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Source: *Evolution*, Jun., 1991, Vol. 45, No. 4 (Jun., 1991), pp. 910–917

Published by: Society for the Study of Evolution

Stable URL: https://www.jstor.org/stable/2409698

EVOLUTION OF PLUMAGE COLOR IN MALE PIED FLYCATCHERS (*FICEDULA HYPOLEUCA*): EVIDENCE FOR FEMALE MIMICRY

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Abstract.—We present the first evidence for sexual deception by female mimicry in birds. Using live, caged birds we show that territorial male pied flycatchers behave aggressively toward bright-colored males but display sexually toward female-like male intruders. We also show that the males that are fooled are those that lack recent sexual experience. All male pied flycatchers are dull-colored in winter. It is possible that young males are more constrained during the spring molt than older males since the former are more dull-colored in spring. According to the molt-constraints hypothesis a subadult plumage would be maladaptive in the breeding season. Analysis of male settling pattern at breeding sites in spring suggests that brownish males are allowed to settle closer to already-established males than dark-colored males. This result suggests an adaptive value of having a subadult plumage color, in particular for young males arriving late from spring migration. However, we also show that mimicry incurs a cost, that of increased aggression from females, which may explain why female-like males have reduced mating success.

Key words.—Delayed plumage maturation, female mimicry, *Ficedula hypoleuca*, plumage color, sexual selection.

In many sexually dichromatic birds the males have a rather female-like plumage color in their first breeding season (Rohwer et al., 1980; Studd and Robertson, 1985*a*; Lyon and Montgomerie, 1986). A number of hypotheses have been proposed to explain this pattern, dealing with individual recognition (Rohwer, 1982), delay of sexual maturation (Selander, 1965), delay of reproductive effort (Procter-Gray and Holmes, 1981; Studd and Robertson, 1985*a*), status signaling (Rohwer et al., 1980; Foster, 1987; Slagsvold and Lifjeld, 1988*a*), and spring molt constraints (Rohwer and Butcher, 1988; Rohwer and Manning, 1990). According to the female mimicry hypothesis (Rohwer, 1978; Rohwer et al., 1980), a female-like plumage color is adaptive, since it would help a young male to establish a breeding territory in an area already occupied by conspecific males. This is because the resident males will be deceived into believing that the intruder is a female and thus react less aggressively. Here we present a test of this hypothesis.

The plumage color of male pied flycatchers *Ficedula hypoleuca* Pallas varies from conspicuous black-and-white (color score I) to brownish and almost female-like (color score VII; Drost, 1936). First-year males are generally more brownish than older males but overlap exists between age groups (Drost,

1936; Røskaft et al., 1986; Slagsvold and Lifjeld, 1988*a*). The species is a common breeding bird in Europe, and it has been subjected to intensive studies. However, the significance of the variation in the plumage color of the males is poorly understood (Haartman, 1985; Järvi et al., 1987; Slagsvold and Lifjeld, 1988*a*; Alatalo et al., 1990). We have studied behavioral responses of males and females to caged conspecifics with different grades of plumage color, looking for aggressive or sexual display. We have also tested the possibility that female-like males are able to settle closer to the territories of already established males than dark-colored males. This is done by analyzing the settling pattern of the males in spring in relation to their plumage color.

MATERIALS AND METHODS

The study was conducted at Oslo, Norway, where the birds were provided with nestboxes in a woodland area (plots Brenna, Sinober, and Tangen, 60°N, 11°E; see Slagsvold et al., 1988). All males seen defending nestboxes at Brenna in 1985–1989 were trapped and color-banded soon after arrival. This made possible a comparison between plumage color and the distance to the nearest resident male at the time of nextbox occupation.

