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Competition for a mate restricts mate search of female pied flycatchers

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Summary. We studied the mate sampling behaviour of female pied flycatchers, *Ficedula hypoleuca*, in a 40-ha area containing 10–12 unmated males whose nestboxes were monitored with videocameras. The main results were: (1) The females undertook a restricted mate search. The females that mated in the area during three monitoring periods ($n = 20$, 12 females released by us and 8 females that arrived naturally) sampled 1–10 males (median 4.5). This was about 40% of the available mating options. (2) Search costs in terms of time and energy were low. The search period was short (median 5.1 h) and only a small proportion of the search period was spent at the nestboxes of males (median 4%). The females visited up to seven different males in 1 h, and the time elapsing between visits to different males was short (median 13 min). The minimum distance travelled during the search was also short (median 1.4 km). (3) There was competition between the females. We recorded seven cases of two females visiting the same male at the same time, including at least one case involving physical fighting. (4) Females that experienced a high level of competition had a more restricted mate search than females that experienced a low level of competition. (5) The search pattern of most of the females did not conform to the best-of-*n*-males rule nor to the threshold criterion rule, because they made repeated visits to many of the males sampled.

Introduction

Basic knowledge of the mate sampling behaviour of individuals is needed to understand mate choice. Information about the extent of the search for a mate in terms of the number and sequences of mates sampled is necessary to determine what rules are used to choose among mating options. This will in turn provide information on the criteria on which choices are based. Data on the sampling behaviour is accumulating for non-resource-based mating systems (e.g. lek species; Kruijt and Hogan 1967; Lill 1974, 1976; Payne and Payne 1977; Borgia et al. 1985; Trail 1985; Gibson and Bradbury 1986; Arak 1988; Moore 1989; Trail and Adams 1989; Pruett-Jones and Pruett-Jones 1990; Trail 1990; Petrie et al. 1991) while for resource-based mating systems (e.g. species with paternal care of young) such data are still scarce (Gronell 1989; Dale et al. 1990). These two general types of mating systems differ widely regarding costs and benefits of sampling behaviour and mate choice (Reynolds and Gross 1990).

Several models for how individuals may choose between mating options have been proposed (Janetos 1980; Wittenberger 1983; Real 1990; Wade and Pruett-Jones 1990). According to the best-of-*n*-males rule (also called a pool-comparison tactic) a female samples *n* males and then chooses the best. Support for this rule comes from lek species (Trail and Adams 1989; Pruett-Jones and Pruett-Jones 1990; Petrie et al. 1991). Individuals using the threshold-criterion rule (also called sequential search or one-step decision process) sample mates until encountering one that exceeds some threshold value. There are indications that some species use this rule (Moore and Moore 1988; Zuk et al. 1990). Alternatively, mate choice may not be involved at all and individuals settle with the first mate encountered (passive attracion or random settlement; O'Donald 1980; Parker 1983; Lightbody and Weatherhead 1987; Arak 1988; Dale and Slagsvold 1990). One could also imagine more complicated decision rules consisting of combinations of some of the above rules and which depend on the costs and benefits of sampling experienced by each individual during the search.

There are indications from several species that individual animals undertake only a restricted mate search (Brown and Downhower 1983; Alatalo et al. 1988; Slagsvold et al. 1988; Dale and Slagsvold 1990). This is expected if there are costs associated with mate search and mate sampling (Daly 1978; Parker 1983; Pomiankowski 1987; Real 1990; Slagsvold and Dale 1991). Search costs may be in terms of time and energy (Parker 1983; Alatalo et al. 1988; Slagsvold et al. 1988), costs of assessing mate quality (Wootton et al. 1986), risk of predation (Arak 1988; Wing 1988), harassment by males (Trail and Adams 1989), or competition between prospecting individuals. In animals that are highly mobile in relation to the density of potential mates it would be surprising if costs in terms of time and energy were important. In fact, there are indications that these costs may be low (Slagsvold and Dale 1991). Furthermore, in some species the cost of assessing mate quality or resource quality may be low (Dale et al. 1990; S. Dale unpublished). On the other hand, competition between individuals searching for mates may be an important factor leading to a restricted mate search, but we know of no evidence for this.

In this study, we present detailed data on the mate sampling behaviour of female pied flycatchers, *Ficedula hypoleuca*. In this species males display at sites such as nestboxes to attract females. The females may visit several males in a short period of time and inspect their nestboxes (Dale et al. 1990). Nestbox quality is important for female mate choice (Alatalo et al. 1986; Slagsvold 1986) but visits nonetheless last only a few minutes (Dale et al. 1990). The males feed the females during the incubation period (Lifjeld and Slagsvold 1986) and provide parental care to the offspring. Though some males are polygynous most pied flycatchers mate monogamously. Here we used videocameras to monitor male and female behaviour at the nestboxes. This provided an almost complete knowledge of the mate sampling behaviour of the females that were released into the study area. Based on these data we address the following questions: (1) Do female pied flycatchers have a restricted mate search? (2) What kind of decision rules do the females use when choosing among males? (3) Do the females obtain a better mate by sampling than by mating with the first male encountered? (4) Is the extent of the mate search influenced by search costs, competition between females for a mate, or some other factor?

