Osmo Rätti

Polyterritorial Polygyny in the Pied Flycatcher

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Academic Dissertation

*To be presented, with the permission of the Faculty of Mathematics
and Natural Sciences of the University of Jyväskylä, for public criticism
in Auditorium S212 on August 10, 1993 at 12 o'clock noon.*

*Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston vanhassa juhlasalissa (S212)
elokuun 10. päivänä 1993 kello 12.*

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To my daughter Essi

ABSTRACT

After having attracted their first female most pied flycatcher (*Ficedula hypoleuca*) males establish a second, spatially separate, territory and attempt to attract a second female there. Some males succeed in attracting the second female. Polygynous mating is costly for a secondary female since males feed primarily the young of the primary female and many of secondary females have to raise their nestlings alone.

Why are males polyterritorial and why do some females accept a secondary status? First, males may space out territories in order to hide their mating status and therefore females are deceived into polygyny against their best interests. Alternatively, males may be polyterritorial to reduce aggression between their two mates. Some females may do their best by accepting polygyny because the cost of searching for an unmated male may exceed the cost of reduced male assistance.

Females did not effectively avoid polygyny even though there were optional unmated males close by and it would have been adaptive to mate with an unmated male. There were some cues females might have been able to use to estimate male's mating status. Already mated polyterritorial males spent less time and sang less on their second territories than did unmated males on their single territories. The overlap in behaviour of males of different mating status might prevent females to accurately determine male's mating status. The power of female aggression seemed to be too weak to prevent male's secondary mating even when the distance between territories was short. The most plausible explanation for polyterritorial polygyny in the pied flycatcher is that males derive benefits from imperfect female choice by being polyterritorial.

Keywords: Pied flycatcher; mating systems; polygyny; polyterritoriality; mate choice; deception; female aggression.

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List of original publications

This thesis is based on the following articles, which will be referred to by their Roman numerals:

I   Rätti, O. & Alatalo, R.V. 1993: Determinants of the mating success of polyterritorial pied flycatcher males. - Ethology (in press).

II   Rätti, O., Dufva, R. & Alatalo, R.V. 1993: Blood parasites and male fitness in the pied flycatcher. - Manuscript (submitted).

III   Rätti, O. & Siikamäki, P. 1993: Female attraction behaviour of radio tagged polyterritorial pied flycatcher males. - Manuscript (submitted).

IV   Alatalo, R.V., Lundberg, A. & Rätti, O. 1990: Male polyterritoriality and imperfect female choice in the pied flycatcher, *Ficedula hypoleuca*. - Behav. Ecol. 1: 171-177.

V   Rätti, O. 1993: Female reactions on male absence at mating in the pied flycatcher. - Manuscript (submitted).

VI   Rätti, O., Alatalo, R.V., Kilpimaa, J. & Siikamäki, P. 1993: Female-female aggression and male polyterritoriality in the pied flycatcher. - Manuscript (submitted).

CONTENTS

1   INTRODUCTION

1.1   Polygynous mating system

The term "mating system" refers to the behavioural strategy employed in obtaining mates (Emlen & Oring 1977). To be more specific it describes the number of mates acquired, how mates are acquired, the presence and characteristics of pair bonds, and pattern of parental care provided by each sex. Polygyny is a mating system where an individual male mates with at least two females.

Females invest more in their offspring at the initial stage of breeding than males (eggs versus sperm, Trivers 1972). Where a male invests relatively less than a female to their offspring female's reproductive success is limited by access to resources rather than by access to males. Instead, a male is able to father offspring at a faster rate than a female can produce them. Thus, male's reproductive success is limited by access to females. Consequently, usually males may maximize their breeding success by deserting their current mate and attempting to search additional mates. When males invest much in rearing their offspring, like in many bird species, also females may gain by having access to more than one male. Still, among bird species polygyny is far more common than polyandry (Emlen & Oring 1977). This may be due to fact that in birds a male is able to desert his mate before she has completed her clutch (cruel bind, Trivers 1972).

Polygyny occurs when individual males are able to monopolize resources essential to females, can control access to females, or dominant

males are chosen more often than others by females (Emlen & Oring 1977). Polygyny is assumed to be always advantageous for males (Orians 1969). Sometimes females may benefit from polygyny due to cooperative nest defence (Altmann et al. 1977) or they may suffer no cost from mating polygynously (Lightbody & Weatherhead 1988). However, when male's assistance is essential for successful reproduction there is a cost of sharing a male. In that case females are suggested to choose polygyny when the costs of sharing a male are compensated by high quality resources offered by an already mated male (polygyny threshold model, Orians 1969) or by high quality offspring fathered by a high quality male (sexy son hypothesis, Weatherhead & Robertson 1979).

Earlier the occurrence of polygyny was emphasized to be due to female choice. However, there is also an alternative view. Individuals are expected to attempt to maximize their breeding success (Emlen & Oring 1977). While aiming to do this the interests of the two sexes do not necessarily coincide (Davies 1989). Sometimes males may gain an advantage at the expense of females since females do not always achieve the preferred option and vice versa. Different mating systems may hence reflect different outcomes of sexual conflict.

1.2 Mating system of the pied flycatcher: theoretical background

Pied flycatchers (*Ficedula hypoleuca* Pallas) exhibit regularly a polygynous mating system (von Haartman 1951, 1956). A proportion of males (3-39 %) mate with more than one female (Lundberg & Alatalo 1992). A special feature of the mating system of this species is polyterritoriality (von Haartman 1951, 1956). When males have attracted the first female many of them establish a second territory that is spatially separated from the first territory. Males take over a second territory usually around the day when the first female starts egg laying (von Haartman 1956, Silverin 1980). After having attracted a secondary female males return to the first nest and help rearing primarily the young of the first female (Alatalo et al. 1982, Lifjeld & Slagsvold 1989a, 1990). Polygynous males feed the young of secondary females only occasionally and many of them have to rear their offspring alone. Also the rate of incubation feeding by a polygynous male is lowered (Lifjeld et al. 1987, Lifjeld & Slagsvold 1989b). Thus, particularly secondary females seem to suffer considerably from reduced male assistance.

