

## Female pied flycatchers *Ficedula hypoleuca* choose male characteristics in homogeneous habitats

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**Summary.** The paper reports the results of a 2-year study of pairing success of male pied flycatchers in a homogeneous habitat. A handicapping experiment was carried out in which certain wing and tail feathers were removed from randomly selected males. Handicapped males had reduced pairing success, they lost weight, and they sang less frequently than control males. Male pairing success was positively correlated with the darkness of the plumage, body-size, and previous breeding experience. Earlier studies on the same species have failed to detect any relationships between pairing success and male characteristics, possibly because of habitat heterogeneity and variation in nest site quality. The evolutionary basis for female choice of male characteristics is discussed. There are reports that males with attractive traits (e.g. black plumage) provide a high quality of parental care. However, the fact that male pairing success was related to male conspicuousness makes it difficult to discriminate between active and passive female choice.

### Introduction

Individual animals would be expected not to pair at random, but to make a choice of mate that maximizes their reproductive success (Halliday 1983). In general, the sex that makes the greatest parental investment would be expected to be the most discriminating sex (Trivers 1972); in most species this is the female. The female may base her choice on two main properties of the male: (1) the quality of the resources he defends, and (2) the quality of the male himself, including his ability to provide parental care and the quality of his genes (Searcy 1982). In species in which the male controls resources essential for the reproductive success of

the female, e.g. territorial birds, it is often difficult to separate the respective influences of resource quality and of male quality on female choice, because the best males usually control the best resources (Davies 1978; Searcy 1982).

In a 7-year study of pied flycatchers *Ficedula hypoleuca*, Askenmo (1984) found that certain nestboxes were occupied more frequently than expected from a random distribution, that nestboxes were occupied in descending order of attractiveness, and that birds bred more successfully in the more attractive boxes. The results indicated that nest site quality was important for male mating success, but it was not possible to decide whether females made their choice directly on nest site quality, or on the properties of the males defending those nest sites. Two recent studies have attempted to test whether female choice in this species is based on nest site quality or on male characteristics. Slagsvold (1986) made a series of experiments using upright and tilted nestboxes. Males preferred the upright nestboxes, but differed in their ability to occupy such sites. Switching of nestbox position after male settlement revealed that females made their choice of where to settle primarily on nest box quality, although in some of the experiments there may have been a slight effect of male quality.

Alatalo et al. (1986a) eliminated the correlation between nest site quality and male quality by successively providing nestboxes of random quality as the males arrived. They found no correlation between male characteristics and pairing order. When the mated females were removed and new females allowed to settle, the same rank order of nestbox occupation was found. Nest site attractiveness could be explained by a combination of nest site and habitat factors.

Although the results of the experiments made by Slagsvold (1986) and by Alatalo et al. (1986a)

emphasized the importance of nest site quality for female choice, they did not rule out the possibility that females also choose their mates on the basis of male quality. The variation in male quality may be of smaller magnitude, and its importance in female choice may therefore be more difficult to detect in such experiments. Thus, to identify the effects of male quality one must minimize, as far as possible, any variation in habitat and nest site quality. This paper reports on an attempt to do so. The study was carried out in a homogeneous habitat, with a standardized set-up of nestboxes. We also tried to increase the natural variability in male attractiveness by experimentally 'handicapping' some of the males: certain tail and wing feathers of randomly selected males were removed shortly after their arrival in the study area in spring, but before they had become mated. Their subsequent pairing success was studied in relation to a control group of untreated males.

## Methods

The study was carried out during the breeding seasons of 1983 and 1984 in two study plots of deciduous woodland, Tillerbrua and Almelia, near Trondheim, Central Norway. In this area very few natural nesting holes exist, and all pied flycatchers included in this study occupied wooden nestboxes provided by us. The vegetation was homogeneously structured and mainly composed of grey alder *Alnus incana* and elm *Ulmus glabra*, providing a favourable habitat for the pied flycatcher. Care was taken in choosing similar, favourable sites when erecting the nestboxes; they were not placed in dense vegetation and there was free space in front of each nestbox. The nestboxes were mounted in a normal, upright position, 1.5 m above ground level. All the nestboxes were of the same age and size, with an entrance hole diameter of 32 mm. The nestboxes were placed only about 40–50 m away from each other, which ensured the presence of a high density of displaying males between which the arriving females could choose.

