff from paternal care for the cuckolded male is lowered. Males that perceive a loss of paternity may then reduce their level of care, although it remains a matter of debate when reduced male care is expected and to what degree it actually occurs (Wright 1998; Whittingham and Dunn 2001; Sheldon 2002; Arnqvist and Kirkpatrick 2007; Griffith 2007; Eliassen and Kokko 2008).

Third, females may or may not benefit from copulating with a male that is not their social partner. A female that does not benefit may be expected to resist copulation attempts by extra-pair males, further reducing the benefits and increasing the costs of EPC behavior for males. Such sexual conflict will always exist to some extent because the optimal copulation pattern for a female will not coincide with the optimal copulation pattern for the social mate and extra-pair males. However, in certain male-female constellations, the conflict may be reduced or even absent, namely in those where the female also gains from EPCs. How would females benefit from EPCs? First and foremost, females need their ova to be fertilized, and the social partner may be unable to provide her with enough gametes to do so (e.g. Sheldon 1994; Hasson and Stone 2009), for instance when he produces too few or low quality sperm. Females could also benefit from EPCs for a variety of other reasons (Westneat et al. 1990; Birkhead and Møller 1992, pp. 198-209). Most controversial amongst these is the idea that females may gain indirect (genetic) benefits from EPCs (Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007; Eliassen and Kokko 2008; Uller and Olsson 2008). The quality of the offspring genome is the result of the combination of the paternal and maternal haplotypes and an extra-pair male may provide alleles that are more adaptive than those from the social mate, either generally ('good genes'), or in combination with the female's alleles ('compatible genes'), or both (Neff and Pitcher 2005). Such a situation could be common under social monogamy, because many females may have to settle with a suboptimal social mate when their partner of choice is mated to another female (Gowaty 1996; Hasselquist and Sherman 2001). However, it remains unclear (a) to what extent these and other benefits occur in different populations and under different conditions (Friedl and Klump 2005; Schmoll et al. 2005; Garvin et al. 2006; O'Brien and Dawson 2007; Dreiss et al. 2008; Fossøy et al. 2008; Dunn et al. 2009; Kawano et al. 2009; Townsend et al. 2010) and (b) whether they are sufficient to cause selection on female pursuit of extra-pair mat-

ings (Westneat and Stewart 2003, Arnqvist and Kirkpatrick 2005). In any case, whenever extra-pair copulations occur, male-male competition will increase, *and* additional opportunities for female choice will arise, either at the precopulatory stage or later in the form of cryptic female choice among male sperm. This provides the link between extra-pair paternity (EPP) and sexual selection.

1-3.1.2 Sexual Selection

Sexual selection is selection acting on differences among individuals in reproductive success caused by variation in their mating success (Andersson 1994). Such variation may be random, but selective effects are then not transferred to the next generation and will not lead to evolutionary change. Sexual selection on phenotypic traits is thus dealing with variation in mating success as the result of non-random mating. Sexual selection is a major force in shaping the structure of animal societies and the behavioral repertoire of individuals, for example through its interaction with the mating system and sex roles (Andersson 1994, ch.7). Sex differences in the strength of sexual selection are the primary cause of the sex differences in behavior and morphology found in many species (Andersson 1994, ch.11-15). Under strict monogamy, the number of mating events is constrained to one per individual, and differences between the sexes in the strength of sexual selection are limited. Nevertheless, pronounced sexual dimorphism is also found in many socially monogamous species (Figure 1; e.g. Knolton 1980; Møller 1986; Leutenegger and Lubach 1987; Boonstra et al. 1993; Kokita and Mizota 2002; Mizuta 2005). Is EPP a candidate to explain sexual dimorphism in socially monogamous species?

Clearly, EPP increases the number of mating events and thereby creates additional opportunities for male-male competition and female choice. Hence, at least in theory, EPP has the potential to dramatically alter the strength of sexual selection experienced by males. However, high levels of EPP do not necessarily lead to increased intensity of sexual selection on males. For instance, if females perform EPCs as insurance against the risk of infertility, they may mate at random with respect to male phenotypic traits. Even then, however, it is unlikely that male mating success is entirely stochastic, because the extra-pair behavior of females will introduce competition among males to secure EPCs and to fertilize the eggs (sperm competition). Furthermore, male extra-pair behavior may trade off with success with their social mate, because males cannot simultaneously pursue EPCs and protect paternity or feed offspring. Variation in mating success may therefore not translate into variation in reproductive success, because within- and extra-pair success may be negatively correlated. It is even conceivable that extra-pair paternity leads to reduced male reproductive skew and hence less intense sexual selection. This would be the case if variation in the apparent success among males – unequal success at securing social mates or variation in female fecundity – is re-

duced via higher extra-pair success of socially less successful males (Webster et al. 1995; Jones et al. 2001; Lawler 2009). In summary, a higher level of EPP will not necessarily cause an increase in sexual selection on males, because extra-pair success may be random or uniformly distributed, or it may be negatively associated with within-pair success.
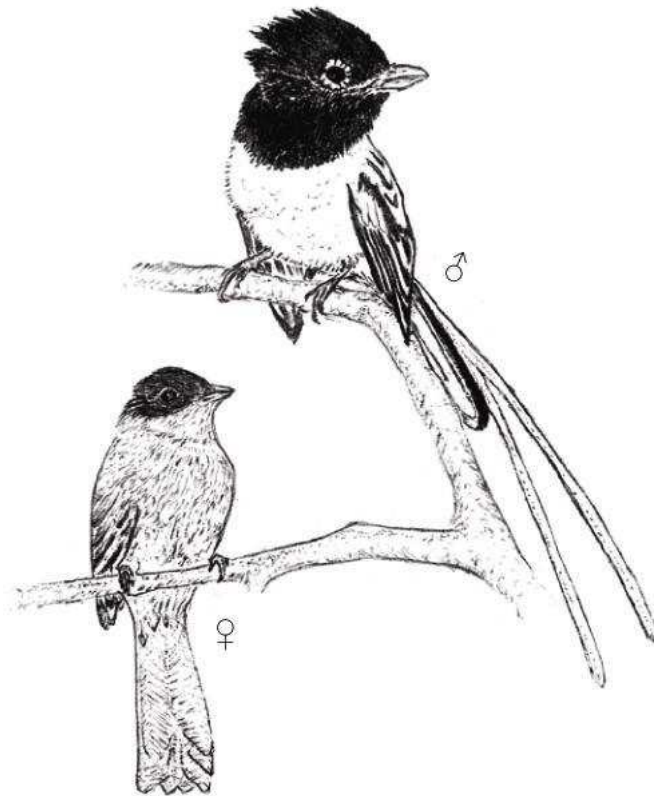

Fig. 1. Male and female of the Madagascar paradise flycatcher (*Terpsiphone mutata*). This is a socially monogamous species with biparental care. Can extra-pair paternity play a role in the evolution of the pronounced sexual dimorphism? A study by Raoul Mulder found that fifty percent of the females had extra-pair young in this species (Eliot 2005).

Comparative studies in birds have shown that higher levels of EPP are associated with increased color and size dimorphism, suggesting that EPP does magnify the intensity of sexual selection on males (Møller and Birkhead 1994; Owens and Hartley 1998; Dunn et al. 2001). However, secondary sexual traits (increased size, 'weaponry', ornaments) are most exaggerated in males of socially polygynous and lekking species. Indeed, the social mating system remains the best predictor of dimorphism across all birds (Owens and Hartley 1998; Dunn et al. 2001). This is not surprising because social monogamy will tend to equalize selection on males and females unless EPP causes highly skewed male reproductive success. EPP

leads to variation in mating systems among species beyond those observable via social pairings, and may be especially important for sexual selection through post-copulatory processes such as sperm competition. Interspecific variation in rates of multiple paternity are related to numerous aspects of male reproductive biology, such as testis size or sperm swimming speed (Møller and Briskie 1995; Garamszegi et al. 2005; Ramm et al. 2005; Bryja et al. 2008; Immler et al. 2008; Kleven et al. 2008; Kleven et al. 2009; Lüpold et al. 2009; but see Schülke et al. 2004).

An effect of EPP on the strength of sexual selection in males probably varies considerably between species and populations, if not between years. It is thus of interest to quantify the effect of multiple mating on the intensity of sexual selection for specific populations. In this review we will discuss studies that have attempted to do this. Because studies of EPP have been conducted overwhelmingly in birds, the majority of examples are from avian species. We first introduce several methods that allow quantifying the strength of sexual selection. We then examine how these estimates are affected by EPP, both theoretically and in empirical studies. For each estimate we also discuss problems that arise in the interpretation and comparison of results, which may be of more general importance for research on the strength of sexual selection and male reproductive skew in multiply mating species (see also chapter 1-1).

1-3.2 Measurements of Sexual Selection

For selection to act, it is necessary that fitness variation among individuals is present. In fact, standing variation in fitness measures the increase in fitness from one generation to the next, if all fitness variance was heritable (Fisher 1930, p.35). The variance in relative fitness (absolute fitness divided by mean absolute fitness), a measurement referred to as **the opportunity for selection I**, quantifies the maximum rate at which fitness can increase over time (Crow 1958; O'Donald 1970) and thus sets an upper limit to the strength of any form of selection, including sexual selection. Note that I is not a measurement that is specifically concerned with sexual selection, but rather encompasses both natural and sexual selection. From its definition, it is clear that sexual selection can act only if variation among individuals in their ability to obtain access to mates exists. This variation can be quantified as variance in relative mating success, referred to as **the opportunity for sexual selection I_{mates}** (Wade 1979; Wade and Arnold 1980). Molecular parentage assignment often reveals that a male's true success in obtaining mates for fertilizations is different than would appear from his number of social mates. Here we define realized mating success, based on parentage analysis, as the number of individuals of the opposite sex with which an individual produces genetic offspring. I and I_{mates} are of interest because they set upper limits to parameters that are relevant to the intensity of sexual selection, and they can be estimated independent of

the phenotypic traits that are the target of sexual selection. The maximum intensity of sexual selection that any phenotypic trait could be subjected to is also interesting in its own right. Estimating variation in relative reproductive (I) and mating success (I_{mates}) is one of many possibilities to measure male reproductive and mating skew (Kokko et al. 1999; Nonacs 2003). I and I_{mates} have the advantage that they are closely linked to selection theory, thus allowing a direct interpretation regarding the evolutionary process (Jones et al. 2002; 2004; for applications of reproductive skew theory in primates and social insects see chapters 1-1 and 1-2).

The strength of selection on a trait depends on how variation in the trait relates to variation in fitness. This relationship can be measured as the partial regression of relative fitness on the trait while all other traits are held constant. The corresponding regression coefficient is called a selection gradient β (Lande 1979). In the context of sexual selection the trait of interest is the 'ability to obtain mates'. The selection gradient for this trait is called the **Bateman gradient β_{ss}** (Andersson and Iwasa 1996). The Bateman gradient thus measures the slope of the least-squares regression of relative fitness on mating success and this is the direct expression of sexual selection resulting from differences in the ability to obtain access to mates (Arnold and Duvall 1994). Including this measurement into quantitative analyses of sexual selection may provide more reliable information than variance-based estimates alone (Jones et al. 2002; Jones et al. 2004; Jones et al. 2005; Mills et al. 2007; see also Bjork and Pitnick 2006). One disadvantage of selection gradients is that they may not be easily comparable between studies because they are affected by the particular choice of phenotypic characters that are included in the multivariate regression analysis (Arnold and Wade 1984; Andersson 1994, pp.91-94). Furthermore, they need to be standardized for comparisons, which may not be straightforward (Hereford et al. 2004; Jones 2009).

Bateman (1948) illustrated that sex differences in all three of the above estimates (I, I_{mates}, β_{ss}) go hand in hand with a sex difference in the strength of sexual selection. This is known as Bateman's principles (Arnold 1994). As a consequence of anisogamy, males are typically subject to stronger sexual selection than females. In other words, in species with 'typical' sex roles males exhibit higher variance in fitness (I) and higher variance in mating success (I_{mates}) than females, because for them there is a greater range of reproductive outcomes as a result of mating competition. Most fundamentally, for males of these species there is a stronger correlation between mating and reproductive success (β_{ss}) than for females.

1-3.3 Realized and Apparent Reproductive and Mating Success

1-3.3.1 $I_{realized}/I_{apparent}$ Ratios

Let us now consider how different levels of EPP influence the measurements of the strength of sexual selection. The most common approach to quantify the effect of EPP on sexual selection in a population is to compare the relative variance in apparent and realized male reproductive success (number of young in social nests and number of young sired), $I_{apparent}$ and $I_{realized}$ (summarized in Table 1). This is based on the idea that EPP will increase sexual selection on males when it increases variation in male reproductive success due to sperm competition or non-random mating. Thus, for EPP to increase sexual selection some males must be consistently more successful at acquiring extra-pair offspring than others, either because they are more successful at acquiring extra-pair mates, or because they are more successful in post-copulatory competition to fertilize the eggs. In that case, offspring are redistributed from the unsuccessful males to the successful sires and we expect an increase in the opportunity for selection from the apparent to the realized mating system. Conversely, if all males are equally successful extra-pair sires or EPP trades off with within-pair success, extra-pair males should simultaneously gain and lose paternity and these paternity exchanges should leave their overall reproductive success largely unaffected (e.g. Ketterson et al. 1997). Furthermore, when EPP reduces sexual selection by providing an alternative route to fertilizations for males with small apparent success (e.g. unpaired males), the opportunity for selection will decrease from the apparent to the realized mating system. Hence, a ratio $I_{realized}/I_{apparent}$ significantly greater than 1 is considered evidence that EPP increases selection on males. Ratios of $I_{realized}/I_{apparent} > 1$ are frequently reported in studies of socially monogamous birds (mean reported $I_{realized}/I_{apparent} = 3.4$, Table 1). However, these estimates suffer from a number of problems.

