Female pied flycatchers trade between male quality and mating status in mate choice

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According to mate choice theory, females should consider both male quality and mating status when choosing a mate. In birds, strong experimental evidence indicates that females prefer males with elaborate traits. No comparable evidence exists to determine whether females take male mating status into account or how they may trade between male quality and male mating status. We studied mate choice of female pied flycatchers (*Ficedula hypoleuca*) in outdoor aviaries where the effect of territory quality could be eliminated and where we could control which males were mated and which were unmated. We used male plumage colour as our measure of male quality. In the aviaries, focal females could easily compare males and assess their plumage colour and mating status, and resident females were prevented from attacking prospecting females because of separation in different compartments. The study provided evidence for a trade-off in mate choice. Females may compromise by choosing an already mated male if he is more brightly coloured and, presumably, of higher quality than available unmated males. The study did not support the idea that polygyny is based on male deception of females, but the results were consistent with the female aggression hypothesis.

Keywords: sexual selection; mate choice; polygyny threshold; plumage colour; *Ficedula hypoleuca*

1. INTRODUCTION

According to mate choice theory (Orlans 1969; Davies 1991; Andersson 1994), females consider both male quality and mating status when choosing a mate. They prefer high-quality males to provide favourable genes for the offspring (ensuring high viability, development of attractive sexual traits, etc.; Weatherhead & Robertson 1979; Andersson 1994; Iwasa & Pomiankowski 1994; Petrie 1994) and they prefer unmated males to ensure male parental care (Orlans 1969; Davies 1991; Slagsvold & Lifjeld 1994). In birds, strong experimental evidence indicates that females prefer males with elaborate traits, such as bright and symmetrical plumage colours (Hill 1991; Swaddle & Cuthill 1994; Bennett *et al.* 1996; Sætre *et al.* 1997), large and symmetrical feather ornaments (Andersson 1982; Møller 1992; Petrie & Halliday 1994) and large song repertoire sizes (Catchpole *et al.* 1984; Lampe & Sætre 1995). No comparable evidence exists to determine whether females take male mating status into account or how they may trade between male quality and male mating status. Here we provide experimental evidence for such a trade-off in pied flycatchers (*Ficedula hypoleuca*).

Polygyny is found in a number of territorial birds in which males provide parental care (Møller 1986; Davies 1991). The polygyny threshold model (Orlans 1969; Wittenberger 1976) predicts under which circumstances a female should prefer an already mated male over an unmated male. This should occur when the difference in

breeding situation quality between the two males is so greatly in favour of the already mated male that it compensates for the expected costs of polygyny, such as reduced male parental care to harem females. Hence, females should prefer unmated males but trade this against male quality and territory quality. In nature, it is difficult to prove that females take male mating status into account in mate choice. This is because females may also pay attention to other factors of importance in breeding success, such as male and territory quality. Mated males may be of higher quality than unmated males and they may occupy better territories and nest sites, making it difficult to prove an effect of mating status *per se*. In addition, prospecting females may be unaware of male mating status (Alatalo *et al.* 1981; Searcy & Yasukawa 1989) and aggressive resident females may prevent intruding females from settling with their mate (Slagsvold & Lifjeld 1994; Sandell & Smith 1996). To circumvent these problems, we studied mate choice of female pied flycatchers in outdoor aviaries, where the effect of territory quality could be eliminated and where we could control which males were mated and which were unmated. In the aviaries, focal females could easily compare males and assess their mating status, and resident females were prevented from attacking prospecting females because of separation in different compartments.

2. METHODS

(a) General methods

Females were allowed to choose between a mated male and an unmated male, which were presented simultaneously, and the chosen male was regarded as the one advertising the nest-box in

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which the female started to build a nest. We used plumage colour as our measure of male quality. In pied flycatchers, black males tend to be older (Lundberg & Alatalo 1992), arrive earlier in spring (Lundberg & Alatalo 1992), have larger song repertoires (Lampe & Espmark 1994) and provide more food to the young (Sætre *et al.* 1995) than brown males. Colour is partly heritable (Lundberg & Alatalo 1992; Slagsvold & Lifjeld 1992).

