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# WHY DO FEMALES ENGAGE IN EXTRA-PAIR COPULATIONS ? A REVIEW OF HYPOTHESES AND THEIR PREDICTIONS

by

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## SUMMARY

Behavioural ecologists have become aware that extra-pair copulations form a major element of avian mating behaviour. Previously, attention was focused primarily on the benefits of this behaviour to males. However now that it is realized that females are not just passive participants, but instead may be largely in control of which male fathers their young, the major goal is to understand what females gain from extra-pair copulations. In this paper we summarize some of the existing hypotheses and we advance and discuss some new predictions that may open perspectives for future research.

*Key-words :* Reproductive behaviour, extra-pair copulations, paternity, female choice, review.

## INTRODUCTION

Copulations outside the social pair bond (known as « extrapair copulations » or EPCs) are now documented for a wide range of bird species (reviews in WESTNEAT *et al.*, 1990 ; BIRKHEAD and MØLLER, 1992) and form an important alternative reproductive behaviour by which males can increase their reproductive success [« mixed reproductive strategy » (TRIVERS, 1972)]. The benefit for males could be proven, using genetic markers, by showing that EPCs can result in fertilizations (e.g. WESTNEAT, 1987 ; LANK *et al.*, 1989 ; BIRKHEAD *et al.*, 1990). Although there are also potential costs for males performing EPCs (reviews in BIRKHEAD and MØLLER, 1992), obviously the benefit of fathering more offspring is very important and males can gain a substantial part of their reproductive success through EPCs (GIBBS *et al.*, 1990 ; MORTON *et al.*, 1990 ; WESTNEAT, 1990).

However, recent studies of different bird species show that in fact extra-pair paternity is likely to be largely controlled by the female (WAGNER, 1991a ; KEMPENAERS *et al.*, 1992 ; LIFJELD and ROBERTSON, 1992 ; BIRKHEAD and MØLLER, 1993a). In most bird species males lack an intromittent organ, and therefore the cooperation of the female might be necessary to make a successful copulation (with sperm transfer) possible (FITCH and SHUGART, 1984), although there is still debate over this topic (discussion in WAGNER, 1991a; BIRKHEAD and MØLLER, 1992). Nevertheless, a number of observers have reported or implied that EPCs require female cooperation (WAGNER, 1991a and references therein). Moreover, in many species it has been observed that females are actively seeking or soliciting EPCs from certain males [e.g. northern fulmar *Fulmarus glacialis* (HATCH, 1987); zebra finch *Taeniopygia guttata* (BIRKHEAD *et al.*, 1988); black-capped chickadees *Parus atricapillus* (SMITH, 1988); house sparrow *Passer domesticus* (MØLLER, 1990); blue tit *Parus caeruleus* (KEMPENAERS *et al.*, 1992)]. Good experimental evidence for female control of extra-pair paternity stems from a recent study of tree swallows *Tachycineta bicolor* (LIFJELD and ROBERTSON, 1992). Since the data suggest that females play an active role in getting EPCs, they should also get some benefits from them.

## HYPOTHESES AND PREDICTIONS

Many hypothetical benefits of EPCs for females have been proposed (reviews in WESTNEAT *et al.*, 1990; BIRKHEAD and MØLLER, 1992) but there are only a few studies that provide good evidence for one or another hypothesis. Good evidence is lacking because of three main reasons. (1) There are still few studies that combine both detailed behavioural work with DNA-fingerprinting results (paternity data) for the same individuals, (2) in the past most people have focused their attention on male behaviour and (3) for several of the hypotheses clear predictions are lacking and only a few attempts have been made to differentiate between the hypotheses (notable exceptions are: WAGNER, 1992a; BIRKHEAD and MØLLER, 1993b; LIFJELD *et al.*, 1993).

BIRKHEAD and MØLLER (1992) reviewed the different hypothetical benefits and discussed the existing evidence for these hypotheses. However, they did not propose any predictions to test the hypotheses. In this paper we will limit ourselves to the discussion of what we think are the seven most likely hypothetical benefits of EPCs for females. The aim of this paper is only to propose and discuss some predictions to differentiate between the hypotheses. It should be noted that the hypotheses are not exclusive and thus the same female might obtain several benefits or different females might benefit in different ways. To understand how EPC behaviour might have evolved, one should also consider the costs of this behaviour to females, but this is beyond the scope of this paper (for a discussion see WESTNEAT *et al.*, 1990).

