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## **Extra-Pair Behaviour**

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In many sexually reproducing organisms, a single well-timed copulation would in theory be sufficient to fertilize all the eggs in a clutch. However, in reality males and females often copulate much more frequently and they also often mate with more than one partner of the opposite sex during a single bout of reproduction. Although such **multiple mating** or **promiscuity** comes with some obvious costs, such as increased risk of predation or increased risk of contracting a sexually transmitted disease, it turns out to be extremely common. Hence, we need an explanation for why multiple mating has evolved. In this chapter, we discuss a special case of promiscuity, which can occur in all species where individuals form pairs for breeding (Box 1). An **extra-pair mating** can be defined as a copulation with an individual of the opposite sex that is not the social partner, and it can lead to **extra-pair paternity** or **mixed paternity** within a brood or litter. The study of promiscuity and extra-pair behaviour is interesting, not only in itself, but also because promiscuity has several interesting evolutionary consequences. For example, it can help explain variation in the morphology of reproductive organs, in sperm production, sperm size, and sperm motility, in copulation behaviour, or in patterns of parental care. It may also lead to selection that favours behaviours such as mate guarding or male aggression. Finally, extra-pair behaviour can substantially affect the fitness of an individual and it can dramatically increase the intensity of sexual selection, particularly in socially monogamous species.

In this chapter we focus exclusively on birds. In this group of vertebrates, a large variety of mating patterns has been described, but **social monogamy** with **biparental care** is by far the most common mating system (Box 1). However, parentage analyses using **DNA fingerprinting** techniques revealed that social monogamy often goes hand in hand with multiple mating and extra-pair paternity. Studies on birds have played a prominent role in our understanding of the evolutionary causes and consequences of extra-pair mating, partly because many aspects of bird behaviour are relatively easy to study in the field. Many of the issues discussed here not only apply to birds and are more generally relevant in the context of understanding promiscuous behaviour.

*Box 1 around here*

# 1. The Occurrence of Extra-Pair Behaviour

## 1.1. Frequency of Extra-Pair Paternity

The **frequency** of extra-pair paternity, as revealed by studies using molecular techniques such as microsatellite markers, varies dramatically among species (Griffith et al. 2002). In some species, extra-pair paternity seems to be absent or extremely rare. For example, in the socially monogamous Lanyu scops owl (*Otus elegans botelensis*) only one extra-pair offspring was detected among a total of 200 genotyped offspring from 108 families (Hsu et al. 2006). In other species, extra-pair males sire the majority of offspring. This is for example the case in the socially monogamous tree swallow (*Tachycineta bicolor*), where 51% of 229 offspring from 49 broods were extra-pair, and extra-pair paternity was found in 75% of all broods (Kempnaers et al. 1999; see Figure 1). The record holder is found in Australia: in the superb fairy-wren (*Malurus cyaneus*), a cooperatively breeding bird, extra-group paternity was detected in almost all broods (95% of 40, Mulder et al. 1994), and 61% of 1895 genotyped offspring were sired by males outside the female's social group (Double and Cockburn 2003). Species also vary in the **distribution** of extra-pair young among broods and in the **number of fathers** within a brood. In many cases, broods show mixed paternity, with some offspring fathered by the social male, and some by an extra-pair male. However, broods that contain exclusively extra-pair young are found in many species (see Figure 1 for example). In the superb fairy-wren, this occurred in no less than 48% of the broods (Mulder et al. 1994). Females may also copulate with several extra-pair males, so that each offspring can have a different father (e.g. in the tree swallow; Whittingham et al. 2006; Dunn et al. 2009).

*Figure 1 around here*

There are two important points to be made regarding the frequency of extra-pair paternity. First, one should be aware that multiple paternity in a brood can occur for reasons other than extra-pair mating. These are: (1) **rapid switching of social mates** (e.g. Mee et al. 2004), (2) **sequential polyandry** and **sperm storage** (e.g. Oring et al. 1992), and (3) **cooperative breeding** with more than one reproductively active male (e.g. Haydock et al. 2001). The second point is that the frequency of extra-pair paternity does not necessarily reflect the **frequency of extra-pair behaviour** (Brommer et al. 2007; Griffith 2007). Thus, it is possible that extra-pair copulations are rather common, but rarely lead to extra-pair paternity. For example, a study on northern fulmars (*Fulmarus glacialis*) found no extra-pair paternity although 2.4% of copulations were extra-pair (Hunter et al. 1992). Extensive behavioural observations suggest that the social males may have sired all the offspring because they *always* obtained the majority of copulations *and* the last copulation before egg laying. Because observing copulation behaviour is time-consuming, and because extra-pair copulations may be harder to observe than within-pair copulations (e.g. extra-pair behaviour may be more cryptic), it is difficult to link behaviour with paternity. Experimental work with bluethroats (*Luscinia svecica*) provides further insight. Fossøy et al. (2006) employed a simple device to prevent social males from transferring sperm during copulation (see photo).

## ||Picture

A male bluethroat (*Luscinia svecica*) with a rubber tube attached around the cloaca to prevent sperm transfer during copulation.

**Photo Jan T. Lifjeld** (reprinted with kind permission from Springer Science+Business Media: Behavioral Ecology & Sociobiology, Evidence of obligate female promiscuity in a socially monogamous passerine, 60, 2006, 256, Fossøy F, Johnsen A & Lifjeld JT, Fig. 1).

Females mated to such males should lay infertile eggs, unless they performed extra-pair copulations. Indeed, Fossøy et al. (2006) showed that most of the experimental pairs had extra-pair offspring in their brood. Because the level of extra-pair paternity in natural broods is much lower, the results suggest that many females that appear truly monogamous (i.e. have no extra-pair offspring) are in fact promiscuous. Note that the opposite is also possible: a single, well-timed extra-pair copulation may sire a disproportionate number of offspring (Michl et al. 2002).

Extra-pair paternity is not only the outcome of copulation behaviour, but also of post-copulatory processes such as **sperm competition** and **cryptic female choice**. The importance of sperm competition is demonstrated in a study on mallards (*Anas platyrhynchos*): when female mallards were artificially inseminated with equal numbers of sperm from a brother and an unrelated male, differences in fertilization success could be explained by between-ejaculate differences in average sperm swimming speed and motility, but not by male relatedness to the female (Denk et al. 2005). Evidence for female sperm selection comes from a study on red junglefowl (*Gallus gallus*): the number of sperm that were counted on the perivitelline membrane of eggs – which reflects the number of sperm at the site of fertilization – was lower when a female was inseminated by a brother compared to an unrelated male (Pizzari et al. 2004). Despite these and other studies, we still lack a general understanding of whether and how processes such as sperm selection and sperm competition, and factors such as the timing of copulations affect the success of extra-pair copulations.

### 1.2. Determinants of Variation in Levels of Extra-pair Paternity

Which factors can explain the observed variation in the frequency of extra-pair paternity that occurs between species, populations and individuals? The frequency of extra-pair paternity in a population is the outcome of processes that play at the level of individuals with potentially strong conflicts of interest between males and females (Petrie and Kempenaers 1998; Westneat and Stewart 2003). Thus, to understand variation in extra-pair paternity, we need to consider the costs and benefits for individuals engaging in extra-pair matings. This is the focus of section 2. Here, we briefly consider four groups of relevant factors and illustrate their complex interactions with some examples.

(1) *Species-specific factors and life-history*. Comparative analyses have shown that variation in the frequency of extra-pair paternity can be explained by variation in general life-history characteristics of the species (Arnold and Owens 2002). Extra-pair paternity is most frequent in species with high adult mortality (Figure 2) and high annual fecundity (**fast life-histories**), in species where males provide less care (relative to the female), or in species where the effect of male care on offspring fitness

is limited. In contrast, extra-pair paternity is generally rare or absent in species that are long-lived and show a low annual fecundity (**slow life-histories**), and in species where male care is more important. Life-history, paternal care, and extra-pair behaviour may be directly linked through the evolutionary response of male behaviour to an increased frequency of cuckoldry. The more common extra-pair paternity becomes, the less it will pay males to care for offspring (Box 2). Extra-pair behaviour and extensive paternal care may then become mutually exclusive and male care in the absence of extra-pair paternity may be the only stable equilibrium for species with slow life-histories. Yet how exactly slow life-history prevents the invasion of cuckoldry remains unclear. Maybe it is the potential costs of extra-pair matings for females, imposed by the males' facultative response to their mate's infidelity (Box 2). Male retaliation in terms of **reduced care** or **divorce** after perceived loss of paternity presumably has a stronger negative impact on female fitness in slow life-history species and might thus prevent females from pursuing extra-pair matings. This is also referred to as the "constrained female hypothesis" (Mulder et al. 1994; Gowaty 1996). Alternatively, the association between life-history characteristics and the frequency of extra-pair paternity may be caused by an unknown factor which has yet to be explored.

*Figure 2 around here*  
*Box 2 around here*

(2) *Population-specific factors and genetic diversity.* If females mate with extra-pair males to increase the genetic quality of their offspring through "good genes" or "compatible genes", levels of extra-pair paternity may vary depending on the availability of males with good or compatible alleles (Kempnaers 2007; Lindstedt et al. 2007). One could then predict a positive relationship between levels of extra-pair paternity and population-wide variation in male genetic quality or genome-wide diversity (Petrie et al. 1998). Indirect evidence comes from the observation that levels of extra-pair paternity are generally lower on island populations (Griffith 2000), which may also be less genetically diverse. For example, an island population of house sparrows (*Passer domesticus*) had both lower levels of extra-pair paternity and reduced genetic diversity compared to several mainland populations (Ockendon et al. 2009). When mainland birds with higher genetic diversity were released on the island, the level of extra-pair paternity strongly increased, as predicted. However, contrary to the idea that females would benefit from mating with immigrant males by maximizing the genetic diversity of their offspring, all extra-pair fathers were island males. What this study shows most clearly is that we are still far from understanding the factors that affect extra-pair paternity within populations.

(3) *Population-specific factors and ecology.* Levels of extra-pair paternity in a population may also vary depending on ecological factors that influence the likelihood of meeting extra-pair partners. For example, the availability of copulation partners may be larger in high-density populations, or in populations with high **breeding synchrony** (because all individuals will be fertile around the same time; Stutchbury and Morton 1995). Note, however, that high breeding synchrony may also lead to lower levels of extra-pair paternity, if males face a trade-off between mate guarding and pursuing extra-pair copulations (Westneat et al. 1990; van Dongen and Mulder 2009). Similarly, one could argue that higher levels of extra-pair paternity are expected in low-density populations, if this forces females to settle with non-preferred

males and hence to pursue extra-pair copulations more often. Although effects of **breeding density** and synchrony have been extensively discussed and tested, they rarely seem important (e.g. Kempenaers 1997; Stewart et al. 2006; Lindstedt et al. 2007; Rowe and Weatherhead 2007, but see the experimental study by Charmantier and Perret 2004). Another example is the potential effect of habitat characteristics on extra-pair paternity. Dense **vegetation** may allow females as well as extra-pair males to hide from guarding males and to sneak extra-pair copulations, whereas open habitats make it easier for territory owners to observe intruding males and may also increase the probability of male retaliation, and thus increase the costs of extra-pair paternity for females (Valera et al. 2003).