In the cage experiments, the live 'intrud-

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er' was presented in a small (38 dm³), wire-netting cage set down on the ground 5 m away from a nestbox already occupied by a male/pair of pied flycatchers. We placed a mark 2 m from the cage and attached a line to the rug covering the cage before hiding 10–20 m away. When the male owner was in position to discover the caged bird, we pulled the rug off and started time recording. In the case of the pairs tested, time was started when both the male and the female were present and at least one member had discovered the caged bird. Each experiment lasted 10 min. Several variables were re-corded, including time spent at the cage and at the nestbox, song activity, and attack dis-play (Sætre, 1989). We compared the re-sponses found for 22 resident, unmated males at Brenna in 1988 toward two dark-colored males (color score II and III) with those recorded toward a caged female, to identify typical components of aggression and sexual advertisement, respectively. Ac-cording to a stepwise discriminant analysis (Sætre, 1989), the following variables were of statistical significance: time spent being aggressive (time spent at and on the cage), number of enticing calls (Curio, 1959; used by the male to attract a female, mostly given at or inside the nesthole), and number of song phrases of the regular territorial, ad-vertising type. The amount of territorial song given by the resident male was reduced compared with the amount of song recorded before starting the trials, and more so when a dark-colored male than when a female was presented in the cage (Sætre, 1989).

Every female that settled on the Brenna plot was trapped and removed soon (mostly 0–1 day) after she had started nest building so that the males were kept unmated most of the breeding season. Males that attracted a female were termed sexually experienced for the rest of that particular breeding sea-son. The caged males used at Brenna to test the responses of the unmated males had col-or scores II, III, and VI in 1988, and IV, V, and VII in 1989. A caged female was used each year (two different individuals).

The responses of females and their mates to caged intruders were tested during the nest-building stage at Sinober and Tangen in 1989. The females are very aggressive toward caged females during this stage of breeding (Breiehagen and Slagsvold, 1988). The caged males used had color scores II, V, VI, and VII (the individuals used were different from those used at Brenna, except the one of color score VII). Pairs were only tested once. The unmated males at Brenna were tested 1–4 times each, but none was tested more than once with a particular caged bird, and at least 24 hr lapsed between tests.

Statistical tests are two-tailed.

RESULTS

Response of Sexually Inexperienced Males

The resident, bachelor males reacted strikingly differently when a dark-colored male, compared with a female, was pre-sented. In the former case the resident male spent most of his time close to the cage (Fig. 1a), perching on top and trying to attack the intruder by pecking; no enticing calls were heard (Fig. 1b). When the female was pre-sented the resident male spent most of his time at the nestbox, demonstrating the nest-hole (Fig. 1a). When he visited the cage it was only for a few seconds each time. He never attacked, but tried to induce the fe-male to follow by uttering many enticing calls (Fig. 1b).

When the most brownish-colored male intruder was presented, all resident males reacted by making a sexual display response similar to that made to the caged female (Fig. 1). None of the 18 males tried to peck the brownest caged male, compared with 8 of 9 males in the case of the experiments with the darkest male intruder [$\chi^2(1) = 18.67, P < 0.001$]. The number of enticing calls made to the caged, brownish male did not differ significantly from that recorded when the female was presented ($z = -0.46$, U test), but was much higher than that re-corded when the darkest male was present-ed ($z = -4.20, P < 0.001$, U test). Thus, not only did the resident males reduce their level of aggression toward a dull-colored male, but they also behaved as if the in-truder was a female, spending time and ef-fort trying to attract the mimic. The re-sponses to male intruders of intermediate color types were intermediate to those de-scribed above (Fig. 1).