Table 1 Overview of studies calculating $I_{realized}/I_{apparent}$ ratios and comparison with $I_{realized}/I_{random}$ ratios from model of random extra-pair mating (bold when $I_{random} > I_{apparent}$).

Species (scientific name)	(common name)	N [a]	p (%) [b]	AR(%) [c]	$\bar{c}$ [d]	MS [e]	$I_{realized}$ [f]	$I_{apparent}$ [g]	I_{random} [h]	$\dfrac{I_{realized}}{I_{apparent}}$	$\dfrac{I_{realized}}{I_{random}}$	ξ [i]	Ref [j]
Acrocephalus arundinaceus	Great reed warbler	121	3	100	4.6	P	1.02	1.00	0.94	1.02	1.08	*4.60*	*1*
Agelaius phoeniceus 1	Red-winged blackbird	13	37	93	5.8	P	0.39	0.25	0.15	1.56	2.63	1.45	*2*
Agelaius phoeniceus 2	Red-winged blackbird	51	25	57	3.2	P	1.20	1.02	0.67	1.17	1.80	3.27	*3*
Agelaius phoeniceus 3	Red-winged blackbird	103	26	78	4.3	P	0.74	0.64	0.41	1.16	1.78	2.72	*4*
Carpodacus erythrinus	Scarlet rosefinch	46	18	73	4.3	M	0.40	0.12	0.12	3.31	3.31	0.52	*5*
Cyanistes caeruleus 1	Blue tit	32	11	73	9.8	M	0.27	0.16	0.14	1.69	1.98	1.57	*6*
Cyanistes caeruleus 2	Blue tit	47	15	74	11.6	M	0.12	0.04	0.04	3.51	**3.26**	0.46	*7*
Delichon urbica	House martin	17	19	100	3.6	M	0.31	0.06	0.09	5.17	**3.51**	**0.21**	*8*
Dendroica caerulescens	Black-throated blue warbler	67	21	62	4.0	M	0.72	0.51	0.37	1.41	1.95	2.04	*9*
Dendroica pennsylvanica	Chestnut-sided warbler	37	47	87	2.9	M	0.70	0.19	0.21	3.75	**3.35**	0.54	*10*
Dendroica petechia	Yellow warbler	14	37	35	4.0	M	0.10	0.03	0.10	3.25	**1.06**	**0.13**	*11*
Ficedula albicollis	Collared flycatcher	44	15	93	5.7	M	0.14	0.03	0.05	5.11	**3.03**	**0.15**	*12*
Geothlypis trichas	Common yellowthroat	21	26	83	4.4	M	0.48	0.28	0.20	1.71	2.36	1.24	*13*

Species (scientific name)	(common name)	N [a]	p (%) [b]	AR(%) [c]	$\overline{c}$ [d]	MS [e]	$I_{realized}$ [f]	$I_{apparent}$ [g]	I_{random} [h]	$\dfrac{I_{realized}}{I_{apparent}}$	$\dfrac{I_{realized}}{I_{random}}$	ξ [i]	Ref [j]
Hirundo rustica erythrogaster	North American barn swallow	86	31	100	5.2	M	0.53	0.07	0.09	7.96	**5.85**	0.35	*14*
Hirundo rustica rustica	European barn swallow	63	28	-	4.1	M	0.36	0.15	0.14	2.37	2.49	0.63	*15*
Icterus galbula bullockii	Bullock's oriole	31	32	45	4.3	M	0.17	0.07	0.10	2.43	**1.65**	**0.30**	*16*
Junco hyemalis	Dark-eyed junco	50	28	55	3.7	M	0.72	0.55	0.35	1.32	2.06	2.03	*17*
Luscinia svecica svecica	Bluethroat	134	29	52	5.4	M	0.37	0.08	0.09	4.63	**3.96**	0.43	*18*
Malurus splendens	Splendid fairy-wren	204	42	91	-	CB	1.42	1.47	-	0.97	-	-	*19*
Melospiza melodia	Song sparrow	299	8	95	1.6	M	1.33	1.21	1.08	1.10	1.23	1.90	*20*
Passerculus sandwichensis	Savannah sparrow	80	47	92	4.6	P	0.48	0.27	0.17	1.78	2.74	1.24	*21*
Poecile atricapillus	Black-capped chickadee	58	9	47	6.2	M	0.10	0.04	0.05	2.50	**2.11**	**0.25**	*22*
Progne subis	Purple martin	41	19	54	3.4	M	0.33	0.05	0.09	6.69	**3.79**	**0.16**	*23*
Sialia currucoides	Mountain bluebird	59	36	70	5.0	M	0.27	0.04	0.09	7.32	**3.15**	**0.19**	*24*
Tachycineta bicolor	Tree swallow	19	51	66	4.9	M	0.79	0.09	0.12	8.78	**6.72**	0.44	*25*
Troglodytes aedon	House wren	68	10	88	8.6	P	0.22	0.18	0.16	1.22	1.40	1.55	*26*
Tyrannus tyrannus	Eastern kingbird	89	47	56	3.0	M	0.85	0.09	0.18	9.44	**4.69**	**0.27**	*27*
Wilsonia citrina	Hooded warbler	100	27	55	3.4	M	0.46	0.18	0.17	2.56	2.66	0.62	*28*

1-3.3.2 Effects of Sampling Limitations on I

Measurements of I are sensitive to sampling effort and limitations (Downhower et al. 1987). In most studies of EPP the focal individuals are part of an open population where reproductive interactions extend beyond the sampled nests. Thus, the males that are included in the study will usually have sired some offspring in non-registered nests. Estimated variances may then be too high or too low if males that are unsuccessful on the study site are more or less successful in unsampled nests (Webster et al. 1995; Freeman-Gallant et al. 2005). Also, in an open population some of the offspring in sampled nests will be sired by unknown males (indicated as assignment rate in Table 1) which are then excluded from further calculations. This will generally cause an increase of $I_{realized}$ over $I_{apparent}$ by lowering mean realized reproductive success (Møller and Ninni 1998; Freeman-Gallant et al. 2005) and may also bias variance calculations when the unknown sires are a non-random sub-sample of males (e.g. unpaired males; Jones et al. 2001).

1-3.3.3 Effects of Random Mating on I

Although the use of relative instead of absolute fitness variance appears to remove scaling effects, estimates of I are not generally independent of mean fitness and the number of competitors (Downhower et al. 1987; Ruzzante et al. 1996; Kokko et al. 1999; Fairbairn and Wilby 2001; Walsh and Lynch 2008; see also Galimberti et al. 2002), because the value of I under the null hypothesis of random success changes systematically as a function of these parameters. This is mostly an expression of the fact that chance can create fitness variance that is unrelated to phenotypic traits (Sutherland 1985a,b).

It is generally accepted that selection and response to selection are two separate issues. Indeed, the extent to which the action of selection on a particular trait is transferred to the next generation depends on the trait's heritability (e.g. Wade and Arnold 1980; Lande and Arnold 1983) and on whether selection acts on the trait's genetic component or on its environmental components (Price 1988). Thus, measurements of I provide an estimate of the standing variation in fitness and selection will act on this variation, both when it is of random origin and when it is not (Shuster and Wade 2003, pp.31-34). As long as some trait with marginal fitness effects exists, selection on this trait will be stronger when I is larger. Still, it is worth noting that an increase in I does not necessarily imply an increase in selection on specific phenotypes, because fitness variance may be stochastic, i.e. unrelated to phenotypic traits. Because the contribution of chance to fitness variance may vary systematically under different scenarios (Sutherland 1985a,b; Hubbell

and Johnson 1987; Gowaty and Hubbell 2005), it is helpful to calculate which value of I we would expect under randomness and use this as a reference when comparing estimates of I (e.g. Wade 1995; Haydock and Koenig 2003; Nonacs 2003; Cerchio et al. 2005).

This may be particularly relevant when considering the effect of different EPP rates on I. In a socially monogamous system almost any deviation from monogamy may increase variance in male fitness, because the apparent mating system should produce a relatively uniform distribution of offspring among males (Jones et al. 2001; Lawler 2009). For example, in the socially monogamous purple martin (*Progne subis*) standard deviation in apparent reproductive success among 41 males was only 0.8 while mean apparent reproductive success was 3.4 (Wagner et al. 1996; Table 1). In such cases, the redistribution of offspring among males via EPP can *just by chance* lead to some males being more successful than others, even if all males are equally likely to gain or lose offspring. It is erroneous to assume that random processes lead to equal extra-pair success of all males and thus to paternity exchanges that leave variance in reproductive success unaffected. Therefore, the correct reference value for $I_{realized}$ can be smaller or larger than $I_{apparent}$. When variation in apparent success among males is high, for instance when many males fail to secure a social mate ('floaters'), introducing random extra-pair mating will lead to a reduction in I, as some of the floaters randomly receive extra-pair fertilizations. Conversely, when variation in apparent success among males is low, for instance when there are no unpaired males and clutch size variation and nest predation are limited (e.g. Whittingham and Lifjeld 1995; Sheldon and Ellegren 1999; Richardson and Burke 2001; Dolan et al. 2007; Balenger et al. 2009), I is expected to increase with the rate of EPP under random mating because some males randomly receive more extra-pair fertilizations (see also simulations in Webster et al. 1995).

Based on a model of random extra-pair mating, we calculated the expected opportunity for selection, I_{random}, and the associated variance ratio for published studies and compared this with the reported variance ratios (Table 1; see Online Supplementary Material for details of the model). The variance ratio obtained in this way was greater than the reported ratio in roughly half of the studies (13 out of 27). In the other half (14 out of 27 studies) the ratio based on random mating was smaller than the reported ratio (bold in Table 1). In nine and three studies the reduction was more than 20% and 50%, respectively. This indicates that for these studies the role of extra-pair paternity in generating stronger sexual selection strength (than under the apparent mating system) may not be as important as previously thought because part of the variance increase is expected even under random mating. Another result from this model of random extra-pair mating is that the opportunity for selection will increase systematically with the rate of extra-pair paternity under random mating for certain parameter constellations that may occur naturally (parameter $\xi < 0.4$, Table 1; see Online Supplementary Material for details).

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Complete randomness of male extra-pair success is unlikely, of course, because some male trait will probably affect extra-pair success to some extent. Since EPP increases the number of mating events, it increases the number of events where sexual selection, if it occurs, comes into action. However, we have seen above that we can imagine biological situations that introduce stochasticity into male extra-pair success, such as random female choice of extra-pair mates as an insurance against the risk of infertility. When a significant increase of $I_{realized}$ over $I_{apparent}$ is found, this undoubtedly reflects an increase in the opportunity for selection caused by EPP. But how this relates to the strength of selection on traits that are the targets of sexual selection is another question. The effect of selection opportunity on sexually selected traits may vary systematically with the frequency of extra-pair paternity, irrespective of the heritability of these traits.

1-3.3.4 Opportunity for Selection in Females

Some studies have used a similar approach and compared variance in relative female fitness $I_{\female}$ to variance in relative male fitness $I_{\male}$ (realized reproductive success; Ketterson et al. 1997; Weatherhead and Boag 1997; Webster et al. 2001; Byers et al. 2004; Kraaijeveld et al. 2004; Freeman-Gallant et al. 2005; Whittingham and Dunn 2005; Albrecht et al. 2007). This has the advantage that it only relates to actual parentage, which may be more relevant biologically. A sex difference in I is thought to be related to a sex difference in the strength of sexual selection (Bateman 1948). However, here too, chance may systematically increase fitness variance, in this case that of males over that of females (Sutherland 1985a,b; Hubbell and Johnson 1987; Gowaty and Hubbell 2005). This is immediately clear when we consider that the majority of studies concern socially monogamous species whereby only breeding males are included, so that apparent male reproductive success and female reproductive success are identical. Calculating $I_{\female}$ is more interesting with respect to sex differences in the opportunity for selection when unpaired males are included (Ketterson et al. 1997; Whittingham and Dunn 2005; Albrecht et al. 2007) or when the study species is socially polygynous (Gibbs et al. 1990; Westneat 1993; Hasselquist et al. 1995; Weatherhead and Boag 1997; Freeman-Gallant et al. 2005; Whittingham and Dunn 2005; Westneat 2006), but then it is difficult to quantify the effect of EPP.

1-3.3.5 Variation in the Number of Mates

The variance in relative mating success I_{mates} has rarely been calculated in studies of EPP (but see Ketterson et al. 1997). Variance in mating success is a necessary prerequisite for sexual selection to occur and the standard deviation in relative mating success also gives an upper bound for the effect of any trait on mating suc-

cess (Jones 2009). In the absence of EPP, variation in mate number among individuals of a socially monogamous species arises only from differences in pairing status (breeding or non-breeding). Variance in mating success is thus expected to dramatically increase with the rate of EPP. However, here it is most obvious that any form of extra-pair mating, even random mating, is bound to increase variance in mate numbers. Comparisons between apparent and realized I_{mates} are therefore not very informative. To assess the effect of EPP on the strength of sexual selection on males or females, a reference value for I_{mates} should be defined based on a random mating process (e.g. McLain 1986; see also Online Supplementary Material). Still, it is interesting to compare male and female variation in mate numbers.