(4) *Individual-specific factors.* Only few studies so far have addressed whether loss or gain of paternity is repeatable for individual males, females or pairs (e.g. Dietrich et al. 2004). At the level of the individual, the question thus remains whether some individuals are more likely to engage in extra-pair behaviour than others (everything else being equal), and what factors play a role. Males or females may intrinsically differ in a variety of ways that influence their propensity to show extra-pair behaviour. For example, individuals may differ in their **genetic predisposition** to be promiscuous (Forstmeier 2007), or individual extra-pair behaviour may depend on maternal effects (e.g. hormone levels in the egg) or on the rearing environment. Males may also differ in quality, as reflected in **age, condition**, or expression of **sexual ornaments**, which may influence their capacity to gain extra-pair matings or to avoid losing paternity. One of the more robust findings in studies on extra-pair paternity is that older males are more likely to sire extra-pair offspring (e.g. Delhey et al. 2003; Bitton et al. 2007; Bouwman et al. 2007; Schmoll et al. 2007a). Similarly, females may differ in quality, condition, size, or experience (age), which may influence their ability to cope with reduced male investment, and hence the potential costs of engaging in extra-pair matings. Alternatively, larger or stronger females might be better at avoiding costly extra-pair copulations and hence are less likely to have extra-pair offspring (Rosivall et al. 2009).

In reality, it will often be difficult to disentangle the factors that play a role in creating a particular level of extra-pair paternity in a population, unless experiments are conducted. The following examples illustrate how difficult it is to unequivocally interpret results even in carefully designed studies. In the coal tit (*Parus ater*) Dietrich et al. (2004) showed that the level of extra-pair paternity increased significantly from first to **second broods** (overall and within pairs). There are several, not always mutually exclusive explanations (see also discussion in Dietrich et al. 2004). (a) Second broods may be less valuable to males so they would invest less in paternity protection strategies. (b) Males whose mates did not lay a second clutch may have invested heavily in extra-pair behaviour causing high paternity loss for males whose mates *did* produce second broods. (c) Young in second broods may face harsher conditions, so that effects of good or compatible alleles on offspring fitness are more important (Schmoll et al. 2005; Kempenaers 2007), and selection would favour females who engage more often in extra-pair behaviour. (d) Females may invest more in extra-pair behaviour because the environmental conditions have improved so that they are less dependent on male care. (e) Females may have increased opportunities to engage in extra-pair copulations for the second brood because the eggs of the second brood are fertilized when the young of the first brood still require care and males have to trade off mate-guarding with offspring care.

The second example concerns studies on the relationship between **weather conditions** and the level of extra-pair paternity. In a Norwegian population of bluethroats low temperatures during the peak fertile period resulted in lower levels of extra-pair paternity (Johnsen and Lifjeld 2003), presumably because individuals invested more in self-maintenance during a spell of bad weather. Moreover, it may be harder for males or females to detect suitable extra-pair partners in adverse weather conditions. Finally, when weather conditions are likely to stay bad during the nestling phase, male care may become more important, and this may cause a shift in female behaviour towards less extra-pair behaviour. Similar reasoning can explain why rainfall during the fertile period caused a decrease in levels of extra-pair paternity in the reed bunting (*Emberiza schoeniclus*, Bouwman and Komdeur 2006). However, in this species, low temperatures led to *increased* levels of extra-pair paternity, which the authors explain by reduced mate guarding because of investment in self-maintenance when temperatures are low. What can we learn from such conflicting results? Clearly, the level of extra-pair paternity is hard to predict even when information about variation in very specific ecological parameters is available. This is because the level of extra-pair paternity is a population parameter that emerges from behavioural interactions between individuals, and we are still far from understanding the complex dynamics causing population level changes. However, we can focus on particular behaviours or behavioural interactions and use the above results to predict the effect of e.g. weather conditions on mate guarding in male reed buntings or on solicitation of extra-pair copulations in female bluethroats. Ultimately, seemingly contradictory results may not be inconsistent after all. Weather conditions likely affect general activity patterns and may do so more in one sex than in the other or more for particular activities depending on the specific ecological situation and on the species.

The final example is an experimental study on song sparrows (*Melospiza melodia*, MacDougall-Shackleton et al. 2006) where food and predator presence was manipulated. Extra-pair paternity was more frequent when the **environment** was more challenging (no extra food, predators present), and females with extra-pair offspring were more stressed than faithful females. This contradicts the hypothesis that females that are more in need of male help are less likely to engage in extra-pair behaviour. Instead, general activity patterns may again have changed in response to the experimental manipulation leading also to changes in the exposition to and opportunities for extra-pair mating attempts. For example, hungry females might move around more and hence meet more extra-pair males, and females might be less likely to conspicuously resist copulation attempts if predators are around.

Arnold and Owens' (2002) comparative analysis showed that 55% of the interspecific variation in the frequency of extra-pair paternity in birds is explained by the taxonomic classification (family and order). They thus suggested a **hierarchical explanation** for the variation in extra-pair paternity. Variation among major avian lineages can best be explained by variation in the potential costs and evolutionary consequences of extra-pair behaviour, as explained above. Variation among closely related species, or among populations of the same species, may be better explained by the opportunities to engage in extra-pair copulations and the benefits that can be gained from this behaviour. It would be interesting to find out whether this hierarchical explanation can be extended to other vertebrates. The available data are too scant to allow formal analysis, but at least indicate that there may be as much

variation in levels of extra-pair paternity in other taxa as observed in birds (Sefc et al. 2008; Cohan and Allainé 2009; While et al. 2009a).

## 2. Evolutionary Causes of Extra-Pair Behaviour

When the existence of extra-pair behaviour is the result of natural and sexual selection, the fitness **benefits** an individual derives from acquiring additional mates must be higher than the **costs** associated with it, at least for some individuals. Costs are not only those that come about directly from performing the behaviour, but also include **opportunity costs**. These arise from missing the opportunity to perform an alternative behaviour. Extra-pair behaviour will trade-off with behaviours such as self-maintenance, mate guarding or parental care. An individual that invests in extra-pair behaviour can only do so at the cost of investing less into such other behaviours, thereby foregoing other fitness benefits.

Generally, the reproductive success of male birds is mainly limited by the access to females, because males can produce more gametes than they can obtain eggs to fertilize. Therefore, males should always copulate with additional females, unless there are substantial costs associated with this behaviour. In contrast, female birds usually cannot increase their offspring number by mating with more males and it is therefore not so clear whether they should mate multiply, even when this behaviour is not costly. Due to this initial difference between the sexes, **conflicts of interest** between the members of a socially monogamous pair (and other individuals) may arise over the level of promiscuity. The observed extra-pair behaviour will be the evolutionary outcome shaped by these conflicts of interest. Here we discuss the costs and benefits of engaging in extra-pair behaviour for males and females separately.

### 2.1. Benefits and Costs of Extra-Pair Matings for Females

#### 2.1.1. *Female Benefits of Extra-Pair Behaviour*

Selection can act on females to mate multiply in two ways (Jennions and Petrie 2000). (1) Selection may favour females who increase their number of mates independent of the quality of their social mate. (2) Selection may favour females who improve on the quality of their social mate by ensuring fertilization by (extra-pair) males of higher quality. In both cases the fitness increase for multiply mated females can be brought about directly via an increase in female fecundity, in female survival, or in the number or non-genetic quality of the offspring that can be raised (**direct benefits**). Alternatively, fitness of multiply mated females can increase indirectly through genetic effects on the fitness of offspring (**indirect benefits**). Most likely direct and indirect benefits of extra-pair behaviour for females often occur jointly in the same species (Jennions and Petrie 2000).

#### A. *Direct Benefits*

##### *Material Benefits*

The fitness of a female can be enhanced directly via extra-pair behaviour when she gains **material benefits** in the form of additional male investment such as courtship

feeding, nutritional resources in the ejaculate, offspring care, access to additional resources etc. In this context, it is important to note that female multiple mating will reduce the fitness benefit of parental investment for males (Box 2). Also, distributing paternal care among several nests would lead to a reduction in efficiency, especially in territorial species. Selection will therefore favour males who focus their care on the brood(s) where their expected paternity is highest (Souzou and Houston 1994; Iwasa and Harada 1998). This makes it unlikely that females can gain additional male investment such as offspring care from extra-pair mates. Furthermore, when females only seek extra-pair copulations to obtain additional investment, a simple way in which males could reduce multiple mating of their female is to provide her with as much care as possible (cf. Hunter and Davis 1998). Taken together this should concentrate material benefits within the social pair (Akçay and Roughgarden 2007) and inhibit selection for female extra-pair behaviour solely through benefits such as paternal care. In line with this, material benefits from extra-pair copulations are generally thought to be unimportant (e.g. Birkhead and Møller 1992, pp.201-203). Nevertheless, a few studies have found evidence for such benefits and we discuss those cases in more detail below.

In the great grey shrike (*Lanius excubitor*), a socially monogamous species with biparental care, males give food to females immediately before copulation. Tryjanowski and Hromada (2005) showed that extra-pair females are provided with prey items of high energy value that are costly to hunt (Figure 3). Why do males not allocate this investment to their social mate? The benefit for males from this investment is twofold: it not only functions as parental effort but also as mating effort (Møller and Thornhill 1998). Forms of male investment that occur after fertilization, such as incubation or feeding young, primarily serve to increase offspring fitness and cannot influence mating success anymore (although they might sometimes influence copulation opportunities for future broods, e.g. Freeman-Gallant 1996). In contrast, providing females with courtship gifts may create extra-pair opportunities that are otherwise absent.

*Figure 3 around here*

Additional access to fertile females may also explain why male red-winged blackbirds (*Agelaius phoeniceus*) allow extra-pair mates to forage on their territory (Gray 1997a). Material benefits in the form of foraging opportunities could further be facilitated because males have to defend a territory for their social nest(s) in any case, and the cost of allowing other females to forage in their territory may be minimal. Finally, in some species, it has been observed that unpaired males provided material benefits to females when they copulated with them (Hunter and Davis 1998; Blomqvist et al. 2005). In this case, the care-providing extra-pair males do not have their own brood to care for. Such a situation shows some resemblance to a cooperative breeding system where several males share in siring offspring and in providing care. Similarly, males may start caring for an “extra-pair brood” after their “social brood” failed (e.g. due to predation; Kempenaers 1993).

