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## The illusion of monogamy

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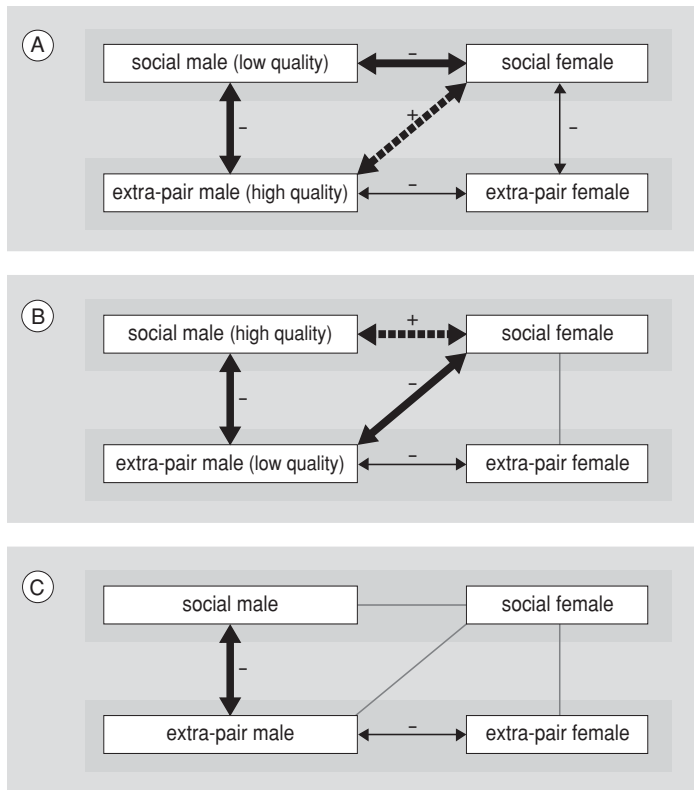
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## General discussion

“Where one sex invests considerably more than the other, members of the latter will compete among themselves to mate with members of the former. Where investment is equal, sexual selection should operate similarly on the two sexes.” (p173; Trivers 1972). In accordance with these ideas, Trivers (1972) was the first to propose ‘mixed reproductive strategies’ regarding the mating behaviour for both males and females. If male parental investment is lower than female parental investment, males should attempt to fertilise additional females, whereas females should not only select their partner for the quality of his territory or paternal care, but also for the quality of his genes. We thus expect conflicts of interests between individuals. There are four individuals involved in extra-pair copulations: the social pair male and female, and the extra-pair male and his mate (‘extra-pair female’). Figure 9.1 shows three scenarios how potential conflicts of interests may act (Petrie & Kempenaers 1998). There will always be a strong conflict between the males, since they directly compete over the paternity of offspring (figure 9.1A,B,C). For females different scenarios are possible, as they can gain (figure 9.1A), lose (figure 9.1B), or suffer no fitness consequences from extra-pair copulations (EPCs; figure 9.1C). In figure 9.1A, the female is paired to a low quality male, and she would gain genetic benefits for her offspring by copulating with a high quality extra-pair male. However, when the female is paired to a high quality male, she would not benefit from EPCs with a low quality extra-pair male (figure 9.1B). In figure 9.1C, only male behaviour drives EPCs, and females do not gain benefits or suffer costs from EPP. Since male extra-pair mating behaviour is likely to conflict with paternal care, a conflict between the extra-pair male and his partner is expected (figure 9.1A,B,C; Eens & Pinxten 1995) and between the social and extra-pair female (figure 9.1A; Mays & Hopper 2004).

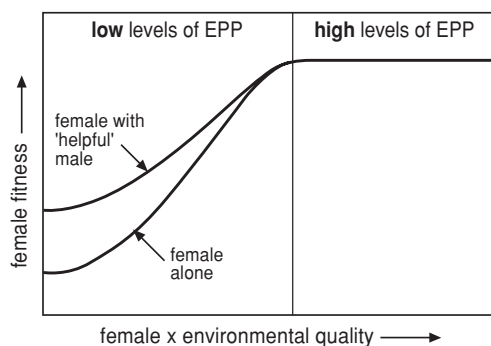
Gowaty (1996) launched a theory of coevolutionary selective pressures to explain the occurrence of and variation in EPP, acting on males for control of female extra-pair mating behaviour, and on females for resisting male efforts to control them. Under the hypothetical condition that females are free to choose the best male available, they are expected to be socially and genetically monogamous. However, females are likely to be prevented from making the best choice, for instance due to an inability to perfectly judge male quality, female competition for the best mates, or having to choose between different male qualities, such as his potential to provide parental care and the quality of his genes. While assuming that females (i) at least partially control EPCs, (ii) gain genetic benefits through EPP and (iii) run the risk of losing paternal care when engaging in EPCs, the ‘constrained female hypothesis’ posits that within species, a female’s options for extra-pair mating behaviour, i.e. to resist the attempts of male control, depends on her own quality and on the quality of the environment she is in (Gowaty 1996). In figure 9.2, the theoretical effects of the interaction between female and environmental quality on female fitness are described when females are ‘helped’ by males