The experiment was conducted under a licence from the Directorate for Nature Management in Norway and was carried out on the campus of the University of Oslo, Norway, in May and June 1995–1998. Females could choose between two males in seven outdoor aviaries (3 m × 3 m × 1.9 m; figure 1) each divided into three compartments: (i) for a male (called mated male) and a female (called resident female) that we had put in the same compartment, (ii) for an unmated male, separated from the pair by an opaque wall and (iii) for the focal female, separated from the male compartments by transparent nylon netting. Nylon netting was also used for the outer walls and roof. We set up a nest-box with two entrance holes, one for the male (and resident female when present) and one for the focal female, between each male compartment and the female one. Internally, the nest-box was divided into two compartments by a cardboard plate. Food (mealworms) and water were available *ad libitum* and dried grass and leaves served as nesting materials (only females build nests). Shelter and small trees were also provided. The two males were allowed to stay in the aviary for at least 4 h (usually 1 d) for habituation before the resident female was introduced. Where to place the males and the resident female was decided by flipping a coin.

Male plumage colour was scored before a trial according to Drost's (1936) seven-point scale. We used a black and a brown male in 18 trials (the difference in colour score was 2.5–4.5 units), whereas both males were black in 13 trials. Most focal females were introduced 5–6 h (range 0–13 d) after the resident female because such a time delay is significant when females compete for nest sites in nature (Dale & Slagsvold 1995). Eighteen of the resident females had started nest building when the focal female was introduced and one of these had also started egg laying. Earlier experiments using the same aviaries showed that male display behaviour may be important in mate choice (Slagsvold & Viljugrein 1999). When the focal female was introduced, we observed the birds' behaviour from a hide ca. 1 m from the aviary for 30 min. As a measure of amount of male display we used the number of minutes (out of 30) during which a male displayed one or more times by song, enticement calls or nest-box visits. In seven trials no observations of behaviour were made because of time constraints.

Trials were terminated at least one day after the focal female had started nest building to see whether she built in more than one nest-box. We used 'first building' as our criterion for mate choice because this was comparable with an earlier aviary experiment on plumage colour (Sætre *et al.* 1994). Only a few females changed their decisions (three females switched building activity from the mated to the unmated male and three switched from the unmated to the mated male).

Males ($n=50$) were caught at four nest-box areas around Oslo. Females ($n=52$) were captured in different areas from those in which the relevant males in a trial had been caught. Keeping of birds followed the procedure used in earlier experiments (Sætre *et al.* 1994; Slagsvold & Viljugrein 1999). A few birds were used in two different trials because of lack of birds and because of the short breeding season of the species. New males were used in each trial except in six cases. In one case

Figure 1. Cross-section viewed from above of the aviary used in mate choice experiments on pied flycatchers. Dashed lines, nylon netting walls; solid line, opaque wall. Nest hole entrances are indicated by a cross.

with a black and a brown male, the males were put in opposite compartments in the second trial and the resident female (a new one) was with the opposite male. In another case, the resident female was introduced 5 h before the focal female in the first trial and 11 d before in the second trial with the same males (but with new females). In four cases, the focal female in the initial trial was let into the chosen mate in the second trial, serving as resident female (she always continued nest building) and a new female was allowed to choose as focal female. This was to save time and to increase the sample of cases with long time intervals between introduction of resident and focal females. This procedure was conservative with respect to the hypothesis tested, i.e. that females prefer unmated males: the unmated males may have been of inferior quality in these trials because they had been rejected in the initial trial. Four more trials were of this kind but in these cases the initial trials were part of another study with a slightly different method used (Slagsvold & Viljugrein 1999) and, therefore, these initial trials are not included here. Hence, the latter males were new with respect to the present study.

Females were only used once as focal females except that one female was given a choice between a black and a brown coloured male in one trial and between two black coloured males in another trial. The two trials were in different cages and with different resident females. Focal females were never used as resident females in an earlier trial. Nine resident females were used in an earlier trial, as focal ($n=8$) or resident females ($n=1$).