1-3.4 Fitness Components

The influence of EPP on sexual selection can also be assessed by estimating the magnitude of fitness components that contribute to fitness variation (Webster et al. 1995). A male's total reproductive success, T, is the product of the number of mates M he has, the average clutch size N of these mates, and the proportion P of young in all these clutches that he sires:

$$T = M\,N\,P.$$

These variables reflect variation in male reproductive success due to the number of mates he can acquire, the quality (fecundity) of these mates, and the success at securing fertilizations with these mates. Furthermore, a male's total reproductive success is the sum of the young he sires in his own and in other males' nests (his within-pair and his extra-pair success):

$$T = W + E.$$

Male total reproductive success can thus be written as

$$T = M_wN_wP_w + M_eN_eP_e,$$

where the indices w and e refer to the variables for within- and extra-pair success, respectively. Each of these six components contributes to variance in male reproductive success. It is thus possible to split up the total variance in reproductive success into terms that correspond to the variation due to each of the six components and to the covariance between components (Webster et al. 1995). For example, when we restrict ourselves to the two variables W and E, without further partitioning, we find that

$$\mathrm{Var}(T) = \mathrm{Var}(W) + \mathrm{Var}(E) + 2\,\mathrm{Cov}(W, E).$$

Thus, one can calculate the proportion of the total variance that is attributable to variance in within-pair and in extra-pair success and to the covariance between the two. This type of variance partitioning can be performed for all six components and their associated covariances.

Table 2 Overview of studies that report variance components in male reproductive success

Species (scientific name)	(common name)	N [a]	p (%) [b]	$I_{realized}$ [c]	% Total variance [d]					MS [e]	outside [f]	floaters [g]		Ref [h]
-	-	-	-	-	W	E	Cov	P_w	M_e	-	-	present	included	-
Agelaius phoeniceus 2	Red-winged blackbird	21	25	0.49	69.3	9.7	20.1	35.2	10.2	P	R	R	N	*3*
Agelaius phoeniceus 3	Red-winged blackbird	103	26	0.74	72.0	15.0	13.0	-	-	P	R	Y	N	*4*
Agelaius phoeniceus 4	Red-winged blackbird	275	40	1.36	76.0	11.0	20.0	19.0	-	P	Y	?	N	*29*
Carpodacus erythrinus	Scarlet rosefinch	46	18	0.40	67.3	22.9	9.8	28.7	18.9	M	R	Y	Y [α]	*5*
Delichon urbica	House martin	17	19	0.31	41.5	56.6	1.9	-	-	M	N	N	N	*8*
Dendroica caerulescens	Black-throated blue warbler	67	21	0.72	76.3	11.0	12.7	-	-	M	R	N or R	N	*9*
Dendroica pennsylvanica	Chestnut-sided warbler	37	47	0.70	55.8	44.2	2.1	18.9	-	M	R	N or R	N	*10*
Geothlypis trichas 1	Common yellowthroat	21	26	0.48	57.7	20.8	21.5	22.6	22.7	M	R	Y	Y [α]	*13*
Geothlypis trichas 2	Common yellowthroat	101	18	0.71	56.3	22.6	21.1	8.5	16.9	M	N or R	Y	Y	*30*
Hirundo rustica erythrogaster	North American barn swallow	86	31	0.53	33.0	48.0	19.0	-	-	M	N or R	N or R	N	*14*
Malurus splendens	Splendid fairy-wren	204	42	1.42	58.8	42.0	−0.8	12.7	42.4	CB	N	N	N	*19*
Passerculus sandwichensis 2002	Savannah sparrow	57	56	0.58	34.6	65.3	−0.6	29.6	56.6	P	N	N	N	*21*
Passerculus sandwichensis 2003	Savannah sparrow	33	37	0.37	75.1	36.9	−11.9	34.0	23.6	P	N	N	N	*21*
Sialia currucoides	Mountain bluebird	59	36	0.27	60.4	33.6	6.0	9.2	9.5	M	Y	Y	N	*24*

Species (scientific name)	(common name)	N [a]	p (%) [b]	$I_{realized}$ [c]	% Total variance [d]					MS [e]	outside [f]	floaters [g]		Ref [h]
-	-	-	-	-	W	E	Cov	P_w	M_e	-	-	present	included	-
Troglodytes aedon	House wren	68	10	0.22	97.3	10.4	–7.7	22.9	8.3	P	R	R	N	*13*
Tyrannus tyrannus	Eastern kingbird	89	47	0.85	42.0	46.0	12.0	36.5	33.0	M	Y	?	N	*27*
Propithecus verreauxi verreauxi	Verreaux's sifaka (primate) [β]	134	46	2.95	37.7 [γ]	33.9 [γ]	10.5 [γ]	-	-	MF	N	'Y' [δ]	'Y' [δ]	*31*

[a] Sample size (number of males).

[b] Frequency of EPP among young in %.

[c] Opportunity for selection based on realized male reproductive success.

[d] Proportion (in %) of total variance in male reproductive success attributable to variation in within-pair (W) and extra-pair (E) success and the covariance between them ($2Cov(W,E)$) as well as to variation in the proportion of young sired in social nest(s) (P_w) and variation in the number of extra-pair mates (M_e). Note that components need not sum up because other terms can be negative (Webster et al. 1995). Fields are empty where values not available.

[e] Social mating system (MS): socially monogamous (M), polygynous (P), cooperative breeder (CB), or multi-male multi-female groups (MF).

[f] opportunities for fertilizations of focal males in non-monitored nests shown as yes (Y), no (N),or restricted (R).

[g] presence of floaters in population shown as yes (Y), no (N), or rare (R) and floaters included in calculations of reproductive success yes (Y) or no (N).

[h] References: see Appendix.

[α] Some floaters may not have been caught.

[β] This is the only non-avian species included. E refers to extra-group paternity in this primate.

[γ] Contribution without remainder terms.

[δ] Males without reproductive success are not floaters but members of the studied groups.

1-3.4.1 Influence of EPP on Fitness Components

Table 2 provides an overview of studies that have used the described method of variance partitioning. Components contributing at least 10% to 15% of the total variance in reproductive success are usually thought to be important (e.g. Webster et al. 2001; Lawler 2007; but see Whittingham and Dunn 2005), whereas contributions below 5% are considered negligible (Webster et al. 1995). The influence of EPP on the total variance in male reproductive success is indicated in three ways.

1. $Var(E)/Var(T)$ directly indicates which proportion of the total reproductive success of males is due to success with extra-pair mates and would thus generate opportunities for selection and sexual selection. The contribution of $Var(E)$ exceeds 20% in more than two thirds of the studies, and is less than 10% in only one study (Table 2). In eight out of nine studies (where it was assessed) the majority of variance in extra-pair success was due to the number of acquired extra-pair mates (M_e), which means that variation in extra-pair success directly reflects the opportunity for sexual selection (because sexual selection is caused by variation in reproductive success that arises from variation in mating success).

2. The effect of $Var(P_w)$ indicates the proportion of the total reproductive success of males that is due to variation in paternity loss in the own brood. Typically, the greatest part of the total variance in reproductive success remains with $Var(W)$. In nine out of eleven studies (where it was assessed) variation in P_w contributed substantially (>10% of total variance) to this variance in within-pair success (Table 2). This is caused by differences among males in their ability to secure paternity in their own nest(s), which is related to their success in competition over mates, either via female choice, via male-male competition (e.g. territory defense), or via sperm competition.

3. A positive covariance between within- and extra-pair success indicates that males that are successful with their social mate(s) are also successful at siring extra-pair offspring. Conversely, when the covariance is negative increased extra-pair success coincides wit lower within-pair success, which suggests a trade-off between investing in the own brood or in extra-pair copulations. In this case EPP may decrease the strength of sexual selection by providing an alternative route to reproductive success, for example for males that fail to nest. In eleven out of sixteen studies the contribution of $Cov(W,E)$ is non-negligible (>5%) and positive (Table 2). In at least three studies, however, the covariance term was very small suggesting no clear relationship between a male's extra- and within-pair success. Extra- and within-pair reproduction then represent two independent pathways through which sexual selection can act. Overall, we expect this to weaken the strength of sexual selection because reproductive skew among males should decrease with the existence of multiple uncorrelated

pathways to mating success (e.g. Candolin 2003). Random mating will also lead to zero covariance between extra- and within-pair success.

Although the studies listed in Table 2 generally seem to support the idea that EPP increases the intensity of sexual selection, there are some caveats to consider.

In some studies estimates are highly inconsistent between years (savannah sparrow, *Passerculus sandwichensis*, in Table 2; Freeman-Gallant et al. 2005; Webster et al. 2007; see also Weatherhead and Boag 1997; Kleven et al. 2006), which would imply that the intensity of sexual selection may vary among years. However, the inconsistency is probably due to the low level of confidence associated with estimates of fitness components based on small sample sizes (Table 2). This uncertainty could be quantified by calculating confidence intervals for all estimates of the intensity of sexual selection, for instance via bootstrapping, as is shown in Table 3 for the contribution of fitness components in the blue tit (*Cyanistes caeruleus*). Note that the contribution of the covariance term in particular is highly variable between years, but confidence intervals overlap. Annual sample sizes are well within the range of the sample sizes reported in other studies (Table 2) and only the collation of data from six years allows a more precise assessment. Confidence intervals for *I* could be constructed in a similar manner to provide information on the quality of the estimate. In any case, results from studies based on relatively small sample sizes should be treated with caution.

Table 3 Confidence intervals for fitness components in blue tits

Year	Sample size (Number of males)	% Total variance		95% CI
1998	40	Var (*W*)	72.6	50.8 to 89.7
		Var(*E*)	10.3	4.1 to 19.4
		2Cov(*W*, *E*)	17.1	3.8 to 32.8
2001	28	Var (*W*)	79.6	46.2 to 104.6
		Var(*E*)	28.5	1.1 to 104.7
		2Cov(*W*, *E*)	−8.2	−50.1 to 12.6
1998 – 2003	274	Var (*W*)	84.9	77.1 to 91.1
		Var(*E*)	10.4	7.3 to 15.4
		2Cov(*W*, *E*)	4.7	−0.7 to 10.6

Proportional contribution of fitness components (within-pair and extra-pair success and their co-

variance) to total variance in male reproductive success (in percent) for a population of blue tits (*Cyanistes caeruleus*). Data for 1998, 2001, and for all six years of the study are shown (see Delhey et al. 2003 for details on the study). 95% confidence intervals were constructed for the proportional contributions via bootstrapping using the package 'boot' (Canty and Ripley 2009) in the software R 2.9.0 (R Development Core Team 2009) based on Davison and Hinkley (1997, ch. 5 and 11). For intervals shown here parameters were set to 10000 replicates, simulation type 'ordinary', and interval type ' 'bca' (adjusted percentile method). Other simulation and interval types lead to similar results.

1-3.4.2 Effects of Sampling Limitations on Fitness Components

Table 2 also contains information concerning the problem of sampling limitation, which may not only bias estimates of *I*, but also of fitness components. As outlined above, extra-pair success may be wrongly assessed when there are abundant opportunities for focal males to sire young in non-monitored nests. Based on the published information this is a potential problem only for three of the studies listed in Table 2. Notably, Dolan et al. (2007) were presumably able to locate all nests, but because of the large distances over which reproductive interactions took place in this population uncertainty remained about whether reproductive success of focal males was registered completely.

Variation in reproductive success and in its components may also be misrepresented if the focal males, which are almost always paired, do not represent a random sub-sample of the entire male population, that is, when there are unpaired males ('floaters', 'satellites', or 'sneakers') in the population. For example, a recent study of EPP in the common yellowthroat (*Geothlypis trichas*), that did include unpaired males, found that differences among inexperienced males in their ability to secure a social mate (M_w) accounted for 70% of the variance in reproductive success in this age group (Freeman-Gallant et al. 2009). In contrast, among experienced males variation in extra-pair success (*E*) became a major factor, explaining 40% of the total variance in reproductive success, because most of these males obtained a social mate. Thus, if unpaired males are common and even sire EPY (e.g. Kempenaers et al. 2001), estimates based solely on the breeding population may be misleading.

In most studies summarized in Table 2 floaters are thought to be rare or absent. However, this is often hard to assess, because non-breeding males may be cryptic and therefore hard to observe despite intensive study. Consider for example that in the ruff (*Philomachus pugnax*), a species that has been studied extensively for many years, only recently a 'sneaky' male type (the 'faeder') was discovered (Jukema and Piersma 2006). Faeders are female mimics that sneak copulations and thus represent an alternative mating strategy (Lank and McRae 2008). Similarly, extra-pair behavior could represent a specialized mating tactic in other species, at least for some males. It is difficult to exclude this possibility as long as the sires of many EPY remain unassigned. The example of the ruff is also illustrative

in another respect. The other two well known alternative reproductive types of male ruffs, the 'independent' and the 'satellite' males, are genetically determined (Lank et al. 1995) and this appears to be the case for faeders as well (McRae et al. 2008). Usually, extra-pair behavior is viewed as a phenotypically plastic trait so that each individual can optimize its mating behavior depending on the situation. It is thus assumed that all individuals will engage in extra-pair behavior, if it is optimal to do so in a particular environment. However, just as for the mating types in ruffs, individuals may differ in their propensity to form a strong or loose pair bond, to invest more or less in parental care or in courtship, to show a low or high sex drive, etc. and this may have a heritable component (Forstmeier 2007; van Oers et al. 2008). If such genetic divergence is common, this is an additional reason why nesting males may not be representative for the entire male population.