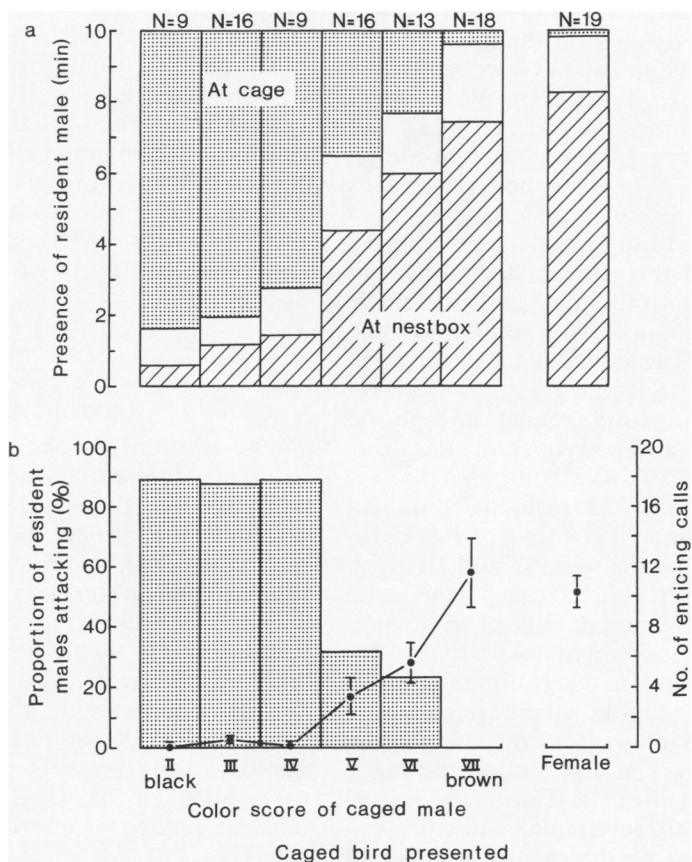Only a single male was used to represent

Fig. 1. Response of sexually inexperienced, male pied flycatchers to caged, male intruders with different grades of plumage color, and to a female intruder. (a) Crossed bars: <2 m from nestbox (sexual display response); shaded bars: <2 m away from cage (aggressive response); open bars: more than 2 m from cage and nestbox. (b) Proportions of resident males that tried to attack the caged intruder (dotted bars), and numbers of enticing calls recorded (mean ± SE). N = number of males tested.

each color score class in Figure 1. Two different females were used, and the numbers of enticing calls given by the resident males to these were similar (mean values of 9.3 and 11.0, $z = -1.20$, NS, U test). The correlation between the color score of the six caged males and the mean time spent at the nestbox, or cage, by the resident males was significant (Spearman $r_s = 1.00$, $N = 6$, $P = 0.01$).

Significance of Sexual Experience

The above analysis includes data only for male residents that had not yet attracted any female in that particular breeding season. To see if the poor sex-recognition ability was improved by prior sexual experience we recorded the response of 23 territorial,

bachelor males to the same brownish male intruder (score VI) between 24 and 27 May at Brenna in 1988. The responses were then compared with the number of females that the respective resident males had attracted prior to the trial. The number of enticing calls (range 0–25) correlated negatively with the degree of prior sexual experience of the respective resident males (range 0–4 females attracted; $r_s = -0.42$, $N = 23$, $P < 0.05$). Thus, sexual experience seemed to improve sex recognition ability.

The significance of prior sexual experience was further investigated in the same study plot in 1989. A brownish male (score VII) was presented twice to 15 resident, unmated males: before mating (soon after arrival, between 17 and 19 May) and when

about half of the males had attracted at least one female (on 23 May). The same caged male was used each time to make the trials comparable. In the first trial, when all males were sexually inexperienced, the males displayed sexually and there was no significant difference between the responses made by the two groups of males ($z = -1.16$, U test; Fig. 2). In the second trial, males still sexually inexperienced once again showed strong advertising display and showed no aggression. In contrast, males that had gained experience were no longer fooled to give enticing calls (Fig. 2). Thus, in the second trial, a significant difference was found between the two groups of males in number of enticing calls ($z = -3.05$, $P < 0.01$, U test). The responses recorded for the first and the second trial, of the males that had attracted females, differed significantly ($z = -2.03$, $P < 0.05$, Wilcoxon matched-pairs signed-ranks test). This was not the case with the other group of males ($z = -0.17$, NS, same test). In the second trial, none of 8 sexually inexperienced males tried to peck the caged male, compared with 4 of 7 males that had gained female experience (Fisher's exact probability test, $P = 0.05$).

Of the 15 males tested in 1989, 5 had mated in the study plot during the preceding breeding season, of which 3 had even shown aggressive behavior when the caged brownish male of color score VI was presented in 1988. All 5 of these males were deceived during the first trial in 1989, which demonstrates the importance of recent sexual experience for correct sex recognition.