**Figure 9.1.** Interactions between individuals involved in extra-pair copulations. Members of a pair are enclosed in a box. Arrows indicate conflicts of interest (solid), or interactions where both individuals would benefit (dashed). Dashed lines indicate no conflict of interest but also no benefit. The strength of the interaction is indicated by the width of the arrows. In these scenarios, there is always a strong conflict over paternity between social and extra-pair male, while the social female may (A) gain benefits from EPCs, (B) suffer costs through EPCs, or (C) not gain or lose from EPCs. In (A) and (B) extra-pair mating behaviour may be both male and female driven, whereas in (C) only male behaviour drives EPCs. For a more detailed description see text.

(e.g. paternal care for the offspring) and when they are not. When the combination of female intrinsic quality and environmental quality is sufficiently high, additional male help may not increase female reproductive success any further. On the other hand when the combination of female intrinsic quality and environmental quality is lower, females fitness may decrease when male help is withdrawn, e.g. as a retaliation for female extra-pair mating behaviour (figure 9.2).

In this thesis we investigated the variation in levels of EPP in a population of reed buntings, a socially monogamous passerine with levels of EPP which are among the highest found so far (Griffith *et al.* 2002). In this final discussion, I will



**Figure 9.2.** The constrained female hypothesis predicts genetic mating patterns of socially monogamous females. The upper curve describes how female fitness varies when females are ‘helped’ by males and when they are not. The curves converge for high female x environmental quality because female fitness is limited by intrinsic variation in females. This model posits that females of poorer quality or in less permissive environments are more vulnerable to manipulation by male helpful coercion than females of higher quality or those in highly permissive environments. The model predicts relative levels of extra-pair paternity (EPP) for females x environments below and above the point at which the curves converge. Modified from Gowaty (1996).

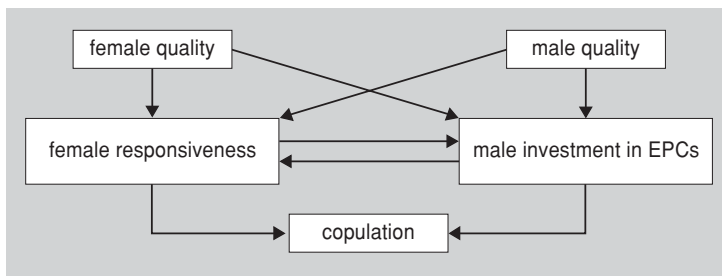
place our results in the framework of the ‘constrained female hypothesis’ (Gowaty 1996), and discuss whether this hypothesis offers a likely explanation for the variation in EPP observed between individuals. First I will discuss whether reed buntings meet the assumptions required for the constrained female hypothesis to act, and second I will consider the validity of the predictions. Furthermore, I will discuss our results in relation to the scenario where male behaviour drives EPCs (figure 9.1C). Wherever relevant I will draw comparisons with other recent work on this topic.

## Constrained female hypothesis

### *Assumption 1: are EPCs female driven?*

There is obviously a conflict between the social male and the extra-pair male over paternity. Hence, early literature on sperm competition has focussed on male-male competition (reviewed in Lifjeld *et al.* 1994). Over the past ten years, more attention has been directed to the role of females, even to the extent that there is currently a general consensus that all adaptive explanations for EPP should focus on female fitness (Westneat & Stewart 2003). This emphasis may however lead to important interactions between the sexes being overlooked (Westneat & Stewart 2003). Generally, EPCs are considered to be at least partly female driven. Females

have been shown to actively participate in EPCs through making forays, soliciting EPCs, or selectively rejecting EPC attempts by extra-pair males (reviewed in Westneat & Stewart 2003). In most species, males will make forays into female territories and attempt EPCs (Westneat & Stewart 2003), while females will have to evaluate these attempts, and subsequently accept or resist (Forstmeier 2004). Both male investment in EPCs and female responsiveness to EPCs may be influenced by the quality of the other sex, or by the interaction between responsiveness and investment in EPCs (figure 9.3). For instance, males of certain quality may be able to invest more in EPCs, but the degree of investment may also depend on female quality or her responsiveness. If EPCs are under total female control, copulations are expected to occur following the left pathway with no interactions with male quality or investment, whereas under total male control, copulations will occur following the right pathway (figure 9.3).