1-3.4.3 Effects of Random Mating on Fitness Components

The last issue to consider in connection with fitness components is the influence of stochastic events. As discussed above, random extra-pair mating can introduce variance in reproductive success and thus be a major contribution to I. When partitioning variance, we are only making a statement about the opportunity for selection mediated by EPP without relating this to phenotypic traits and heritability. This is probably less problematic than for $I_{realized}/I_{apparent}$ ratios because we may expect systematic contributions of chance to influence different components roughly equally. However, this assumption may not always hold. For the model of random extra-pair mating mentioned above, the contribution of variance in extra-pair success to total reproductive success increases with the rate of extra-pair paternity (Figure 2). The opposite is true for the contribution of variance in within-pair success under parameter constellations that prevail in natural systems ($\xi < 4$, Table 1; see Online Supplementary Material for details). Comparing results from variance partitioning from different populations may be problematic when there is evidence that stochastic effects may be influential (e.g. when the contribution of covariance is close to zero).
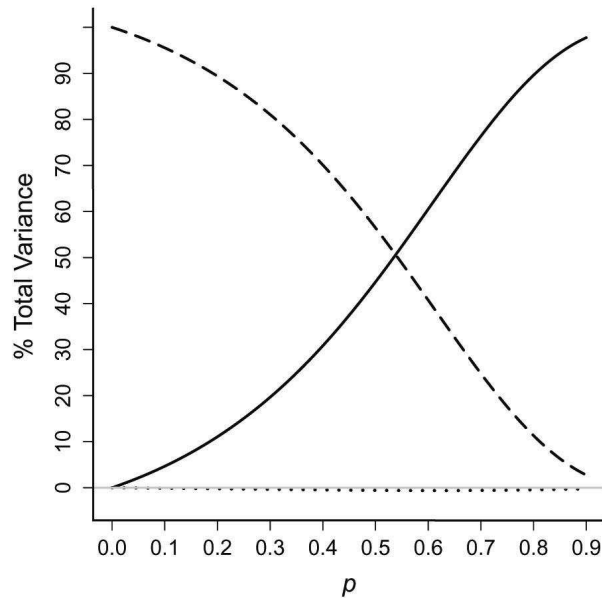
Fig. 2. Fitness components in relation to the frequency of extra-pair paternity based on a model of random extra-pair mating. Shown is the contribution of variance in extra-pair success (solid line) and within-pair success (dashed line) and their covariance (dotted line) to total variance in reproductive success (in %) with changing frequency of extra-pair paternity among offspring, p. This example is for model A with parameters $N = 100$, $\bar{c} = 5$, and $I_{apparent} = 0.5$ (see Online Supplementary Material for details).

1-3.5 The Bateman Gradient

The Bateman gradient is a direct reflection of the influence of additional mates on reproductive success and should thus provide the most accurate measure of sexual selection strength. Bateman gradients based on parentage analysis are expected to differ strongly between the sexes. For females of most species, additional mates should not lead to additional offspring. In some cases the relationship between the number of surviving offspring (e.g. fledglings) and the number of sires could be negative as a result of sexual conflict, or even slightly positive, for example if extra-pair young are more likely to survive until fledging. For males, on the other hand, we expect a strong positive relationship between the total number of sired young and the number of mates, unless there is a trade-off between within- and extra-pair success.

Calculating the Bateman gradient for males and females based on apparent and realized measurements of reproductive and mating success should thus reveal no

differences in slope for females, but an increase for males, if EPP increases the strength of sexual selection on males. In socially polygynous species, it is not immediately clear whether variation in reproductive success due to additional social mates (Bateman gradient based on apparent mating system) or to additional extra-pair mates (influence of EPP on Bateman gradient based on realized mating system) has a stronger effect on sexual selection. Here, calculating Bateman gradients from measurements of apparent and realized reproductive and mating success may be particularly informative.

The Bateman gradient has been calculated in three studies of extra-pair paternity on socially monogamous species (Ketterson et al. 1997; Webster et al. 2007; Balenger et al. 2009). All support the view that EPP drives sexual selection on males (Figures 3, 4a, and 5a). Still, the interpretation of these results is less straightforward than it may seem, as explained below.
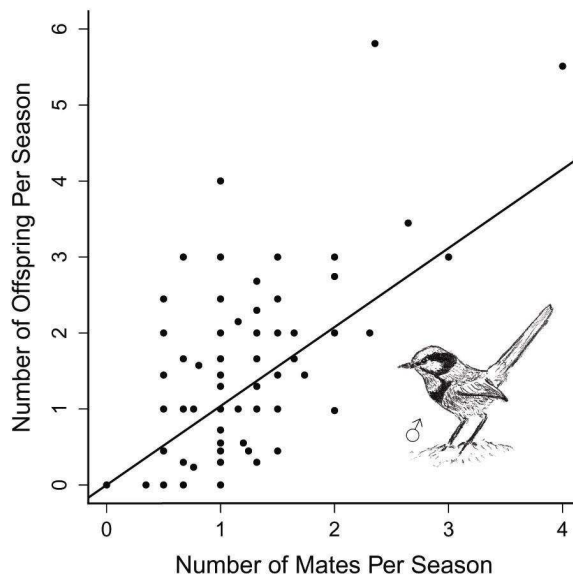
Fig. 3. Bateman gradient in male splendid fairy-wrens (*Malurus splendens*). Shown is the relationship between mating success (number of females with which a male sired genetic offspring) and reproductive success (log-transformed data: N=204, R^2= 0.68, P<0.0001). This is a cooperatively breeding species and helper males (auxiliaries) are included here. Results are very similar when analysis is restricted to breeding males only. Redrawn with permission from Webster et al. 2007.
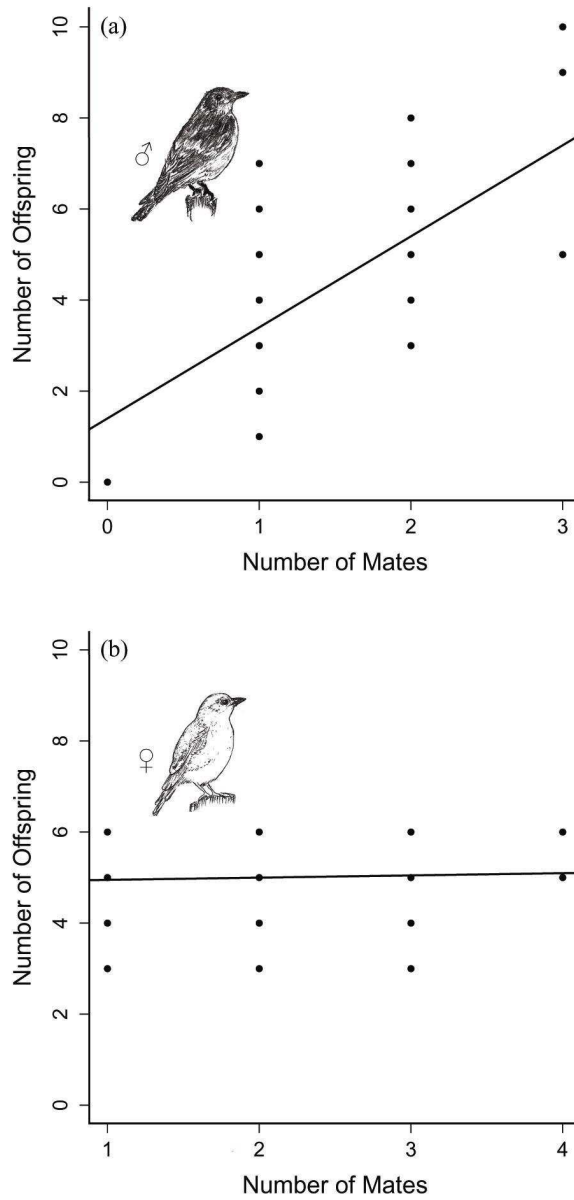
Fig. 4. Bateman gradients for (**a**) males and (**b**) females of the socially monogamous mountain bluebirds (*Sialia currucoides*). Shown is the relationship between mating success (number of individuals with which genetic offspring are produced) and reproductive success. The Bateman gradient is significant and steep in males (β_{ss}=2.0, N=59, R^2=0.42, P=0.003) and non-significant in females (β_{ss}=0.0, N=59, R^2<0.01, P=0.75). Redrawn with permission from Balenger et al. 2009.
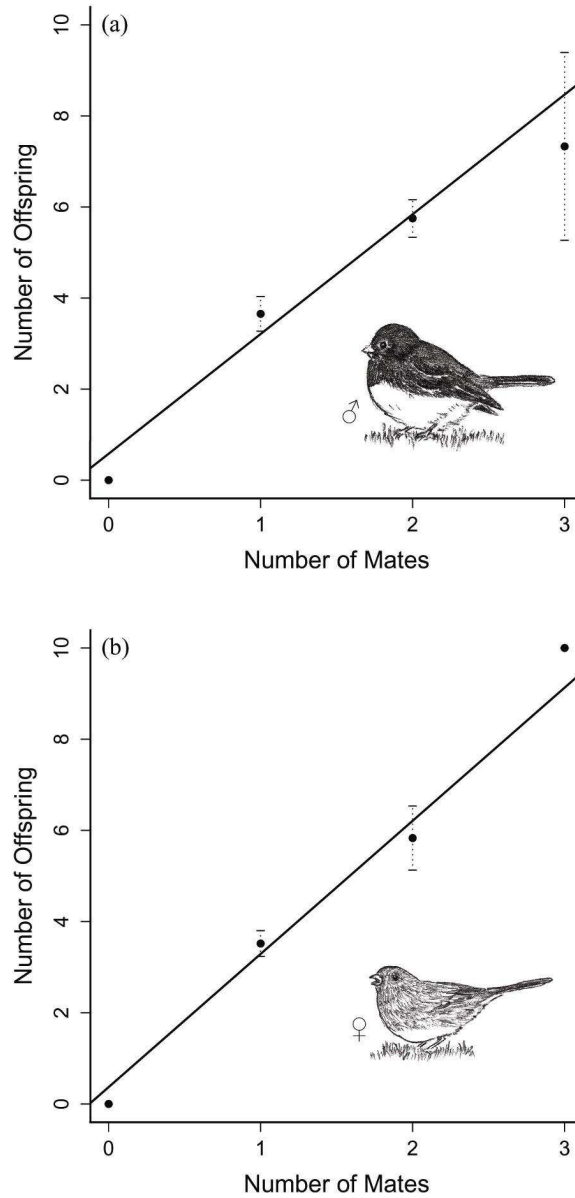
Fig. 5. Bateman gradients for (**a**) males and (**b**) females of the socially monogamous dark-eyed juncos (*Junco hyemalis*). Shown is the relationship between mating success (number of individuals with which genetic offspring are produced) and reproductive success (mean ± SE). The Bateman gradient is significant and steep in males (β_{ss}=2.6, N=50, R^2=0.61, P<0.0001). In females, it is also significant and even steeper (β_{ss}=2.9, N=45, R^2=0.59, P<0.0001). Redrawn with permission from Ketterson et al. 1997.

1-3.5.1 The Bateman Gradient in Females

Figures 4b and 5b show the Bateman gradient for females from two of the three studies. As we would expect, reproductive success is independent of mating success for female mountain bluebirds (*Sialia currucoides*, Figure 4b). However, female dark-eyed juncos (*Junco hyemalis*) seem to increase their reproductive success when mating with more males (Figure 5b), and this increase is at least as strong as in males (Fig. 5a). This seems to suggest that females obtain substantial benefits from mating with multiple males. However, female mating and reproductive success may covary without a causal relationship. When extra-pair fertilization of any one egg is equally likely for all females, we expect a higher number of extra-pair mates in larger clutches (Ketterson et al. 1997; Parker and Tang-Martinez 2005).

The causality between mating and reproductive success may also be reversed for females. For example, when more fecund females are the target of more copulation attempts by extra-pair males, they may end up with a higher number of mates fertilizing their offspring (Ketterson et al. 1997). Hence, females may produce the same number of offspring in the absence of multiple mating and higher fitness is not necessarily the result of higher mate number (sexual selection), but may be the cause of an increase in mate numbers. This explanation is unlikely to apply for male Bateman gradients, because males that are the target of female EPC attempts will not, only because they are more fertile, sire the same number of offspring in the absence of multiple mating.

1-3.5.2 Effects of Sampling Limitations on the Bateman Gradient

Male Bateman gradients could also be biased due to sampling limitations. When focal males sire EPY in non-monitored nests, both reproductive and mating success are underestimated. This is unlikely to affect calculations of the Bateman gradient, unless male fertilization success per extra-pair mate is different for these nests. However, when unassigned EPY are sired by socially unsuccessful males (e.g. floaters), the effect of EPP on sexual selection may be very different than it appears from the calculations restricted to nesting males.