In general there are two types of female benefits from EPCs: phenotypic or direct effects and genotypic effects (WESTNEAT *et al.*, 1990). There is one major difference between them. Females can only receive genetic benefits if the EPCs lead to extra-pair young, while for the non-genetic benefits to occur, the EPCs do not have to result in the fertilization of an egg. Therefore, important differences in female behaviour can be expected, depending on the type of benefit.

### Hypothesis 1 : courtship feeding before copulation

This hypothesis can only explain why females engage in EPCs if males do indeed feed the female before the EPC. TASKER and MILLS (1981) showed that in red-billed gulls (*Larus novaehollandiae scopulinus*) within-pair copulation success increased when males provided courtship feeding before the copulation attempt, suggesting that in some species females indeed trade copulations against food. Observations of EPCs should make it clear whether this benefit can occur.

### Hypothesis 2 : male parental care

This hypothesis states that females try to obtain extra help for feeding their young, by copulating with other males. It is based on the idea that males will provide parental care in relation to their certainty of paternity (cue is access to the fertile female). This idea is supported by copulation patterns and male help in the polyandrous mating system of the dunnock *Prunella modularis* (BURKE *et al.,* 1989). Apart from this, the only existing evidence is the observation that after females are widowed, they start copulating with new males showing interest and this has been interpreted as the females trying to deceive these males into helping them (GJERSHAUG *et al.,* 1989 ; MEEK and ROBERTSON, 1991). However, so far there is no evidence that EPCs result in male help. Broods fathered by different males can thus also be a result of such « rapid mate switching » (PINXTEN *et al.,* in press).

Regardless of the fact that one should indeed observe that females receive help from extra males (with which they copulated), one can make the following predictions. (1) EPCs should be performed with males that are likely to give parental care (e.g. unpaired males, males that lost their mate or nest). (2) Those females that engage in EPCs should badly need the extra help or expect little male help later (e.g. secondary females of polygynous males). Also, the extra help should result in an increase of the female's reproductive success. This is more likely in situations where food is scarce and where providing parental care is costly.

### Hypothesis 3 : mate appraisal and acquisition

Females may engage in EPCs in order to appraise and acquire future mates (COLWELL and ORING, 1989 ; WAGNER, 1991b). This hypothesis does not require an insemination or fertilization, so EPCs could take place outside the fertile period. One should be able to show that females that have performed EPCs with certain males, will later choose these males as a partner. This may be in the same year (second breeding attempt or new male of polyandrous female) or in consecutive years (e.g. WAGNER, 1991b).

### Hypothesis 4 : avoiding rejection costs

Females might passively accept EPCs to avoid a potentially larger cost of rejecting a persistent male. In this case females do not benefit from the EPCs, but from not refusing them. This hypothesis cannot be valid if one observes females actively seeking or soliciting EPCs. In species where the male closely guards the female, it is unlikely that females cannot avoid an EPC by warning their mate when another male approaches them, unless the copulation attempts are made by multiple males [e.g. sexual chases in bank swallows *Riparia riparia* (BEECHER and BEECHER, 1979); communal displays in house sparrows (MØLLER, 1987a)]. However, in colonial species with a high level of nest-site competition or where nests can be destroyed, nest guarding may prevent continuous mate guarding (BIRKHEAD and MØLLER, 1992), and females that are left alone may be attacked by males [e.g. white ibis *Eudocimus albus* (FREDERICK, 1987)]. This hypothesis is also likely to be valid for species where males have an intromittent organ and can forcibly copulate [e.g. « rape » in waterfowl where females might even be killed during an EPC attempt (MCKINNEY *et al.*, 1983)]. In some species the threat of infanticide can also be a rejection cost (ROBERTSON, 1990).

