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The illusion of monogamy

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Document Version

Publisher's PDF, also known as Version of record

Publication date:
2005

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Bouwman, K. M. (2005). *The illusion of monogamy: Patterns of extra-pair paternity in the reed bunting (Emberiza schoeniclus)*. s.n.

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General introduction

Variation in extra-pair paternity

Social monogamy, i.e. where one male pairs with one female to produce offspring, is the most common mating system found in birds (Lack 1968). However, since the use of molecular techniques has become integrated in the study of avian mating systems, our perception of monogamy has changed radically. True genetic monogamy (i.e. all offspring are fertilised within the social pair-bond) occurs only in 14% of studied passerines, while extra-pair paternity (EPP; i.e. offspring resulting from fertilisations outside the social pair-bond) occurs regularly in the remaining 86% (Griffith *et al.* 2002). On average, 11% of offspring in 19% of broods have been found to be extra-pair, while in a quarter of the socially monogamous passerine species studied over 25% of offspring are extra-pair (Griffith *et al.* 2002). The reed bunting (*Emberiza schoeniclus*) is among the most promiscuous, with 55% of offspring sired by extra-pair males and at least one extra-pair offspring in 86% of broods (Dixon *et al.* 1994; Griffith *et al.* 2002). The most promiscuous species detected up till now is not socially monogamous, but breeds cooperatively; the superb fairy wren (*Malurus cyaneus*) was found to have up to 76% extra-pair offspring in 95% of broods (Mulder *et al.* 1994; Griffith *et al.* 2002).

Factors explaining variation in extra-pair paternity

The large variation in EPP between species has a strong phylogenetic basis, as 55% of the variation occurs at or above the taxonomic level of family (Arnold & Owens 2002). This variation between bird families is suggested to be a result of the variation in costs of cuckoldry, so that EPP should be most common in species where the risks of punishment are low. Punishment is predicted to be low in species where (i) the social male partner contributes little to the care of offspring (Gowaty 1996; Møller 2000), as the withdrawal of paternal care would not affect the female to a large extent, and (ii) high mortality rates occur, leading to males investing in their current breeding attempt, as the chances of surviving to the next breeding attempt are low (Mauck *et al.* 1999). In agreement, high rates of EPP were associated with high rates of adult mortality and low levels of paternal care in an interspecific comparison (Arnold & Owens 2002).

Not only between avian families, but also between related species, between populations within species and between individuals within populations a large degree of variation in levels of EPP is found (Petrie & Kempenaers 1998). The variation on these levels is suggested to be a result of the variation in the opportunities and genetic benefits of cuckoldry (Arnold & Owens 2002). In agreement, breeding density and synchrony (i.e. factors influencing the

opportunities of cuckoldry) were identified as potentially important factors in determining variation in EPP in an intra-species comparison (Westneat & Sherman 1997; Møller & Ninni 1998), but not in an inter-species comparison (Westneat & Sherman 1997; Bennett & Owens 2002). Furthermore, factors possibly influencing the genetic benefits of cuckoldry, such as male attractiveness and genetic diversity, were also found to explain variation in levels of EPP within species (Møller & Ninni 1998; Petrie *et al.* 1998; Griffith 2000).

Present study

One of the best examples of the costs of EPP has been published from a previous study on EPP in reed buntings: when using a strong within-male comparison, male reed buntings reduced their level of paternal care with reduced paternity (Dixon *et al.* 1994). In order to test the generality of behaviors, it is important to compare populations of the same species (Griffith *et al.* 2003). We therefore set out to repeat this study in a Dutch population, using the same methodology.

With the advancement of molecular techniques, and the possibility to learn these methods in the same lab as where the previous work on reed buntings was done (under supervision of Prof. T.A. Burke), we were able to take the study of EPP in reed buntings a step further. Besides determining a male's cuckoldry rate in his own brood, we were also able to assign the paternity of offspring to extra-pair males, which has opened a whole range of possibilities to explain variation in EPP between individual reed buntings.

Outline of the thesis

Benefits of EPP to females

As most birds species lack an intromittant organ, females are assumed to have at least some control over whether insemination occurs (Birkhead & Møller 1992) and females have been seen to actively seek and solicit EPCs from extra-pair males in several species (Kempnaers *et al.* 1992; Gray 1996; Neudorf *et al.* 1997; Double & Cockburn 2000). Since potential costs are involved (Birkhead & Møller 1992b), females are expected to engage in EPCs only if they benefit. Benefits may be either direct, i.e. beneficial for the female herself, or indirect, i.e. beneficial for her offspring. Since extra-pair males generally do not contribute anything else but sperm (but see Gray 1997), direct benefits are expected to be of less importance (Birkhead & Møller 1992).