Male pied flycatchers were trapped on the day of their arrival in spring or the following day. At this time they can easily be trapped while they are inspecting empty nestboxes. Each male was individually colour-ringed and its wing length, tarsus length, and body weight recorded. The colour of the upper parts was scored on a scale from 1 (completely black) to 7 (completely brown) (Drost 1936). The females were caught on their nests 1–3 days after the start of incubation. Each was ringed and the body measurements recorded. In 1984, most of the females were also aged, as either first-year or older birds, according to the colour pattern of their outermost secondary coverts (Lifjeld and Slagsvold 1986).

In our study area, some 30%–40% of the males return to the same study plots in subsequent years (Slagsvold and Lifjeld 1988). Those males that had been ringed as adults in a previous year were designated 'experienced' males, and the degree of experience was scored as the number of breeding seasons in which they had been present in the area. Breeding males had been ringed for the first time in 1981 at Tillerbrua, and in 1982 at Almelia.

Male pairing success was studied up to 5 June in 1983 and to 7 June in 1984; all nests containing complete clutches on

these dates were then robbed experimentally (see Slagsvold and Lifjeld 1986). No data on reproductive success in relation to the initial choice of mate are therefore available. An analysis of mate fidelity and reproductive success of the re-nesters will be published elsewhere (Lifjeld and Slagsvold 1988).

In an attempt to reduce male attractiveness, thereby experimentally increasing the normal variation in attractiveness of different males, we removed certain feathers from randomly selected birds when they were trapped after arrival in spring. The 7th and 9th primaries (counted ascendantly) were removed from each wing, together with six central tail feathers. In 1983 every fourth, and in 1984 every second, male trapped before pairing was 'handicapped' in this way. The lack of such a number of feathers is a familiar situation for a bird during moult (Stresemann and Stresemann 1966). The handicapped males appeared to behave just like the other males. They resumed singing soon after release, and those that did become mated fed their mates during incubation, and the nestlings later on (Lifjeld and Slagsvold 1986). The rate of return in 1984 of the males that had been handicapped in 1983 was not lower than that of the control group of males (34% and 29%, respectively).

The study plots were surveyed daily in order to map nestbox ownership, to trap any newly-arrived males, and to inspect the nestboxes. Pairing date was defined as the day on which nest-building started. Data for males that were not observed occupying any nestbox, after capture, have been excluded from all analyses.

All statistical tests are two-tailed, unless otherwise specified.

## Results

### *Arrival times of males and females*

Males that arrived early were more experienced and had darker plumage, a higher body weight, and longer wings than those that arrived late (Table 1). These traits were in general intercorrelated, e.g. the dark-coloured males had longer wings and a higher body weight than the browner males, and the experienced males were darker-coloured than the inexperienced males.

The males arrived before the females, but there was a considerable overlap in the arrival times (Fig. 1). Both males and females arrived approximately 1 week earlier in 1983 than in 1984. In both years the males had to wait, on average, for 7.2 days before they became paired. A substantial proportion of the males remained unmated throughout the breeding season, viz. 22% in 1983 and 45% in 1984. Only two cases of bigyny were recorded, one in each year.

### *Variation in nestbox attractiveness*

Out of all the nestboxes used for nesting by the pied flycatchers in 1983, 40% (21/53) also contained a pied flycatcher nest in 1984. Among the nestboxes that were empty in 1983, 32% (12/38)

**Table 1.** Correlation matrix of some characteristics of male pied flycatchers. Coefficients above diagonal refer to 1983 data ( $n=85$ ), those below to 1984 data ( $n=84$ )

	Arrival date	Body weight	Plumage colour	Experience	Tarsus length	Wing length
Arrival date		-0.15	0.33**	-0.18	-0.13	-0.16
Body weight	-0.34***		-0.24*	0.22*	0.41***	0.38***
Plumage colour	0.18	-0.15		-0.41***	-0.06	-0.42***
Experience	-0.32**	0.35***	-0.42***		0.32**	0.33**
Tarsus length	-0.23*	0.34***	-0.13	0.30**		0.40**
Wing length	-0.26*	0.52***	-0.26*	0.32**	0.28**	

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

were used in 1984 ( $\chi^2_1 = 0.32$ , NS). For those nestboxes that were used by nesting pied flycatchers in both years, the orders of settling by the females were uncorrelated ( $r_s = -0.021$ ,  $N = 21$ , NS). Experimental predation of the initial nests was carried out in 1983 without manipulating the availability of nestboxes (see Slagsvold and Lifjeld 1986). Nestboxes that had previously been empty proved to be just as popular for re-nesting attempts as those that had previously contained a nest (23% and 20% were used, respectively,  $\chi^2_1 = 0.001$ , NS; the nestboxes in question were those observed to be defended by a male after nest removal, but excluding all cases in which a female re-nested with the same male). These results demonstrate the low variation in nestbox attractiveness.