### Hypothesis 5 : insurance against male infertility

In the first place females want their eggs to be fertilized. Therefore, they could copulate with more males as an insurance against the possible infertility of their own mate. This hypothesis is not easy to test because (1) male infertility is difficult to examine (BIRKHEAD and MØLLER, 1992) and (2) the hypothesis may predict both a positive and a negative association between extra-pair paternity and the occurrence of infertile eggs. WETTON and PARKIN (1991) argued that for a male with low viable sperm counts there will be an increased risk of his mate laying infertile eggs. At the same time, the male might have a reduced success in sperm competition resulting in an increased likelihood of extra- pair fertilization. Alternatively, females that engage in extra-pair copulation should enjoy a higher fertilization success than those who do not, resulting in fewer, not more, infertile eggs in nests with extra-pair offspring. Some confusion may also arise because one can make different starting assumptions. (1) It is possible that males are only temporarily infertile (or less fertile) because they copulated at a high frequency [sperm depletion hypothesis (WETTON and PARKIN, 1991)]. However, sperm depletion through frequent copulation could also be « organized » by the female, because then she has more control over paternity. In this case the benefits have to come from either « good genes » or genetic diversity (see further). (2) Females are aware of the fertility status of their male. If this is the case, one expects only some females to perform EPCs (those females paired to infertile/less fertile males) and one should find that most nests contain no extra-pair young, while in a few nests all young are sired by an extra-pair male. (3) Females are unaware of the fertility status of their male. In this case all females should perform at least some EPCs. The resulting pattern of extra-pair paternity would then be that again a few nests contain only extra-pair young (those of infertile males), but a lot of nests should contain a low proportion of extra-pair young (assuming that infertility is rare).

To further examine this hypothesis, we should have an idea of the occurrence of male (and female) infertility in wild populations and of the effect of copulation frequency on sperm depletion (see BIRKHEAD, 1991 ; BIRKHEAD and FLETCHER, 1992).

### Hypothesis 6 : genetic diversity

In an unpredictable environment females might benefit from genetically diverse offspring (WILLIAMS, 1975 ; GLADSTONE, 1979). The following predictions can be made for this hypothesis.

(1) Pattern of extra-pair paternity in the population : few extra-pair young per nest in most nests or, if many extra- pair young per nest, they should all have different fathers. In principle, a female could have each egg fertilized by a different male, but there are actually few examples from DNA fingerprinting studies which record more than two males as the fathers of chicks within a single brood (BIRKHEAD and MØLLER, 1993b). Extra-pair young could be randomly distributed over the nests. (2) If genetic diversity is important, females should perform EPCs both with neighbours and with floater males and they should not refuse EPCs from certain males. In conclusion, females should not be selective. (3) Most or all females should engage in EPCs. (4) Nests with extra-pair young (high genetic diversity) should result in more recruits than nests without extra-pair young if genetic diversity is really beneficial to the female. One could also argue that the females perform EPCs as an « insurance » against an unpredictably fluctuating environment. (5) The variance in male reproductive success in the population should not increase, because males should both lose paternity and father young in other nests. (6) Extra-pair paternity should be more common if pair members are relatives, because then the genetic diversity obtained through sexual reproduction is lower and inbreeding can be costly [e.g. splendid fairy-wren Malurus splendens (BROOKER *et al.,* 1990 ; ROWLEY and RUSSELL, 1990)].

### Hypothesis 7 : genetic quality

This hypothesis states that females benefit from EPCs if their offspring are fathered by males with « good genes », either genes for general vigor or genes for attractiveness (BIRKHEAD and MØLLER, 1992).

Two versions of this hypothesis should be considered.

A. Under the assumption that all females have identical preferences, we can make the following predictions. (1) General pattern of extra-pair paternity : bimodal distribution of extra-pair young, i.e. no extra-pair young in some nests, a lot of extra-pair young in other nests. In an extreme case, when assuming that (a) it is very important to have your offspring fathered by a « good » male and (b) all females are able to copulate with the same male(s), one could find a lot of extra-pair young in a lot of nests [e.g. Reed Bunting *Emberiza schoeniclus* (DIXON, A. pers. comm.)]. Thus, extra- pair young are not randomly distributed amongst nests and they are never reciprocal. (2) Females should be selective in that they only perform EPCs with certain (« better ») males. Unless females can judge the quality of a male very quickly (if males have honest indicators of genetic quality), they should only perform EPCs with known males (e.g. territorial neighbours). (3) Females paired to low quality males should engage in EPCs while females paired to high quality males should refuse EPCs (or cooperate in mate guarding). Thus, some females refuse EPCs or do not solicit them. On the other hand females might resist extra-pair matings as a ploy to test the quality of males or to incite male-male competition (McKinney *et al.,* 1983). (4) Some males should be clearly preferred for EPCs and this should result in these males obtaining a higher reproductive success both through within- and extra-pair young. Thus, the variance in reproductive success between males increases. (5) In nests with extra-pair young, the extra-pair young should recruit better than the legal (within-pair) young or should have a higher reproductive success when breeding later, because they live longer or attract more females. Also, offspring of males that get EPCs should recruit better than offspring of other males. However, the last prediction is much more difficult to test, because of the many confounding variables that might play an important role (female quality, territory quality, parental investment). The first comparison is easier to make because extra-pair and within-pair young have the same mother and are raised together in the same nest. (6) Males that have fathered extra-pair young should be of high quality and thus for example live longer or attract more females (polygyny) and they should recruit more young from their own nest than males that suffer lost paternity.