(b) Statistical analysis

We used logistic regression to analyse the data. The dependent variable was whether the focal female chose the male in the right or the left compartment. The independent variables were mating status of the male in the right compartment (mated or unmated; the left male had opposite mating status), the difference in colour score between the two males, number of hours elapsing between introduction of resident and focal females ($\log_{10}(X+1)$ transformed), whether or not the resident female

Figure 2. Percentage of female pied flycatchers choosing a mated male (open bars) or an unmated male (solid bars) in paired tests, depending on plumage colour of the males compared. Sample sizes above bars.

had started nest building when the focal female was introduced, number of days (0–5) elapsing from when the focal female was introduced until she started nest building, difference in display score between the two males, year of study, date of introduction of focal female (16 May–11 June) and aviary used.

The statistical tests were two-tailed unless stated otherwise. We had reason to expect that male mating success would be higher for black than for brown males (Sætre *et al.* 1994) and higher for unmated than for mated males (Slagsvold & Dale 1994; Dale & Slagsvold 1996). Hence, in these comparisons one-tailed tests were employed.

3. RESULTS

Focal females preferred the black male in 14 of the 18 trials that included a black and a brown male (figure 2; $\chi^2_1 = 5.56$ and $p = 0.009$, one-tailed). They chose the unmated male in 19 of the 31 trials, which was not significantly different from random choice ($\chi^2_1 = 1.58$ and $p = 0.10$, one-tailed), showing that male quality was more important than male mating status. However, multiple logistic regression analysis of the total sample ($n = 31$) showed that focal females considered both male mating status ($\chi^2_1 = 4.36$ and $p = 0.018$, one-tailed) and male plumage colour ($\chi^2_1 = 6.40$ and $p = 0.006$, one-tailed) in mate choice. The result held true when potentially confounding factors were included in the analysis (table 1). There was no significant effect of amount of time elapsing between introduction of resident and focal females into the aviary, whether the resident female had started nest building when the focal female was introduced or of time elapsing from when the focal female was introduced until she started nest building (table 1). Further analyses of female mate choice with male mating status and male plumage colour as independent variables showed no effect of male display behaviour ($\chi^2_1 = 0.14$, $p = 0.70$ and $n = 24$), year of trial ($\chi^2_3 = 0.49$, $p = 0.92$ and $n = 31$), date of trial ($\chi^2_1 = 0.76$, $p = 0.38$ and $n = 31$) or aviary used in a trial ($\chi^2_6 = 0.49$, $p = 0.99$ and $n = 31$).

Two other sources of data suggest that male mating status was important. First, as explained in §2, some focal females added nesting materials to both nest-boxes

Table 1. Multiple logistic regression analysis of mate choice of 31 female pied flycatchers

variable	χ^2_1	p
male mating status	4.39	0.018 ^a
male plumage colour	5.83	0.008 ^a
time elapsing between entry of resident and focal female	0.22	0.640
nest building of resident female before entry of focal female	0.05	0.820
time elapsing between entry and onset of nest building by focal female	0.24	0.620

^a One-tailed test.

provided. When the brown male was mated and the black male was unmated, the focal female started nest building with the brown male in none of seven trials (figure 2) but added some nesting materials to his nest-box later on in one trial. When the brown male was unmated and the black male was mated, the focal female started nest building with the brown male in four out of 11 trials (figure 2) and she added some nesting material to the nest-box of the brown male in another four trials. Hence, in total, the focal female added nesting materials to the nest-box of the brown male in eight out of 11 trials when the brown male was unmated and the black male was mated, but this occurred in only one out of seven trials when the brown male was mated and the black male was unmated ($p = 0.024$, Fisher exact probabilities test, one-tailed).

Second, in an earlier study on pied flycatchers using the same aviaries, we found that, when given a choice between two black, unmated males, two different females preferred the same male independently of each other in seven out of eight trials (Slagsvold & Viljugrein 1999). In some of the present trials, two different focal females were also allowed to choose between the same pair of males. However, in eight cases the male preferred by the focal female in the first trial was mated in the second trial (with the focal female from the first trial; see §2). We found that only three of the eight focal females repeated the mate choice of the first female, which is nearly significantly different from the earlier result when both males were unmated (namely seven out of eight; $p = 0.056$, Fisher exact test, one-tailed).

4. DISCUSSION

We found that both male mating status and male plumage colour were important in female choice of mate, confirming current mate choice theory (Davies 1991; Andersson 1994). This shows that the polygyny threshold is not only influenced by differences in the quality of breeding resources defended by males (Orlans 1969) but by differences in quality among males, females being willing to accept an already mated male if he is of higher quality than available unmated males.