#### Handicapping experiment

Male pairing success can be expressed in two ways. Firstly, attractive males will become paired before less attractive ones, hence the time of pairing will be an expression of pairing success. Secondly, pairing success can be expressed as success or failure in becoming paired at all. The pairing success of handicapped and control males is shown graphically in Fig. 1. In the group of males that succeeded in mating, the pre-mating period of the handicapped ones was significantly longer than that of the controls (Mann-Whitney  $U$  test, 1983:  $P = 0.08$ , 1984:  $P = 0.11$ ; Fisher's combined probability test:  $\chi^2_4 = 9.46$ ,  $P = 0.05$ ).

A greater proportion of the handicapped than of the control males remained unpaired throughout the breeding season (Fig. 1; Table 2). In 1983, 50% of the handicapped and 18% of the controls failed to get a mate ( $\chi^2_1 = 6.00$ ,  $P < 0.05$ ). In 1984, the corresponding figures were 64% and 37% ( $\chi^2_1 = 4.38$ ,  $P < 0.05$ ). When all the males were divided into two groups, according to the median trapping date, no differences in the pairing success of the early arrivers were found. Thus, the differ-

ence in pairing success of the handicapped and the control males was mainly due to the late arrivers (Table 2).

Since it was the males themselves that were manipulated in this experiment, not their territory resources, the data indicate that female choice of mate was based on the quality of the male himself. Before this conclusion can be finally drawn, the question of whether or not the handicapped males occupied nestboxes of inferior quality has to be answered.

There is a possibility that the handicapped males were forced to occupy lower-quality nestboxes by the other males. Only 31% ( $n = 177$ ) of the males that remained in the study plots after their release were later found to occupy/breed in the same nestbox in which they had been trapped (Fig. 2). This proportion was much lower in the early spring (16%,  $n = 89$ ) than later on (47%,  $n = 88$ ,  $\chi^2_1 = 18.26$ ,  $P < 0.001$ ), probably because of the decrease in availability of empty nestboxes during the season. There was a tendency for those males that remained at their original nestbox to have less success in pairing than those males that occupied a different nestbox. In 1983, 57% ( $n = 23$ ) of males that remained obtained a mate, compared with 83% ( $n = 52$ ) of those that switched nestboxes ( $\chi^2_1 = 4.47$ ,  $P < 0.05$ ). The corresponding figures for 1984 were 38% ( $n = 21$ ) and 55% ( $n = 53$ ) ( $\chi^2_1 = 1.06$ , NS). One may therefore ask whether the handicapped males showed a stronger tendency to stay put after their release than the control males, particularly in the late spring, when a difference in pairing success was found: in late spring 38% ( $n = 32$ ) of the handicapped males stayed put compared with 52% ( $n = 56$ ) of the control males ( $\chi^2_1 = 1.15$ , NS). The values for early spring were 16% ( $n = 37$ ) and 15% ( $n = 52$ ) respectively ( $\chi^2_1 = 0.01$ , NS). Males probably moved to another nestbox because of the bad experience they had had (trapping and handling), and not because of displacement by another male. In most cases, at the time when a male