B. The alternative assumption is that females have variable preferences, for example if genetic complementarity is important. Variation in female preference has often been neglected and is poorly studied (see Kirkpatrick and Ryan, 1991), but causes a difference in the above predictions. Extra-pair paternity may be reciprocal, males may be cuckolded with one female but not with another and the variance in male mating success may not be as big as for identical preferences.

A special case of the good genes hypothesis is direct sperm competition to allow the best sperm to fertilize the eggs (e.g. study on adders, *Vipera berus* (Madsen *et al.,* 1992)). If the female has no way of telling the genetic quality of a male, she could engage in multiple copulations and let the sperm « decide » which is the best male through competition in the female reproductive tract. The sperm fertilizing her eggs are (by definition) the best at sperm competition. Since many aspects of ejaculate/copulation behaviour are probably highly heritable, the female will tend to have sons who are also good at sperm competition. Madsen *et al.* (1992) suggested that sperm that is more successful in fertilizing the ova could also be more effective in producing viable offspring. If females benefit from direct sperm competition, one predicts that all females engage in EPCs (see also Lifjeld *et al.,* 1993) and that this still leads to a few males getting all the extra-pair young.

## THE STUDY OF MALE BEHAVIOUR

The behaviour of the male, which has received most attention up until now because of the obvious male benefits, might give few insights to explain the detected pattern of extra-pair paternity. This is because all males clearly benefit from having extra-pair young, and one can thus expect that all males will try to get them when the possibilities arise and that all males will also try to avoid being cuckolded themselves. If females control copulations, then differences in the benefits of EPCs to different females will result in different female behaviour and might then determine the pattern of extra-pair paternity.

## MATE GUARDING AND OTHER PATERNITY PROTECTION BEHAVIOURS

Whatever the benefits females might obtain, if the EPCs lead to the fertilization of one or more eggs, they are very costly to the cuckolded male. Therefore males should always adopt behaviour that minimizes the risk of being cuckolded, either through guarding the fertile partner, frequent copulation or retaliatory copulations (reviewed in BIRKHEAD and MØLLER, 1992). One can expect to find a negative correlation between the intensity of mate guarding and the number of extra-pair young in the nest if mate guarding is an effective protection against extra-pair paternity. However, if the male quality hypothesis is true, then high quality males that have no better quality neighbours should not invest in mate guarding, because their female will not engage in EPCs anyway. Then a positive relation between mate guarding and extra-pair paternity could be found [e.g. eastern bluebirds *Sialia sialis* (GOWATY and BRIDGES, 1991)]. This does not mean that mate guarding is not important, but that it is not very effective [as shown for the blue tit (KEMPENAERS *et al.*, 1992)]. In that case, males of lower quality that guard their mate are probably making the best of a bad job. Frequent copulation is perhaps more effective, but it is also possible, given that last male sperm precedence seems to be the mechanism of sperm competition in birds (BIRKHEAD and MØLLER, 1992), that the timing of the copulation is more important than the number of copulations. In that case, the female has a strong possibility of control. In some species the anti-cuckoldry tactics seem to be remarkably ineffective. Despite close mate guarding or high within-pair copulation rates, one can find a high rate of extra-pair paternity in e.g. eastern bluebirds (GOWATY *et al.*, 1989 ; GOWATY and BRIDGES, 1991), swallows *Hirundo rustica* (MØLLER, 1987b ; 1989), tree swallows (VENIER and ROBERTSON, 1991 ; LIFJELD *et al.*, 1993), house sparrows (MØLLER, 1987a ; WETTON and PARKIN, 1991). It thus seems that in some species females are a step in front in this sexual conflict.