First, when some males do not secure a social mate there is variation in apparent mating success and a significant and high apparent Bateman gradient can be expected, because the success of floaters is zero, whereas the success of breeders equals the clutch or brood size. Second, when floaters are successful at siring EPY, the relationship between realized mating and reproductive success may be weakened or even absent. In species with larger clutches and relatively low proportions of EPY within broods, floaters may have to secure several extra-pair mates to sire as many offspring as the average mated male with his social mate.

In the studies on mountain bluebirds and on dark-eyed juncos, unmated males may have been present (Ketterson et al. 1997; Balenger et al. 2009). The study on the splendid fairy-wrens (*Malurus splendens*; Webster et al. 2007) is special in that this species is a cooperative breeder where 17% to 42% of males are helpers with no apparent reproductive and mating success. Given that 25% of EPY are sired by such males, EPP might reduce the intensity of sexual selection by providing an alternative path to reproductive success for auxiliaries (Webster et al. 2004). (Note that the $I_{realized}/I_{apparent}$ ratio observed in this study is smaller than 1; Table 1.) Thus, counterintuitively, similar species with lower EPP rates might experience stronger sexual selection on males, arising from competition between males to enter the breeding pool. Still, in the splendid fairy-wren EPP drives sexual selection – independent of its effect on the absolute strength – because it is the major source of variation in reproductive success between males (Table 2).

Just as for opportunity estimates and fitness components there may be systematic influences of EPP rate on the size of the Bateman gradient under random mating. However, these are not further considered here. Comparisons between published studies are hampered by the fact that only unstandardized Bateman gradients are reported.

1-3.6 Conclusions

We reviewed studies that quantify effects of extra-pair paternity on the strength of sexual selection and briefly described the methods used to do this. So far, all measurements have been presented as point estimates. Including confidence intervals for these estimates may be a simple way to add information on their reliability. We emphasized two issues about the interpretation of the measurements of the intensity of sexual selection, which we now briefly discuss further.

The first issue is the sensitivity of the measurements to sampling limitations. For studies that are unable to account for all offspring of focal males the Bateman gradient is probably the estimate of choice, but all measurements can be strongly affected by the presence of floaters in the population. Attempts to maximize the number of identified sires or to obtain information about non-breeders through extensive behavioral observations are therefore valuable. Where this is impossible, at least the potential role of EPP in shaping sexual selection for this subset of males can be investigated. To compare different populations or species, it might be useful to concentrate on paternity loss, because this can always be recorded completely for the focal males (as long as the brood is genotyped). One can then search for patterns that indicate a reshuffling of paternity in favor of a subset of males as a consequence of EPCs. For example, when extra-pair sires lost less paternity in their own brood compared to other males in the population or compared to the males they cuckolded, EPP probably increases reproductive skew among nesting males (Stutchbury et al. 1997). Conversely, when reciprocal cuckoldry is

common this indicates a lack of strong directional selection on males through EPP (Freeman-Gallant et al. 2005).

Modern methods of sibship analysis allow estimating the number of males involved in siring unassigned EPY (e.g. Jones 2001; Wang 2004; Croshaw et al. 2009). This can provide an indication of the size of the unmonitored population of reproductively active males. Furthermore, paternity assignment to 'virtual' sires allows assessing the reproductive skew for these males. When paternity is spread widely among the unknown sires, measurements of sexual selection based only on part of the male population probably suffer less from sampling limitations than when a few unknown sires would have fathered a large number of offspring (Westneat 2006).

The second recurring issue is the question how random mating would affect the measurements of the strength of sexual selection. We do see selection measurements as a sign of current selection strength, even when it does not lead to evolutionary change. Still, systematic stochastic effects may be an important issue for comparisons between populations and it may be instructive to consider this in future studies. Specifically, it may be useful to construct reference values for selection measures based on an appropriate random mating process and include the deviation of the realized estimates from these reference values (see Online Supplementary Material for an example).

Although the current evidence is still limited, it suggests that extra-pair matings provide a major path to male reproductive success in some bird species (e.g. Dolan et al. 2007; Webster et al. 2007). This does not necessarily imply a strong increase of the strength of sexual selection with the rate of extra-pair paternity (Dunn et al. 2001), because – as we have seen above – sometimes sexual selection might even be stronger in the absence of EPP. How universal the role of EPP is for sexual selection remains debatable (Whittingham and Dunn 2005), even though in several species it appears to be important (Table 2). The next step then is to examine whether differences in mating and reproductive success mediated by EPP are linked to phenotypic traits, that is, to identify the targets of sexual selection. The quantitative estimates discussed here, particularly fitness components, can be helpful in establishing the main arena of sexual selection and predicting which traits may be important. In some cases, it has been confirmed that among-male variation in sexually dimorphic traits is linked to variation in extra-pair success (e.g. Kleven et al. 2006; Dolan et al. 2007; Albrecht et al. 2009; see also Møller and Ninni 1998), whereas in others there is no such relationship (e.g. Westneat 2006; Neuman et al. 2007; see also Akçay and Roughgarden 2007). Variation among species and populations in life-history (Albrecht et al. 2007), geography (Neuman et al. 2007), or habitat (Kingma et al. 2009) is an important determinant of these differences. Molecular techniques are now routinely used and have made it possible to assess reproductive interactions with much greater accuracy (see also chapters 1-1 and 1-2). This will allow further study on how multiple mating affects sexual selection and through which mechanism.

List of Abbreviations EPC, extra-pair copulation; EPP, extra-pair paternity; EPY, extra-pair young

Appendix

References for Table1 and Table 2: *1*, Hasselquist et al. 1995; *2*, Gibbs et al. 1990; *3*, Westneat 1993, fitness components calculated by Webster et al. 1995; *4*, Weatherhead and Boag 1997; *5*, Albrecht et al. 2007; *6*, Kempenaers et al. 1992; *7*, Delhey et al. 2003; *8*, Whittingham and Lifjeld 1995, fitness components calculated by Whittingham and Dunn 2005; *9*, Webster et al. 2001; *10*, Byers et al. 2004; *11*, Yezerinac et al. 1995, 'lower bound estimate'; *12*, Sheldon and Ellegren 1999; *13*, Whittingham and Dunn 2005; *14*, Kleven et al. 2006; *15*, Møller and Tegelström 1997 and Møller and Ninni 1998; *16*, Richardson and Burke 2001; *17*, Ketterson et al. 1997; *18*, Johnsen et al. 2001; *19*, Webster et al. 2007 and Webster et al. 2004; *20*, O'Connor et al. 2006, averaged over years; *21*, Freeman-Gallant et al. 2005; *22*, Otter et al. 1998 and Whittingham and Dunn 2005; *23*, Wagner et al. 1996 and Møller and Ninni 1998; *24*, Balenger et al. 2009; *25*, Kempenaers et al. 2001, among residents; *26*, Whittingham and Dunn 2005; *27*, Dolan et al. 2007; *28*, Stutchbury et al. 1997; *29*, Westneat 2006; *30*, Freeman-Gallant et al. 2009; *31*, Lawler 2007 and Lawler et al. 2003

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A Model of Random Extra-Pair Mating

Online Supplementary Material to

Extra-Pair Paternity and Sexual Selection

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To illustrate effects of random mating on measures of the strength of sexual selection we describe the influence of the rate of extra-pair paternity on the opportunity for selection and fitness components based on a simple model of random mating.

1. The Model

We assume a population of N males and N females of a socially monogamous species where all males and females are mated (N broods). The model is easily extendable to cases where a proportion x of all males and females remains unmated. The frequency of extra-pair paternity among all offspring is p ($0 \leq p \leq 1$) and the average number of young in a male's nest is $\overline{c}$. Thus, the total number of young is $N\overline{c}$, of which $pN\overline{c}$ are extra-pair. In the following we will assume no mortality between laying and the stage where reproductive success is assessed, and refer to the apparent reproductive success of male i as his clutch size c_i, and to average apparent reproductive success as average clutch size $\overline{c}$. The associated variance in clutch size is $\mathrm{Var}(c)$. The realized reproductive success r_i of male i ($i = 1, \ldots, N$) is his clutch size c_i, plus g_i, the number of young he sires in other nests (his paternity gains), minus l_i, the number of young he loses to other males (his paternity losses): $r_i = c_i + g_i - l_i$. Average realized reproductive success is the same as average apparent reproductive success: $\overline{r} = \overline{c}$. This means that all reproductive interactions take place within the population.

$N, p, \overline{c}$, and $\mathrm{Var}(c)$ are given parameters, while c_i, g_i, l_i, and r_i are dependent random variables following certain distributions which are identical for all i. (Supplementary Table 1 provides a list of all variables and parameters.) To model opportunity ratios and fitness components it is necessary to inspect the variances of r_i, g_i, and l_i in our population. This is equivalent to inspecting the variance of the variables for a randomly picked individual of the population, which we will call c, r, g, and l. For simplicity, we examine the following two possibilities (models A and B). In model A, we allow for any population size N. The variances of r, g, and l in this model are those that we would expect to find on average after complete sampling of many populations with identical parameters. In model B our population is assumed to be very large and the variances of r, g, and l in this model are those that we would expect to find for $N \rightarrow \infty$.

In our model of random mating we make the following assumptions:

1. *The proportion of extra-pair young is the same in all nests.* This implies that paternity losses are not randomly distributed, but deterministic. It could arise when all females follow the same strategy of having a certain fraction of their eggs sired by extra-pair males, for instance as an insurance against infertility of the social mate. Thus, each male loses a proportion p of his clutch: $l_i = pc_i$.

2. *The sire of each extra-pair young is determined by random choice from the male population (excluding the social father).* This implies that paternity gains follow a random process. For instance, females could mate with a random extra-pair male in the population.

In **model A**, for each male there are $pN\overline{c} - pc$ extra-pair young he can sire (all extra-pair young except the young in his own nest). The probability of a certain male to sire one of these young is $v = \dfrac{1}{N-1}$ (all males except the social father compete for fertilization and they all have the same success rate). Thus, in model A, paternity gains, given c, are binomially distributed for each male with mean $v(pN\overline{c} - pc)$ and variance $v(1-v)(pN\overline{c} - pc)$. In this model, a male's paternity gains are not independent of his losses and hence his clutch size. Since the total number of extra-pair young in the population is fixed, males with small paternity losses (males with small clutches) are in the run for more extra-pair fertilizations and are likely to have higher paternity gains. This causes a negative covariance between a male's extra- and within-pair success (see also equation (A7) below).

In **model B**, the population is very large ($N \to \infty$). In this case, a male's paternity gains are (almost) independent of his losses and of clutch size, because in- or excluding a male as a potential sire of an extra-pair young in his own nest makes (almost) no difference. Thus, in model B gains are Poisson distributed for each male with mean and variance $p\overline{c}$.

These assumptions imply that the random process only extends to paternity gains while each male loses the same proportion p of his clutch to other males. Also, we assume that extra-pair young from the same nest are assigned independently to a sire. Arguably, these model assumptions are rarely met in natural systems. In particular, extra-pair fertilizations in the same nest may be the result of the same copulation event, which would cause non-independence of extra-pair success within nests and make a two-step modeling procedure necessary (see Brommer et al. 2007). Our simple model is a first attempt to illustrate our approach and to evaluate potential consequences of stochasticity on measurements of sexual selection. Despite its limitations, our model uses more realistic assumptions than previous simulations (Webster et al. 1995).

We now calculate variances for the variables of interest and consider how the frequency of extra-pair paternity p influences values of $I_{realized}/I_{apparent}$ and fitness components in this model.

Supplementary Table 1 Parameters, variables, and functions of the model for random extra-pair mating

Frequency of extra-pair paternity among offspring	p
No. of males, females, broods	N
Average clutch size	$\bar{c}$
Reproductive success	r
Within-pair success	w
Extra-pair success	e
Clutch size	c
Paternity gain	g
Paternity loss	l
Probability for a male to sire a particular extra-pair young in other male's nests in model A	$v = \dfrac{1}{N-1}$
Opportunity for selection based on realized reproductive success	$I_{realized}$
Opportunity for selection based on apparent reproductive success	$I_{apparent}$
Opportunity for selection generated by random extra-pair mating	I_{random}
Variance in extra-pair success as a function of p	$V_e(p)$
Variance in within-pair success as a function of p	$V_w(p)$
Variance in total (realized) reproductive success as a function of p	$V_r(p)$
Contribution of variance in extra-pair success to variance in total reproductive success as a function of p	$R_e(p)$
Contribution of variance in within-pair success to variance in total reproductive success as a function of p	$R_w(p)$

2. Variance Calculations

Let us examine variance in realized reproductive success r, within-pair success w, and extra-pair success e, as well as their covariance for a randomly chosen male:

$$
\begin{aligned}
\mathrm{Var}(r) &= \mathrm{Var}(c + g - l) \\
&= \mathrm{Var}\big((1-p)c + g\big) \\
&= (1-p)^2\,\mathrm{Var}(c) + \mathrm{Var}(g) + 2(1-p)\,\mathrm{Cov}(c,g)
\end{aligned} \tag{1}
$$

$$
\mathrm{Var}(w) = \mathrm{Var}(c - l) = \mathrm{Var}\big((1-p)c\big) = (1-p)^2\,\mathrm{Var}(c) \tag{2}
$$

$$
\mathrm{Var}(e) = \mathrm{Var}(g) \tag{3}
$$

$$
\mathrm{Cov}(w,e) = \mathrm{Cov}(c - l, g) = \mathrm{Cov}\big((1-p)c, g\big) = (1-p)\,\mathrm{Cov}(c,g). \tag{4}
$$

We now find expressions for $\mathrm{Var}(g)$ and $\mathrm{Cov}(c,g)$ in models A and B. In the following, let $\mathrm{E}(V)$ denote the expected value of variable V.