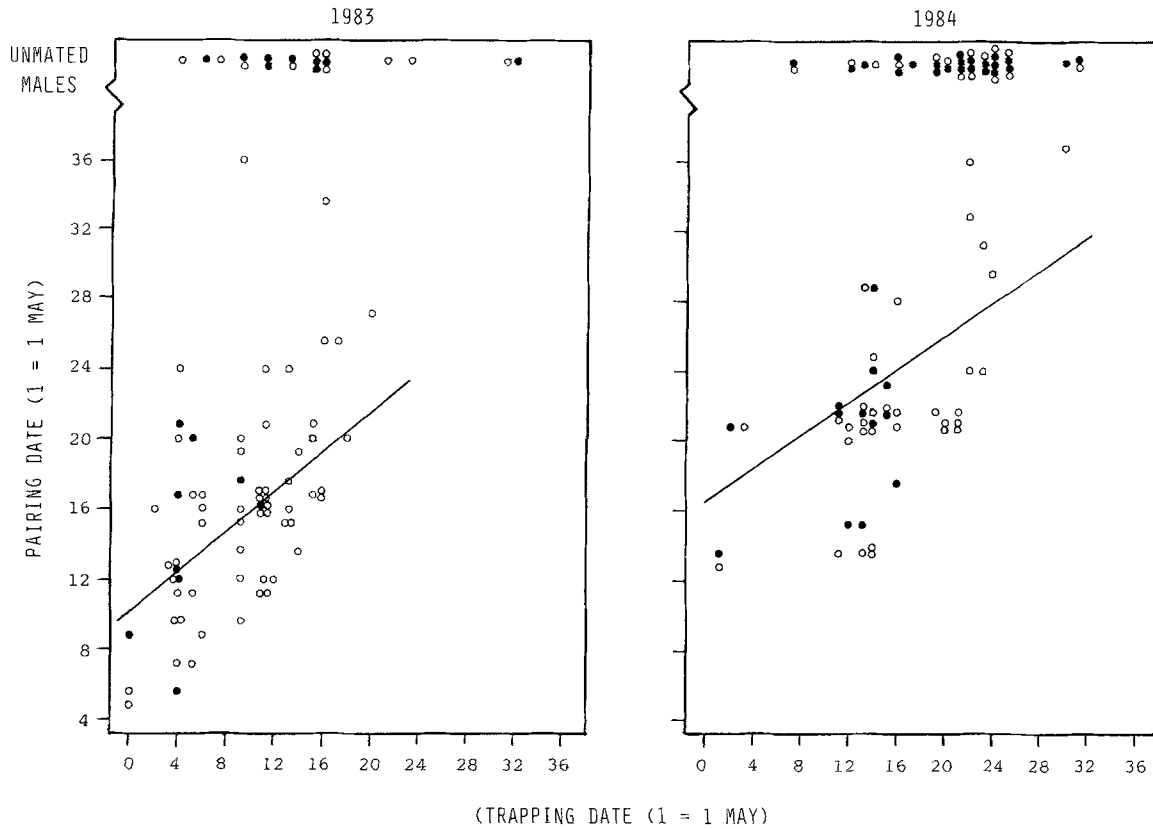


Fig. 1. Pairing success of pied flycatcher males. Filled circles handicapped males, open circles control males. Regression lines for the paired males are indicated

Table 2. Pairing success of handicapped and control pied flycatcher males. "Early" and "late" males refers to the median date of arrival

Year	Time of season	Male category	Paired	Un-paired	Test
1983	Early	Handicapped	8	2	$\chi^2=0.03$
		Control	24	3	NS
	Late	Handicapped	1	7	$\chi^2=8.59$
		Control	23	7	$P<0.01$
1984	Early	Handicapped	13	6	$\chi^2=0.14$
		Control	15	4	NS
	Late	Handicapped	0	17	$\chi^2=8.36$
		Control	9	10	$P<0.01$

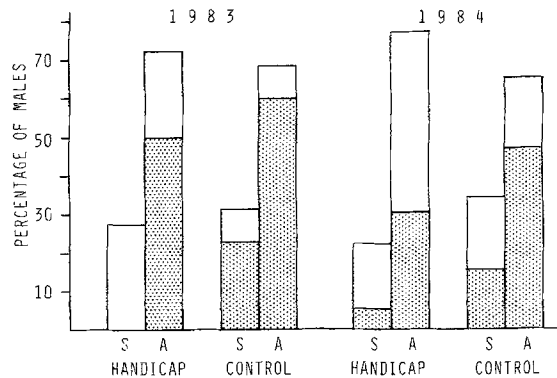


Fig. 2. Nestbox occupation and subsequent pairing success of handicapped and control males after trapping. S same nestbox occupied as the one in which they were trapped; A a different nestbox occupied. Stippled areas indicate the proportion of males that subsequently succeeded in getting a female

moved to another nestbox, a new male had not yet settled at the previously-occupied nestbox.