## EXTRA-PAIR PATERNITY AND FEMALE CHOICE

Females of many bird species are known to be choosy in that they show clear preferences for certain males (e.g. MØLLER, 1988 ; ANDERSSON, 1992) or for males holding certain high value resources [e.g. high quality territories (VERNER, 1964 ; ALATALO *et al.*, 1986). This preference for certain males can lead to these males pairing earlier (e.g. CATCHPOLE, 1980 ; MØLLER, 1988), getting more females (e.g. VERNER, 1964), having more broods within one season (e.g. MØLLER, 1988) and getting more copulations (e.g. HOGLUND and LUNDBERG, 1987). And now recent studies clearly suggest that females are also exerting some choice over which male(s) father their offspring through EPCs (KEMPENAERS *et al.*, 1992; LIFJELD and ROBERTSON, 1992).

The study of female benefits from EPCs could perhaps also shed more light on the paradox of the lek, because one can draw a number of important parallels between female choice in a lek and female choice for EPCs. (1) In both cases females choose from among a number of males (assembled in a lek, members of the colony or territorial neighbours), and in both cases the females seem to receive little else than ejaculates. Females often show strong unanimity in their choice of copulation partner. The result of this unanimity among females is that a few males acquire most of the matings (e.g. HOGLUND and LUNDBERG, 1987). In a recent study of razorbills (*Alca torda*) WAGNER (1992b) describes the EPC behaviour occurring on mating arenas outside the colony and explicitly refers to it as lekking behaviour. He argues that in this species lekking is a secondary mating system. In a lot of lekking species, female preference has already been studied in great detail and it has been shown that male characteristics such as tail length (ANDERSSON, 1992), tail morphology (HOGLUND *et al.*, 1990), and fighting ability (ALATALO *et al.*, 1991) determine male mating success. For EPCs it is far from clear what male characteristics females might be choosing (KEMPENAERS *et al.*, 1992; LIFJELD and ROBERTSON, 1992) and this should be a priority in future research.

## CONCLUSION

We hope that the above discussion will help to unravel the problem of female benefits from EPCs. As already pointed out by WAGNER (1991b), one of the major problems in testing these hypotheses is that they make overlapping predictions. Therefore, we think that it is essential to collect data on male and especially female behaviour and extra-pair paternity for the same individuals. Only a combination of these data and eventually data on offspring survival can give a clear picture.

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## REFERENCES

ALATALO, R. V., J. HOGLUND and A. LUNDBERG (1991) — Lekking in the black grouse — a test of male viability. *Nature*, **352** : 155-156.

ALATALO, R. V., A. LUNDBERG and C. GLYNN (1986) — Female pied flycatchers choose territory quality and not male characteristics. *Nature,* **323** : 152-153.

ANDERSSON, S. (1992) — Female preference for long tails in lekking Jackson's widowbirds : experimental evidence. *Anim. Behav.,* **43** : 379-388.

BEECHER, M. D. and I. M. BEECHER (1979) — Sociobiology of bank swallows : reproductive strategy of the male. *Science,* **205** : 1282-1285.

BIRKHEAD, T. R. (1991) — Sperm depletion in the Bengalese finch, *Lonchura striata. Behav. Ecol.,* **2** : 267-275.

BIRKHEAD, T. R., T. BURKE, R. ZANN, F. M. HUNTER and A. P. KRUPA (1990) — Extra-pair paternity and intraspecific brood parasitism in wild zebra finches *Taeniopygia guttata,* revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.,* **27** : 315-324.

BIRKHEAD, T. R., K. CLARKSON and R. ZANN (1988) — Extra-pair courtship, copulation and mate guarding in wild zebra finches *Taeniopygia guttata. Anim. Behav.,* **35** : 1853- 1855.

BIRKHEAD, T. R. and F. FLETCHER (1992) — Sperm to spare ? Sperm allocation by male zebra finches. *Anim. Behav.,* **43** : 1053-1055.

BIRKHEAD, T. R. and A. P. MØLLER (1992) — *Sperm competition in birds : evolutionary causes and consequences.* Academic Press, London (282 pp).

BIRKHEAD, T. R. and A. P. MØLLER (1993a) — Female control of paternity. *TREE,* **8** : 100-104.

BIRKHEAD, T. R. and A. P. MØLLER (1993b) — Why do male birds stop copulating while their partners are still fertile ? *Anim. Behav.,* **45** : 105-118.