2.1 Variance Calculations for Model A

In model A, we need to recognize the dependency of g on c before using the mean and variance of the binomial distribution:

$$
\begin{aligned}
\mathrm{Var}(g) &= \mathrm{E}(g^2) - \mathrm{E}(g)^2 \\
&= \mathrm{E}\big(\mathrm{E}(g^2\,|\,c)\big) - \mathrm{E}\big(\mathrm{E}(g\,|\,c)\big)^2 \\
&= \mathrm{E}\big(\mathrm{E}(g^2\,|\,c) - \mathrm{E}(g\,|\,c)^2\big) + \mathrm{E}\big(\mathrm{E}(g\,|\,c)^2\big) - \mathrm{E}\big(\mathrm{E}(g\,|\,c)\big)^2 \\
&= \mathrm{E}\big(\mathrm{Var}(g\,|\,c)\big) + \mathrm{Var}\big(\mathrm{E}(g\,|\,c)\big) \\
&= \mathrm{E}\big(v(1-v)(pN\bar{c} - pc)\big) + \mathrm{Var}\big(v(pN\bar{c} - pc)\big) \\
&= (1-v)\,p\bar{c} + \mathrm{Var}(-vpc) \\
&= (1-v)\,p\bar{c} + v^2 p^2\,\mathrm{Var}(c)
\end{aligned}
\tag{A1}
$$

$$
\begin{aligned}
\mathrm{Cov}(c,g) &= \mathrm{E}(cg) - \mathrm{E}(c)\,\mathrm{E}(g) \\
&= \mathrm{E}\big(\mathrm{E}(cg\,|\,c)\big) - \mathrm{E}\big(c\,\mathrm{E}(g)\big) \\
&= \mathrm{E}\big(c\,\mathrm{E}(g\,|\,c)\big) - \mathrm{E}\big(c\,\mathrm{E}(\mathrm{E}(g\,|\,c))\big) \\
&= \mathrm{E}\big(c\,v(pN\bar{c} - pc)\big) - \mathrm{E}\big(c\,\mathrm{E}(v(pN\bar{c} - pc))\big) \\
&= vpN\bar{c}\,\mathrm{E}(c) - vp\,\mathrm{E}(c^2) - vpN\bar{c}\,\mathrm{E}(c) + vp\,\mathrm{E}(c)^2 \\
&= -vp\big(\mathrm{E}(c^2) - \mathrm{E}(c)^2\big) \\
&= -vp\,\mathrm{Var}(c).
\end{aligned}
\tag{A2}
$$

2.2 Variance Calculations for Model B

In model B, g is independent of c and we can thus use the variance of the Poisson distribution directly:

$$
\mathrm{Var}(g) = p\bar{c}
\tag{B1}
$$

$$
\mathrm{Cov}(c,g) = 0 \qquad (g \text{ and } c \text{ independent}).
\tag{B2}
$$

Equations (B1) and (B2) also result from equations (A1) and (A2) for $N \to \infty$.

3. $I_{realized}$ in the Model

3.1 $I_{realized}$ in Model A

Inserting equations (A1) and (A2) into equation (1) gives for model A:

$$
\begin{aligned}
\mathrm{Var}(r) &= \mathrm{V}_r(p) \\
&= (1-p)^2\,\mathrm{Var}(c) + (1-v)\,p\bar{c} + v^2 p^2\,\mathrm{Var}(c) - 2(1-p)vp\,\mathrm{Var}(c) \\
&= \big(1 - 2p(1+v) + p^2(1+v)^2\big)\mathrm{Var}(c) + (1-v)\,p\bar{c} \\
&= (1 - pNv)^2\,\mathrm{Var}(c) + (1-v)\,p\bar{c}.
\end{aligned}
\tag{A3}
$$

Hence,

$$I_{realized} = \frac{\text{Var}(r)}{\bar{r}^2} = \frac{\text{Var}(c)}{\bar{c}^2} \cdot (1 - pN\nu)^2 + \frac{1}{\bar{c}} p(1-\nu)$$

$$= I_{apparent} \cdot (1 - pN\nu)^2 + \frac{1}{\bar{c}} p(1-\nu) \qquad (A4)$$

$$= \frac{\xi}{\bar{c}} (1 - pN\nu)^2 + \frac{1}{\bar{c}} p(1-\nu),$$

where

$$\xi = \frac{\text{Var}(c)}{\bar{c}} = I_{apparent} \cdot \bar{c}. \qquad (5)$$

We can now study the behavior of $I_{realized}$ with changing frequency of extra-pair paternity p:

$$I_{realized}{}'(p) = p \cdot 2N^2\nu^2 \frac{\xi}{\bar{c}} + \frac{1}{\bar{c}}(1-\nu) - 2N\nu\frac{\xi}{\bar{c}}.$$

$I_{realized}$ is an increasing function of p when its first derivative is positive:

$$I_{realized}{}'(p) > 0 \Rightarrow p > \frac{1}{N\nu}\left(1 - \frac{N-2}{2N\xi}\right).$$

Thus, in model A, $I_{realized}$ is an increasing function of p when $p > t_A$, where $t_A = \frac{1}{N\nu}\left(1 - \frac{N-2}{2N\xi}\right)$.

If $\xi < \frac{N-2}{2N}$, $t_A < 0$. Assuming that the population comprises at least 10 broods ($N \geq 10$), $\frac{N-2}{2N}$ is minimally 0.4 and approaches 0.5 for large N. Hence, if $\xi < 0.4$, $t_A < 0$ and $p > t_A$, since p (the frequency of extra-pair paternity) is a value between 0 and 1. Therefore, in model A, $I_{realized}$ is an increasing function of p over the whole range of p, if

$$\xi < 0.4. \qquad (A5)$$

3.1 $I_{realized}$ in Model B

Inserting equations (B1) and (B2) into equation (1) gives for model B:

$$\text{Var}(r) = V_r(p) = (1-p)^2 \text{Var}(c) + p\bar{c}. \qquad (B3)$$

Hence,

$$I_{realized} = \frac{\text{Var}(r)}{\bar{r}^2} = \frac{\text{Var}(c)}{\bar{c}^2} \cdot (1-p)^2 + \frac{1}{\bar{c}} p$$

$$= I_{apparent} \cdot (1-p)^2 + \frac{1}{\bar{c}} p \qquad (B4)$$

$$= \frac{\xi}{\bar{c}} (1-p)^2 + \frac{1}{\bar{c}} p,$$

defining ξ as above (equation (5)). (Equations (B3) and (B4) also result from equations (A3) and (A4) for $N \to \infty$.)

This gives

$$I_{realized}{}'(p) = p \cdot 2\frac{\xi}{\bar{c}} + \frac{1}{\bar{c}} - 2\frac{\xi}{\bar{c}}$$

and

$$p > 1 - \frac{1}{2\xi}$$

as condition for $I_{realized}{}'(p) > 0$. Thus, in model B, $I_{realized}$ is an increasing function of p when $p > t_B$, where $t_B = 1 - \frac{1}{2\xi}$. (We also obtain t_B from t_A for $N \to \infty$.) If $\xi < \frac{1}{2}$, $t_B < 0$. Hence, if $\xi < 0.5$, $t_B < 0$ and $p > t_B$, since $0 \le p \le 1$. Therefore, in model B, $I_{realized}$ is an increasing function of p over the whole range of p, if

$$\xi < 0.5. \tag{B5}$$

3.3 Comparing I_{realized} in Model A and Model B

Comparing the results of model A and model B for $I_{realized}$ gives:

$$(\text{B4}) - (\text{A4}) = \frac{p v}{\bar{c}} \xi \big(2 - p v (2N - 1)\big) + \frac{p v}{\bar{c}}.$$

Assuming $N \ge 10$ (at least 10 broods in the population) and $p < 0.9$ (less than 90% of offspring are extra-pair), $2 - p v (2N - 1)$ is positive, as are all the parameters. Thus, the value of $I_{realized}$ obtained for model A is smaller than the value obtained for model B. Random extra-pair mating produces less variance in model A and we will use this more restrictive definition:

$$I_{random} = I_{apparent} \cdot (1 - pN v)^2 + \frac{1}{\bar{c}} p(1 - v). \tag{6}$$

Merging the conditions of model A and B for an increase of $I_{realized}$ with p (inequalities (A5) and (B5)), we find that in both models $I_{realized}$ is an increasing function of p over the whole range of p, when

$$\xi < 0.4. \tag{7}$$

4. Fitness Components in the Model

We now consider $\mathrm{Var}(w)$, $\mathrm{Var}(e)$, and $\mathrm{Cov}(w,e)$. In both models $\mathrm{Var}(w) = V_w(p) = (1 - p)^2 \mathrm{Var}(c)$ (equation (2)).

4.1 Fitness Components in Model A

Inserting equations (A1) and (A2) in equations (3) and (4) we obtain for model A:

$$\mathrm{Var}(e) = V_e(p) = (1 - v) p \bar{c} + v^2 p^2 \mathrm{Var}(c) \tag{A6}$$

$$\mathrm{Cov}(w, e) = -v p (1 - p) \mathrm{Var}(c) < 0. \tag{A7}$$

Using equation (A3) we can calculate

$$V_r(p) - V_e(p) = \big(1 - 2pN v + p^2 v (N + 1)\big) \mathrm{Var}(c) \tag{A8}$$

and

$$V'_r(p) - V'_e(p) = \left(-2N\nu + 2p\nu(N+1)\right)\mathrm{Var}(c) \tag{A9}$$

from this.

The contribution of variance in extra-pair success to variance in total reproductive success is $\dfrac{\mathrm{Var}(g)}{\mathrm{Var}(r)}$, which we can now write for model A as

$$R_e(p) = \frac{V_e(p)}{V_r(p)} = \frac{\mathrm{Var}(g)}{\mathrm{Var}(r)} = \frac{(1-\nu)p\overline{c} + \nu^2 p^2\,\mathrm{Var}(c)}{(1-pN\nu)^2\,\mathrm{Var}(c) + (1-\nu)p\overline{c}}$$

(using equations (A6) and (A3)). The behavior of $R_e(p)$ with changing p can be examined by inspecting its first derivative

$$R'_e(p) = \frac{V'_e(p)\cdot V_r(p) - V_e(p)\cdot V'_r(p)}{\left(V_r(p)\right)^2},$$

the sign of which is given by its numerator $V'_e(p)\cdot V_r(p) - V_e(p)\cdot V'_r(p)$. This we can rewrite using equations (A8) and (A9):

$$
\begin{aligned}
&V'_e(p)\cdot V_r(p) - V_e(p)\cdot V'_r(p) \\
&= V'_e(p)\cdot\left(V_r(p) - V_e(p)\right) - V_e(p)\cdot\left(V'_r(p) - V'_e(p)\right) \\
&= \left((1-\nu)\overline{c} + 2p\nu^2\,\mathrm{Var}(c)\right)\cdot\left(1 - 2pN\nu + p^2\nu(N+1)\right)\mathrm{Var}(c) \\
&\quad - \left((1-\nu)p\overline{c} + \nu^2 p^2\,\mathrm{Var}(c)\right)\cdot\left(-2N\nu + 2p\nu(N+1)\right)\mathrm{Var}(c) \\
&= \mathrm{Var}(c)\cdot\overline{c}(1-\nu)\left[\left(1 - 2pN\nu + p^2\nu(N+1)\right) - p\left(-2N\nu + 2p\nu(N+1)\right)\right] \\
&\quad + \left(\mathrm{Var}(c)\right)^2\cdot 2p\nu^2\left[\left(1 - 2pN\nu + p^2\nu(N+1)\right) - p\left(-N\nu + p\nu(N+1)\right)\right] \\
&= \mathrm{Var}(c)\cdot\overline{c}(1-\nu)\left(1 - p^2\nu(N+1)\right) + \left(\mathrm{Var}(c)\right)^2\cdot 2p\nu^2(1 - pN\nu).
\end{aligned}
$$

Assuming $N \geq 10$ (at least 10 broods in the population) and $p < 0.9$ (less than 90% of offspring are extra-pair), both $1 - p^2\nu(N+1)$ and $1 - pN\nu$ are greater than zero, which makes the whole term positive. Thus, for model A, the contribution of variance in extra-pair success to variance in total reproductive success increases with increasing frequency of extra-pair paternity under realistic parameter constellations (Supplementary Figure 2).