It has been suggested that polygyny in some species, such as the pied flycatcher, is based on deception, mated males trying to hide their mating status by moving some distance away from their first nest to advertise for a new mate (Alatalo *et al.* 1981). The present study does not support this idea because polygyny occurred when it was

easy for females to assess male mating status. The results are consistent with the alternative female aggression hypothesis, stating that mated males defend separate territories to avoid aggression from the primary female (Slagsvold *et al.* 1992; Slagsvold & Lifjeld 1994). In the aviaries, resident females were prevented from attacking the focal female. This may explain the high proportion of females choosing the mated male (12 out of 31; figure 2), a higher proportion than that found among prospecting females sampling both mated and unmated males in the field (Slagsvold & Dale 1994; Dale & Slagsvold 1996). The present study shows that females do not regard a nest site and a male as being totally unavailable simply from encountering another female near the nest site in company with the male. Hence, they do not seem to respect ownership without testing the owner. The results are similar to those of a field experiment on the same species in which resident females were experimentally prevented from attacking intruding females by enclosing them in their own nest-box; this increased the mating success of their mates (Slagsvold *et al.* 1999). The results are also consistent with an earlier aviary study suggesting that female pied flycatchers do not copy the mate choice of others but choose a mate independently (Slagsvold & Viljugrein 1999). Finally, we found that most females preferred black males and rejected brown males, which is similar to the results of descriptive field studies and also to the result of an aviary experiment where effects of male age were controlled for by painting one of two brown males black (Sætre *et al.* 1994).

The aviary conditions may have limitations in expressing the natural situation with regard to male and female mating status. Mated males seemed to court females normally by frequently displaying at the nest-box, entering it and uttering enticement calls. Resident and focal females often tried to attack each other. We did not quantify such aggression because of time constraints; we focused on male behaviour because this was found to be important in another mate choice study (Slagsvold & Viljugrein 1999). However, aggression by resident females can hardly explain the results with regard to male plumage colour and male mating status, because we can see no reason why resident females should behave more aggressively when their own mate was brown than when he was black.

When choosing the mated male, the focal female built her nest in the same nest-box as the resident female. Hence, she may have regarded the situation as if she had displaced the resident female and, thereby, succeeded to mate monogamously. This explanation is not likely, however, because the resident female was still together with the male and involved in normal breeding activities, such as entering the nest-box with nesting materials and copulating with the male. Notice also that the nest-boxes had separate entrances and that the interiors were completely separated by a cardboard plate (figure 1). Field studies have shown that secondary females do not usually visit or enter the nest site of the resident (primary) female when they settle (H. Rinden and T. Slagsvold, unpublished telemetric data).

The resident female may have regarded the situation as if she was defending her own nest site and not a secondary nest site of her mate. We do not think this

confounded our conclusion because we can see no reason why a resident female should defend her own nest site to a lesser extent than her mate's secondary nest site. Under natural conditions, resident females show similar behaviour at both sites. They try to prevent intruding females from entering the nest cavity by jumping inside and blocking the entrance hole (Slagsvold *et al.* 1992; Dale & Slagsvold 1995). In the present study, such behaviour was prevented by separation of the females in the aviary.

In birds with biparental care, including the pied flycatcher, harem females often fledge fewer chicks than females mated with monogamous males. This seems to be caused by less male assistance in the case of polygyny (Slagsvold & Lifjeld 1994). Why then do some females settle with already mated males? One explanation is lack of unmated males and restricted mate search by females (Stenmark *et al.* 1988; Slagsvold & Lifjeld 1994). Another explanation is that females trade between male quality and male mating status, as shown in the present study. Females may compromise by choosing a mated male of high quality that can provide favourable genes for the offspring, or by choosing an unmated male of lower quality but which can provide higher amounts of parental care. When monogamously mated, a black male may provide more food to the brood than a brown male (Sætre *et al.* 1995) and, hence, in cases of high risk of nest and adult predation, as may occur in hole-nesting flycatchers (e.g. Walankiewicz 1991; Slagsvold & Dale 1996), some females may benefit from choosing a black male even when he is mated because the brood will receive high amounts of male care if the other female and nest fail (Bensch & Hasselquist 1991; Lifjeld & Slagsvold 1991; Sonerud 1992).

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