BROOKER, M. G., I. ROWLEY, M. ADAMS and P. R. BAVERSTOCK (1990) — Promiscuity : an inbreeding avoidance mechanism in a socially monogamous species ? *Behav. Ecol. Sociobiol.,* **26** : 191-199.

BURKE, T., N. B. DAVIES, M. W. BRUFORD and B. J. HATCHWELL (1989) — Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature,* **338** : 249-251.

CATCHPOLE, C. K. (1980) — Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus. Behaviour,* **74** : 149-166.

COLWELL, M. A. and L. W. ORING (1989) — Extra-pair mating in the spotted sandpiper : a female mate acquisition tactic. *Anim. Behav.,* **38** : 675-684.

FITCH, M. A. and G. W. SHUGART (1984) — Requirements for a mixed reproductive strategy in avian species. *Am. Nat.,* **124** : 116-126.

FREDERICK, P. C. (1987) — Responses of male white ibises to their mate's extra-pair copulations. *Behav. Ecol. Sociobiol.,* **21** : 223-228.

GIBBS, H. L., P. J. WEATHERHEAD, P. T. BOAG, B. N. WHITE, L. M. TABAK and D. J. HOYSAK (1990) — Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. *Science,* **250** : 1394-1397.

GJERSHAUG, J. O., T. JARVI and E. RØSKAFT (1989) — Marriage entrapment by « solitary » mothers : a study on male deception by female pied flycatchers. *Am. Nat.,* **133** : 273- 276.

GLADSTONE, D. E. (1979) — Promiscuity in monogamous colonial birds. *Am. Nat.,* **114** : 545-557.

GOWATY, P. A. and W. C. BRIDGES (1991) — Behavioral, demographic, and environmental correlates of extra-pair fertilizations in eastern bluebirds, *Sialia sialis. Behav. Ecol.,* **2** : 339-350.

GOWATY, P. A., J. H. PLISSNER and T. G. WILLIAMS (1989) — Behavioural correlates of uncertain parentage : mate guarding and nest guarding by eastern bluebirds, *Sialia sialis. Anim. Behav.,* **38** : 272-284.

HATCH, S. A. (1987) — Copulation and mate guarding in the northern fulmar. *Auk,* **104** : 450-461.

HOGLUND, J., R. V. ALATALO and A. LUNDBERG (1990) — Copying the mate choice of others ? Observations on female black grouse. *Behaviour,* **114** : 221-231.

HOGLUND, J. and A. LUNDBERG (1987) — Sexual selection in a monomorphic lek-breeding bird : correlates of male mating success in the great snipe *Gallinago media. Behav. Ecol. Sociobiol.,* **21** : 211-216.

KEMPENAERS, B., G. R. VERHEYEN, M. VAN DEN BROECK, T. BURKE, C. VAN BROECKHOVEN and A. A. DHONDT (1992) — Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature,* **357** : 494-496.

KIRKPATRICK, M. and M. J. RYAN (1991) — The evolution of mating preferences and the paradox of the lek. *Nature,* **350** : 33-38.

LANK, D. B., P. MINEAU, R. F. ROCKWELL and F. COOKE (1989) — Intraspecific nest parasitism and extra-pair copulation in lesser snow geese. *Anim. Behav.,* **37** : 74-89.

LIFJELD, J. T., P. O. DUNN, R. J. ROBERTSON and P. T. BOAG (1993) — Extra-pair paternity in monogamous tree swallows. *Anim. Behav.,* **45** : 213-229.

LIFJELD, J. T. and R. J. ROBERTSON (1992) — Female control of extra-pair fertilization in tree swallows. *Behav. Ecol. Sociobiol.,* **31** : 89-96.

MADSEN, T., R. SHINE, J. LOMAN and T. HAKANSSON (1992) — Why do female adders copulate so frequently ? *Nature,* **355** : 440-441.

MCKINNEY, F., S. R. DERRICKSON and P. MINEAU (1983) — Forced copulation in waterfowl. *Behaviour,* **86** : 250-294.

MEEK, S. B. and R. J. ROBERTSON (1991) — Adoption of young by replacement male birds : an experimental study of eastern bluebirds and a review. *Anim. Behav.,* **42** : 813-820.