Similarly, when we consider the contribution of variance in within-pair success to variance in total reproductive success in model A, we write

$$R_w(p) = \frac{V_w(p)}{V_r(p)} = \frac{\mathrm{Var}(c)}{\mathrm{Var}(r)} = \frac{(1-p)^2\,\mathrm{Var}(c)}{(1-pN\nu)^2\,\mathrm{Var}(c) + (1-\nu)p\overline{c}}$$

(using equations (2) and (A3)) and

$$R'_w(p) = \frac{V'_w(p)\cdot V_r(p) - V_w(p)\cdot V'_r(p)}{\left(V_r(p)\right)^2},$$

where we again examine the numerator. This we can rewrite:

$$V'_w(p) \cdot V_r(p) - V_w(p) \cdot V'_r(p)$$
$$= -2(1-p)\,\mathrm{Var}(c) \cdot \left((1-pN\nu)^2\,\mathrm{Var}(c) + (1-\nu)p\overline{c}\right)$$
$$- (1-p)^2\,\mathrm{Var}(c) \cdot \left(-2N\nu(1-pN\nu)\,\mathrm{Var}(c) + (1-\nu)\overline{c}\right)$$
$$= -(1-p)(1-\nu)\overline{c}\,\mathrm{Var}(c) \cdot \left(2p + (1-p)\right)$$
$$- (1-p)(1-pN\nu)\left(\mathrm{Var}(c)\right)^2 \cdot \left(2(1-pN\nu) + (1-p)(-2N\nu)\right)$$
$$= -(1-p)\,\mathrm{Var}(c) \cdot \left(\nu(N-2)\overline{c}(p+1) + (1-pN\nu)\,\mathrm{Var}(c) \cdot (-2\nu)\right)$$
$$= (1-p)\nu\,\mathrm{Var}(c) \cdot \left(2(1-pN\nu)\,\mathrm{Var}(c) - (N-2)(p+1)\overline{c}\right).$$

Here, the sign is determined by the sign of the term $2(1-pN\nu)\,\mathrm{Var}(c) - (N-2)(p+1)\overline{c}$. This term is maximal when N ($N \geq 10$) and p ($0 \leq p \leq 1$) are minimal and then reads $2\,\mathrm{Var}(c) - 8\overline{c}$, which is negative for $\dfrac{\mathrm{Var}(c)}{\overline{c}} < 4$. Thus, under this condition, the term is always negative. Therefore, in model A, the contribution of variance in within-pair success to variance in total reproductive success decreases with increasing frequency of extra-pair paternity for

$$\xi < 4 \tag{A10}$$

(defining ξ as above, equation (5); see also Supplementary Figures 1 and 2).

Finally, we already know that the covariance of extra- and within-pair success in model A is always negative (equation (A7)). Its absolute contribution to total variance in reproductive success is greatest for intermediate values of p.

4.2 Fitness Components in Model B

Inserting equations (B1) and (B2) in equations (3) and (4) we obtain for model B:

$$\mathrm{Var}(e) = V_e(p) = p\overline{c} \tag{B6}$$

$$\mathrm{Cov}(w,e) = 0. \tag{B7}$$

Considering the contribution of variance in extra-pair success to variance in total reproductive success for model B we find

$$R_e(p) = \frac{V_e(p)}{V_r(p)} = \frac{\mathrm{Var}(g)}{\mathrm{Var}(r)} = \frac{p\overline{c}}{(1-p)^2\,\mathrm{Var}(c) + p\overline{c}}$$

(from equations (B6) and (B3)) and for the numerator of the first derivative

$$V'_e(p) \cdot V_r(p) - V_e(p) \cdot V'_r(p)$$
$$= \overline{c}\left((1-p)^2\,\mathrm{Var}(c) + p\overline{c}\right) - p\overline{c}\left(-2(1-p)\,\mathrm{Var}(c) + \overline{c}\right)$$
$$= \overline{c}(1-p)\,\mathrm{Var}(c) \cdot \left((1-p) + 2p\right)$$
$$= \overline{c}(1-p^2)\,\mathrm{Var}(c),$$

which is positive. Thus, in model B, the contribution of variance in extra-pair success to variance in total reproductive success increases with increasing frequency of extra-pair paternity without restrictions.

For the contribution of variance in within-pair success to variance in total reproductive success in model B, we write

$$R_w(p) = \frac{V_w(p)}{V_r(p)} = \frac{\mathrm{Var}(c)}{\mathrm{Var}(r)} = \frac{(1-p)^2\,\mathrm{Var}(c)}{(1-p)^2\,\mathrm{Var}(c) + p\overline{c}}$$

(using equations (2) and (B3)) and for the numerator of the first derivative

$$V'_w(p) \cdot V_r(p) - V_w(p) \cdot V'_r(p)$$
$$= -2(1-p)\,\mathrm{Var}(c) \cdot \left((1-p)^2\,\mathrm{Var}(c) + p\bar{c}\right) - (1-p)^2\,\mathrm{Var}(c) \cdot \left(-2(1-p)\,\mathrm{Var}(c) + \bar{c}\right)$$
$$= -\bar{c}(1-p)\,\mathrm{Var}(c) \cdot \left(-2p + (1-p)\right)$$
$$= -\bar{c}(1-p^2)\,\mathrm{Var}(c),$$

which is negative. Therefore, in model B, the contribution of variance in within-pair success to variance in total reproductive success decreases with increasing frequency of extra-pair paternity also without restrictions.

The contribution of the covariance of extra- and within-pair success to total variance in reproductive success in model B is always zero (equation (B7)).

4.3 Comparing Fitness Components from Model A and Model B

Both models produce essentially the same results, namely that under random mating an increase in the rate of extra-pair paternity leads to an increase in the contribution of extra-pair success to total reproductive success and a decrease in the contribution of within-pair success for all biologically relevant parameter constellations ($N \leq 10$ and $p \leq 0.9$). For model A the latter is only fulfilled under the condition $\xi < 4$ (inequality (A10)).