#### *Insurance Benefits*

An increase in the number of mates can also lead to higher fecundity because it **ensures fertilisation** when some males are unable to fertilise a female's eggs

(Sheldon 1994). Even if a male produces functional sperm, he may be unable to fertilise the ova of his social mate due to temporary sperm depletion (Wetton and Parkin 1991) or due to a failure to overcome female barriers against polyspermy (Morrow et al. 2002). There is considerable variation among bird species in hatching success, but no positive relationship with the rate of extra-pair paternity has been found (Morrow et al. 2002). However, such a relationship is not necessarily expected because the present state may represent an evolutionary response to past selection against infertility (Sheldon 1994), so that species with high levels of extra-pair paternity are now best insured against infertility (Lifjeld 1994).

Fertility benefits are difficult to study both for theoretical and practical reasons. First, with observational data it is almost impossible to exclude the hypothesis that females obtain indirect benefits from extra-pair behaviour. Whenever there is some heritable component to an extra-pair male's ability to fertilise a female's eggs that her social mate failed to fertilise, genetic benefits are inevitable and it is difficult to quantify the evolutionary importance of one benefit relative to the other (Sheldon 1994; Griffith et al. 2002; Griffith 2007). Second, it may be problematic to ascertain whether eggs have failed due to lack of fertilisation or due to early embryo death (e.g. Kempenaers et al. 1996; Friedl and Klump 2005, but see Birkhead et al. 2008). Temporary sperm depletion is perhaps most likely in polygynous species where mated males always copulate with several females. Indeed, the strongest evidence for fertility benefits comes from two socially polygynous species (Gray 1997b; Friedl and Klump 2005), whereas evidence from studies of socially monogamous species is relatively weak (Wetton and Parkin 1991; Wagner 1992; Lifjeld 1994; Krokene et al. 1998).

Extra-pair behaviour may not only function as an insurance against male infertility but also against **mate loss** through death of the partner, if it enables multiply mating females to find a new male more quickly (Petrie and Kempenaers 1998). This hypothesis has not been explicitly studied, but interspecific variation in the rate of extra-pair paternity is positively associated with variation in mortality rates (see above, Arnold and Owens 2002). However, such a pattern can easily be explained in other ways because mortality will fundamentally influence the costs and benefits of infidelity in several respects (Mauck et al. 1999; Wink and Dyrce 1999; Arnold and Owens 2002; Jeschke and Kokko 2008).

Insurance benefits could also come into play as a result of genetic **pleiotropy** when the same genes control the frequency of within- and extra-pair copulations (positive genetic correlation; Arnqvist and Kirkpatrick 2005; Forstmeier 2007). It is likely that there is an optimal frequency of within-pair copulations, for example to avoid infertility of eggs, to secure male care, or to strengthen the pair bond. Hence, selection may favour female extra-pair behaviour indirectly because only unfaithful females copulate frequently enough with their social partner to avoid infertility or mate loss.

A related benefit of female extra-pair behaviour could lie in **mate sampling** (Heg et al. 1993) and **pair formation** (Colwell and Oring 1989). Females in suboptimal pair bonds could assess available males via extra-pair behaviour and initiate new social relationships for the following season. In socially monogamous bird species a high divorce rate was positively associated with a high rate of extra-pair paternity (Cézilly and Nager 1995). Again, it is easy to come up with alternative explanations for such an association, because the divorce rate of a species also emerges as a trait

from complex interactions between individuals (Cézilly and Nager 1995; Catry and Furness 1997).

### *Diversity Benefits*

Multiple paternity broods will show a higher genetic diversity. This may directly increase the success of the brood, if it leads to **positive interactions** among nestlings (Yasui 1998; for tests and discussion see Schmoll et al. 2007b and Dunn et al. 2009). For example, genetic diversity may hinder the transfer of infectious diseases among offspring (Jennions and Petrie 2000). Here it is considered a direct and not an indirect benefit because it is independent of offspring genomic quality itself. It has to be kept in mind, however, that the presence of half-siblings will lead to an **increase in sibling-competition** as an ecological (Boncoraglio and Saino 2008) or evolutionary (Briskie et al. 1994) response to decreased relatedness among nest-mates. This might be beneficial in some cases when it eliminates genetically inferior competitors quickly (Jennions and Petrie 2000), but in general is expected to be against the parents' interest (Birkhead and Møller 1992, p.204).

### *B. Indirect Benefits*

The genetic quality of an offspring will influence its fitness and thus indirectly maternal fitness. Females could therefore benefit from extra-pair behaviour by optimising the genetic quality of their offspring. How females should behave will depend on the information they can obtain about expected fitness returns.

It may sometimes be impossible to maximize offspring genetic quality, because the optimal male genotype is uncertain or not readily identifiable. In such a situation **genetic bet hedging** may be adaptive (Yasui 1998; for tests and discussion see e.g. Schmoll et al. 2007b). Multiple mating produces offspring of variable genetic quality, whereas broods sired by only one male contain young that are more or less of the same (superior or inferior) genetic quality. The average genetic quality of a brood with multiple sires is therefore less likely to be extreme. Hence, **increasing genetic diversity** by mating multiply causes a reduction in fitness variance between broods. In the long run, this reduction in between-brood variance in offspring quality is associated with increased fitness. This is because over evolutionary time, above-average success with one mate cannot compensate similar below-average success with another (the geometric mean is more relevant for long-term fitness than the arithmetic mean; Gillespie 1977; Philippi and Seger 1989). However, it has been convincingly argued that fitness benefits from genetic bet-hedging are usually limited and unlikely to be important in maintaining female promiscuity, except in special cases (Yasui 2001).

When females are able to determine the optimal genetic constellation for their offspring, their choice of a paternal genotype should be influenced by two effects: allelic quality and allelic compatibility. The former refers to the absolute, additive effects certain paternal alleles ("**good genes**") have on the fitness of the offspring genotype (Jennions and Petrie 2000; Neff and Pitcher 2005). These will be alleles that increase viability or attractiveness (mating success) and they confer their fitness effects relatively independent of the genetic background in which they happen to occur. **Genetic compatibility** refers to the effects of interactions within a genome

between alleles at the same locus (e.g. heterozygote advantage) or at different loci (epistasis). In the context of mate choice, genetic compatibility issues might arise when the fitness effects of the alleles from the maternal haplotype and other maternal genetic elements depend in a non-additive way on the paternal haplotype they are combined with. This means that the quality of offspring genotypes does not only depend on the sum of the effects of the maternal and paternal alleles, but also on their interaction (Zeh and Zeh 1996; Brown 1997; Neff and Pitcher 2005). Female choice for allelic quality and compatibility are not mutually exclusive (Jennions and Petrie 2000) and it is expected that females trade off one benefit against the other when they are negatively associated (Neff and Pitcher 2005).

When female preferences for genetically superior or compatible males drive female extra-pair behaviour, infidelity is expected only when females can improve on the social mate's genotype via extra-pair copulations. Thus, females that secured the genetically optimal male as social mate should not engage in extra-pair copulations for genetic benefits. The good genes and the compatible genes hypothesis make different predictions about the congruence among females in their extra-pair mate choice: additive effects lead to agreement about who is the "top-quality" male, whereas non-additive effects lead to a different ranking of males for different females (Zeh and Zeh 1996; Brown 1997; Neff and Pitcher 2005). However, both hypotheses predict that extra-pair young should have higher quality genomes than within-pair young of the same brood (**maternal half-sib comparisons**; Griffith et al. 2002; Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007). A recent meta-analysis found only small and presumably evolutionary irrelevant effects of paternity status on offspring fitness (Arnqvist and Kirkpatrick 2005; see also Akçay and Roughgarden 2007 who additionally find small effects for two other measures of indirect benefits). This suggests that selection on females to pursue extra-pair copulations for genetic benefits is absent.

However, the estimates on which this meta-analysis is based can be criticized for three reasons. (1) Estimates of offspring fitness that can be obtained from data in the field and that are reported in studies on extra-pair paternity do not necessarily represent an important component of total fitness, because they often do not give information on residual reproduction or offspring reproduction (Eliassen and Kokko 2008). (2) Differences in genetic quality among offspring within a brood need not transfer into easily measurable differences in fitness when genetic effects explain only a small amount of the variation in offspring fitness (Møller and Alatalo 1999). Yet they might constitute the most important fitness consequence of a female's mating decision, which is then shaped by these minor differences because a small fitness benefit can still be selected for over evolutionary time. (3) Parental effects may differ among the young in a brood (Price 1998). This could confound the genetic differences (Griffith et al. 2002) and conceal them when parents invest more into within-pair offspring. Such compensatory allocation (Bluhm and Gowaty 2004) can be very difficult to control for because it can occur already at the stage of egg production (Saino et al. 2002; Bolund et al. 2009; see also Magrath et al. 2009).

*Figure 4 around here*

There is evidence for both good genes and genetic compatibility benefits from studies on a variety of species (e.g. Hasselquist et al. 1996; Blomqvist et al. 2002; Forstmeier

et al. 2002; Eimes et al. 2005; Fossøy et al. 2008; Kawano et al. 2009). For example, in a study on the blue tit (*Cyanistes caeruleus*) extra-pair offspring were more heterozygous than within-pair offspring from the same nest (Fig. 4a). Heterozygosity is associated with reproductive success and sexual attractiveness in this species presumably because it reduces the number of recessive deleterious alleles expressed or increases the diversity of gene products synthesized (Foerster et al. 2003; García-Navas et al. 2009). Interestingly, the difference in heterozygosity was only present when extra-pair sires were not close neighbours (Fig. 4a). This is because females were generally less related to more distantly breeding males (Foerster et al. 2006). Hence, females that copulated with extra-pair males breeding further away obtained compatibility benefits (Foerster et al. 2003). Further, it could be shown that only close neighbours, but not non-neighbours, were older and larger than the social male they cuckolded (Fig. 4b). This suggests that females may have obtained good genes benefits from mating with neighbouring extra-pair males. Thus, in this population the details are more complicated because different females may obtain different genetic benefits from their extra-pair behaviour. Similarly, in bluethroats, extra-pair offspring were more heterozygous and showed a higher cell-mediated immune response than their within-pair maternal half-sibs (Figure 4c,d). However, both these effects were independent of each other (Fossøy et al. 2008), again suggesting that females may obtain different genetic benefits from engaging in extra-pair copulations.