Female Response

When a caged, dark-colored male was presented at the nestbox occupied by a pair, the resident male, but not the female, responded very aggressively; when a brownish male was presented, the female was the more aggressive member of the pair (Fig. 3). In the 18 trials with the two darker male intruders, the resident males spent more time at the cage than their mates ($z = -3.72$, $P < 0.001$, Wilcoxon matched-pairs signed-ranks test); the males tried to peck the caged bird in 17 of the trials, the females did so only once [$\chi^2(1) = 25.78$, $P < 0.001$]. In the 12 trials with the two brownish male intruders, the female spent more time at the
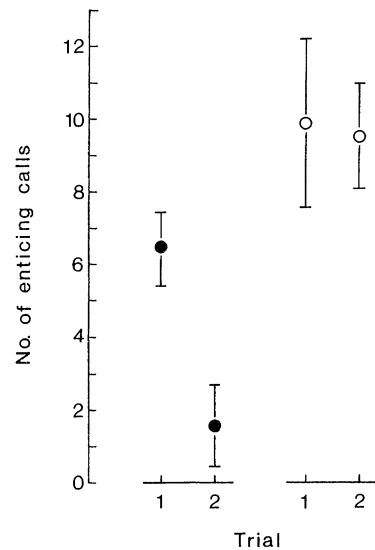

FIG. 2. Mean number ($\pm$SE) of enticing calls uttered by unmated, male pied flycatchers, on two separate occasions, to a caged, brownish male (color score VII). Filled symbols: males that attracted at least one female during the interval between the two trials ($N = 7$); open symbols: males that attracted no females ($N = 8$).

cage than the male ($z = -2.04$, $P < 0.05$, Wilcoxon matched-pairs signed-ranks test); the caged male was attacked in 10 of the trials by the female, and in 6 by the male [$\chi^2(1) = 1.69$, NS]. Thus, the females tried to peck the browner male intruders much more often than in case of the trials with the two darker caged males [$\chi^2(1) = 15.56$, $P < 0.001$], whereas their mates were more eager to peck dark than brownish intruders [$\chi^2(1) = 5.66$, $P < 0.02$].

To sum up, after mating, most females and some males were fooled by brownish male intruders.

Male Settling Pattern

Female-like males settled closer to resident males than dark-colored males (Table 1, Fig. 4). The former males tend to arrive later in the breeding season than the latter ones (Slagsvold and Lifjeld, 1988a; Alatalo et al., 1990). Hence, in the present analysis, intruders settling before the first male of color score VI had arrived in any particular year were excluded. Confounding correlations between arrival day and plumage color, and between arrival day and the distance
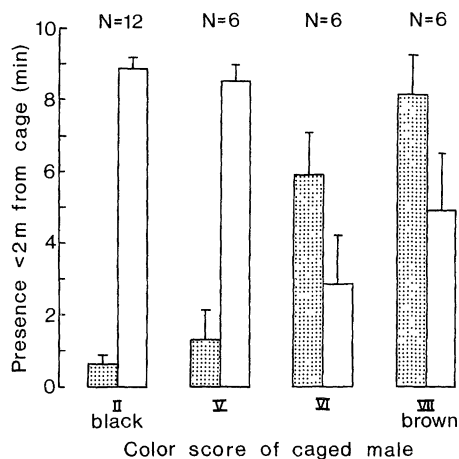
FIG. 3. Aggressive response (mean values ± SE) made by newly mated pied flycatchers to intruding caged males with different grades of plumage color. Shaded bars: female responses; open bars: male responses. N = number of pairs tested.

measure were thus reduced; the latter correlations were now insignificant ($r_s = -0.08$, $N = 111$, and $r_s = 0.06$, $N = 111$, respectively).