Secondary females produce offspring of lower phenotypic quality. The weight of their offspring at the time of fledging is lower than that of monogamous and primary females (Alatalo et al. 1982, Stenmark et al. 1988, Lifjeld & Slagsvold 1989a). The heritability of male mating success is also low at best (Alatalo & Lundberg 1986). Therefore, any compensation in the form of high quality offspring is unlikely. Also the number of fledglings produced by secondary females is lower compared to the success of simultaneously laying primary and monogamous females (Alatalo & Lundberg 1990). Secondary females do not seem to be able to compensate the cost of male sharing by any quality differences in breeding sites. The polygyny threshold hypothesis may not be applicable to explain occurrence of polygyny in the pied flycatcher since there are no compensatory benefits for secondary females.

To fully understand the mating system of the pied flycatcher two important questions need to be answered. (1) Why are males polyterritorial and (2) why do some females accept a secondary status? Von Haartman (1969) suggested that females might be ignorant about the another female of a male at the time of second mating because of spatially separated territories. Alatalo et al. (1981) extended this idea to consider also the male behaviour by suggesting that males establish a separate second territory to hide their mating status from females (Table 1). Consequently, females are deceived into polygyny against their own best interests. This view has been challenged by Stenmark et al. (1988). They suggested that females should be aware of male's mating status because of behavioural differences between already mated and unmated males. Still, some females do better by accepting a secondary female status since the costs of searching for an unmated male exceed the costs of reduced male assistance.

TABLE 1   Hypotheses about male polyterritoriality and polygyny (female point of view) of the pied flycatcher (partly after Alatalo & Lundberg 1990).

Polyterritoriality	Polygyny
Deception[1]	Deception[1]
Female-female aggression[2]	Search costs[3]
Taking the next best nest site/territory available[4]	?
Spreading the risk of nest predation[5]	?
Reducing competition for food between two females[6]	?
Female retention/quick renesting[7]	?

References: 1. Alatalo et al. 1981, 2. Breiehagen & Slagsvold 1988, 3. Stenmark et al. 1988, 4. Meier 1983, 5. Winkel & Winkel 1984, 6. Alatalo & Lundberg 1984, 7. Slagsvold & Lifjeld 1986.

Continuing the mate search is costly for pied flycatcher females because delayed breeding reduces reproductive success (e.g. Lundberg & Alatalo 1992). This cost is associated with both the deception hypothesis and the search cost hypothesis. However, the difference between these hypotheses is that according to the deception hypothesis there is an additional cost, the cost of perfectly assessing male's mating status. Polyterritoriality hides easy cues, like the presence of the primary female, from a prospecting female. There are two mechanisms how deception by males could operate. These are not mutually exclusive and they may as well act together. First, polyterritorial males may mimic perfectly enough the behaviour of unmated males while attracting an additional female. Secondly, females may not have evolved appropriate responses to any differences in male behaviour.

Since the search cost hypothesis alone does not explain polyterritoriality males are suggested to space out territories to reduce the aggression between their two mates thus making polygyny feasible (Breiehagen & Slagsvold 1988, Slagsvold et al. 1992; Table 1). In addition to the deception and the female-female aggression hypotheses several other factors have been proposed to favour male polyterritoriality (Table 1). Males may space territories out in order to avoid competition for food between broods (Alatalo & Lundberg 1984) or to decrease the risk of nest predation (Winkel & Winkel 1984). Males may also establish a second territory to be able quickly renest in the case of predation of the first nest (Slagsvold & Lifjeld 1986) or they may take over the next best nest site irrespective of the distance (Meier 1983). However, none of these additional hypotheses alone can explain why females accept secondary status. Furthermore, all of these factors seem to provide far too small benefits for males to become polyterritorial (see Alatalo & Lundberg 1990).

In this dissertation I will study polyterritorial behaviour of males in detail. Especially I will examine if there are possible cues for a female that may be used to avoid polygyny. Further, I investigate experimentally whether females are able to elude polygyny and what is the role of aggression between females in polyterritoriality of males. I will also discuss how well these results agree with the proposed hypotheses.

2 MATERIAL AND METHODS

2.1 The pied flycatcher and the study area

The pied flycatcher is a small migratory passerine bird. Pied flycatchers overwinter in tropical West Africa. The first males usually arrive to the breeding grounds in Central Finland in early May and most males normally have arrived before the end of May. Females arrive on average one week after males.

The pied flycatcher breeds in natural cavities. However, when nest boxes are available it readily accepts them as nesting sites. This feature makes the pied flycatcher very fruitful species to study. Nests are easy to find and nesting in nest boxes gives better opportunities to design experiments. Moreover, pied flycatchers are not very sensitive for any disturbance which makes this species profitable to study.

These studies have been carried out at the Konnevesi Research Station (62°37'N, 26°20'E) and the surroundings of it. The habitat was mainly coniferous forest with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) mixed with birches (*Betula spp.*). Nest boxes were provided in several plots containing up to about 30 nest boxes. Nest boxes were put up on tree trunks at the height of 1.6 m.

Pied flycatchers included in these studies were all individually marked by using plastic colour rings as well as numbered aluminium rings. Birds were aged as yearlings and older on the basis of wear in primary and outermost greater coverts (Karlsson et al. 1986).