5. Implications

5.1 $I_{realized}/I_{apparent}$ *Ratio*

According to both variants of the model, random mating generates an opportunity of selection at least as strong as given by I_{random} from equation (6). The parameters of this equation can be retrieved from published studies that measure the effect of extra-pair paternity on the strength of sexual selection by estimating $I_{realized}/I_{apparent}$ ratios. Thus $I_{realized}/I_{random}$ can be calculated for these studies (Table 2 of main text). In a third (9 out of 27) of studies the variance ratio obtained in this way is considerably smaller than the ratio reported in the study. This indicates that for these studies the role of extra-pair paternity in generating stronger sexual selection strength (than under the apparent mating system) may not be as important as previously thought, because part of the variance increase is to be expected even under random extra-pair mating.
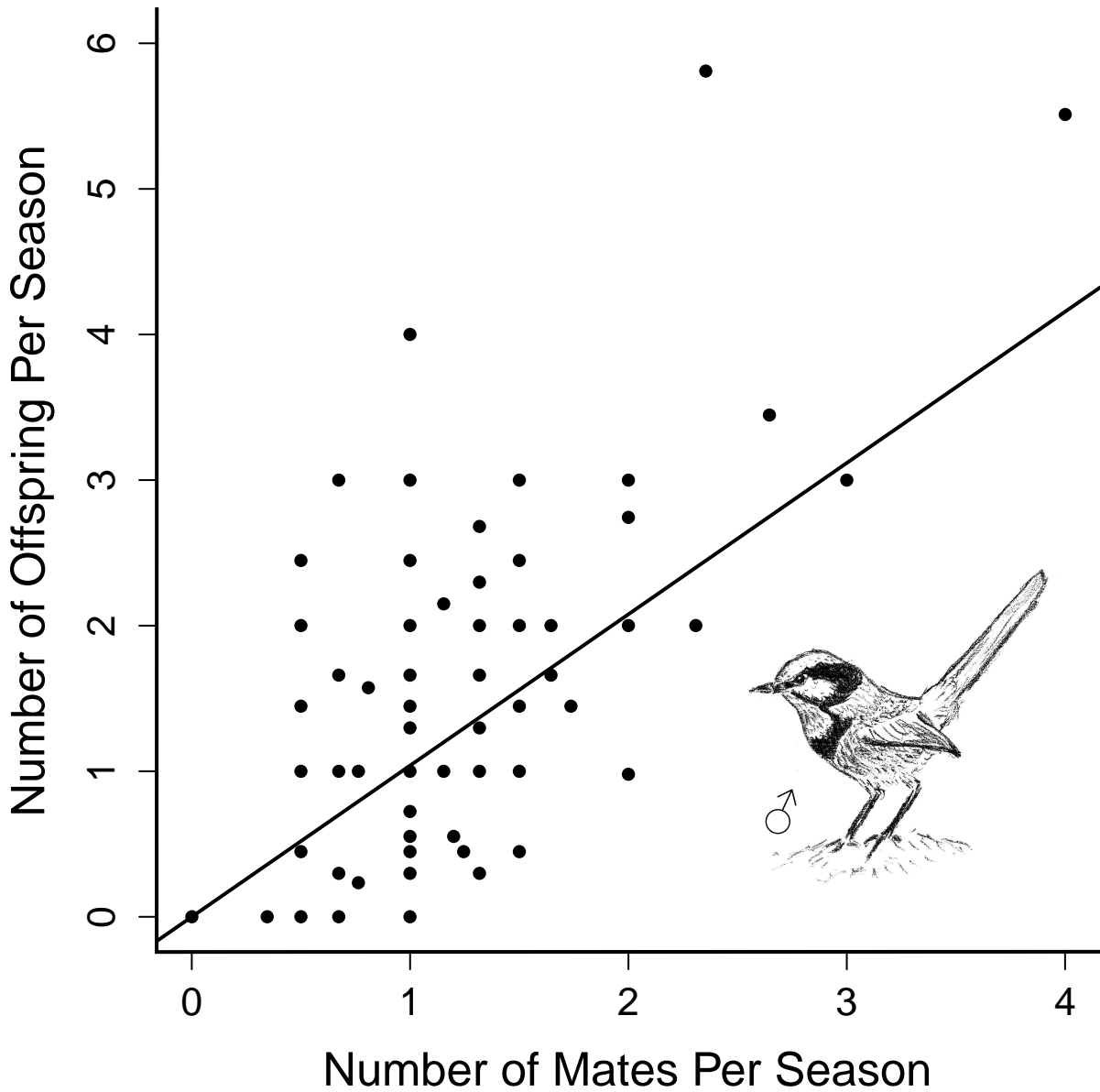
Furthermore, we have seen that in both variants of the model $I_{realized}$ is an increasing function of p over the whole range of p, whenever $\xi < 0.4$ (inequality (7)). Parameter constellations for which this inequality is fulfilled occur repeatedly in studies (Table 2 main text, Supplementary Figure 1). Thus, we may often expect a systematic influence of the extra-pair paternity rate on the estimate of sexual selection strength, at least based on this model of random mating.
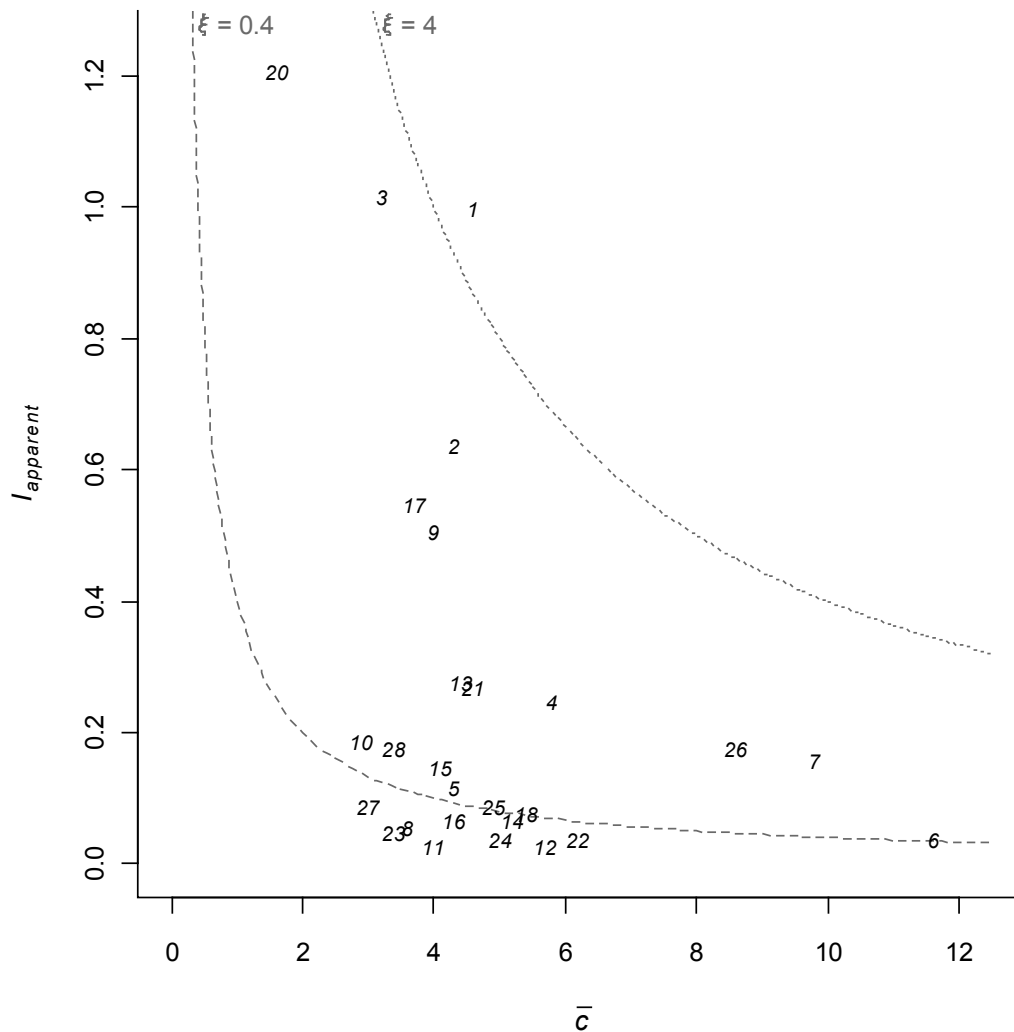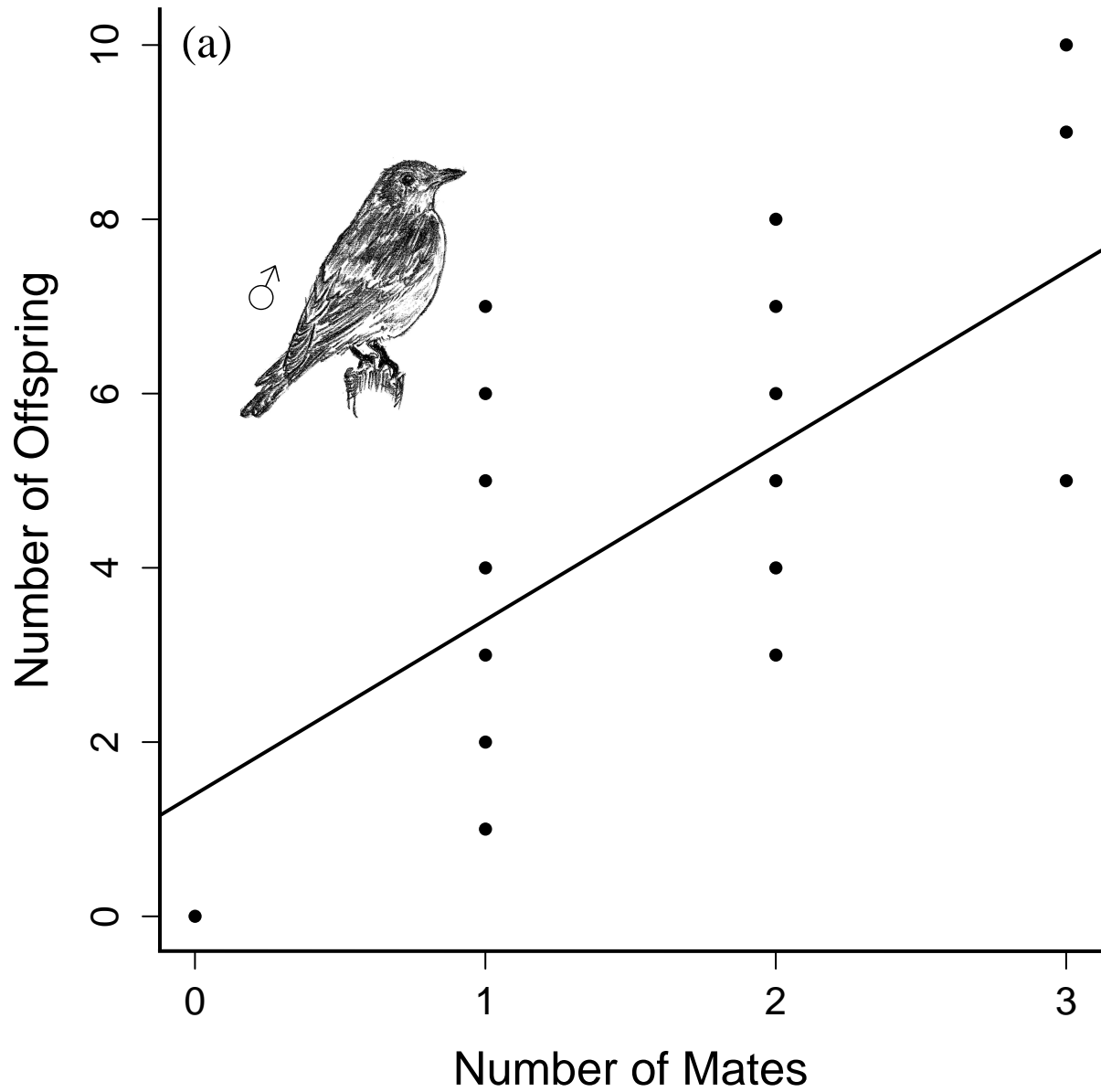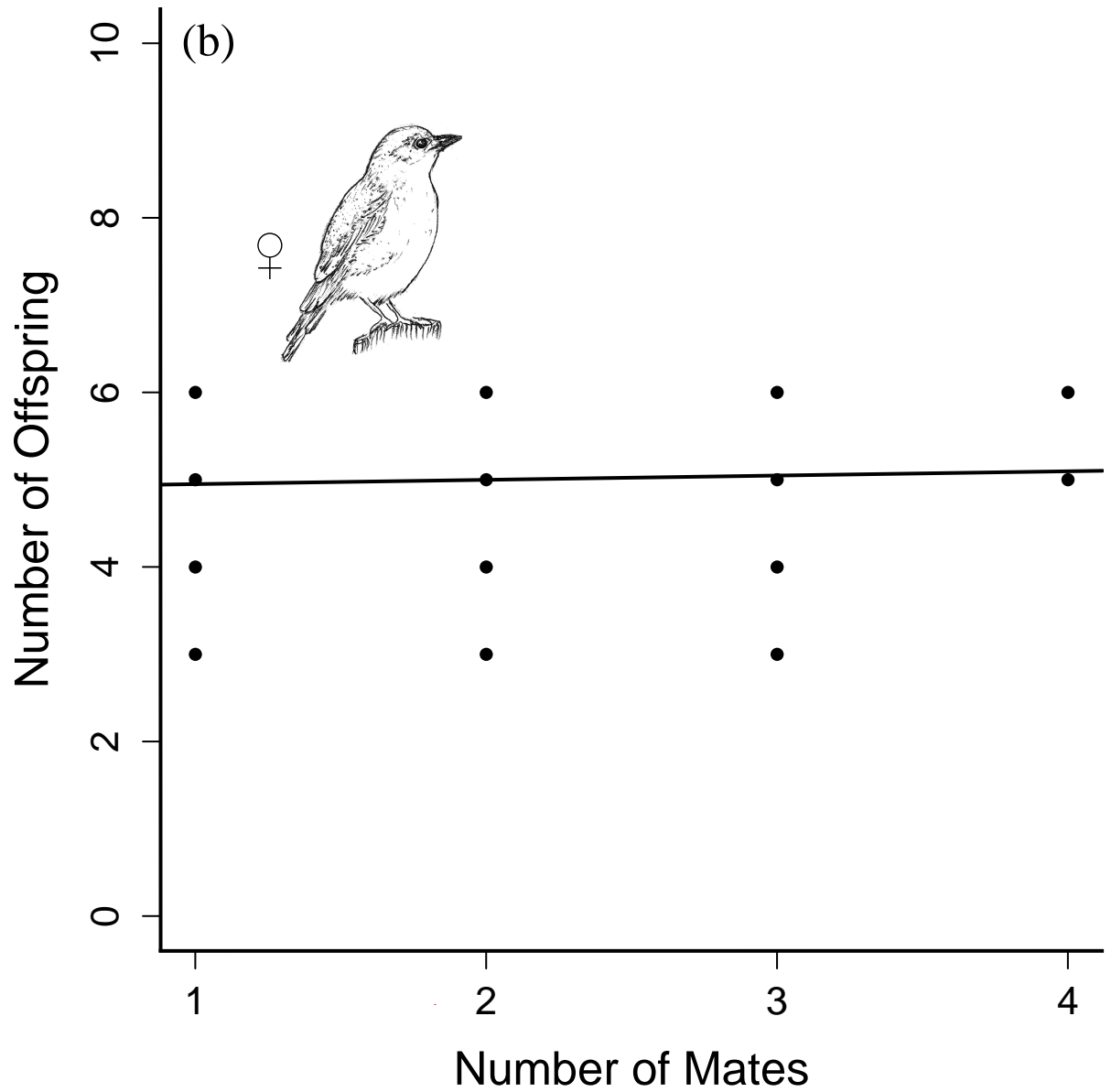
Supplementary Fig. 1 Mean apparent reproductive success ($\bar{c}$) and standardized variance in apparent reproductive success ($I_{apparent}$) reported in studies of extra-pair paternity. Numbers refer to the last column of Table 1. The dashed and dotted gray lines indicate $\xi = 0.4$ and $\xi = 4$, respectively. For points below and left of a line ξ is smaller than indicated by the line, for points above and right of a line ξ *is* greater than indicated by the line.
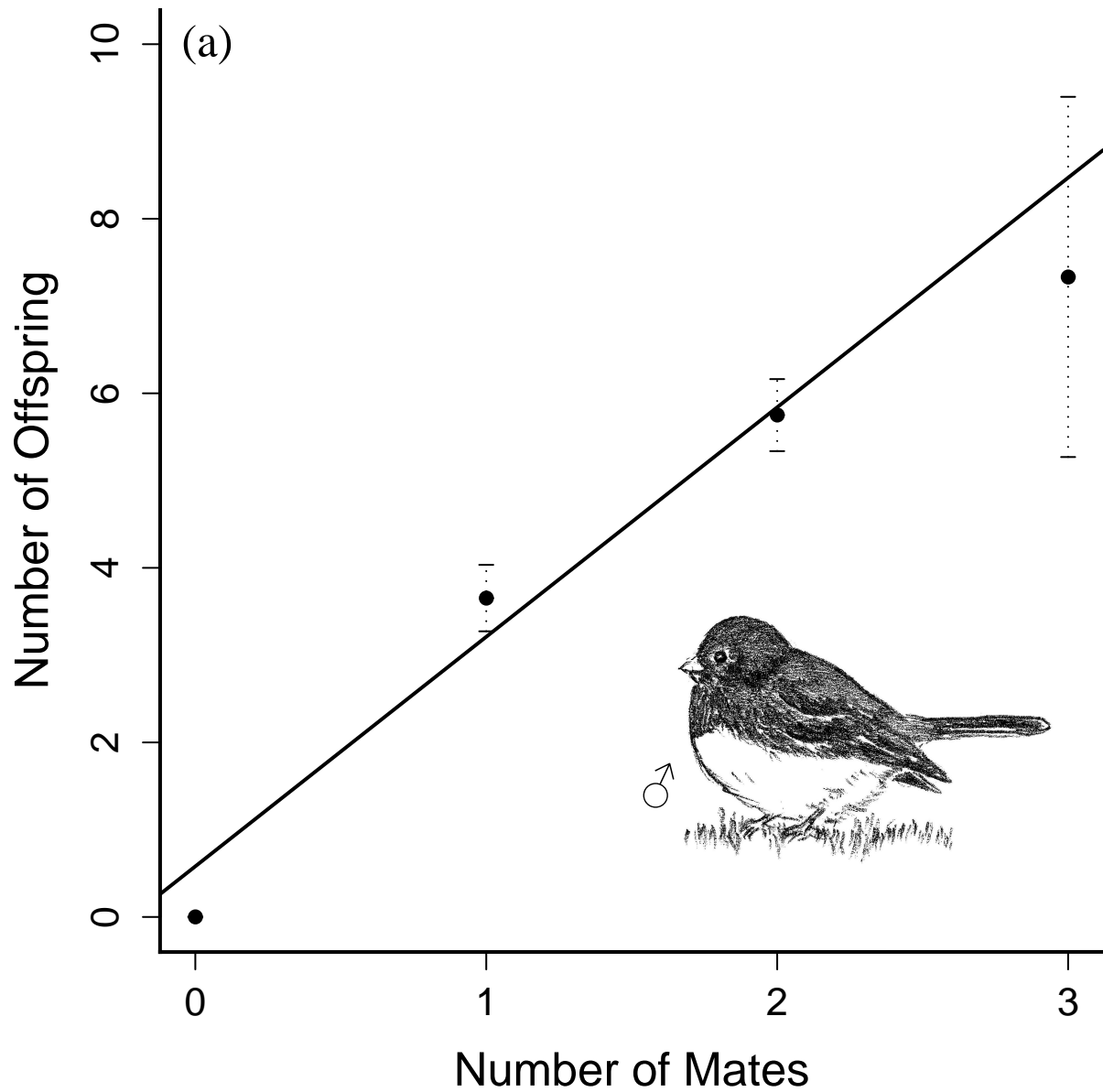
5.2 Fitness Components

Both variants of the model also indicate that measuring the effect of extra-pair paternity on the strength of sexual selection based on fitness components may be biased. The contribution of variance in extra-pair success to the opportunity for selection is an increasing function of the extra-pair paternity rate (Figure 1 of main text). Thus, the effect of random mating on this fitness component changes systematically with the rate of extra-pair paternity. If $\xi < 4$ (inequality (A10)), as may often be the case (Table 2 main text, Supplementary Figure 1), the contribution of variance in within-pair success decreases with increasing p, causing systematic effects also for this fitness component (Figure 1 of main text).

(a)

(b)

(a)

(b)

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