The previous example illustrates that the type of selection on female extra-pair behaviour is likely to vary not only between species and populations but also between individuals (Petrie and Kempenaers 1998; Westneat and Stewart 2003). Hence, measuring an average effect size by drawing together measurements across many studies on different species might not be very meaningful (Eliassen and Kokko 2008). Complex patterns can also arise when individual females differ in the benefits they derive from extra-pair behaviour depending on their condition (Friedl and Klump 2005; Dreiss et al. 2008), or on environmental conditions (e.g. Johnsen and Lifjeld 2003; Schmoll et al. 2005; Bouwman et al. 2006; Garvin et al. 2006; O'Brien and Dawson 2007). As discussed above (see section 1.2.), intricate relationships are probably the rule rather than the exception. Direct and indirect benefits or different types of indirect benefits may often occur simultaneously. It should further be kept in mind that whenever extra-pair copulations occur, indirect benefits will necessarily be invoked because all females possess pre- or post-copulatory mechanisms that make fertilizations more probable for certain paternal haplotypes (e.g. conspecific haplotypes). The question is thus “What is the importance of female genetic benefits for maintaining extra-pair behaviour *relative* to other female benefits, to female costs, and to male costs and benefits?”

Another genetic benefit of female extra-pair behaviour may result when alleles causing an increase in extra-pair behaviour have opposite effects on male and female fitness (**intralocus sexual conflict**). If the genetic basis underlying promiscuity is identical for both sexes (i.e. if there is a positive genetic correlation between male and female extra-pair behaviour), strong selection favouring male extra-pair behaviour will result in increased extra-pair behaviour of both sexes (Halliday and Arnold 1987). The evolutionary stable level of promiscuity could then be above the level optimal for females because it reflects a compromise between the costs to females and the benefits to males. However, there would also be positive selection acting on females to express such a high level of extra-pair behaviour because without this the

male descendants of their line would be unsuccessful as extra-pair sires. Hence, in this case the genetic benefit for females is the increased extra-pair behaviour of their sons and grandsons. Benefits of extra-pair copulations are then rather concealed and females may even appear to suffer a cost, although the behaviour increases their overall fitness.

### *2.1.2. Female Costs of Extra-Pair Behaviour*

There are at least four types of costs associated with engaging in extra-pair copulations (listed in Westneat et al. 1990). First, as with any behaviour, the costs of extra-pair mating to females are associated with the time and energy needed to express the behaviour, that is, with the availability of additional mates. Second, copulations with additional mates may increase the risk of predation or of infection with parasites or sexually transmitted diseases. Third, a male may react to potential infidelity of his mate with mate guarding, frequent copulation, physical punishment, reduced care or divorce which may all be costly for females. This group of costs is thus a manifestation of sexual conflict between females and their social mates. Fourth, producing broods containing half- instead of full-siblings tends to increase sibling competition, which in most cases will be costly to parents (see “Diversity Benefits” in previous section).

Should males reduce their investment in parental care when their paternity is lower? And do they? It remains a challenge both to *predict* how males should respond (Box 2) and to *test* whether they respond (Box 3). To date there is no generally accepted study design that allows a decisive evaluation of the hypothesis of facultative male responses to reduced (certainty of) paternity (Sheldon 2002). The strongest experimental setup to address this question has been developed in a study on bluegill sunfish (*Lepomis macrochirus*, Neff 2003). It makes use of the fact that males that tend a nest can assess their relatedness to the fry (recently hatched young) via chemical cues, but not to the unhatched eggs (Neff and Sherman 2003, 2005). By experimentally reducing perceived (but not real) paternity during the egg stage and then revealing the true paternity during the fry stage, Neff has been able to induce an increase in paternal care from the egg to the fry stage that was not found in untreated controls. Furthermore, when true paternity was experimentally lowered without providing the male with a cue of cuckoldry at the egg stage, the opposite response (i.e. a decrease in paternal care) occurred. Thus, when males are able to assess true paternity reliably at a well-defined point in time, manipulations of perceived and true paternity become much more meaningful, especially because the response was shown in a randomly selected sample of males and in opposite directions between the two experiments.

*Box 3 around here*

*Figure 5 around here*

Irrespective of these theoretical and experimental issues, **reduced male care** is often considered the most important cost of extra-pair matings to females (e.g. Birkhead and Møller 1992, p.217). Across species the rate of extra-pair paternity and the level of paternal care are inversely associated (Møller 2000; Møller and Cuervo 2000; Arnold and Owens 2002). A high male contribution to brood care may have

constrained the evolution of extra-pair behaviour, so that divergence in parental care patterns between major avian lineages has led to different extra-pair paternity rates (Arnold and Owens 2002; Griffith et al. 2002; but see Møller 2000 and Møller and Cuervo 2000 for alternative explanations). Could the importance of paternal care also constrain female extra-pair behaviour at the population or the individual level? A recent meta-analysis emphasized that the cost of reduced male care, measured for individual females, appears to be high, especially when compared to the benefits (in the form of good or compatible genes; Arnqvist and Kirkpatrick 2005). However, the cost measurements on which this conclusion is based may not reflect responses of males to female extra-pair behaviour (Box 3, Eliassen and Kokko 2008). Leaving this aside, the estimates of these costs (Arnqvist and Kirkpatrick 2005) *are* negatively correlated with the rate of extra-pair paternity for this selection of species (Albrecht et al. 2006), supporting the idea that at the species level females that suffer the highest costs of extra-pair copulations are the least likely to engage in this behaviour. The costs of loss of male care can be reduced experimentally, for example by providing females with additional food. One would then predict that such females are more likely to engage in extra-pair behaviour, but studies that used this approach produced mixed results, depending on the study system (Hoi-Leitner et al. 1999; Václav et al. 2003). Hence, the evolutionary relevance of the cost of reduced male care in shaping patterns of female extra-pair behaviour probably varies between species.

## 2.2. Benefits and Costs of Extra-Pair Matings for Males

### 2.2.1. Male Benefits of Extra-Pair Behaviour

In general, males may gain the same benefits from extra-pair behaviour as females. However, unlike for females, the reproductive success of males is limited by the number of eggs they can fertilize, so males should always accept additional copulations when these can be acquired cheaply (Trivers 1972). Hence, selection will strongly favour males that increase their number of mating partners, independently of the quality of their social mate. In contrast, selection to improve the quality of the offspring through extra-pair copulations with high-quality females will be relatively unimportant. Thus, male benefits from extra-pair behaviour are mostly **direct benefits**, namely acquiring additional female investment in the form of eggs.

Males can also gain benefits from extra-pair paternity that do not apply to females, that is, benefits that arise from distributing offspring among several nests or from exploiting the care of other males. This requires that the female does not place the extra-pair eggs in the nest of the sire (quasi-parasitism), a behaviour that appears to be rare in birds (Griffith et al. 2004). For example, by siring young in multiple broods, males could **bet-hedge** against the effects of total offspring loss through nest predation (Webster et al. 2007), but such benefits are generally thought to be small (Bulmer 1984; Hopper and Rosenheim 2003; but see Pöysä 2007). Furthermore, if extra-pair young are of higher quality than their within-pair half-sibs (see above), they might experience reduced sib competition compared to the level of competition they would experience among their full siblings (Holen and Johnstone 2007). However, as outlined above, the decreased relatedness among young of a mixed paternity brood

can also cause an increase in sibling competition (Boncoraglio and Saino 2008), which would work against any such benefits to the extra-pair male.

### ***2.2.2. Male Costs of Extra-Pair Behaviour***

For males the cost of extra-pair copulation itself is probably small. Whenever copulations can be acquired cheaply, males only pay the costs associated with performing the copulation and producing viable sperm. As for females, the most important costs of copulating are an increased risk of predation and the risk of infection with parasites or with a sexually transmitted disease.

In contrast to females, the cost associated with the **availability of additional mates** is most likely a major factor for males. Fertile females will always be a limited resource because males should accept all extra-pair copulations that can be acquired cheaply. When competition for females is high, the costs associated with attempts to obtain extra-pair copulations (**opportunity costs**) are high and this can lead to selection favouring male investment in other behaviours (cf. Kokko and Jennions 2008). Specifically, extra-pair behaviour may trade off with **securing paternity** in the nest of the social mate, because females may be free to pursue extra-pair copulations when their social mate is absent. This will lead to males that invest into paternity protection behaviours such as frequent copulation or mate guarding rather than courting additional females (Westneat et al. 1990; Westneat and Stewart 2003). Pursuing extra-pair copulations may also trade off against **providing care** for the offspring in the nest of the social mate (Westneat et al. 1990), especially when material investment is needed to acquire extra-pair mates. Thus, males may refrain from extra-pair copulations because caring for offspring has a higher fitness pay-off. Note that such a trade-off can also explain the relationship found across species between the level of paternal care and the rate of extra-pair paternity discussed earlier (section 2.1.2; Møller 2000; Møller and Cuervo 2000). Independent of the availability of mates and the opportunity costs of extra-pair behaviour there can be a **fixed cost** for every additional mate a male acquires when material benefits are important for maintaining female extra-pair behaviour.

### **2.3. Is Extra-Pair Behaviour Male or Female Driven?**

The question whether extra-pair behaviour is **male or female driven** has received much attention in the recent literature (e.g. Westneat and Stewart 2003; Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007; Eliassen and Kokko 2008). We use the term “male (or female) driven” in the sense of evolutionary changes in extra-pair behaviour resulting from selection on males (or females). The question is tightly linked to the net-effect of extra-pair behaviour on male and female fitness. If the costs of extra-pair behaviour for females outweigh the benefits, infidelity is selected against in females and will only occur as a result of selection on males to pursue extra-pair copulations. Note however, that extra-pair behaviour can also be male driven when females gain a net benefit from cuckoldry, as long as selection for infidelity is much stronger in males than in females, which seems likely. Then, evolutionary changes in extra-pair behaviour would occur chiefly through selection on males, even though selection favouring the behaviour acts on both sexes. Furthermore, as discussed

above, male and female extra-pair behaviour may be genetically correlated, so that expression of extra-pair behaviour in females may be non-adaptive and a consequence of strong selection on male behaviour. Then females appear to suffer a net cost, but extra-pair behaviour is not the result of male pursuit alone.