2.2 Singing performance and male presence (I, IV)

We sampled the singing performance of polyterritorial males by counting the number of song phrases during at least two 10-min periods (I). Further, we standardized song rates for any variation due to observation time and prevailing temperature. Additionally, we noted the presence of a male at the territory during each minute of the observation period.

To be able to compare singing performance of already mated males at the secondary territory and unmated males we estimated the song rates in the same manner except that the minimum observation time was three 10-min periods (IV). The males of each pair were visited about the same time to standardize any temporal variation in singing behaviour. Likewise, for each minute of the observation period we noted presence of a male at the territory.

2.3 Radio tagging (III)

To obtain precise information about movements and behaviour of pied flycatcher males of different mating status we used radio tagging. Radio transmitters were provided by Biotrack and by Holohil. The Biotracks were attached by harnesses and they weighed about 0.9 grams with harnesses. The Holohils were glued on back feathers and they weighed about 0.7 grams. The weights of transmitters corresponded approximately 7 % and 6 % of the weight of the pied flycatcher male. Transmitters were removed immediately after observations had been completed. In total we tagged 8 polyterritorial and 6 unmated males.

For each minute of the observation period we entered the position of the male on a map and counted the number of song phrases. We also determined the territory where the males were in each minute.

2.4   Sampling of blood parasites (II)

Soon after males had arrived we captured them for blood sampling. One drop of blood was taken from brachial or tarsus vein with a microcapillary tube and smeared on a glass slide. The blood smears were air-dried and fixed in absolute methanol. The Giemsa stain solution was used to stain fixed smears. Blood smears were microscopically examined for parasites. We recorded the prevalence of five blood parasite genera (*Haemoproteus*, *Plasmodium*, *Leucocytozoon*, *Trypanosoma* and *Microfilaria*).

2.5   Breeding success of secondary females (IV)

The crucial question when studying a polygynous mating system is if there are any costs for a female who mated with a polygynous male as a secondary female. We compared breeding success of secondary females to that of females who later mated with an unmated male nearby (<200 m). Both males were available at the moment when a female mated as a secondary female. Altogether we have 36 such comparisons. We measured clutch size, number of fledglings and mean fledgling weight. Further, we estimated the relative number of recruits produced by using the likelihood of survival for fledglings of different weights (Alatalo & Lundberg 1989). We also observed the feeding rates of males by counting all feedings by each parent during a 30 min period when nestlings were 4-6 and 11-13 days old.

2.6   Female choice experiment (IV)

We arranged situations where a female can choose between two males of different mating status, i.e. an unmated and an already mated male. At the start of the experiment we had one already mated male attempting to attract an additional female to his second territory and one unmated male attracting a first female. These two males advertised their nest boxes separated by at most 100 m. This arrangement was made to minimize the costs of searching for an unmated male and to allow females easily to

compare males. Then we observed which of these two males mated earlier. If females were able to distinguish between mating statuses we would expect unmated males to be mated first. In total we had 20 such pairs of males.

2.7 Male removal experiment (V)

Females could use occasional male absence from territory as a cue to ascertain male's mating status after mating (Stenmark et al. 1988). I removed a male soon after the female settlement in order to mimic occasional absence of a polyterritorial male and to study female reactions to this treatment. Fourteen times I removed a male for 30-60 min soon after the female settlement and 8 times in the day after settlement. During removals I noted if there were any singing unmated males available in my study area. After trials I checked if the females have either remained or deserted the male.

2.8 Moving experiment for secondary females (VI)

We moved the secondary female of a male closer to the male's first female after her mating to test whether the first female is able to to prevent the settlement of the secondary female. As soon as the secondary female has started nest building we put up an additional nest box 10-20 m ahead at the direction of the male's first nest. After a while we changed the initial nest box at the place of the additional nest box and moved the additional nest box ahead again. Usually quite soon the male advertised this new nest site for the female and she continued nest building there. When the female has continued nest building some time we performed the next step and so on. If a female remained we, in most cases, stopped moving at the distance of 20 m from the nest of primary female.

3   RESULTS AND DISCUSSION

3.1   Polyterritorial behaviour of males

In the study population males usually established their secondary
territories some days after their first female had started her egg laying (I).
Some males occupied a secondary territory four days before the primary
female had started egg laying, whereas some of them did this nine days
after the onset of egg laying. The distance between male's territories
ranged from 60 m up to 1300 m (I). These results are consistent with
earlier studies (cf. Lundberg & Alatalo 1992). When the nest box density
was lower males occupied significantly more distant secondary territories
(I).

There was much variation in the proportion of time males spent
on the second territory while attempting to attract a secondary female (I,
III, IV). Males seemed to trade between guarding the primary territory
and attracting a secondary female. The intrusion rate of other males may
explain the variation in behaviour among polyterritorial males (see
Alatalo et al. 1987). Males might be able to assess intrusion rates and
adjust the defence of the primary territory as needed (see Hasselquist &
Bensch 1991). Losing the primary territory while attempting to attract a
secondary female is not exceptional (Slagsvold et al. 1992, own obs.).
Another cost of polyterritoriality might be an increased risk of extra pair
paternity in their first brood (Alatalo et al. 1984, 1989; Westneat et al.
1990; Lifjeld et al. 1991; Birkhead & Møller 1992; Gelter & Tegelström
1992). However, when a female appeared on the secondary territory, all

males relaxed the guarding of their primary territory/female and instead stayed most of their time on the secondary territory (III). Presumably they took a greater risk of losing the first territory and suffering from extra pair paternity. On the other hand, the only way for a male to successfully mate with a secondary female may be to spend as much time as possible with her during the early period of pair formation.