**Figure 9.3.** Interactions between males and females possibly leading to the occurrence of extra-pair copulations (EPCs). Whether EPCs occur depends on male investment in EPCs and on the readiness of the female to copulate (responsiveness). Male EPC investment is likely to depend on the quality of the male, but may also be influenced by female quality and responsiveness. On the other hand, female responsiveness may depend on her own quality, the extra-pair male's quality and his investment in EPCs. Modified from Forstmeier (2004).

In different reed bunting populations, males have been observed intruding in a fertile female's territory (chapter 8), whereas female extra-pair mating forays were reported only in a Polish population of reed buntings (Buchanan 2001). Females may have performed covert forays in all reed bunting populations studied, as was found through using radio telemetry in superb fairy wrens (*Malurus cyaneus*; Double & Cockburn 2000) and hooded warblers (*Wilsonia citrina*; Neudorf *et al.* 1997). EPCs are seldom seen in reed buntings (chapter 8), and therefore it is unknown whether female reed buntings selectively accept and reject EPC solicitations. Generally, since female reed bunting behaviour is secretive, we cannot exclude female control of EPP (Westneat & Stewart 2003).

Patterns of EPP as a result of interactions between individual reed buntings do not provide conclusive results. Males in many species attempt to protect their paternity by closely following their mate, to either prevent her from seeking EPCs (Lifjeld *et al.* 1994), or to prevent other males from gaining EPCs (Beecher & Beecher 1979). Whether or not the female has an active role in seeking EPCs will largely determine the effectiveness of male mate guarding behaviour with regard to preventing cuckoldry (Lifjeld *et al.* 1994). Mate guarding was found to be an effective paternity guard in Norwegian reed buntings, and thus EPCs were suggested to be a result of male, and not female forays (Marthinsen *et al.* 2005). However, this still does allow females to be selective in their choice. In the Dutch population we found that higher levels of EPP occur when the minimum temperature during the female fertile period was low (chapter 7). We suggested this to be a consequence of mate guarding behaviour being restricted, thus allowing EPCs to occur more easily. However, no distinction could be made whether the increase in EPP is a result of increased female or extra-pair male investment.

Breeding density and synchrony may limit the number of potential extra-pair partners available, and thus influence whether individuals engage in extra-pair mating behaviour (Westneat & Sherman 1997; Møller & Ninni 1998). In the tree swallow (*Tachycineta bicolor*), a socially monogamous species with levels of EPP comparable to reed buntings, females control the occurrence of EPCs (Lifjeld & Robertson 1992). In this species no effect of breeding density nor synchrony on the level of EPP was found, for which the authors provide an explanation based on female control of EPCs (Dunn *et al.* 1994; Kempenaers *et al.* 1999; Conrad *et al.* 2001). Female tree swallows appear to actively seek their extra-pair partners outside the study area (only 20% of extra-pair offspring was assigned to a known male), and thus are not likely to be limited by the number of copulation partners. The absence of a relationship between breeding density and synchrony and levels of EPP in the reed bunting (chapter 6), may thus be explained by female control over whom they mate with. However, in reed buntings, extra-pair sires are mainly close neighbours (chapter 2). Female control of EPCs does not always obviate an association between breeding density and EPP. Thus, in Bullock's orioles (*Icterus galbula bullockii*), Richardson & Burke (2001) reported that levels of EPP increased with breeding densities, despite the fact that females actively seek and solicit EPCs.

Based on the general assumption that female participation is necessary for a copulation to be successful (Birkhead & Møller 1992), at this moment we can merely state that it is likely that female reed buntings exercise some control over whom they mate with. Detailed behavioural observations are needed to determine to what extent females control extra-pair mating behaviour in the reed bunting.



*Assumption 2: do females gain genetic benefits from EPP?*

Using three approaches, we attempted to determine whether the patterns of EPP in our population matched the predictions of the hypothesis that female reed buntings gained genetic benefits for their offspring. First, we investigated the distribution of EPP among broods and individual females (chapter 2). We found that more broods than expected contained no EPP and that more broods than expected were sired by a single male, which was in agreement with the predictions of the genetic benefit hypothesis. Second, we determined whether male characteristics were related to cuckoldry risk and success in siring extra-pair offspring (chapter 3). We found that older males were more successful in protecting paternity in their own brood as well as in siring offspring in other broods. Although females may gain genetic benefits from engaging in EPCs with older males, this is not necessarily the case (BOX 1).