It is not easy to determine whether the extra-pair behaviour observed in a population is the result of selection on males, females or both. The answer to this question may appear obvious if judged by the behaviour of females. For example, in the New Zealand Stitchbird (or Hihi, *Notiomystis cincta*) groups of extra-pair males perform prolonged chases of fertile females which alarm call and apparently try to evade the males. When a male can successfully get hold of a female, the female is pinned with her back to the ground during copulation (Castro et al. 1996). Observations such as these have been made in a variety of species and have been referred to as “forced copulations” (McKinney et al. 1983; Birkhead and Møller 1992, p.104-106; Westneat and Stewart 2003). They strongly suggest that in many instances females actively avoid extra-pair copulations, reflecting a sexual conflict. However, **resistance** against copulation attempts does not necessarily equal female avoidance of costly copulations, because females may ensure copulations with high quality males by allowing only the most persistent males to copulate (**resistance as a ploy**; Cox and LeBoeuf 1977; Westneat et al. 1990). Furthermore, females are often not equally resistant towards all males (**female manipulation hypothesis**; Westneat et al. 2003) and even solicit copulations from some while fleeing from others.

In the blue tit and in the superb fairy-wren fertile females conduct **forays** to the territories of extra-pair or extra-group males which are the sires of some of the offspring in their brood (Kempnaers et al. 1992; Double and Cockburn 2000). In the fairy-wrens these forays occur very early in the morning when it is still dark and are the first movement of females after leaving their roost site. They consist of rapid flights directly to the centre of the visited territory and back (Double and Cockburn 2000). Upon arrival at the male’s territory, females were observed to perch near the male, and to closely approach the male after he started a courtship display until copulation took place (Cockburn et al. 2009). Thus, females of some species apparently actively pursue extra-pair copulations, which – at least for an adaptationist – is hard to reconcile with the idea that extra-pair copulations come at a net cost for females. Similarly, in the Adélie Penguin (*Pygoscelis adeliae*) females have been observed to join extra-pair males at their nest site and **solicit** courtship and copulation (Hunter and Davis 1998). After copulation however, these females picked up a stone from the extra-pair male’s nest which they then brought to their own nest. Adélie Penguins’ nests consist of a pile of stones and these stones are a limited resource in their breeding area. Females therefore probably trade nesting material for copulations and it is impossible to determine whether they leave their nest site for extra-pair copulations or in search of stones. This illustrates the general problem to determine the function of female forays (Westneat and Stewart 2003). When the copulation itself is not observed – which can be exceedingly difficult – it is impossible to rule out that females visit the territories of extra-pair males in search of nesting material or food and copulations are the result of male coercion upon encounter. In sum, studying female behaviour can give strong indications in one or the other direction, but it does not allow a conclusive decision about whether extra-pair behaviour comes at a net cost or benefit to females, because all forms of female behaviour are open to alternative explanations (Westneat et al. 1990; Westneat and Stewart 2003).

Nevertheless, in most bird species it seems that some **female cooperation** is necessary for *successful* copulation (Gowaty and Buschhaus 1998). Also, females can **control paternity** to a certain degree *after* copulation, at least in some species (Birkhead and Møller 1993; Pizzari et al. 2004). When the female has evolved the ability to prevent fertilization by sperm from particular males and extra-pair fertilizations still occur, this suggests a net benefit of extra-pair paternity to females. However, because such control is never perfect, and because males will be selected to exploit the “gaps” (Holland and Rice 1997), extra-pair offspring could be the result of fertilizations escaping cryptic female choice. In conclusion, the issue about who is in control and about whether females obtain a net benefit from extra-pair behaviour remains controversial.

Interestingly, a cost-benefit analysis of male extra-pair behaviour has rarely been made, probably because it is assumed that the benefits from siring additional young cared for by other males are overwhelming. However, a study on great tits (*Parus major*) that examined the net effect of extra-pair behaviour for individual males found that males that gained extra-pair young also had a higher than average probability to lose paternity in their nest (Figure 6a, Lubjuhn 2005). It is not necessarily true that paternity loss could have been avoided if those males would not have engaged in extra-pair copulations. Yet, if there is indeed a trade-off, males pursuing extra-pair copulations might not do better than those that guard their mate (i.e. alternative reproductive strategies with equal pay-off). In the great tit study this was not the case: the number of young gained in extra-pair nests more than compensated for the number of young lost in the social nest (Figure 6b).

*Figure 6 around here*

Up to now we have treated the male and female perspective separately to simplify the line of argument. However, it is important to realize that in reality these two viewpoints are merged. Every extra-pair copulation involves the reproductive interests of at least the copulating male and female, and the female’s social partner. Therefore, male *and* female costs and benefits inescapably come into play simultaneously and the behaviour of all “players” determines the adaptive value of the realized outcome (extra-pair offspring). Let us return to the superb fairy-wrens where females appear to seek extra-group copulations with particular males. Paternity analysis showed that satellite males were successful in securing on average one third of extra-group fertilizations by mimicking the behaviour of attractive males in a sort of reproductive parasitism (Cockburn et al. 2009). Thus, despite strong behavioural evidence for female “control”, males are obviously often able to evade this control. In the superb fairy-wren males do so inconspicuously, but in other species they resort to more overt behaviour such as harassing and coercing females. The selective effect in both sexes drives evolutionary changes in mating behaviour and both sexes will evolve adaptations to maximize their fitness payoff from mating interactions. The often very different costs and benefits from the male and female perspective outlined above emphasize the **sexual conflict** that is inherent in the evolution of extra-pair behaviour (Petrie and Kempenaers 1998; Snook 2001; Chapman et al. 2003; Westneat and Stewart 2003; Wedell et al. 2006).

### 3. Evolutionary Consequences of Extra-Pair Mating

#### 3.1. Overview

The occurrence of extra-pair paternity has a range of important evolutionary consequences, some of which have already been discussed above. We first provide a brief general overview of these consequences, and then discuss one of them in detail.

- (1) Selection on male and female **copulation behaviour**. Selection will favour males who develop behavioural strategies that allow them to maximize the chances to obtain extra-pair copulations. This could for example lead to selection on male display behaviour, or on sneaky behaviour in search of fertile females. Similarly, females may develop behavioural strategies that increase the probability to obtain extra-pair copulations from favoured males at peak fertility and that avoid copulations with unattractive males (see Westneat and Stewart 2003 for a review).
- (2) Selection on male **parental behaviour**. See Box 2 and 3.
- (3) Evolution of **paternity protection behaviour**., If males risk losing paternity either because other males intrude on their territory or because females leave the territory to visit other males, selection may favour paternity protection behaviour such as territory defence, close mate guarding, and frequent copulation during the period when their mates are fertile (see Birkhead and Møller 1992, chapters 7-9 for further information).
- (4) Selection on sperm production and sperm characteristics. Female birds can store sperm in special organs (sperm storage tubules) for a period of at least a week (Birkhead and Møller 1992, pp.60-64). This means that when females copulate with multiple males, sperm from different males will compete for the fertilization of the egg(s), a process known as **sperm competition**. This will lead to selection on male traits that improve their success in sperm competition, such as increased sperm production, increased sperm swimming speed and increased sperm longevity.
- (5) Selection on **sperm selection mechanisms**. If females benefit from having their offspring sired by a particular male, mechanisms may have evolved that increase the likelihood that the “right” sperm will fertilize the egg. This **cryptic female choice** is expected to be more important in species where females have less behavioural control over copulations, for example species where males have an intromittent organ and can force copulations on females (see Eberhard 2009 for a short and recent review on sperm competition and cryptic female choice).
- (6) Selection on **offspring behaviour**. If offspring in a brood are half-sibs rather than full-sibs, increased competition is expected, which may manifest itself in the loudness of begging or in aggression among offspring (for more information on relatedness and sibling competition see e.g. Royle et al. 1999; Kilner and Hinde 2008).

(7) Effects on the **intensity of sexual selection**. See next section.

## 3.2. Extra-Pair Paternity and Sexual Selection

### 3.2.1. *Variance in Mating Success is the Basis for Sexual Selection*

**Sexual selection** is selection acting on variation among individuals in their ability to obtain access to mating partners. The extent of this variation often differs considerably between males and females, most commonly males showing higher variance. Because variation provides the substrate for selection (Box 4), greater variance in mating and reproductive success generally causes males to experience stronger sexual selection than females. This is known as **Bateman's principle**.

Sex differences in the strength of sexual selection are the primary cause of many of the sex differences in behaviour and morphology that can be found in organisms. They can explain the evolution of conspicuous traits, such as ornamentation, weaponry or display behaviour in one sex and they may account for the particular expression of sex roles and mating systems in different species (Andersson 1994). Pronounced sexual dimorphism is thought to be a sign of a strong sex difference in the strength of sexual selection (Dale et al. 2007).

*Box 4 around here*

In a strictly monogamous species there is no variation in mate number and variation in offspring numbers is constrained to be equal for males and females. As a consequence, selection pressures on males and females are identical and there is little scope for sexual conflict. A priori, the evolution of **sexual dimorphism** and sex-specific roles is suppressed. In a strictly monogamous species one would therefore – at least theoretically – expect both sexes to exhibit similar levels of intrasexual competition for mates and intersexual mate choice. Because of the similarity in the intensity of sexual selection one would also expect that males and females are endowed with ornaments and armaments to the same degree.

However, in many apparently monogamous bird species males and females differ substantially in characteristics such as size, plumage colour, ornaments, song, etc. Prior to the discovery of extra-pair paternity, when birds were thought to raise their own genetic offspring, this presented a conundrum (Mock 1985; Møller and Birkhead 1994). Sexual dimorphism in monogamous species can sometimes be explained by a biased sex ratio (causing many males to obtain no mates) or by competition related to mate quality instead of mate number (Darwin 1871, pp. 221-222). However, such explanations should in principle apply equally to males and females. It thus remains difficult to see why female choice and male-male competition should be more important than male choice and competition among females. Extra-pair paternity allows a relaxation of the constraints imposed on sexual selection by strict monogamy. Could extra-pair paternity cause sex differences in sexual selection in socially monogamous birds and account for the observed sexual dimorphism?

## || Pictures

Male (left) and female (right) red-winged blackbirds (*Agelaius phoeniceus*) obviously differ in size and plumage colour. This species breeds in North and Central America and is socially polygynous. Successful males defend territories with up to 15 females, so it is assumed that higher variance in male compared to female reproductive success led to the evolution of sexually selected ornaments (e.g. red epaulets) in males, but not in females. Could extra-pair paternity act in a similar way as polygyny and enhance the strength of sexual selection in males, leading to sexual dimorphism also in socially monogamous species?