3.2 Mating success of polyterritorial males

The distance between the primary and secondary territory was the most important determinant of the mating success of a polyterritorial male (I). The mating success of males with a distant secondary territory was better than that of males with close territories. Not only the probability of attracting a secondary female was increased but also time until mating was reduced. This result confirms a crucial assumption of both the female-female aggression and the deception hypothesis. Males who have established a distant secondary territory may have been able to reduce aggression between their two mates or to hide their mating status from a mate seeking female.

The timing of establishment of a secondary territory or male's singing activity at the secondary territory did not affect the mating success of a male (I). However, males with a distant secondary territory seemed to allocate more time in singing there (I). Even though the singing activity did not have independent effect on male's mating success it still may partly explain the better mating success of males with more distant territories. If females are using singing behaviour to assess a male's mating status the already mated males with distant territories are most difficult to discriminate from unmated males. These are also the males who allocate least to parental care of the secondary brood (Lifjeld & Slagsvold 1989a, 1990).

The role of parasites on host ecology has been a neglected topic (see Toft & Karter 1990). It has been thought that well adapted parasites do not harm their hosts. However, nowadays there is growing evidence that parasites have an impact on great variety of host fitness components (e.g. Loye and Zuk 1991, references in reviews by Møller et al. 1990 and Clayton 1991). In pied flycatcher especially *Trypanosoma* infection was associated with male's arrival time to breeding grounds (II). Healthy males arrived on average earlier than infected males. The *Trypanosoma* infection may have lowered the condition of males and their ability to

moult and migrate. Early arriving males are usually those who successfully attract a secondary female (Lundberg & Alatalo 1992). Therefore, it is likely that healthy males most often succeed in obtaining an additional female and infected males may most often remain unmated.

3.3   Sexual conflict

When studying a polygynous mating system the crucial question is what are the benefits and costs for both sexes. Pied flycatcher males benefit from mating with more than one female (Alatalo & Lundberg 1990). They produce about one and half times so many fledglings than monogamous males. There is no evidence that polygynous males suffer from a greater risk of extra pair paternity than other males (Lifjeld et al. 1991).

Primary females of polygynous males seem to have somewhat reduced breeding success compared to simultaneously laying monogamous females (Stenmark et al. 1988, Alatalo & Lundberg 1990), because males reduce their assistance in the later part of nestling period (Stenmark et al. 1988, Alatalo & Lundberg 1990). Males primarily feed the nestlings in the first brood (Alatalo et al. 1982, Lifjeld & Slagsvold 1989a, 1990, Alatalo & Lundberg 1990). Therefore, secondary females seem to suffer a major cost from polygyny.

The breeding success of secondary females has been found to be 68 % of that of simultaneously laying monogamous and primary females (Alatalo & Lundberg 1990). However, this kind of comparison tells nothing about options available for females at the time of mating. Some females may well have acquired secondary status because there were no other options at the time of mating.

In study IV we used pairs of neighbouring (within 200 m) males attracting a female, one already mated male and one unmated male. We compared the breeding success of females who had chosen an already mated male to that of females who later mated with a neighbouring unmated male. In this comparison where females have freely mated polygynously it was possible to measure if females suffered from being secondary females or were they able to compensate the reduced assistance by males. Females that mated with an already mated male produced significantly fewer fledglings and with significantly lower body mass than females that mated later with a neighbouring unmated male. The estimated number of recruits produced by secondary females was 77 % of that of monogamous females. Therefore, secondary females suffered

a net cost from polygyny. There was no evidence that females who mated with an already mated male were poorer in quality. Secondary broods received about 50 % less male help than monogamous broods. The reduced breeding success of secondary females seems to be solely caused by reduced male assistance.

There is a clear conflict between sexes in the pied flycatcher. Males benefit from having more than one female and we may expect them to be selected to behave in the manner that increase the probability of achieving this goal. Polygyny is the preferred mating status for males. On the other hand, females do not benefit from polygyny. Instead, especially the secondary female suffers a considerable net cost from polygyny due to reduced male assistance during the nestling period. Therefore, monogamy is the most preferred mating status for females and we may expect them to be evolved to avoid polygynous matings. Polyandry might be even better for a female but very difficult to achieve.

3.4   Male polyterritoriality and female choice

There are some potential cues available for females that they could use to assess male's mating status. Already mated males behave somewhat differently compared to unmated ones (Stenmark et al. 1988, Searcy et al. 1991, III, IV). Hence, females might use the behaviour of males to estimate male's mating status. Another cue is the presence of the primary female. If a female discovers the primary female that will directly reveal male's mating status. The search cost hypothesis suggests that females are able to determine male's mating status irrespective to the distance between territories of a male. The probability for a secondary female to observe the existence of the primary female should decrease as the distance between male's territories increases. This is supported by the observation that primary females visited most often a secondary territory of a male when distance from their own nest was short (Slagsvold et al. 1992). Therefore, if females are able to determine male's mating status irrespective to the distance between male's territories, as suggested by the search cost hypothesis, they should base this on differences in male behaviour. The presence of the primary female is an easy cue that males, according to the deception hypothesis, are attempting to hide by being polyterritorial.

Polyterritorial males sometimes visited the primary territory while attempting to attract a secondary female (III). Consequently,

polyterritorial males were less present and sang at reduced rate on their secondary territories than did monoterritorial unmated males on their territories (III, IV). Even if there is a statistically significant difference in male behaviour we can not directly assume that females are using this difference to avoid polygyny or that it is easy to use this as a cue. There was a considerable overlap between mating categories both in the male presence and singing performance (III, IV). This may make it difficult for a female to correctly distinguish all polyterritorial males from unmated ones. From these two cues the singing performance is not as reliable indicator of male's mating status than male's presence at the territory because also some external factors, like weather, availability of food and time of the day, affect singing performance (Gottlander 1987, Alatalo et al. 1990b). Too exacting demands in addition would lead to increased risk of rejecting also unmated males and a further prolongation of the mate search process.