DISCUSSION

Sexual Deception

Natural selection favors those individuals that are able to increase their own fitness by manipulating the behavior of others (Dawkins and Krebs, 1978). One way to manipulate this is to convey false sexual signals to conspecifics (Otte, 1975; Gross and Charnov, 1980; Weldon and Burghardt, 1984; Trivers, 1985). There has often been an im-
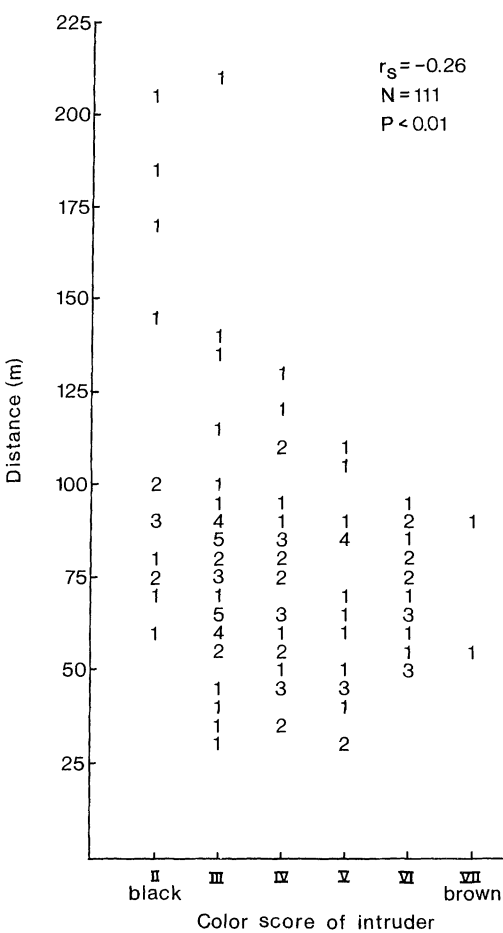

FIG. 4. Distance to nearest resident male on the day of nestbox occupation of male pied flycatchers in relation to plumage color of intruder.

plicit assumption in the biological literature that animals experience little difficulty in discerning sex. However, the sex recognition ability of many animals is not perfect (Otte, 1974; Burley, 1982; Ten Cate, 1985; Butcher and Rohwer, 1989), which may allow such sexual deception. This would be of particular importance if the time and resources thereby gained could be used for reproductive activities (Dominey, 1984; Trivers, 1985). Sexual mimicry includes cases of deceptive behavior (Le Boeuf, 1974; Arnold, 1976; Thornhill, 1979; Massey, 1988), appearance (Morris, 1952; Dominey, 1980; Gross, 1982; Clarke et al., 1985; Robertson, 1985), and chemical signaling (Jallon, 1984; Scott, 1986; Peschke, 1987).

TABLE 1. Spearman rank correlation analysis of plumage color of male pied flycatchers in relation to distance to nearest resident male on the day of nestbox occupation.

Year	Period (1 = 1 May)	Distance (m) Mean	SD	N	r_s	P[1]
1985	15–49	62	24	25	−0.19	0.351
1986	18–35	62	14	15	−0.38	0.163
1987	16–25	61	19	22	−0.18	0.411
1988	11–20	101	61	29	−0.29	0.121
1989	15–35	100	29	20	−0.47	0.039
Total	11–49	79	41	111	−0.26[2]	0.006

[1] Combined probabilities test for the five years gave χ^2 (10) = 18.21, $P = 0.05$.
[2] The distance score for each male was divided by a year-specific ratio, calculated as the ratio between the mean distance for the year in question and the overall mean distance (79 m).

The present study presents the first evidence for sexual deception by female mimicry in birds. The resident males did not only reduce their level of aggression toward a dull-colored male, as has been shown earlier for other bird species (Rohwer, 1978; Flood, 1984; Studd and Robertson, 1985b), including the pied flycatcher (Järvi et al., 1987), but behaved as if the intruder was a female. Females were also fooled by caged, brownish males.

It is puzzling that pied flycatchers have not evolved a more perfect sex recognition ability. In pigeons and doves, individuals are not easily able to tell the sex of conspecifics (Burley, 1982), but such birds are less dimorphic in color than pied flycatchers. When we first observed a brownish male pied flycatcher in the field, we recorded it as a female until it started singing and breeding. Later on we found that males, including brownish ones, have a darker tail and have more white in their wings than females. Apparently, pied flycatchers also need some degree of experience to improve their sex recognition ability, and this experience has to be refreshed each year. Tentatively, we suggest that the cost of being deceived is relatively low; it is probably more costly for a resident male to drive away a potential mate, and more costly for a mated female not to behave aggressively toward a potential female competitor.