In **chapter 2** we adopt a female point of view by determining patterns of EPP in broods of individual reed buntings, both within and between seasons, to tests

three hypothesised female benefits. First, females may engage in EPCs to increase the probability of successful remating, should this be necessary (Birkhead & Møller 1992). In a comparative analysis between species, evidence was found for a relation between divorce and levels of EPP (Cézilly & Nager 1995). Second, females may increase the genetic diversity of their offspring through mating with multiple males (Birkhead & Møller 1992). Increased genetic diversity of offspring increases the chance of at least some offspring performing well in unpredictable environments (Williams 1975). Third, if males vary in genetic quality, females can gain benefits for their offspring by acquiring high quality or ‘good genes’ through EPFs with higher quality males (Birkhead & Møller 1992). Reed buntings are capable of producing multiple broods in a single season and adults show high site fidelity between seasons, thereby presenting an ideal opportunity to study patterns of EPP in successive broods within individuals.

In chapter 3, we adopt a male point of view to test hypothesised female benefits, firstly by determining characteristics related to male fertilisation success, and secondly by determining differences in fitness related characteristics between extra-pair young and their half-siblings. In this chapter we test predictions following three female benefit hypotheses: females may benefit through gaining ‘good genes’, compatible genes, or insurance against infertility. Sexually selected signals may provide females with cues to judge male genetic quality (Andersson 1994). Females seeking good genes for their offspring may also benefit through selecting older males, as older males will on average be of higher quality than younger males demonstrated through their survival (Trivers 1972; Manning 1985; Kokko 1998). Age, size, plumage characteristics and song have all been shown to be positively related with male fertilisation success in many bird species (reviewed in Griffith *et al.* 2002), and females selecting these characteristics may actually produce offspring with higher fitness (Petrie 1994; Hasselquist *et al.* 1996). If however the quality of the offspring depends on the combination of maternal and paternal genotypes, rather than on the absolute quality of the paternal genotype, females may seek extra-pair males that are genetically more compatible than their social mate (Tregenza & Wedell 2000). This hypothesis predicts no relationship between male characteristics and fertilisation success, but does predict that extra-pair young are fitter than their half-siblings. The good genes and the genetic compatibility hypotheses need not be mutually exclusive, as females may choose high quality as well as compatible genes (Jennions & Petrie 2000). Female blue tits gained different benefits from different males, as copulations with local males produced offspring with good genes, while copulations with non-local males increased offspring heterozygosity (Foerster *et al.* 2003). Alternatively, females may directly benefit through insurance against (temporary) infertility of the mate. Although the incidence of male sterility is expected to be too low for female promiscuity to evolve (Birkhead & Møller 1992), male fertility may covary with

male characteristics, allowing females to choose the most fertile male (Sheldon 1994). In this case no difference in fitness between extra-pair young and their half-siblings is expected.

Costs of EPP to females

As parental effort is considered to be costly (Williams 1966), males are expected to provide less care to offspring sired by other males (Trivers 1972). Depending on a male's ability to discriminate between related and non-related offspring, he may choose to reduce care to all offspring, or direct his care to his kin (Westneat & Sherman 1993). Either way, females are expected to suffer the cost of decreased paternal investment, which may lead to lower survival of the offspring, or, in case of compensatory behaviour, to lower survival of the females themselves (Birkhead & Møller 1992; Petrie & Kempenaers 1998). Although many studies found no reduction of paternal effort with decreased paternity (reviewed in Whittingham & Dunn 2001), evidence was found that this is a potential cost to females (Burke *et al.* 1989; Sheldon & Ellegren 1998; Lifjeld *et al.* 1998). One of the best examples of reduction of paternal effort with decreased paternity was found in reed buntings. Dixon *et al.* (1994) used two broods of the same pair within one season to show that males provisioned less to broods in which they sired a lower proportion of the offspring. In **chapter 4** we repeat the study by Dixon *et al.* (1994) to investigate whether males reduce their parental effort in relation to increased cuckoldry rates in our Dutch population of reed buntings. Furthermore, we investigate whether males discriminate between related and unrelated offspring in broods of mixed paternity.