We also analysed whether the nestboxes occupied by handicapped and control males in one year differed in popularity in the other year, and vice versa (Table 3). 50% of the nestboxes occupied by the handicapped males in 1984 contained a pied

flycatcher nest in 1983, compared with only 35% of those occupied by the control males ( $\chi^2_1=1.25$ , NS). Similarly, 26% of the nestboxes defended by handicapped males in 1984 contained a pied flycatcher nest in 1983, compared with 33% for the control males ( $\chi^2_1=0.09$ , NS). Furthermore, the proportion of nestboxes occupied by handicapped

**Table 3.** Nestbox occupation by handicapped and control male pied flycatchers in 1983 and 1984 in relation to nestbox occupation in the inverse year

Year	Male category	Mating status	<i>n</i>	Nestbox occupation in the inverse year (%)				
				Pied flycatcher		Tit nest	Empty	Added/removed
				Nest	Empty <sup>a</sup>			
1983	Handicapped	Mated	10	30	20	30	20	–
		Unmated	9	22	78	–	–	–
	Control	Mated	56	32	34	23	7	4
		Unmated	10	40	30	20	10	–
1984	Handicapped	Mated	13	46	–	8	15	31
		Unmated	23	52	17	17	4	9
	Control	Mated	33	45	24	9	3	18
		Unmated	15	13	33	20	13	20

<sup>a</sup> Defended by an unmated or a polyterritorial male

males, but either previously or subsequently occupied by tits *Parus* spp., was no lower than that of the control males (14% and 13% in 1983 and 16% and 23% in 1984, respectively). In other words, the handicapped males had not been obliged to defend inferior nestboxes.

#### *Effects of handicap on male behaviour*

The removal of certain primaries and tail feathers should have made flight less effective and would probably have forced the birds to increase their metabolic rate. In 1983 the mean body weight of the control males increased, from their arrival in spring up to the start of the incubation period, by 0.32 g ( $n=20$ ), whereas that of the handicapped males decreased during the same period by 0.07 g ( $n=8$ ;  $t=2.09$ ,  $P<0.05$ , one-tailed test; no data available for 1984). Handicapping obviously reduced the condition of the males over that period of time.

The intensity of the advertising display may depend on the physical condition of the male. On the day following the experimental nest predation, in both 1983 and 1984, we censused the singing activity of bachelor males (i.e. those that were still unpaired at the time of clutch removal) by walking through the study plots and recording which males were singing and which not. In both years a greater proportion of the controls than of the handicapped males were singing. The difference was significant in 1983 and for the pooled data for both years (Table 4). In addition, we have data from the 1986 breeding season that show that the volume of song per minute (strophe length  $\times$  number of strophes) of handicapped males is also less than that of con-

**Table 4.** Song survey results for handicapped and control bachelor male pied flycatchers

Survey date	Male category	Re-recorded singing	Not re-recorded singing	Fisher exact test
6 June 1983	Handicapped	2	7	$P=0.012$
	Control	9	1	
8 June 1984	Handicapped	14	9	$P=0.215$
	Control	12	2	
Total	Handicapped	16	16	$P=0.007$
	Control	21	3	

trol males, viz. respective mean values of 12.6 s/min and 15.9 s/min ( $t=2.29$ ,  $n=30$ ,  $P<0.05$ ).

#### *Pairing success and male characteristics*

In order to identify the male characteristics that are important in female choice, we used two kinds of data analysis, partial correlation and multiple linear regression. Pairing date was used as an expression of pairing success, but since the time of pairing depended on the time of male arrival (cf. Fig. 1), arrival date was controlled for. Separate analyses were made of the data for paired males, and of the pooled data for the paired and unpaired males. In the latter analyses the unpaired males were assigned a very late pairing date, viz. their arrival date + 28 days; this calculated pre-mating period was one day longer than the longest recorded period.

*1983.* A characteristic of the males that soon became paired was their defence of more than one

**Table 5.** Relationships between male pairing day and male characteristics. Unmated males were assigned a pairing day of their arrival day + 28 day

Male characteristic	Partial correlation coefficients, controlling for male arrival day				Multiple regression, standardized regression coefficients, $\beta$			
	1983		1984		1983		1984	
	Mated males (n=66)	All males (n=85)	Mated males (n=46)	All males (n=84)	Mated males (n=66)	All males (n=85)	Mated males (n=46)	All males (n=84)
Arrival day					0.40**	0.56***	0.57***	0.55***
Control/handicapped	0.10	0.40***	0.06	0.38***	0.03	0.27***	0.06	0.27***
No. of nestboxes defended <sup>a</sup>	-0.37**	-0.19	-0.09	-0.22*	-0.22	0.01	-0.06	-0.15
Experience	-0.11	-0.18	-0.31*	-0.20	0.11	0.09	-0.26	-0.14
Plumage colour	0.26*	0.48***	0.10	0.04	0.17	0.34***	-0.13	-0.08
Wing length	-0.30*	-0.33**	-0.29	-0.15	-0.07	0.00	-0.16	-0.11
Tarsus length	-0.35**	-0.26*	-0.15	-0.11	-0.23*	-0.18*	0.02	-0.05
Body weight	-0.30*	-0.29**	-0.17	-0.11	-0.10	-0.11	-0.03	0.04