Third, if females gain genetic benefits for their offspring, extra-pair offspring are expected to be of a higher quality than within-pair offspring. Of all measured characteristics (i.e. biometrics, heterozygosity and survival probabilities), we found that only tarsus length differed between extra-pair young and within-pair young, in that extra-pair young had longer tarsi (chapter 3). Increased growth rate resulting in longer tarsi may be a result of superior paternal genes. However, at an early age (< 4 days old), extra-pair offspring were heavier than their maternal half-siblings, whereas this difference disappeared at a later age ( $\pm$  7 days old). Since differences in mass at an early age may indicate differences in hatching time (Slagsvold 1986), we suggest that extra-pair offspring have longer tarsi, simply because they hatch earlier (chapter 3). Hatching early may provide fitness benefits compared to hatching late (Krebs 1999 and references therein), and it may thus be an adaptive strategy for females and extra-pair males to bias extra-pair offspring towards eggs early in the laying sequence.

Fitness benefits may only be revealed on a long-term basis. Due to the low recruitment rates of reed bunting offspring, we have only been able to measure short-term benefits, and thus have not been able to test the genetic benefits hypothesis rigorously. Although we did not find any direct evidence of increased fitness for extra-pair offspring, at this moment we cannot reject this hypothesis. To date, only one study has managed to measure reproductive success of offspring; in coal tits (*Parus ater*), extra-pair offspring did not have a higher recruitment rate, nor did they produce more fledglings or have a lower risk of cuckoldry in their first year of breeding than within-pair offspring (Schmoll *et al.* 2003). However, this study was likewise unable to determine whether extra-pair offspring survived better or were more successful in gaining extra-pair fertilisations.

Variations in differences between half-siblings have been found between populations of the same species. In a Belgian population of blue tits (*Parus caeruleus*), strong support was found for females gaining good genes for their

offspring through EPCs (Kempnaers *et al.* 1992; Kempnaers *et al.* 1997). Successful males were older, had longer tarsi, sang longer songs and survived better, while extra-pair offspring were more likely to survive to fledging. In an Austrian population of blue tits, females appeared to gain compatible genes for their offspring through EPCs, possibly in addition to good genes (Foerster *et al.* 2003). Extra-pair offspring sired by non-local males were significantly more heterozygous than their maternal half-siblings, while this was not the case for extra-pair offspring sired by neighbouring males. These neighbouring males were older and larger than the cuckolded male, suggesting females may acquire good genes through mating with these males, as was found in the Belgian population. In three Mediterranean populations of blue tits, no differences in size, age, survival or relatedness with the female between successful and unsuccessful males were found (Charmantier *et al.* 2004), which suggests that genetic benefits through good genes or genetic compatibility are absent. However, survival to fledging was higher for extra-pair offspring than for their half-sibs (Charmantier *et al.* 2004), which in turn does suggest that females gained genetic benefits. In contrast to these populations, in a Norwegian population of blue tits, no evidence for genetic benefits was found (Krokene *et al.* 1998). EPP was randomly distributed among broods, there was no difference in morphology, age or survival between successful and nonsuccessful males, and extra-pair offspring did not differ from their half-siblings in growth rate, fledging mass or survival. The patterns of EPP in this population were consistent with the fertility insurance hypothesis.

Although differences between half-siblings are absent in some species, populations or years, they may still exist under different environmental circumstances (Schmoll *et al.* 2003). Genetic benefits, which are generally assumed to be small (Møller & Alatalo 1999), may only be detectable under relatively poor environmental conditions. An experimental approach, in which environmental conditions are selectively made more stressful (i.e. by brood size manipulations), may help clarify the environmental context dependence of the performance of 'good genes' (Schmoll *et al.* 2003).

### *Assumption 3: do females risk losing male assistance?*

Generally it is assumed that the largest cost of EPP to females is reduction in paternal effort (Birkhead & Møller 1992). However, so far little support has been found for such costs of EPP to females. Only a few studies found evidence that with decreased paternity, males reduce their provisioning rates to nestlings (Burke *et al.* 1989; Sheldon & Ellegren 1998; Lifjeld & Dunn 2001b) or their degree of nest defence (Weatherhead *et al.* 1994), whereas many others found no relation between paternal care and paternity (reviewed in Whittingham *et al.* 1992). In the reed bunting, conflicting results were found with respect to the adjustment of parental care in relation to paternity. In an English population, males reduced their

feeding rates to broods when their paternity was reduced (Dixon *et al.* 1994), whereas no relation was found between paternal feeding rates and paternity in our Dutch population (chapter 4). Despite this difference in the costs of EPP to females between the populations, levels of EPP were similar (chapters 4 and 8). However, male reed buntings from the English population did not decrease their feeding rates to a large extent, since even when paternity decreased by 100% (i.e. from full paternity to no paternity at all), males reduced their paternal feeding rate only by 4% (chapter 4). Hence, the risk of losing male care did not appear to be large in either population and is not expected to affect female decisions with respect to engaging in EPCs. However, both male and female provide care to fledglings after leaving the nest (Cramp & Perrins 1994; pers.obs.), but the male provides the largest share of care (Cramp & Perrins 1994). The length of post-fledging care is not exactly known, but fledglings are expected to receive parental care up to approximately 20 days after leaving the nest (Cramp & Perrins 1994). The relation between a male's parental care to fledglings and his level of paternity has not yet been investigated in the reed bunting. During this period of post-fledging care, female reed buntings may still suffer the cost of reduced paternal care.