Photos Bruce E. Lyon

### 3.2.2. *Extra-Pair Paternity and Sexual Selection: Measurements*

#### *Realized and Apparent Variance in Mating Success*

Several studies have attempted to assess the role of extra-pair paternity for the sex difference in the strength of sexual selection by comparing standardized variances (Box 4) in two measurements of male reproductive success: (1) the reproductive success a male would have had without extra-pair paternity, that is, the number of young raised with the social mate (**apparent reproductive success**), and (2) the number of young a male actually sired in his and other males' nests (**realized reproductive success**). When extra-pair paternity contributes to the sex difference in sexual selection, variance in realized reproductive success should be larger than variance in apparent reproductive success (Gibbs et al. 1990; Mock and Fujioka 1990). This is because an increase in sexual selection on males through extra-pair paternity is only expected when some males can gain paternity at the cost of others (instead of males merely exchanging paternity). In order to affect sexual selection extra-pair paternity should thus increase the variation among males in their reproductive success, that is, the ratio  $I_{\text{realized}} / I_{\text{apparent}}$  should be larger than 1. The published studies that report this ratio have produced mixed results (Tables in Møller and Ninni 1998, Freeman-Gallant et al. 2005, Whittingham and Dunn 2005, and Albrecht et al. 2007). The interpretation is difficult because unassigned extra-pair sires can artificially inflate standardized variances of realized reproductive success (Freeman-Gallant et al. 2005). Comparisons of  $I_{\text{realized}} / I_{\text{apparent}}$  ratios between studies may therefore be of limited value.

#### *Fitness Components*

An alternative approach to estimate the effect of extra-pair paternity on the strength of sexual selection is based on variance in realized male reproductive success. This variance can be partitioned into a component due to extra-pair success, a component due to within-pair success, and a component due to the covariance between the two (Webster et al. 1995). Further partitioning allows accounting for the relative importance of mate number, mate quality as reflected by investment in reproduction (e.g. clutch size), and fertilization success (as well as their covariances) in producing each component. Figure 7 illustrates this method of **variance partitioning**. Based on this example, the effect of extra-pair paternity can now be assessed in three different ways.

*Figure 7 around here*

- (1) **Variance in extra-pair success** explains almost half (46%) of the total variance in male reproductive success. This shows that extra-pair paternity constitutes an important path through which sexual selection can act in this species.
- (2) The **covariance between extra-pair and within-pair success** is positive. This indicates that males that are successful as extra-pair sires also tend to be successful with their social mate. Thus, increased extra-pair success is not generally cancelled out by decreased paternity in the own nest. Rather, extra-pair paternity shifts offspring towards successful sires, thereby increasing the variance in male reproductive success and the opportunity for (sexual) selection on males.
- (3) **Variance in within-pair fertilization success** is also high (36% of total variance). This is variance among males in their ability to secure paternity in their own nest. When paternity loss constitutes an important part of the total variance in reproductive success, as is here the case, much of the observed opportunity for selection is mediated by extra-pair paternity.

Many studies have found at least one of these three indications for an effect of extra-pair paternity on the opportunity for selection (e.g. Webster et al. 1995; Weatherhead and Boag 1997; Kleven et al. 2006; Albrecht et al. 2007). In other studies evidence is equivocal or weak (Webster et al. 2001; Freeman-Gallant et al. 2005; Whittingham and Dunn 2005). Again, differences between populations and species are probably important and deserve further study. However, there are two caveats that should be kept in mind. First, there is no general agreement on the size of variance proportions needed to infer an important role of extra-pair paternity (e.g. compare Webster et al. 2001 with Whittingham and Dunn 2005). Second, in some studies estimates are highly inconsistent between years (Freeman-Gallant et al. 2005; Webster et al. 2007; see also Weatherhead and Boag 1997; Kleven et al. 2006). This indicates that estimates may not be representative of long-term selection pressures either because annual fluctuations are highly influential or because of the low level of confidence associated with one-year estimates of fitness components (cf. Griffith et al. 2002).

The rationale of using variance-based estimates is that they represent opportunity measurements. Thus these approaches rest on the assumption that the strength of sexual selection on males can be compared by calculating the **opportunity for selection  $I$**  (Box 4). It is important to remember here that the opportunity for selection is not a measurement of sexual selection itself.  $I$  only provides an upper limit to the strength of directional selection on any trait and thus also limits sexual selection. Sexual dimorphism however is thought to rest on a sex difference in the strength of sexual selection. The variance-based estimates presented above are not necessarily strongly associated with the effect of extra-pair paternity on this sex difference. For example, much of the variation in male reproductive success may stem from effects outside sexual selection and females may also experience strong sexual selection.

### *Bateman Gradients*

An alternative method to estimate the strength of sexual selection, the **Bateman gradient**, directly links mating and reproductive success (Box 5). Including this

measurement into analyses of sexual selection may add to the picture and provide more reliable information on the strength of sexual selection than variance-based estimates alone (Box 5; Jones et al. 2004, 2005; Mills et al. 2007; see also Bjork and Pitnick 2006).

*Box 5 around here*

In the context of extra-pair mating, Bateman gradients have potential to reveal the role of extra-pair paternity for creating a sex difference in sexual selection. In an otherwise monogamous system, extra-pair mating can create variation between individuals in the number of mates (copulation partners) within a season. We can then estimate the Bateman gradient for both sexes, reflecting the presence of variation in mate number in both sexes. We can further estimate the difference in the male and female Bateman gradient, which corresponds to the sex difference in sexual selection caused by extra-pair paternity.

Only few studies on birds have calculated Bateman gradients (Woolfenden et al. 2002; Webster et al. 2007; Krakauer 2008; Balenger et al. 2009). In a study of the splendid fairy-wren (*Malurus splendens*), a strong positive effect of extra-pair mates on male reproductive success has been found (Figure 8; Webster et al. 2007). This is further corroborated by variance partitioning, which showed that a high proportion of the total variance in male reproductive success (>30 %) is caused by variation in extra-pair success. Thus, in this study the Bateman gradient suggests that extra-pair paternity is an important source of sexual selection on males and might contribute to the sex difference in sexual selection. This could be the ultimate cause of the pronounced plumage dimorphism of splendid fairy-wrens: the body of breeding males is covered in different shades of lustrous blue while females are mostly brown. It could also be the reason why male splendid fairy-wrens exhibit rather extreme reproductive morphology (Tuttle et al. 1996) with large testes, large cloacal protuberances and huge numbers of stored sperm (up to 8.3 billion). Indeed, these are common characteristics of all Australian members of the fairy-wrens (genus *Malurus*), with the exception of the purple-crowned fairy-wren (*M. coronatus*), incidentally the only species with little sexual dimorphism and low levels of extra-pair paternity (Kingma et al. 2009).

*Figure 8 around here*

### **3.2.3. Extra-Pair Paternity and Sexual Selection: Correlates and Consequences**

Exaggeration of male traits such as plumage brightness, tail length or testes size is thought to be a sign of intense sexual selection on males. The estimates of sexual selection intensity from the studies mentioned above indicate that extra-pair paternity can sometimes help explain the presence of such traits in socially monogamous species. Extra-pair paternity probably has a stronger influence on sexual selection in species where it is common than in species where it is rare or absent. Based on this logic, comparative studies have tested for a correlation between the frequency of extra-pair paternity and indicators of sexual selection on males. Across species high levels of extra-pair paternity are associated with relatively larger testes and brighter plumage in males (Møller and Birkhead 1994; Møller and Briskie 1995), as well as

pronounced sexual dimorphism in plumage coloration (Møller and Birkhead 1994; Owens and Hartley 1998; Dunn et al. 2001), and in wing and tail length (Dunn et al. 2001). In many species sexual selection thus appears to operate through the path opened by extra-pair mating. Still, evolutionary effects of extra-pair paternity are less important than effects of the social mating system (i.e. dimorphism in polygynous and lekking species is often even more pronounced; Dunn et al. 2001). This is not surprising because social monogamy will tend to equalize selection on males and females as long as it is not completely annulled by extra-pair paternity, whereas in polygynous species many males may not obtain a single mate.

The fact that higher levels of extra-pair paternity can cause an increase in sexual selection on males beyond that observed in species with less infidelity has two important consequences. First, sexual selection on males via extra-pair copulations goes hand in hand with a potential for genetic benefits from extra-pair behaviour to females (see section 2.1.1.). Sexual selection on males through extra-pair mating is selection on heritable variation among males in their ability to obtain extra-pair paternity. As a result, the genetic constitution of extra-pair young will differ from that of within-pair young in fitness-relevant traits, at least for male offspring. Second, the effect of extra-pair paternity on the strength of sexual selection on males provides indirect information about the net effect of extra-pair behaviour on male fitness (section 2.3.). The estimates of the strength of selection mentioned above can be used to examine the balance between costs and benefits of male infidelity. When (a) additional mates lead to additional offspring (positive Bateman gradient), (b) extra-pair success positively covaries with within-pair success (analysis of fitness components), and (c) extra-pair paternity increases variance in male reproductive success (higher  $I_{\text{realized}} / I_{\text{apparent}}$  ratios), extra-pair fertilizations increase the success of certain males at the expense of others. Thus, an increase in the strength of sexual selection on males through extra-pair paternity is indicative of a net benefit of male extra-pair behaviour.

In summary, several studies have attempted to quantify the effect of extra-pair paternity on sexual selection by estimating selection strength or by comparing indicators of sexual selection. Some studies have found evidence for an important role of extra-pair paternity (e.g. Owens and Hartley 1998; Dolan et al. 2007), but some of the more recent studies caution against an overestimation (Dunn et al. 2001; Freeman-Gallant et al. 2005; Whittingham and Dunn 2005). Independent of quantification, the effect of extra-pair paternity on sexual selection in the context of social monogamy is of a fundamental nature. It releases the constraint of equal mate and offspring numbers for males and females. Thus extra-pair paternity generates greater plasticity in avian mating systems, which sets the stage for sexual conflict and for a far wider field of evolutionary processes than possible under the restrictions of genetic monogamy.

#### **4. Outlook**

In the sections above, we provided an overview of what is currently known about the causes and consequences of extra-pair behaviour in birds. As usual in science, new insights generate new questions and many older questions are still not fully answered.

Let us finish this chapter by sketching some of the problems that await to be tackled and some approaches that might be useful.