MØLLER, A. P. (1987a) — House sparrow *Passer domesticus* communal displays. *Anim. Behav.,* **35** : 203-210.

MØLLER, A. P. (1987b) — Extent and duration of mate guarding in swallows *Hirundo rustica. Ornis Scand.,* **18** : 95-100.

MØLLER, A. P. (1988) — Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature,* **332** : 640-642.

MØLLER, A. P. (1989) — Frequency of extra-pair paternity in birds estimated from sex-differential heritability of tarsus length : reply to LIFJELD and SLAGSVOLD's critique. *Oikos,* **56** : 247-249.

MØLLER, A. P. (1990) — Sexual behaviour is related to badge size in the house sparrow *Passer domesticus. Behav. Ecol. Sociobiol.,* **27** : 23-29.

MORTON, E. S., L. FORMAN and M. BRAUN (1990) — Extra-pair fertilizations and the evolution of colonial breeding in purple martins. *Auk,* **107** : 275-283.

PINXTEN, R., O. HANOTTE, M. EENS, R. F. VERHEYEN, A. A. DHONDT and T. BURKE (1993) — Extra-pair paternity and intraspecific brood parasitism in the European starling *Sturnus vulgaris* : evidence from DNA fingerprinting. *Anim. Behav.,* **45** : 795-809.

ROBERTSON, R. J. (1990) — Tactics and counter-tactics of sexually selected infanticide in tree swallows. In : *Population Biology of Passerine Birds,* BLONDEL, J., A. GOSLER, J.-D. LEBRETON and R. McCLEERY (Ed.) — Springer-Verlag, Berlin : 381-390.

ROWLEY, I. and E. RUSSELL (1990) — « Philandering » — a mixed mating strategy in the splendid fairy-wren *Malurus splendens. Behav. Ecol. Sociobiol.,* **27** : 431-437.

SMITH, S. M. (1988) — Extra-pair copulations in black-capped chickadees : the role of the female. *Behaviour,* **107** : 15- 23.

TASKER, C. R. and J. A. MILLS (1981) — A functional analysis of courtship feeding in the red-billed gull, *Larus novaehollandiae scopulinus. Behaviour,* **77** : 221-241.

TRIVERS, R. L. (1972) — Parental investment and sexual selection. In : *Sexual selection and the descent of man.* CAMPBELL, B. (Ed.) — Aldine Press, Chicago : 136-179.

VENIER, L. A. and R. J. ROBERTSON (1991) — Copulation behaviour of the tree swallow, *Tachycineta bicolor* : paternity assurance in the presence of sperm competition. *Anim. Behav.,* **42** : 939-948.

VERNER, J. (1964) — Evolution of polygamy in the long-billed marsh wren. *Evolution,* **18** : 252-261.

WAGNER, R. H. (1991a) — Evidence that female razorbills control extra-pair copulations. *Behaviour,* **118** : 157-169.

WAGNER, R. H. (1991b) — The use of extra-pair copulations for mate appraisal by razorbills, *Alca torda. Behav. Ecol.,* **2** : 198-203.

WAGNER, R. H. (1992a) — The pursuit of extra-pair copulations by monogamous female razorbills : how do females benefit ? *Behav. Ecol. Sociobiol.,* **29** : 455-464.

WAGNER, R. H. (1992b) — Extra-pair copulations in a lek : the secondary mating system of monogamous razorbills. *Behav. Ecol. Sociobiol.,* **31** : 63-71.

WESTNEAT, D. F. (1987) — Extra-pair fertilizations in a predominantly monogamous bird : genetic evidence. *Anim. Behav.,* **35** : 877-886.

WESTNEAT, D. F. (1990) — Genetic parentage in the indigo bunting : a study using DNA fingerprinting. *Behav. Ecol. Sociobiol.,* **27** : 67-76.

WESTNEAT, D. F., P. W. SHERMAN and M. L. MORTON (1990) — The ecology and evolution of extra-pair copulations in birds. In : *Current ornithology,* vol. 7. POWER, D. M. (Ed.) — Plenum Press, New York : 331-369.

WETTON, J. H. and D. T. PARKIN (1991) — An association between fertility and cuckoldry in the house sparrow, *Passer domesticus. Proc. R. Soc. Lond. B,* **245** : 227-233.

WILLIAMS, G. C. (1975) — *Sex and evolution.* Princeton University Press, Princeton.