Some support for this third assumption was found in the dusky warbler (*Phylloscopus fuscatus*): females breeding late in the season, that do not expect to receive male assistance, were more likely to have EPP in their broods than females that did expect to receive male assistance (Forstmeier 2003). Other support was found in an interspecies comparison: in species where male care was essential for the survival of the offspring, the observed level of EPP was low, whereas in species where females were able to raise a brood without male help, the observed level of EPP was relatively high (Birkhead & Møller 1996).

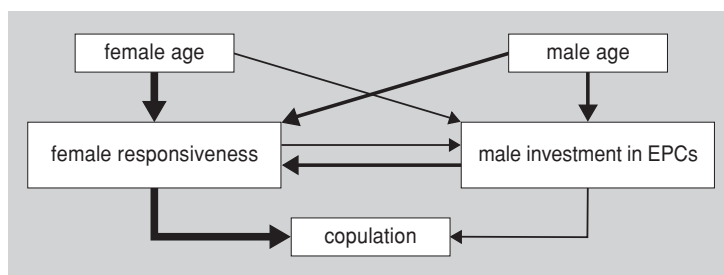
*Prediction: 'high female x environmental quality' leads to high levels of EPP*

Gowaty's 'constrained female hypothesis' predicts that high quality females, or females living in high quality environments, are more likely to have high levels of EPP in their broods, since they will not suffer from a decrease in male help (figure 9.2; Gowaty 1996). Individual differences in female extra-pair behaviour may thus be explained by (i) the intrinsic ability of females to raise offspring without male help, and (ii) food availability, which may facilitate female care without male help. These possible explanations are discussed below and summarised in table 9.1.

We found that with an increase in female age, the levels of EPP in the brood tended to increase (chapter 5). More specifically, we found that when mated to a young male, old females had higher levels of EPP in their broods than young females, whereas this was not the case when mated to an old partner (chapter 5). These results suggest that female responsiveness to EPCs may not be influenced by male quality or investment alone, but also by female age (figure 9.4). With age, individuals often increase their reproductive success due to an increase in breeding

**Table 9.1.** Summary of the assumptions and predictions posited by the ‘constrained female hypothesis’ (Gowaty 1996) and whether these are met in our study of the reed bunting. ‘+’ indicates that support was found in the reed bunting, while ‘-’ indicates that the issue remains unresolved.

‘Constrained female hypothesis’	Reed bunting
<b>Assumptions:</b>	
EPCs are female driven	-
Females gain genetic benefits	-
Females risk losing male help	-
<b>Predictions:</b>	
High quality females have high levels of EPP	+
High quality environments give rise to high levels of EPP	-



**Figure 9.4.** Interactions between males and females possibly leading to the occurrence of extra-pair copulations (EPCs). Female responsiveness to EPCs is not only determined by male age or male investment, but also by her own age. The width of the arrows indicate the strength of the effect. For a more detailed description see text. Modified from Forstmeier (2004).

experience (Saether 1990). Hence, female ability to raise offspring without male help may increase with age, allowing an increase in levels of EPP. An increase of the levels of EPP with female age was also found in coal tits (*Parus ater*; Dietrich *et al.* 2004) and, though non-significantly, in tree swallows (*Tachycineta bicolor*; Kempnaers *et al.* 1999) and pied flycatchers (*Ficedula hypoleuca*; Ratti *et al.* 2001). As a result of differences in the depth of their bill, female dusky warblers (*Phylloscopus fuscatus*) differed in their ability to collect large prey items and hence in their ability to raise a brood without male help (Forstmeier *et al.* 2001). However, females differing in bill morphology or age did not differ in the level of EPP in their broods (Forstmeier 2003).