- As discussed in some detail (section 2.1.1) benefits of extra-pair behaviour to females remain controversial and are currently debated. There is a need for research in two directions here. First, studies that compare fitness-relevant traits of maternal half-sibs, should separate genetic and non-genetic (e.g. hatch order) effects. Such studies should also examine the influence of environmental factors on the relative performance of extra-pair young, for instance by comparing broods under various levels of environmental stress. This is necessary because fitness differences between maternal half-sibs may only reveal themselves under more stressful environmental conditions. Second, experiments should be performed whereby the fitness of females that are free to pursue extra-pair copulations is compared with the fitness of females that are forced to be monogamous. A comparable experimental design has been successfully used in a variety of other taxa to address the fitness benefits of polyandry for females (e.g. Tregenza and Wedell 1998; Fisher et al. 2006; Firman and Simmons 2008). Transferring it to birds in the wild – to obtain the most relevant fitness measures – is going to be quite a challenge, however.
- So far, most studies have focused on male quality and differences among males in explaining variation in paternity loss or gain. It appears interesting to extend this type of inquiry to females. How does female quality affect female extra-pair behaviour? Do females change their mating behaviour depending on age, or on their condition? Along similar lines, do females change their mating behaviour depending on variation in environmental stress?
- Many of the cost-benefit considerations we described above assume total behavioural flexibility of individuals. That is, we assume that an individual bird is able to freely adapt its behaviour so as to optimize its fitness in every feasible situation it might be confronted with during its lifetime. This is undoubtedly an overly adaptationist view. In fact, behaviour might not be this plastic. Research on (avian) personality shows that an individual's behaviour may be correlated over a wide range of different contexts, such as escape situations, object handling, exploration, social dominance or aggressiveness. This means that expressing a particular behaviour comes with a whole suite of other behaviours which may or may not be adaptive in the individual's environment. In mating system research the existence of a 'sexual personality' has not been explicitly considered, but first attempts have been made at linking variation in personality traits with variation in extra-pair behaviour (Van Oers et al. 2008, While et al. 2009b). Indeed, it might well be that an individual's propensity to form a strong or loose pair bond, to invest more in parental care or in courtship, to show a low or high sex drive, etc. are correlated characteristics that lead to variation in extra-pair behaviour. Newly developed methods from quantitative genetics now make it feasible to unravel the underlying genetic basis of these traits.
- Many behavioural ecologists that study extra-pair mating still focus exclusively on an individual's behaviour before and up to copulation. However, much insight can be gained from studying post-copulatory processes, including behaviour (e.g. sperm ejection; Pizzari and Birkhead 2000). In the arena of avian sperm

competition and cryptic female choice, where it is likely that outcomes are determined by intrinsic individual characteristics and that restricted flexibility is the rule rather than the exception, there is still much scope for discovery.

- Above, we mentioned the ongoing debate on whether extra-pair behaviour is male or female driven (section 2.3) and emphasized that the male and female side have to be considered simultaneously. One interesting challenge here is to pinpoint the antagonistic and synergistic evolutionary dynamics, that is, to answer the question when is it cooperation, when conflict?

The discovery of extra-pair behaviour in birds and the study of its causes and consequences would not have been possible without molecular techniques that allow reliable paternity assessment. However, studying paternity is not the same as studying behaviour, and the former has become easier than the latter. It is remarkable how little we still understand about how the pattern of paternity in a brood relates to the copulation behaviour of the female. The difficulties of studying behaviour in the wild are clear, but even in captive birds, few researchers have undertaken in-depth investigations of the link between copulation behaviour and paternity. Many of the issues discussed above would be much better understood if more was known about the behaviour. The challenge thus has changed from developing new molecular tools to developing new methods to study behaviour in the field in much more detail (as for example in Cockburn et al. 2009).

The study of extra-pair paternity in birds has revealed a plasticity in mating systems formerly unknown and produced much insight into the multitude of factors underlying these dynamics. Because birds have been studied for so long and in so much detail they offer the unique opportunity to tackle problems that go deep into the biology of the species and require much background knowledge. However, birds represent only a fraction of animal diversity. The findings on avian extra-pair paternity should be an incentive for students of other animal taxa to extend our understanding beyond birds.

## **Suggested Further Reading**

- Birkhead T, Møller A (1992) Sperm competition in birds: evolutionary causes and consequences. Academic Press, London.
- Jennions M, Petrie M (2000) Why do females mate multiply? A review of the genetic benefits. *Biol Rev* 75:21–64
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## Box 1 - Pair-living and parenting patterns

Pair-living or social monogamy is uncommon and unevenly distributed across the animal kingdom, but it does occur in a wide range of taxa among invertebrates (e.g. Lorenzi and Sella 2000; Lombardo et al. 2004; Baeza 2008; Beltran and Boissier 2009) and vertebrates (e.g. Sefc et al. 2008; Cohas and Allainé 2009; While et al. 2009a). Birds are unusual in that most avian species are socially monogamous (Bennett and Owens 2002, pp.79-82).

We define extra-pair behaviour as a special case of promiscuity where copulations occur with more mates than are included in the social mating system. How do behavioural ecologists know which individuals form a social pair? The male and female of a pair have social interactions that are linked to reproduction but go beyond what is required for the act of fertilization. These interactions lead to an association of pair members in space and time, in particular during the female's fertile period, that is not observed between unpaired individuals (Westneat et al. 1990). For example, in many birds members of a social pair typically engage in behaviours such as prolonged courtship, mate guarding, territory defence, nest building, incubation of the eggs, feeding or protecting the young, and so on. In birds, parenting patterns often reflect the social mating system (Bennett and Owens 2002, p.79) and in the majority of species social monogamy goes hand in hand with biparental care.

||picture

A male of the socially monogamous American robin (*Turdus migratorius*) feeding the offspring in his nest. Whether he sired those offspring is another issue.

**Photo Bruce E. Lyon**

Biparental care and hence social monogamy may be especially common in birds because avian eggs and offspring need considerable parental investment to survive (Thomson et al.1998, Tullberg 2002), and male birds can contribute substantially to all parental activities except egg production. Furthermore, it has been suggested that a high mortality cost of caring as compared to competing for mates will lead to selection favouring egalitarian sex roles and hence biparental care (Kokko and Jennions 2008). To understand this, we need to consider that different sex roles can cause sex-specific mortality, which may feedback on the availability of mates. Assume that sex roles have diverged a little bit so that females tend to care more than males and males are investing more in competing. Further sex role divergence may now be prevented if caring is the more costly activity. This is because females will become rarer as they suffer the higher risk of mortality due to caring, and the mating pool will become more strongly biased towards males. Hence, it will take deserting males longer to find another mate, and despite the higher mortality cost for caring than for competing, caring may become the better option. Irrespective of its ultimate causes, pair-living is especially dominant among birds and this makes them ideal for studying the causes and consequences of extra-pair behaviour.



## Box 2 - Multiple paternity and paternal care

It is characteristic for birds that males allocate their care to clutches in which other males may have fertilized some or all of the eggs. There is no empirical evidence that males can identify the extra-pair young and theory suggests that the evolution of kin recognition is unlikely in this context (Westneat et al. 1995; Kempenaers and Sheldon 1996; Pagel 1997; but see Johnstone 1997). Female extra-pair behaviour will then not only cause a direct reduction in a male's fitness (fewer offspring fathered), but will also lead to males spending part of their parental investment on unrelated young (Trivers 1972). Should males with reduced paternity – and hence reduced benefits from caring – reduce their care? Intuitively the answer seems “yes”, but in fact it depends on the behavioural options available to the male (Grafen 1980). Even when the payoff from paternal care is reduced, it may remain larger than the payoff from alternative behaviours, for instance when chances of survival or remating are remote (Clutton-Brock 1984; Kempenaers and Sheldon 1997). Thus, reduced care is only expected if reallocation to alternative forms of investment (i.e. ultimately to future broods) leads to greater fitness.

In general, changes in the level of extra-pair paternity can cause an **evolutionary response** in the care behaviour of all males or a **facultative response** in the care of individual males (Westneat and Sherman 1993). On an evolutionary timescale, a population-wide increase in female promiscuity reduces benefits from paternal care for males and increases mating opportunities outside the pair. The first effect alone will not cause selection for reduced male care because males will on average have similar paternity in future broods (Maynard Smith 1978, p. 178; Grafen 1980; Westneat and Sherman 1993), but due to the second effect – an increased probability of future mating – reduced paternity in a species should lead to a reduction in paternal care (Queller 1997; Houston and McNamara 2002).

On the individual level, a male that can assess his paternity in a brood should adjust his level of paternal care so as to maximize his fitness. Depending on the circumstances, he may achieve this by ignoring paternity loss, by reducing his care, or even by increasing his care (Kempenaers and Sheldon 1997; Whittingham and Dunn 2001; Holen and Johnstone 2007). It is not possible to identify a universally optimal male response to paternity loss. This is because (a) the effect of paternal care on the success of the brood may vary among species (Whittingham et al. 1992; Houston 1995), (b) not all males are equal, so that males differ in how their care decisions affect their prospects of survival and future matings (Westneat and Sherman 1993), and (c) the opportunity costs of male care relate to the care decisions of other individuals (Houston and McNamara 2002). For example, whether other males decide to desert or care will influence a male's extra-pair mating opportunities. It is thus a matter of some intricacy to determine how an individual male should optimally respond when he perceives paternity loss.

### Box 3 – Studying male facultative responses

In species with biparental care, selection can favour individual males that adjust their level of care to their (perceived) share of paternity (Box 2). Many studies have attempted to empirically test such facultative male responses using correlational or experimental approaches (Wright 1998; Whittingham and Dunn 2001; Sheldon 2002). Unfortunately, **correlations** between levels of male care and share of paternity are hard to interpret (Kempnaers and Sheldon 1997; Wright 1998; Sheldon 2002). The main issue is that young of unfaithful females may receive less paternal care than those of faithful females even without the existence of facultative male responses. This is because a third factor, such as male quality, territory quality, male condition, or male age, can cause a decrease both in male investment and in within-pair success. Most of these factors can be excluded by comparing successive breeding attempts of the same pairs in the same season, but even here alternative explanations are possible (Sheldon 2002, Figure 5).

**Experimental** approaches are more promising to test for a facultative male response (Kempnaers and Sheldon 1997; Sheldon 2002). However, here the difficulty is to ensure that the experimental treatment is effective in manipulating a male's perception of his paternity (Wright 1998). Studies that manipulated male certainty of paternity or perceived paternity (reviewed by Whittingham and Dunn 2001 and Sheldon 2002) provide some support (Arnqvist and Kirkpatrick 2005), though not unequivocal evidence (Sheldon 2002; Griffith 2007), for the existence of facultative male responses. Yet this does not mean that males that had their confidence of paternity experimentally reduced and invested less in the brood in response would ever have suffered paternity loss or that all males would have responded in this way. It is possible and often even expected that the males with the lowest risk of losing paternity suffer the highest opportunity costs of care and are selected to react strongest to paternity loss, and vice versa (Eliassen and Kokko 2008). The experimental studies can be seen as evidence for the existence of strong facultative responses at least in some males. These males could be mated to females that remain faithful, maybe also because of the risk of losing male care otherwise. Nevertheless, the females that are most strongly selected to have extra-pair young could well be the females whose social mates cannot provide a high amount of care *and* are selected to ignore paternity loss, because these males cannot improve their fitness otherwise. Thus, even if females that engage in extra-pair behaviour receive only a small amount of paternal care – as indicated by some observational studies – this does not imply that extra-pair behaviour comes with the cost of reduced male care for females that engage in it.