In study IV females were allowed to choose between neighbouring already mated polyterritorial male and unmated monoterritorial male who were simultaneously attempting to attract a female. The experimental design eliminated any temporal differences in male behaviour and minimized differences in territory quality and the cost of searching another male. Therefore, it is likely that the only remarkable difference between these two breeding opportunities was the male's mating status. Eleven females out of 20 mated with an already mated male. This result suggests clearly that females are not able to effectively distinguish already mated polyterritorial males from unmated ones even though they would have succeeded better in breeding by choosing unmated ones.

Further evidence for imperfect female behaviour comes from study V. Polyterritorial males occasionally visit the primary territory after having attracted a secondary female (Stenmark et al. 1988, III). Such brief visits, if anything else, are suggested to reveal male's mating status. Males were removed for a 30 to 60-min period from their territories soon after they had attracted a female there. This was to mimic a visit of a polyterritorial male to his primary territory and hence to show to a female that the male was likely to have another female elsewhere. Only three out of 14 females deserted their mates. There were unmated males available for females during male removals. Therefore the low desertion rate can not be explained by high search costs for an unmated male. A plausible explanation is that females have not evolved appropriate responses to such differences in male behaviour.

The search cost hypothesis does not explain why males are polyterritorial. To explain this feature of the mating system it has been proposed that males space out their territories to reduce aggression

between their two mates (Breiehagen & Slagsvold 1988). Slagsvold et al. (1992) tested five predictions derived from female-female aggression hypothesis and their results gave positive answers to each of their five predictions. They interpreted these results to be most consistent with the female-female aggression hypothesis. However, they do not clearly exclude the deception hypothesis as an alternative explanation as authors themselves also noted in their introduction. The results of the study by Slagsvold et al. (1992) suggest that a female may meet strong aggression by the already mated female when trying to settle close to that female's own nest. However, that study tells very little about the power of aggression by a primary female since they used caged females as intruders.

We moved secondary females closer to the primary females after their mating (VI). Our aim was to define closest distance where a secondary female can settle. This was to evaluate if monoterritorial polygyny is prevented by the aggression of the primary female. However, we were unable to find such threshold and in most cases we stopped moving female when the distance between nest boxes of two females was 20 m. Seven out of 9 secondary females remained with their mate during moving and the final distance in these trials ranged from 5 m to 20 m. Two secondary females deserted their nest boxes during the moving. One desertion was most probable due to interference by another pair of pied flycatchers which attempted to occupy the additional nest box used to assist moving. Results of this experiment suggest that the power of the aggression of primary females is too weak to prevent a secondary female to settle close by if the secondary female is willing to do it. A male with two females within 20 m can be regarded as monoterritorially polygynous.

3.5 Maladaptive female choice

Pied flycatcher females behave in a seemingly maladaptive way in their mate choice. They mate with an already mated male even though they have optional unmated males close by and they would do much better by choosing such an unmated male. We may ask why females have not evolved to effectively avoid polygyny?

One might expect selective forces to shape the behaviour of animals to be adaptive. However, evolution has its constraints and animals may not be as perfect as they could be (Maynard Smith 1978,

Gould & Lewontin 1979, Lewontin 1979, Dawkins 1982). For example adaptations need time to develop, there may not be genetic variation available for selection, or the costs of developing sensory systems exceed the benefits from it. Such evolutionary constraints may have restricted behaviour of pied flycatcher females to evolve in a perfectly adaptive way with regard to the polygyny avoidance. One more constraint may be that females are presumably selected to mate with a male of good quality. Polyterritorial males are likely to be of good quality, except that they do not assist in feeding of young. Hence, the polygyny avoidance presupposes rejecting males of good quality and this kind of behaviour is unlikely to evolve.

We might expect females to choose a breeding situation where their expected breeding success is highest. This may not be an easy task for females.

> In choosing among potential breeding situations, females are faced with a difficult sampling problem. They must depend on an array of predictive cues, each with differing reliability, and the use of one set of cues may often preclude the use of another. The actual criteria used by females to make their choices depends on how reliable potential cues are as predictors of success and how costly they are to assess. (Wittenberger 1979).

In the pied flycatcher two most important factors that affect breeding success of an individual female are nest predation and male's assistance during breeding (Alatalo et al. 1982, 1990a, Nilsson 1984, Lundberg & Alatalo 1992). Pied flycatcher females are forced to make a fast decision concerning mate and territory choice since breeding prospects of a female decrease rapidly as the season progresses (e.g. Lundberg & Alatalo 1992). The time consuming inspection of breeding opportunities is costly and therefore females are likely to use simple rules when choosing a breeding situation.

Even though nest predation is not strictly predictable the risk of nest predation is related to properties of the nest site (Alatalo et al. 1990a). Females may effectively reduce the risk of predation by choosing safe nest holes. Indeed, females are clearly choosing their breeding situation according to nest hole characteristics (Alatalo et al. 1986, Slagsvold 1986, Alatalo et al. 1988). On the contrary, the evidence of female preference for male characteristics is controversial (Alatalo et al. 1986, 1990c, Slagsvold 1986, Järvi et al. 1987, Lifjeld & Slagsvold 1988). There is a great variation in the behaviour of polyterritorial males and it is, moreover, overlapping with the behaviour of unmated males (Searcy et al. 1991, III, IV). It could be very difficult and costly for a female to effectively distinguish between already mated polyterritorial males and

unmated males even though there are possible cues available. Predation may affect more strongly on the breeding success and survival prospects of a female than male's mating status (Alatalo et al. 1982, 1990a, Nilsson 1984, Lundberg & Alatalo 1992, IV) and it might well be that females base their choice of a breeding situation primarily on the characteristics of the territory, e.g. quality of nest hole, and not on the male characteristics.