Females may not require male assistance in raising offspring if the food availability is high enough, and thus females with good quality territories are expected to accept higher levels of EPP in their broods. Approximately half of all reed bunting foraging trips during nestling care are made to neutral grounds (chapter 8), and thus food availability in the territory is not an appropriate measure. Support was found in serins (*Serinus serinus*), where levels of EPP were higher in territories with high food availability (Hoi-Leitner *et al.* 1999). In contrast, in house sparrow broods (*Passer domesticus*) levels of EPP were lower when the social parents were food-supplemented (Vaclav *et al.* 2003). The time budget of especially the female house sparrow was affected by the availability of additional food. With extra food, females spent more time at the nest, resulting in partners being together for a longer period of time and consequently lower levels of EPP in the brood (Vaclav *et al.* 2003). Similarly, lower levels of EPP were found in broods of food-supplemented red-winged blackbirds (*Agelaius phoeniceus*; Westneat 1994). However, in this species, males, but not females, spent more time on their territories when extra food was available. As EPCs only occurred on the female's territory, the increased presence of the social male on the territory allowed him to prevent more EPCs (Westneat 1994). No effect of variation in food availability was found on the levels of EPP in the dusky warbler (Forstmeier 2003).

To conclude, the assumptions of the constrained female hypothesis were not all met in the reed bunting, since we did not find evidence that EPCs are female-driven, that females gain genetic benefits through EPCs, or that females suffer large costs in terms of decreased paternal care when engaging in EPCs. Nevertheless, we found some support for the constrained female hypothesis, since when paired to a young partner, old female reed buntings had higher levels of EPP in their broods than young females. However, this does not necessarily mean that older females can afford to seek EPCs because they are better able to raise offspring without male assistance. Instead, when assuming that females do actively seek EPCs, older females may have become more choosy when selecting their extra-pair partner, or alternatively, have increased their experience in circumventing their partner's mate guarding (chapter 5).

## Male driven EPCs

Through EPFs, males gain obvious benefits in terms of increased reproductive success, often without the additional cost of providing paternal care. The gains through EPFs are generally larger than the losses in their own broods (Yezerinac *et al.* 1995; Webster *et al.* 2001). Reed bunting males that gained EPFs produced 2.8 times as many offspring compared to males that did not gain EPFs. Realised reproductive gain may be small due to high predation rates, but males may salvage

some reproductive success through siring offspring in different nests (Perreault *et al.* 1997). Since we used nest protection techniques during most of our study, male reproductive success cannot be related to natural predation rates. Male reed buntings did not gain more EPFs following a predated nest than following a fledged nest (chapter 6). However, such a bet-hedging strategy may be followed by all males and may not necessarily be induced by a predation event. We might imagine that in species where the risk of predation is particularly high, there would be strong selective advantage for those males that manage to sire young in a variety of nests, thus spreading the risk of total failure. Interestingly, when comparing six different ground or near ground nesting species within the family of Fringillidae, we indeed found that high predation rates were associated with high levels of EPP (table 9.2; figure 9.5). However, large variations in levels of EPP and nest predation rates may be found between populations, and since in most cases both types of data were not collected in the same population, the results must be interpreted with care. An inter-species comparison relating nest predation risk to levels of EPP may explain variation in EPP between species, but so far we are not aware of any study including this variable in their analysis.

Egg-dumping rarely occurs in reed buntings (chapter 2) and thus a female bet-hedging strategy to compensate for predation risk is not likely. Possibly females do not gain any benefits through engaging in EPCs, but also do not suffer any costs, in which case a male bet-hedging strategy could be the sole driving force behind EPCs (figure 9.1C). Previously in this chapter we have discussed that we have not measured any large costs (i.e. reduced paternal care) or benefits (genetic benefits for offspring) of EPP to female reed buntings. Although at this time we cannot exclude that there are costs and benefits connected to EPP, it may be rewarding to further investigate the possibility that male reed buntings determine extra-pair mating behaviour as a response to high levels of predation.

**Table 9.2.** Relation between the percentage of offspring that result from extra-pair paternity (“%EPP”) and the percentage of nests that are predated (“% predation”) in six related ground or near ground nesting species belonging to the family of Fringillidae. Sample sizes are shown in brackets.

Species	% EPP	% predation
Reed bunting <i>Emberiza schoeniclus</i> (Es)	46% (1468) <sup>1</sup>	63% (435) <sup>2</sup>
Yellowhammer <i>Emberiza citrinella</i> (Ec)	37% (123) <sup>3</sup>	48% (845) <sup>4</sup>
Indigo bunting <i>Passerina cyanea</i> (Pc)	35% (63) <sup>5</sup>	57% (46) <sup>6</sup>
Savannah sparrow <i>Passerculus sandwichensis</i> (Ps)	23% (160) <sup>7</sup>	35% (266) <sup>8</sup>
Song sparrow <i>Melospiza melodia</i> (Mm)	10% (38) <sup>9</sup>	29% (140) <sup>10</sup>
Corn bunting <i>Miliaria calandra</i> (Mc)	4% (44) <sup>11</sup>	19% (74) <sup>12</sup>