#### Box 4 - Fitness variance and the strength of selection

Fitness variance is caused by variation between individuals in reproductive success, which in turn can arise from variance in mating success. When fitness is completely heritable, directional selection causes a change in fitness from one generation to the next with a rate that is equal to the variance in fitness before selection (Fisher 1930, p.35). The traits that cause variation in fitness will change at a rate depending on their contribution to heritable fitness, but their rate of change can never exceed that of fitness itself. Hence, fitness variance places an upper bound on the change in any phenotypic trait from one generation to the next and can be used to measure the maximum strength of selection (Crow 1958; O'Donald 1970). For standardization, variance in *relative* fitness is compared, which is equivalent to dividing variance in (absolute) fitness by mean (absolute) fitness squared. This estimate is now independent of the particular study system and is called the **opportunity for selection  $I$**  (Arnold and Wade 1984). Because they are standardized, measurements of  $I$  are frequently used to compare the strength of selection between populations or species. However, this can be criticized for three main reasons. Measurements of  $I$  are (1) expected to increase with mean fitness values (Downhower et al. 1987; Ruzzante et al. 1996), and (2) expected to increase with sample size (Ruzzante et al. 1996). Furthermore, (3) measurements of  $I$  may not correlate with the strength of selection when the importance of random variance differs between the compared groups (Sutherland 1985a,b).

The (standardized) variance in fitness is only one of many possibilities to estimate inequality of fitness among individuals (Kokko et al. 1999; Fairbairn & Wilby 2001). Several alternative indices have been developed all of which behave differently with respect to changes in inequality (Kokko et al. 1999). Unfortunately, all of them suffer to some degree from the problems described above. The great advantage of estimating inequality by the opportunity for selection  $I$  is the close connection to selection theory, allowing a direct interpretation with regard to the evolutionary process (Jones et al. 2002, 2004).

### Box 5 - The Bateman gradient

The strength of selection on a particular trait depends on how fitness is affected by the trait in question. This can be formally estimated by regressing (relative) fitness on the phenotypic trait value and illustrated by plotting fitness against the trait value. Fitness can also covary with a trait due to selection on correlated traits (indirect selection). To remove these fitness effects the partial regression of relative fitness on the trait in question is used, which then estimates only direct selection on a trait. The **selection gradient  $\beta$**  is the corresponding partial regression coefficient (Lande 1979).

In the context of sexual selection we are interested in the trait “ability to obtain mates”. The selection gradient for this trait is called the **Bateman gradient** (Bateman 1984; Andersson & Iwasa 1996). It measures the association between the number of mates (phenotypic trait) and the number of offspring produced (fitness value), that is, it shows the influence of additional mates on reproductive success and is thus a direct measure of the strength of sexual selection. Furthermore, a combination of a positive male and a negative female Bateman gradient may be an indicator of sexual conflict over mating events. A negative Bateman gradient in females can result when additional matings are harmful to them (Levitan 2008).

In general, selection gradients provide an estimate of evolutionary change for given fitness and error variances. For example, different Bateman gradients (values of  $\beta$ ) for males and females imply a sex difference in the strength of sexual selection. This is true as long as the larger gradient is not associated with greater scatter (large error variance) or with smaller selection opportunity (small fitness variance), which generally applies for comparisons between the sexes. However, these assumptions need not hold for other comparisons. Furthermore, the size of  $\beta$  is specific to the particular situation in which it is measured (Arnold and Wade 1984; Andersson 1994, p.91-94). Therefore it is problematic to use  $\beta$  for comparisons of the strength of selection between traits, populations, and species. The opportunity for selection (Box 4) provides a standardized and comparable measure of the maximal strength of selection  $I$ . However, comparing estimates of  $I$  instead of  $\beta$  ignores some of the information contained in the Bateman gradient, which might be biologically meaningful (Jones et al. 2004, 2005; Mills et al. 2007).

## Figure legends

Figure 1. Patterns of extra-pair paternity in a population of tree swallows (*Tachycineta bicolor*). Each square represents a nestbox. The numbers inside each box refer to the number of extra-pair young and the total number of offspring in the brood. Arrows indicate extra-pair males that sired offspring in a particular nest and the number next to the arrow shows how many offspring they sired. The encircled birds on the right cared for a brood elsewhere, whereas the other three birds were unpaired “floaters” without their own brood. Nestboxes marked with the same colour belonged to one of four socially polygynous males. Reprinted with kind permission from Springer Science+Business Media: Behavioral Ecology & Sociobiology, Extra-pair paternity and the reproductive role of male floaters in the tree swallow (*Tachycineta bicolor*), 49, 2001, 254, Kempenaers B, Everding S, Bishop C, Boag P & Robertson RJ, Fig. 1.

Figure 2. The relationship between the frequency of extra-pair paternity and adult mortality rate. Each dot represents one species. Reprinted with permission from Royal Society Publishing; source: Fig 2a in Arnold KE & Owens IPF (2002), Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation, Proceedings of the Royal Society B, 269, page 1267.

Figure 3. Number of courtship gifts offered by male great grey shrikes (*Lanius excubitor*) to females in the context of within-pair copulations (open bars) or extra-pair copulations (filled bars). Handling time of hunting shrikes is longer for vertebrate prey (birds, voles, lizards) than for insects. Successful copulation attempts are associated with gifts of higher energy content. Reprinted from Animal Behaviour, 69, Tryjanowski P and Hromada M, Do males of the great grey shrike, *Lanius excubitor*, trade food for extrapair copulations?, Fig. 1, page 531, Copyright (2005), with permission from Elsevier.

Figure 4. Evidence for genetic benefits of extra-pair behaviour in blue tits (*Cyanistes caeruleus*; panel a and b on the left) and bluethroats (*Luscinia svecica*; panel c and d on the right).

*Top panels* (a,c): in both species extra-pair young (EPY) were more heterozygous than their within-pair half-sibs (WPY). In the blue tit this difference was found only when the extra-pair sires bred far away from the focal female (non-neighbours and non-locals in panel a).

*Bottom panels* (b,d): in the blue tit extra-pair sires (EP♂) that were close neighbours to the female were older (not shown) and larger than the males they cuckolded (WP♂; panel b). In the bluethroat, extra-pair offspring showed a stronger immune response (PHA test) than their within-pair half-sibs (panel d).

The two effects in the bluethroat (panel c and d) were independent from each other and both were present only when the extra-pair sire was a local male. Left panels: adapted from Fig. 1 by permission from Macmillan Publishers Ltd: Nature (Foerster et al. 2003, 425: 714-717), copyright (2003). Right panels: reprinted from Fig. 3 in Føssøy et al. (2008) Multiple genetic benefits of female promiscuity in a socially

monogamous passerine, *Evolution*, 62(1), 145-156, with permission from Wiley-Blackwell.

Figure 5. Paternity and paternal effort in three studies of the reed bunting (*Emberiza schoeniclus*) using the same study design. To exclude confounding factors, the relationship between the change in the level of extra-pair paternity and the change in male provisioning rate (feeds per hour per nestling) between two sequential broods of the same pair is considered. (a) UK population (Dixon et al. 1994). (b) Dutch population (Bouwman et al. 2005). (c) Swiss population (Suter et al. 2009). In (a) and (c) the negative correlation is significant, whereas in (b) there is no significant association (note that in (a) changes in provisioning are rather small in absolute terms). A significant relationship can be seen as evidence that individual males adjust their parental effort to their level of paternity in the nest. However, a similar pattern could arise when males trade off somatic effort (investment in survival) against mating and parental effort combined (Magrath and Komdeur 2003). This trade-off may vary for individual males over the course of a season. Males that invest more into survival early in the season will have lower paternity (low mating effort) in the first brood and care less (low parental effort) for this brood, whereas males that invest more into survival later in the season will have lower paternity and care less in the second brood. (a) Adapted from Fig. 2a in Dixon et al. (1994) by permission from Macmillan Publishers Ltd: *Nature* (371: 698-700), copyright (1994). (b) Reprinted from Fig. 1c in Bouwman et al., Male reed buntings do not adjust parental effort in relation to extrapair paternity, *Behavioral Ecology*, 2005, 16(3), 499-506, by permission from Oxford University Press and the International Society for Behavioral Ecology. (c) Reprinted from Fig. 3a in Suter et al., The cost of infidelity to female reed buntings, *Behavioral Ecology*, 2009, 20(3), 601–608, by permission from Oxford University Press and the International Society for Behavioral Ecology.

Figure 6. (a) Comparison of the proportion of broods containing extra-pair young in the great tit (*Parus major*). The proportion observed among the broods of 42 males identified as extra-pair sires is higher than the proportion expected based on the population mean. (b) Comparison of paternity loss (in own brood) and paternity gain (extra-pair offspring sired) for the same 42 males. Shown are mean and standard deviation.

Figure 7. Estimates of components of variance in reproductive success in male eastern kingbirds (*Tyrannus tyrannus*). Variance in total (T) male reproductive success (number of young) is partitioned into components due to within-pair (WP) success, extra-pair (EP) success, and the covariance between the two.  $\text{Var}(T) = \text{Var}(W) + \text{Var}(E) + 2 \cdot \text{Cov}(WP, EP)$ ; see Webster et al. (1995). Variance in within- and extra-pair success is further partitioned into components due to mate number, mate quality (clutch size), and fertilization success (proportion of clutch sired). Shown are the percentages of the total variance explained by each component. Terms indicative of the importance of extra-pair paternity for variance in male reproductive success are highlighted. Data from Table 4 in Dolan et al. (2007).

Figure 8. Bateman gradient illustrating the relationship between number of mates and reproductive success in the splendid fairy-wren (*Malurus splendens*). Male reproductive success is strongly correlated with mate number ( $F_{1,159}=261.7$ ,  $R^2=0.62$ ,  $P<0.0001$ ). This is a cooperatively breeding socially monogamous species where auxiliary males associate with a breeding pair and help raising the offspring. Auxiliary males routinely sire young in their own group. Therefore only the reproductive success of breeding males is shown here. Breeding males can obtain multiple mates only through extra-pair copulations. Lifetime reproductive success was recorded, but success per season is shown to remove the effect of differences in lifespan. Reprinted from Fig. 2 in Webster et al. (2007) Promiscuity drives sexual selection in a socially monogamous bird, *Evolution*, 61(9), 2205-2211, with permission from Wiley-Blackwell.

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