<sup>a</sup> Ln transformation\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ 

nestbox. They were also larger-sized and had higher body weights and darker plumage than the others (Table 5; partial correlations). When the data for the unpaired males were included in the analysis the correlation with plumage colour in particular was strengthened. Because the male characteristics are interdependent (Table 1), multiple regression analyses were made, in which all the variables studied, including male arrival time, were entered. The partial effect of each variable, allowing for variation in the others, was expressed by the standardized partial regression coefficients (Table 5). In the separate analysis of the data for paired males, only tarsus length proved to have a significant effect. When data for unpaired males were included plumage colour proved to be the most important factor. In both sets of multivariate analyses the effect of male handicap was significant only when the data for the unpaired males were included.

**1984.** Pairing time showed the strongest partial correlation with male experience (paired males:  $P = 0.036$ , all males:  $P = 0.066$ ). In addition, for the pooled data, pairing time was significantly correlated with male handicap and the number of nestboxes defended. In the multiple regression analyses none of the partial regression coefficients were significant, except for the one for male handicap in the analysis of all males.

We also carried out two additional sets of multivariate analyses, in which the unpaired males were assigned (1) a fixed pre-mating period of 50 days, and (2) a fixed pairing day, viz. 6 June

in 1983 and 8 June in 1984. Results were similar to those given by assigning the unpaired males a pre-mating period of 28 days, and only small deviations in the  $P$ -values were found.

#### *Variation in female choice*

Females may differ in their individual preferences. To examine this possibility, we assumed that the quality of any particular males, as a breeding partner, would be reflected in his arrival time, because the high quality males arrive early (Table 1), and because early-arriving males have the opportunity to select the best territories and nest sites. We calculated a selectivity index for each female using the formula  $(2 \times \text{rank} - 1) / 2n$  (cf. Alatalo et al. 1986a), where  $n$  is the number of unmated males on the study plot at the time the female makes her choice, and  $\text{rank}$  denotes the rank order of the particular male chosen with respect to his arrival time. This index yields a standardized rank, ranging from 0 to 1, with an expected mean value of 0.5 if the females do not discriminate between males according to their order of arrival. The data for handicapped males were excluded from these calculations.

The mean index value for 1983 was 0.44 (SD = 0.27,  $n = 55$ ), and that for 1984 was 0.47 (SD = 0.29,  $n = 32$ ). The values did not deviate significantly from a random distribution (1983:  $\chi^2_1 = 2.20$ , NS, 1984:  $\chi^2_1 = 0.50$ , NS), and therefore it can not be claimed that the females chose to mate with early-arriving males. We were unable to find any significant correlations between the selectivity in-

**Table 6.** Pairing of experienced and inexperienced males in relation to the age and experience of their mates. Experienced bird = one ringed as a breeding adult in a previous year

Year	Female group	Male group		Test
		Experienced	Inexperienced	
1983	Experienced females	7	3	$\chi^2 = 3.76$ $P = 0.052$
	Inexperienced females	20	34	
1984	Experienced females	8	4	$\chi^2 = 2.07$ NS
	Inexperienced females	14	19	
1984	Inexperienced females <sup>a</sup>			
	Old females	7	7	$\chi^2 = 0.10$
	First-year females	6	10	NS

<sup>a</sup> Three females were not aged

dex values and various female characteristics (body size, body weight, clutch size, or arrival time).

We also compared the data for females that had nested in the study plots in a previous year with those that were new and inexperienced in the area. No significant differences in selectivity for male arrival time were found. The choices of the experienced and of the inexperienced females showed no difference in regard to male characteristics ( $P > 0.05$ ), except that the experienced females showed a stronger preference for experienced males than the inexperienced females (Table 6; pooled data for 1983 and 1984:  $\chi^2_1 = 4.89$ ,  $P < 0.05$ ). That difference can hardly be explained by earlier arrival of experienced females, since the mean arrival dates for the experienced and the inexperienced females in 1983 were respectively 15.2 and 16.4 May ( $P > 0.50$ ), and 21.7 and 23.3 May in 1984 ( $P > 0.60$ ). In only one case did a female pair up with the same male as in the preceding year. The proportions of first-year and of older females pairing with experienced males were similar (Table 6).