<sup>1</sup> Chapter 8

<sup>2</sup> Chapter 2; Crick *et al.* 1994

<sup>3</sup> Sundberg & Dixon 1996

<sup>4</sup> Crick *et al.* 1994; Stoate & Szczur 2001

<sup>5</sup> Westneat 1990

<sup>6</sup> Thompson *et al.* 1999

<sup>7</sup> Freeman-Gallant 1996

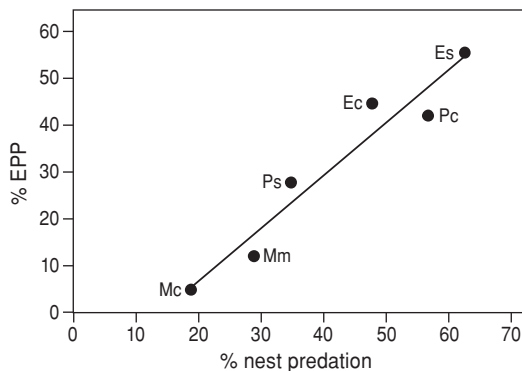
<sup>8</sup> Wheelwright *et al.* 1997

<sup>9</sup> Smith & Zach 1979; Major & Barber 2004

<sup>10</sup> Larison *et al.* 2001

<sup>11</sup> Hartley *et al.* 1993

<sup>12</sup> Hartley & Shepherd 1994; Crick *et al.* 1994



**Figure 9.5.** Correlation between the percentage of offspring that results from extra-pair paternity (“%EPP”) and the percentage of nests that are predated (“% nest predation”) in six closely related Fringillidae species ( $r_s = 0.94$ ,  $n = 6$ ,  $p = 0.005$ ). Sample sizes, explanations to the abbreviations and references to the different species are shown in table 9.2.

**BOX 2: Why are older males more successful in gaining within and extra-pair fertilisations?**

The high fertilisation success of old males, both in their own and in other broods, may be determined by several mechanisms, which are not mutually exclusive. Since active female choice is not a prerequisite for gaining viability genes for offspring, the first three mechanisms described below may allow extra-pair offspring to be genetically superior to within-pair offspring (Jennions & Petrie 2000). If females gain direct benefits for themselves rather than genetic benefits for their offspring (# 4; see below), no differences between within- and extra-pair offspring are expected.

**1- Female choice for high quality males**

Females may actively choose to copulate with older males, as is suggested for Bullock's orioles (*Icterus galbula bullockii*; Richardson & Burke 1999). Older males will on average be of higher quality than younger males, as they have shown to be able to survive longer (Trivers 1972; Manning 1985; Kokko & Lindstrom 1996; Kokko 1998; but see Hansen & Price 1995). If females seek viability genes, they may benefit from selecting older males. We found that older males have an increased song output (chapter 3), which may be used to attract females for EPCs. Female responsiveness may thus be influenced by male age, reflecting male quality, but also by male song output (figure box 2.1A).

**2- Male experience**

Older males may be more persistent or better able to exploit EPC opportunities, as was suggested for red-winged blackbirds (Weatherhead & Boag 1995). More experience due to ageing generally increases success, for instance in breeding (Saether 1990), thus experience can also be expected to affect success in gaining EPCs. Aggression, persistence and frequent intrusions by extra-pair males may increase female participation in EPCs, simply as a response to higher costs of resistance (Dickinson 2001; figure box 2.1B, following pathway 'A'). However, if females generally resist all extra-pair males, they will eventually copulate with males that are persistent or good at forcing copulations (Westneat *et al.* 1990; figure box 2.1B, following pathway 'B'). These traits may then be passed on to the next generation, leading to a higher fitness and thus in support of the good genes hypothesis.