4   CONCLUSIONS

Females did not avoid polygynous matings even though they had optional unmated males close by. Females would have succeeded much better in breeding by choosing an unmated male. Already mated polyterritorial males spent on average less time on their second territory than did unmated males on their single territory. They also sang at reduced rate compared to unmated males. Therefore, females might be able to estimate male's mating status by using the behaviour of a male as a criterion. However, due to overlap in the behaviour of males females may not be able to accurately distinguish males of different mating status.

The aggression of primary female seems not to be a sufficient explanation to polyterritoriality of males. Secondary females were not prevented by the aggression of the primary female to settle close to the primary female's nest when they were moved closer to that nest.

The results of this study support the view that males are polyterritorial in order to make it more difficult for females to obtain reliable information about male's mating status. Evolutionary constraints may have restricted the behaviour of pied flycatcher females to evolve in a strictly adaptive way in regard to the polygyny avoidance. Females may also base the choice of their breeding situation primarily on nest site quality and not on male characteristics.

Acknowledgements

Yhteenveto

Kirjosiepon monireviirinen moniavioisuus

Polygynia on pariutumisjärjestelmä, jossa yksi koiras pariutuu useamman kuin yhden naaraan kanssa. Kirjosieppo (*Ficedula hypoleuca*) on tällainen moniavioinen lintulaji. Osa koiraista onnistuu houkuttelemaan toisen ja joskus jopa kolmannenkin naaraan. Kirjosiepon moniavioisuuden erityispiirre on monireviirisyys (polyterritoriaalisuus). Koiras ei yritä houkutella toista naarasta reviirille, jossa ensimmäinen . naaras pesii, vaan valtaa toisen erillisen reviirin kauempaa. Yleensä koiraat siirtyvät toiselle reviirille heti kun ensimmäinen naaras on aloittanut muninnan. Riippumatta siitä, onnistuuko koiras toisen naaraan houkuttelussa, se palaa ensimmäisen naaraan luokse ja auttaa sitä poikasten ruokinnassa. Toinen naaras saa vain vähän apua poikasten ruokinnassa, ja monet niistä joutuvat kasvattamaan pesyeensä yksin. Koiraan ruokinta-avun vähäisyyden vuoksi toisen naaraan pesimä-menestys on pienempi kuin ensimmäisen tai yksiavioisen naaraan.

Ymmärtääksemme paremmin kirjosiepon pariutumisjärjestelmän meidän täytyy pyrkiä vastaamaan kahteen tärkeään kysymykseen: (1) Miksi koiraat yrittävät houkutella toisen naaraan erilliselle reviirille, ja (2) miksi jotkut naaraat pariutuvat jo pariutuneen koiraan kanssa, vaikka se heikentää pesimämenestystä? Tässä tutkimuksessa pyrin vastaamaan näihin kysymyksiin.

Eräs esitetyistä hypoteeseista pystynee vastaamaan molempiin kysymyksiin. Koiraiden on arveltu siirtyvän erilliselle toiselle reviirille salatakseen sen, että ne ovat jo pariutuneita (pettämishypoteesi). Näinollen naaraat pariutuisivat aikaisemmin pariutuneiden koiraiden kanssa vastoin parempaa tietoa. Toinen ratkaisumalli koostuu kahdesta eri hypoteesistä. Koiraiden monireviirisyyden syy voisi olla se, että ne näin vähentävät naaraiden välistä agressiivisuutta (naaraiden välinen agressiivisuus -hypoteesi). Naaraiden on arveltu kykenevän erottamaan pariutuneen koiraan pariutumattomasta, mutta osa pariutuisi jo pariutuneiden koiraiden kanssa tietoisesti, koska pariutumattoman koiraan etsintäkustannukset olisivat suuremmat kuin kustannukset koiraan ruokinta-avun vähäisyydestä (etsintäkustannushypoteesi).

Pariutuneet koiraat viettivät vähemmän aikaa toisella reviirillään kuin pariutumattomat koiraat ainoalla reviirillään. Siten naaraat voisivat pystyä arvioimaan koiraan käyttäytymisestä, onko se jo pariutunut vai ei. Kaikkien koiraiden luokitteleminen oikein ei ole kuitenkaan helppoa,

koska useat monireviiriset koiraat käyttäytyvät samalla tavalla kuin pariutumattomatkin.

Naaraille järjestettiin tilaisuus valita puoliso kahdesta lähekkäisestä koiraasta, joista toinen oli toisella reviirillään oleva jo pariutunut koiras ja toinen pariutumaton koiras. Yksitoista naarasta 20:stä valitsi jo pariutuneen koiraan. Naaraat eivät selvästikään välttäneet pariutuneita koiraita, vaikka niiden pesimämenestys olisi ollut parempi, jos ne olisivat valinneet pariutumattoman koiraan. Myöskään toisessa kokeessa, jossa jäljiteltiin monireviirisen koiraan käyttäytymistä heti pariutumisen jälkeen, naaraat eivät reagoineet siten, että ne olisivat välttäneet jo pariutuneet koiraat.

Naaraiden välisen agressiivisuuden vaikutusta testattiin siirtämällä toinen naaras pariutumisensa jälkeen lähemmäksi ensimmäistä naarasta. Seitsemässä tapauksessa yhdeksästä lopullinen etäisyys koiraan kahden naaraan välillä oli 20 m tai vähemmän. Siten naaraiden välinen agressiivisuus ei näyttäisi olevan syynä koiraiden monireviirisyyteen.