As mentioned previously, because the experienced males arrive earlier in spring (Table 1) they have a chance to occupy higher-quality nestboxes and may also retain a memory of the location of such sites from the previous breeding season. We tried to test whether, in one year, the experienced males obtained nestboxes that were also more attractive in the other year. In 1984, male pied flycatchers occupied 36 of the nestboxes that had housed a pied flycatcher nest in 1983. The popularity of these nestboxes can be indicated by the respective pairing dates in 1983. We found no difference in pairing date between the nestboxes defended by inexperienced ( $n = 19$ ) and by experi-

enced ( $n = 17$ ) males; the mean dates were 15.8 and 16.6 May, respectively (Mann-Whitney  $U$  test,  $z = -1.12$ , NS). This analysis can also be reversed, by comparing the popularity in 1984 of nestboxes held by males in 1983. The mean pairing dates in 1984 for nestboxes held by inexperienced ( $n = 16$ ) and by experienced ( $n = 11$ ) males in 1983 were 21.5 and 24.3 May, respectively ( $U = 60.5$ , NS). In other words, there was no tendency for the experienced males to occupy more popular nestboxes than the inexperienced males.

## Discussion

### *Pairing success and male characteristics*

The handicapping experiment revealed that in the pied flycatcher, female choice of mate is based on male characteristics as well as on nest site quality. This is one of the few experimental studies on a territorial bird species that has demonstrated an effect of male quality on female choice. Previously, Andersson (1982) manipulated the tail length of the long-tailed widowbird *Euplectes progne* and found that males with elongated tails had an increased pairing success.

The present study has pinpointed certain male traits, especially plumage colour in 1983, that were correlated with pairing success. Järvi et al. (1987) also found that black males had a greater pairing success than brownish ones. They found a significant partial correlation between male plumage colour and pairing date when differences in male arrival time were allowed for, as also for differences in habitat/nestbox quality. However, they did not allow for differences in both male arrival time and habitat/nest site quality in the same analysis, nor were the data for single years analysed separately. We found no effect of plumage colour on pairing success in 1984, which suggests that, in this species, female choice of mate is not based exclusively on male plumage colour. More likely, the choice is based on multiple characteristics (cf. Burley 1981), or on some factor correlated with plumage colour.

Males of the indigo bunting *Passerina cyanea* and the Darwin's medium ground finch *Geospiza fortis* also exhibit an age-related variation in plumage colour. In both these species brightly-coloured males have greater pairing success than dull-coloured ones (Payne 1982; Price 1984). However, if these brightly-coloured males also possessed better territories, then female choice may have been based on territorial quality rather than on plumage colour.

So far all studies on mate choice in the pied flycatcher have been carried out in nestbox areas, and the divergence in the results obtained, especially as regards the significance of male characteristics, may to some extent have been related to local variations in nestbox attractiveness. Nestbox attractiveness depends on several factors, such as bottom area, entrance diameter, and vertical position (Nilsson 1984; Alatalo et al. 1986a; Slagsvold 1986, 1987).

For an assessment of the partial influences of nest site and of male qualities on female choice, variation in nest site quality is of crucial importance. If the variation in nest site quality is great any potential influences of male quality on pairing success may be difficult to detect. Alatalo et al. (1986a) concluded that females choose exclusively on nest site quality, since they found that pairing order was correlated with certain nest site parameters, but not with any male traits. However, their findings may have resulted from great variation in nest site quality, and therefore do not rule out the possibility of an effect of male quality on mate choice in this species.

Slagsvold et al. (1988) found that males that defended peripherally-situated nestboxes attracted more females than males defending nestboxes in the central part of a nestbox study area. Such a pattern of female settlement indicates that females have a restricted search strategy, since they will first encounter the peripheral males. Thus, the order of occupation does not necessarily reflect differences in nestbox or habitat quality; occupation of a nestbox may depend on its position relative to other potential nest sites and to the routes by which the females enter an area.