Female Mimicry and Molt Constraints

Pied flycatchers spend the winter in tropical Africa and all males are then dull-colored. It is possible that young males are more constrained during the spring molt than older males; if so, this may explain why young males remain more dull-colored in spring. According to the molt-constraints hypothesis a subadult plumage color would be maladaptive in the breeding season (Rohwer and Butcher, 1988). The present data on male settlement suggest that males may benefit from having a brownish plumage color when trying to occupy a breeding territory in an area with many males already present. The cage experiments also support this view, since dull-colored males met little aggression from resident males. The resident males did not change their behavior in any consistent way during the 10-min period of the trial (Slagsvold and Sætre, pers. obs.). Occasionally, we have observed unmated male residents advertising to naturally occurring brownish male intruders; the resident male has entered the nestbox, giving enticing calls, and has even allowed the intruder to follow into the cavity. Thus, female mimicry may help a male to obtain information about territory and nest site quality.

Probably, young, late-arriving males would have a greater advantage of mimicking females than older, early-arriving males (Rohwer et al., 1980; Slagsvold and Lifjeld, 1988a). Indeed, brownish males tend to arrive later in the breeding season than dark-colored males, the former arriving only a short time before the females (Slagsvold and Lifjeld, 1988a). The relationship between plumage color and time of arrival is primarily an age effect, older males returning before yearlings (Slagsvold and Lifjeld, 1988a; Alatalo et al., 1990). A suitable time for mimics to establish would be when the resident males have become mated, since male territorial behavior seems to be relaxed after mating: initially males defend several nest sites, if available, to increase mating success (Lifjeld and Slagsvold, 1988; Dale and Slagsvold, 1990), but most additional sites are given up after mating (Slagsvold and Lifjeld, 1988a, 1988b). Further studies are needed to determine if female mimicry also helps nonbreeders to stay in high-quality habitats and if subsequent survival rate is improved.

The present study indicates some benefits for young males of having a female-like plumage color, and thus provides support for the female mimicry hypothesis proposed to explain delayed plumage maturation in sexually dichromatic birds (Rohwer, 1978; Rohwer et al., 1980). On the other hand, the molt-constraints hypothesis cannot yet be excluded, since mimicry also incurs a cost of not being recognized as a male when it is important. This may be a problem when defending a territory and a mate against intruding males, and a problem when attracting a mate. The present study showed that females behaved aggressively against a caged, brownish male even after having gained sexual experience. Failure to recog-

nize true sex may explain why dull-colored males tend to have a lower mating success than dark-colored males occupying territories within the same woodlot (Järvi et al., 1987; Lifjeld and Slagsvold, 1988; Alatalo et al., 1990). Because of female aggression, brownish males may also have low success in managing to achieve any extra-pair copulations. The problem of quick sex recognition seems to have been a neglected point in recent analyses on the evolution of plumage coloration in birds.

To sum up, our results indicate both costs and benefits of female mimicry. The bottleneck for reproduction in male pied flycatchers is primarily a problem of obtaining a suitable breeding territory. This would in particular be the case for inexperienced, late-arriving males. These males may gain a net benefit from being female-like, making the best out of a bad situation. However, these males are also the most likely candidates to have problems with the spring molt.

Previous Studies

Previous studies have shown that dull-colored mounts are treated less aggressively by resident males than bright-colored dummies (Rohwer, 1978; Flood, 1984; Studd and Robertson, 1985b; Järvi et al., 1987; Hill, 1989). However, since only degree of aggressiveness has been measured, and not degree of sexual display, it has not been possible to discriminate between the female mimicry hypothesis and the alternative status signaling hypothesis (Rohwer et al., 1980; Lyon and Montgomerie, 1986). The fact that male pied flycatchers have an enticing call and an enticing behavior makes this species an excellent one for demonstrating deception about sexual identity.

Slagsvold and Lifjeld (1988a) reported an experiment performed at Brenna in 1985 in which extra nestboxes were added 50–100 m away from nest sites already occupied by unmated pied flycatchers. They found that males that managed to outcompete prior owners by taking over one of their nestboxes were not more brownish in color than those who settled at one of the additional nestboxes provided. They therefore concluded that female mimics did not seem to have any advantage over dark-colored intruders in competition for nest sites. The present

analysis of the 5-year data from Brenna showed a weak though significant relationship between plumage color and settling distance in the direction predicted from the female mimicry hypothesis (Fig. 4). Thus, a female-like plumage color may not necessarily help to outcompete a resident male, but may nevertheless help to settle in the vicinity.

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