### 3- More sperm

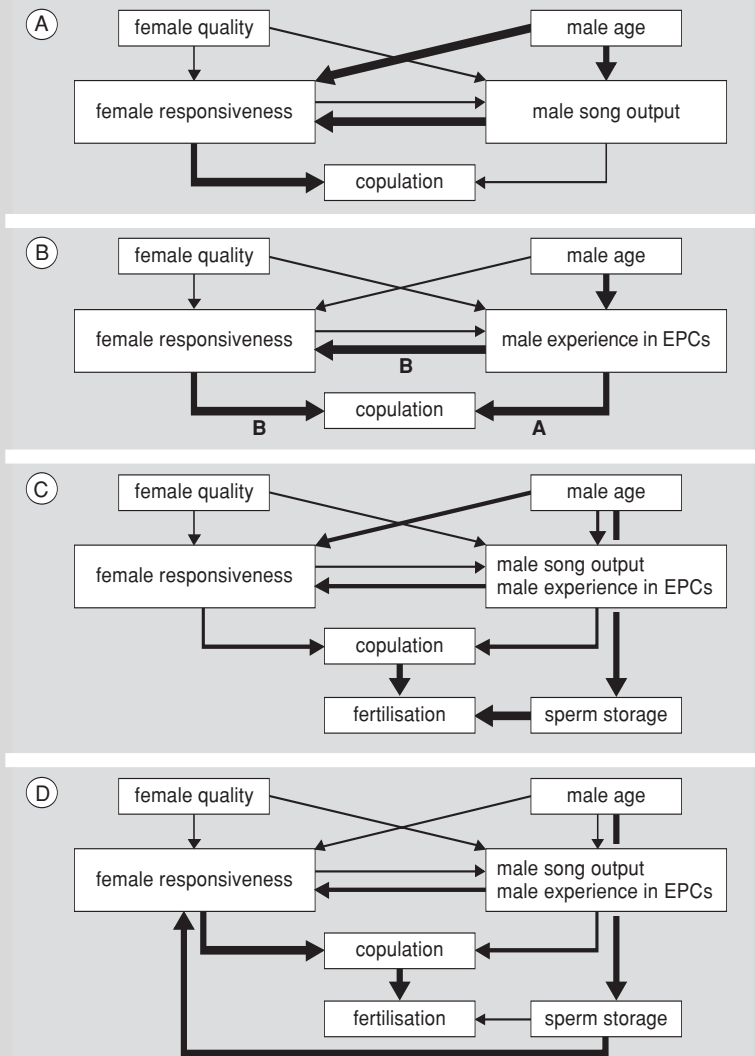
Older males may be more successful through post-copulatory sperm competition within the female reproductive tract. Older male reed buntings have an increased sperm storage capacity (chapter 3), therefore their sperm may be able to swamp other males' sperm by inserting larger ejaculates (Martin *et al.* 1974). Copulations may occur either following female choice (figure box 2.1A) or male experience (figure box 2.1B), but the eventual successful fertilisation may be a result of the amount of sperm (figure box 2.1C). This may lead to females gaining genetic benefits, if male offspring inherit the extra-pair male's viability genes. Increased sperm storage capacity with age has been found in some other species as well, such as dark-eyed juncos (*Junco hyemalis*; Deviche *et al.* 2000) and mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*; Morton *et al.* 1990b), but not in others, such as superb fairy-wrens (*Malurus cyaneus*; Mulder & Cockburn 1993).

### 4- Fertility insurance

Young males may suffer from functional infertility (i.e. the success of ejaculates in fertilising eggs), resulting in females engaging in EPCs with older males to insure against infertility of her eggs (Sheldon 1994b). Although permanent infertility would be very strongly selected against (Birkhead & Møller 1992), temporary infertility, low sperm counts or reduced sperm mobility may be caused by injury, disease or malnutrition (reviewed by Sheldon 1994b). If females seek insurance against the infertility of their partner (i.e. direct benefit) rather than genetic benefits for their offspring, they are likely to select older males on account of their higher sperm storage capacity (figure box 2.1D).

If total loss of paternity is a result of functional infertility of the social male, as suggested for blue and great tits (*Parus major*; Krokene *et al.* 1998), then possibly 32% of males ( $n = 71$  males) have suffered from infertility in our reed bunting population. This appears to be an unlikely high percentage of males to be infertile; in comparison, 2 to 4% of males in blue and great tits suffered from total loss of paternity (Krokene *et al.* 1998). The fertility insurance hypothesis is difficult to evaluate, since studies showing opposite results claimed their findings to be consistent with this hypothesis; nests with mixed paternity contained more unhatched eggs in house sparrows (*Passer domesticus*; Wetton & Parkin 1991), but less unhatched eggs in red-winged blackbirds and tree swallows (Gray 1997a; Kempenaers *et al.* 1999). However, egg failure may also be due to early embryo mortality, and this can only be excluded by checking for absence of sperm on the inner perivitelline

layers around the ovum (Birkhead *et al.* 1994). In tree swallows, all unhatched eggs were fertilised (Kempnaers *et al.* 1999), while in house sparrows 85% of unhatched eggs were fertilised (Birkhead *et al.* 1995), and thus failed to hatch due to embryonic mortality. In reed buntings, hatching success did not differ between nests with and without EPP (chapter 3).



**Figure box 2.1.** Interactions between males and females possibly leading to the occurrence of extra-pair copulations (EPCs) with old males. The width of the arrows indicate the strength of the effect. For a detailed description see text. Modified from Forstmeier (2004).