#### *Why do females choose mates on their characteristics?*

Pied flycatcher males frequently feed their mates during the incubation period (Lifjeld and Slagsvold 1986). They also take a considerable part in feeding the young (von Haartman 1954). Male parental investment is of crucial importance for reproductive success (Alatalo et al. 1982), so we would expect a female to choose a mate that will provide a high quality of parental care. Because the assessment of male help will be difficult at the time when the female has to make her choice, she may utilise some characteristic that is correlated with the parental quality of the male.

In 1983, when the weather was cold during the days preceding the predation experiment, the experienced males fed their incubating mates at a higher

rate than the inexperienced ones (Lifjeld and Slagsvold 1986). In another study on polygynous males, the rate of incubation feeding was positively correlated with male body weight (Lifjeld et al. 1987).

Järvi et al. (1987) and Alatalo et al. (1984) found that black and brown males reared the same numbers of young, but Järvi et al. (1987) reported that the young of black males were heavier than those of brown ones. In our experimental study the initial clutches were removed, so that no data on reproductive success of that sample of males exist, but we do have such data for the re-nestings. The mean body weight of the young was lower in broods of handicapped males than in broods of the control group of males. Furthermore, the mean body weight of the young of black males tended to be higher than that of those of brown males (Lifjeld and Slagsvold 1988). Some evidence does therefore exist that the quality of parental care provided by the pied flycatcher male is correlated with other characteristics, such as his plumage colour.

Female fitness can also be enhanced by choice of a mate that possesses 'good genes' which will be passed on to the offspring. However, female choice on male genotypic quality is a controversial issue (Kirkpatrick 1985), mainly because the traits that are closely correlated with fitness tend to have low heritability (Falconer 1981; Gustafsson 1986). The heritability of male plumage colour is not known, but it is probably low. Male plumage colour is to a large extent phenotypically plastic (Slagsvold and Lifjeld 1988).

Male age has been proposed as an indicator of genotypic quality, because old males have proved their ability to survive (Halliday 1978; Järvi et al. 1982; Weatherhead 1984). The assortative mating pattern of the experienced females (Table 6) and the high pairing success of the experienced males in 1984 (Table 5), might reflect female choice based on good male genes. Experienced males did not defend more favourable nestboxes than inexperienced males, and, for the repeat nests, we found no difference in reproductive success of the experienced and the inexperienced males (Lifjeld and Slagsvold 1988). Alatalo et al. (1986b) found no difference in reproductive success of first-year and of older males, but in the great tit *Parus major*, first-year males have lower reproductive success than older males (Harvey et al. 1979; Perrins and McCleery 1985). Whatever the reasons underlying the preference for experienced males by female pied flycatchers, it is striking that it was primarily the females that had previously nested in the study plots that preferred such males. The



age or experience of a male must be difficult for a female to assess; perhaps the females are able to recognize individual males from a previous breeding season?

#### *Active choice or passive attraction?*

As with many other field studies of mate choice, the present results only refer to the outcome of the pairing process. No information is currently available about the behaviour, and the decision-making process, of the individual females. Evidence that females actively reject some males in favour of others is needed to establish the existence of active choice (Partridge and Halliday 1984), since females may simply be passively attracted to those males that are more readily detected (Parker 1983). The restricted search pattern of female pied flycatchers ought to have favoured the evolution of male conspicuousness (Slagsvold et al. 1988). If so, any characteristics that increase the probability of a male being rapidly discovered by a prospecting female would clearly be favoured by sexual selection, without any necessary pre-condition that choice of these characteristics should enhance the fitness of the female.

Studies of mate choice in several species have shown that mating success is correlated with male conspicuousness and display rate (e.g. Bischoff et al. 1985; Gibson and Bradbury 1985; Kodric-Brown 1985). Black male pied flycatchers are more conspicuous than brown ones, and this difference is particularly obvious before the leafing time of the vegetation, i.e. at the time of female arrival. When advertising for a mate, the probability of any male being detected will be largely dependent on his singing activity. The function of song in attracting females has been clearly documented for the pied flycatcher (Eriksson and Wallin 1986). Thus, the low pairing success of the handicapped males may have been due to their low singing activity.

The slight increase in the pairing success of the males that were defending more than one nestbox can also be explained by 'passive attraction'. Males defending many nestboxes possess larger territories, and the visiting rate of prospecting females may be proportional to territory size (cf. O'Donald 1980).

Further studies are therefore needed before a discrimination between the mechanisms of active and of passive choice of mate can be made, and especially data on the searching pattern and the decision-making process of the females are required.

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