Constraints on extra-pair mating behaviour

Currently EPP is often assumed to be the result of an active female choice for extra-pair matings, however, it is unlikely that females can freely engage in EPCs. The occurrence of EPP is a result of the interaction between the three players of the extra-pair mating game (i.e. social male, social female, and extra-pair male) and their conflicts of interest (Lifjeld *et al.* 1994; Petrie & Kempenaers 1998; Westneat & Stewart 2003). There will always be a strong conflict between the social and extra-pair male, as they directly compete over siring offspring. A conflict between the social male and social female can only be expected if the female benefits from gaining EPCs, for instance when paired to a low quality social male. Alternatively, if the female does not benefit from EPCs, for instance when paired to a high quality social male or when EPCs lead to injury, she is in conflict with the extra-pair male and would benefit from cooperating with her social male. These conflicts of interests have led to both physiological and behavioural adaptations by males and females, in what is likely to be an ongoing armsrace (BOX 1).

The importance of the age of the partner for the interaction between pair-members was determined in a study on coal tits (*Parus ater*; Dietrich *et al.* 2004). Old female coal tits had higher levels of EPP in their broods, but only when paired to a young male. Dietrich *et al.* (2004) suggested this to be a result of the lower mate guarding capacity of young males compared to old males in combination with an increased capacity to escape mate guarding by old females compared to young females. In **chapter 5** we investigate the importance of the combination of age of the pair-members on the levels of EPP in reed bunting broods.

In **chapter 6** we determine the effect of breeding density, synchrony and predation on the levels of EPP, since these factors may influence the degree of interactions between individuals. Breeding density and synchrony may determine the number of potential extra-pair partners available (Birkhead & Møller 1992), while predation may affect the relative investment in extra-pair mating behaviour of both males and females, thereby influencing levels of EPP in the replacement brood. In **chapter 7** we investigate the effect of weather conditions during the peak fertile period of the female on the proportion of EPP in her brood. Daily minimum temperature and rain duration may influence energy expenditure or food availability, and thus the time budgets of both males and females.

In the last two chapters, I will view our results in a broader perspective. In **chapter 8**, I have combined the results of six studies on EPP in reed buntings, conducted in five different populations across Europe, and will discuss the consistency between populations. Finally, in **chapter 9**, I will summarise the most important results and discuss them in relation to current views and other studies on patterns of EPP in other bird species.

BOX 1: Physiological and behavioural adaptations to high levels of sperm competition

The testis size relative to body mass is a measure for sperm production rate, and has been shown to be larger in species with high levels of sperm competition (Birkhead & Møller 1992). Females store sperm after copulation and before fertilising their eggs, increasing the possibility of direct sperm competition between sperm of different males in the female reproductive tract (Birkhead & Møller 1992). A large variation in the number and size of the sperm storage tubules has been found between species, although this was not related to the degree of sperm competition in that species (Birkhead & Møller 1992a). In reed buntings, both males and females exhibited physiological adaptations to high levels of sperm competition. The relative volume of the

cloacal protuberance (i.e. site of sperm storage) of reed bunting males was large compared to that of other socially monogamous passerines, the weight of the testis was 23% larger than expected for a bird the size of a reed bunting, and the spermatozoa were among the longest recorded for any bird species (Dixon & Birkhead 1997). On the other hand, female reed buntings possessed extremely long sperm storage tubules (Dixon & Birkhead 1997).

In addition to physiological adaptations, behavioural adaptations have also been found in response to sperm competition. Two of the main behavioural strategies of the male to prevent cuckoldry are mate guarding (i.e. close following of the female by her social partner during the fertile period) and frequent copulation (Birkhead & Møller 1992). 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). EPCs may occur by females moving away from her own territory and seeking extra-pair males (i.e. a foray), so that guarding is aimed at preventing female forays (Lifjeld *et al.* 1994), which would require almost full-time mate guarding to be effective. Alternatively, extra-pair males may initiate encounters by moving towards the females, so that guarding is aimed at dissuading other males from approaching (Beecher & Beecher 1979), in which case lower levels of mate guarding may already prove to be effective.

Possibly as a result of differences in active female pursuit of EPCs, the results regarding the effectiveness of mate guarding are controversial, as positive (Chuang-Dobbs *et al.* 2001), negative (Gowaty & Bridges 1991; Kempnaers *et al.* 1995) and also no relationships (Johnsen *et al.* 2003) with levels of EPP have been reported. The importance of interactions between pair-members has been shown by temporarily removing a male from his territory. This reduced the effect of mate guarding, which lead extra-pair males to increase their intrusions rates (Westneat 1992; Sundberg 1994; Dickinson 1997; Komdeur *et al.* 1999). However, in these experiments, all EPCs occurring during male removal occurred through male intrusions, and not through female forays (Westneat & Stewart 2003).