Todennäköisin selitys kirjosiepon monireviiriselle moniavioisuudelle on se, että koiraat siirtyvät houkuttelemaan toista naarasta erilliselle reviirille salatakseen olevansa jo pariutuneita ja että osa naaraista pariutuu monireviiristen koiraiden kanssa tietämättä niiden olevan jo pariutuneita.

REFERENCES

Alatalo, R.V. & Lundberg, A. 1984: Polyterritorial polygyny in the pied flycatcher Ficedula hypoleuca - evidence for the deception hypothesis. - Ann. Zool. Fennici 21: 217-228.

Alatalo, R.V. & Lundberg, A. 1986: The sexy son hypothesis: data from the pied flycatcher Ficedula hypoleuca. - Anim. Behav. 34: 1454-1462.

Alatalo, R.V. & Lundberg, A. 1990: Polyterritorial polygyny in the pied flycatcher. - In: P.J.B. Slater, J.S. Rosenblatt & C. Beer (eds), Advances in the study of behaviour 19: 1-27. San Diego, Academic Press.

Alatalo, R.V., Carlson, A., Lundberg, A. & Ulfstrand, S. 1981: The conflict between male polygamy and female monogamy: the case of the pied flycatcher Ficedula hypoleuca. - Am. Nat. 117: 738-753.

Alatalo, R.V., Lundberg, A. & Ståhlbrandt, K. 1982: Why do pied flycatcher females mate with already-mated males? - Anim. Behav. 30: 585-593.

Alatalo, R.V., Gustafsson, L. & Lundberg, A. 1984: High frequency of cuckoldry in pied and collared flycatchers. - Oikos 42: 41-47.

Alatalo, R.V., Lundberg, A. & Glynn, C. 1986: Female pied flycatcher choose territory quality and not male characteristics. - Nature 323: 152-153.

Alatalo, R.V., Gottlander, K. & Lundberg, A. 1987: Extra-pair copulations and mate guarding in the polyterritorial pied flycatcher, Ficedula hypoleuca. - Behaviour 101: 139-155.

Alatalo, R.V., Carlson, A. & Lundberg, A. 1988: The search cost in mate choice of the pied flycatcher. - Anim. Behav. 36: 289-291.

Alatalo, R.V., Gustafsson, L. & Lundberg, A. 1989: Extra-pair paternity and heritability estimates of tarsus length in pied and collared flycatchers. - Oikos 56: 54-58.

Alatalo, R.V., Carlson, A. & Lundberg, A. 1990a: Polygyny and breeding success of pied flycatchers nesting in natural cavities. - In: J. Blondel, A. Gosler, J.-D. Lebreton & R. McCleery (eds), Population biology in passerine birds. An integrated approach: 323-330. Berlin, Springer.

Alatalo, R.V., Glynn, C. & Lundberg, A. 1990b: Singing rate and female attraction in the pied flycatcher: an experiment. - Anim. Behav. 39: 601-603.

Alatalo, R.V., Lundberg, A. & Sundberg, J. 1990c: Can female preference explain sexual dichromatism in the pied flycatcher, Ficedula hypoleuca? - Anim. Behav. 39: 244-252.

Altmann, S.A., Wagner, S.S. & Lenington, S. 1977: Two models for the evolution of polygyny. - Behav. Ecol. Sociobiol. 2: 397-410.

Birkhead, T.R. & Møller, A.P. 1992: Sperm competition in birds: Evolutionary causes and consequences. London, Academic Press.

Breiehagen, T. & Slagsvold, T. 1988: Male polyterritoriality and female-female aggression in pied flycatchers Ficedula hypoleuca. - Anim. Behav. 36: 604-606.

Clayton, D.H. 1991: The influence of parasites on host sexual selection. - Parasitology Today 7: 329-334.

Davies, N.B. 1989: Sexual conflict and the polygamy threshold. - Anim. Behav. 38: 226-234.

Dawkins, R. 1982: The extended phenotype. 307 p. Oxford, W.H. Freeman and Company.

Emlen, S.T. & Oring, L.W. 1977: Ecology, sexual selection, and the evolution of mating systems. - Science 197: 215-223.

Gelter, H.P. & Tegelström, H. 1992: High frequency of extra-pair paternity in Swedish pied flycatchers revealed by allozyme electrophoresis and DNA fingerprinting. - Behav. Ecol. Sociobiol. 31: 1-7.

Gottlander, K. 1987: Variation in the song rate of the male pied flycatcher Ficedula hypoleuca: causes and consequences. - Anim. Behav. 35: 1037-1043.

Gould, S.J. & Lewontin, R.C. 1979: The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. - Proc. R. Soc. Lond. B205: 581-598.

von Haartman, L. 1951: Successive polygamy. - Behaviour 3: 256-274.

von Haartman, L. 1956: Territory in the pied flycatcher (Muscicapa hypoleuca). - Ibis 98: 460-475.

von Haartman, L. 1969: Nest-site and evolution of polygamy in European passerine birds. - Ornis Fennica 46: 1-12.

Hasselquist, D. & Bensch, S. 1991: Trade-off between mate guarding and mate attraction in the polygynous great reed warbler. - Behav. Ecol. Sociobiol. 28: 187-193.

Järvi, T., Røskaft, E., Bakken, M. & Zumsteg, B. 1987: Evolution of variation in male secondary sexual characteristics: a test of eight hypotheses applied to pied flycatcher. - Behav. Ecol. Sociobiol. 20: 161-169.

Karlsson, L., Persson, K. & Wallinder, G. 1986: Ageing and sexing in pied flycatchers, Ficedula hypoleuca. - Vår Fågelv. 45: 131-146. (In Swedish with English summary)

Lewontin, R.C. 1979: Sociobiology as an adaptationist program. - Behav. Sci. 24: 5-14.

Lifjeld, J.T. & Slagsvold, T. 1988: Female pied flycatchers Ficedula hypoleuca choose male characteristics in homogenous habitats. - Behav. Ecol. Sociobiol. 22: 27-36.

Lifjeld, J.T. & Slagsvold, T. 1989a: Allocation of parental investment by polygynous pied flycatcher males. - Ornis Fennica. 66: 3-14.

Lifjeld, J.T. & Slagsvold, T. 1989b: Female nutritional state influences the allocation of incubation feeding by polygynous pied flycatcher males. - Anim. Behav. 38: 903-904.

Lifjeld, J.T. & Slagsvold, T. 1990: Manipulations of male parental investment in polygynous pied flycatchers, Ficedula hypoleuca. - Behav. Ecol. 1: 48-54.

Lifjeld, J.T., Slagsvold, T. & Stenmark, G. 1987: Allocation of incubation feeding in a polygynous mating system: a study on pied flycatchers Ficedula hypoleuca. - Anim. Behav. 35: 1663-1669.

Lifjeld, J.T., Slagsvold, T. & Lampe, H.M. 1991: Low frequency of extra-pair paternity in pied flycatchers revealed by DNA fingerprinting. - Behav. Ecol. Sociobiol. 29: 95-101.

Lightbody, J.P. & Weatherhead, P.J. 1988: Female settling patterns and polygyny: tests of neutral-mate-choice hypothesis. - Am. Nat. 132: 20-33.

Loye, J.E. & Zuk, M. (eds) 1991: Bird-parasite interactions: ecology, evolution, and behaviour. 406 p. Oxford, Oxford University Press.

Lundberg, A. & Alatalo, R.V. 1992: The pied flycatcher. 267 p. London, T & A D Poyser.

Maynard Smith, J. 1978: Optimization theory in evolution. - Ann. Rev. Ecol. Syst. 9: 31-56.

Meier, P.T. 1983: Polyterritorial polygyny in the pied flycatcher: male deception or female choice? - Am. Nat. 121: 145-147.

Møller, A.P., Allander, K. & Dufva, R. 1990: Fitness effects of parasites on passerine birds: a review. - In: J. Blondel, A. Gosler, J.-D. Lebreton & R. McCleery (eds), Population biology of passerine birds. An integrated approach: 269-280. Berlin, Springer.

Nilsson, S.G. 1984: Clutch size and breeding success of the pied flycatcher Ficedula hypoleuca in natural tree-holes. - Ibis 126: 407-410.

Orians, G.H. 1969: On the evolution of mating systems in birds and mammals. - Am. Nat. 103: 589-603.

Searcy, W.A., Eriksson, D. & Lundberg, A. 1991: Deceptive behavior in pied flycatchers. - Behav. Ecol. Sociobiol. 29: 167-175.

Silverin, B. 1980: Effects of long-acting testosterone treatment on freeliving pied flycatchers, Ficedula hypoleuca, during the breeding period. - Anim. Behav. 28: 906-912.

Slagsvold, T. 1986: Nest site settlement by the pied flycatcher: does the female choose her mate for the quality of his house or himself? - Ornis Scand. 17: 210-220.

Slagsvold, T. & Lifjeld, J.T. 1986: Mate retention and male polyterritoriality in the pied flycatcher Ficedula hypoleuca. - Behav. Ecol. Sociobiol. 19: 25-30.

Slagsvold, T., Amundsen, T., Dale, S. & Lampe, H. 1992: Female-female aggression explains polyterritoriality in male pied flycatchers. - Anim. Behav. 43: 397-407.

Stenmark, G., Slagsvold, T. & Lifjeld, J.T. 1988: Polygyny in the pied flycatcher, Ficedula hypoleuca: a test of the deception hypothesis. - Anim. Behav. 36: 1646-1657.

Toft, C.A. & Karter, A.J. 1990: Parasite-host coevolution. - Trend. Ecol. Evol. 5: 326-329.

Trivers, R.L. 1972: Parental investment and sexual selection. - In: B. Campbell (ed.), Sexual selection and the descent of man: 136-179. Chicago, Aldine.

Weatherhead, P.J. & Robertson, R.J. 1979: Offspring quality and the polygyny threshold: 'the sexy son hypothesis'. - Am. Nat. 113: 201-208.

Westneat, D.F., Sherman, P.W. & Morton, M.L. 1990: The ecology and evolution of extra-pair copulations in birds. - In: D.M. Power (ed.), Current Ornithology 7: 331-369. New York, Plenum Press.

Winkel, W. & Winkel, D. 1984: Polygynie des Trauerschnäppers (Ficedula hypoleuca) am Westrand seines Areals in Mitteleuropa. - J. Ornithol. 125: 1-14.

Wittenberger, J.F. 1979: The evolution of mating systems in birds and mammals. - In: P. Master & J. Vandenburgh (eds), Handbook of behavioral neurobiology: social behavior and communication, vol. 3: 271-349. New York, Plenum Press.

ORIGINAL PAPERS

I

Determinants of the mating success of polyterritorial pied flycatcher males

by

Osmo Rätti & Rauno V. Alatalo

II

Blood parasites and male fitness in the pied flycatcher

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Female attraction behaviour of radio tagged polyterritorial pied flycatcher males

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IV

Male polyterritoriality and imperfect female choice in the
pied flycatcher, *Ficedula hypoleuca*

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Rauno V. Alatalo, Arne Lundberg & Osmo Rätti

V

Female reactions on male absence at mating in the pied flycatcher

by

Osmo Rätti

Manuscript (Submitted), 1993

VI

Female-female aggression and male polyterritoriality in the pied flycatcher

by

Osmo Rätti, Rauno V. Alatalo, Janne Kilpimaa & Pirkko Siikamäki

Manuscript (Submitted), 1993