Methods

Study area. The study was carried out during May–June 1989 in a 40-ha deciduous forest near Oslo, south-eastern Norway [see Slagsvold et al. (1988) for a detailed map over the area]. Males arrived during 9–17 May and were trapped and colour-ringed soon after arrival. On 17 May all excess nestboxes were closed to restrict each male to one nestbox and to prevent additional males from settling. All nestboxes were of the same size and shape. Females were released into the area during three experiments (see below). During the first experiment (26–27 May) ten males were present. Two new males were allowed to settle on 28–29 May, so 12 males were present during the second experiment (2–3 June). There were also 12 males present in the third experiment (7–8 June); however, four of the males from the second experiment had been replaced by males that had been captured before the first experiment and held in captivity since then. Half of the males in the second and third experiments were handicapped by removing three of the primaries on each wing and six central tail feathers, but this did not have any obvious influence on the results. The surroundings of the study area had a very sparse population of pied flycatchers and many of these males were probably mated at the time of our experiments. Other nestboxes areas were at least 3–4 km away. On the days before and in between each experiment all naturally arriving females were removed and released in other areas so as to keep all males in the study area unmated at the start of each experiment. However, during this year most of the naturally arriving females mated before the first experiment and none after the third experiment. Males ≤ 200 m apart with common territory boundaries were classified as neighbours (Dale and Slagsvold 1990).

Released females. The females that were released into the study area had been captured in two nestbox areas located 16 and 23 km away from the study area, respectively. The 15 females used in the first experiment were captured during 17–21 May and held in captivity until released (mean 6.7 days). All were captured during the nest building stage. The 15 females used in the second experiment were captured during 28 May–1 June; about half of the females were in the nest building stage and the others were in the incubation stage, and they were held in captivity for a mean of 3.3 days. The 20 females used in the third experiment were captured on 6 June; all were in the incubation stage and they were held in captivity for less than 1 day. The females were given unique combinations of colour-rings on both legs and were also given a unique combination of black ink spots on the head and bars on the white wing patch.

Monitoring of females and definitions of behaviour. The females were released during 0717–0748 hours on 26 May, 0750–0819 hours on 2 June, and 0709–0744 hours on 7 June, on evenly spaced sites throughout the study area. Their subsequent mate sampling behaviour was monitored with videocameras. The cameras were placed on tripods about 2 m from the nestbox of each male and the view covered the nestbox from the side. In the first experiment the cameras monitored the nestboxes of all males during 0704–2222 hours on 26 May and 0457–2000 hours on 27 May, in the second experiment during 0729–2043 hours on 2 June and 0515–2022 hours on 3 June, and in the third experiment during 0651–2123 hours on 7 June and 0929–1954 hours on 8 June. The late start on 8 June was due to heavy rain during the morning. During the experiments sunrise varied from 0422 to 0403 hours and sunset varied from 2209 to 2232 hours. During the experiments nestboxes were approached only to change videocassettes every 3 h, and to remove females that had mated (we did this in nine cases to provide new mating options for unmated females).

During the three experiments females appeared at the nestboxes of the males on a total of 1027 occasions, including both released and naturally occurring females, but excluding all appearanes of nest-building females. In 979 cases (95.3%) we were able to identify them either as a specific released female or as a naturally occurring female. There was a bimodal distribution of the times between the appearances of females that made several appearances at one nestbox in a row. We interpret this as being a methodological artefact due to the restricted field of view of the videocameras. Reappearances after a short time are probably within the same visit and the females have probably been close to the nestbox in the whole period while reappearances after a longer time indicate that the female left the male in the meantime. Thus, we classify appearances of one female at the same nestbox separated by less than 1 min as pertaining to the same visit. The particular value of 1 min is chosen from the form of the curve in Fig. 2A. In these cases the expression 'time spent at the nestbox during the visit' includes the time of less than 1 min between two appearances.

The search period is defined as the time elapsing from the first visit a female made until the last visit the female made. The last visit is defined as the first appearance at the nestbox of the chosen male after the female had stopped visiting other males. Mating time is defined as the onset of nest building. The premating period is defined as the time elapsing from the time of release until mating time. The post-search period is defined as the time from the end of the search period until mating time.

Behaviour of naturally arriving females. To see whether the behaviour of the released females was comparable to that of naturally arriving females, we reconstructed the probable search pattern of the eight females of the latter category that mated during the experiments (four, three and one in each of the experiments, respectively). Plumage variation among females is too small to permit identification of individuals. Therefore, we used the temporal and geographical pattern of visits by unmarked females to distinguish between individual females. Visits were usually temporally and geographically well separated and this coincided with matings of naturally arriving females. In addition, the reconstructions were based on the following assumptions: (1) Females usually start sampling males soon after arrival in the area, mostly early in the morning, and settle later the same day if weather conditions are good (as they were during and before the days these particular females mated). This assumption is supported by observations of the temporal mating pattern of unmanipulated females. In 1987 the number of matings per day in this study area varied from 0 to 12 and the peaks were on days following nights with favourable conditions for migration, suggesting sampling periods of less than 1 day. (2) Females sometimes visit males that are mated, and even after they are mated to one male occasionally also visit other males. (3) A series of visits to one male, usually separated by less than half an hour, leading up to the onset of nest building are attributed to the same female. Assumptions (2) and (3) are supported by the behaviour of the released females in this study. (4) Most of the naturally arriving females visiting males in the study area also settle in the study area. This may seem to be contradicted by the fact that several of the released females disappeared but we assume that this was due to stress during our handling of them since these females were those in worst condition (see also Slagsvold et al. 1988).

Of the 294 appearances of naturally occurring females, 27 remained ambiguous using this method; these were assigned to individual females according to the principle that visits of one female occurring in a short time should be among males in one part of the study area; movements between neighbours is the general rule. This was also supported by the behaviour of the released females. This method introduces some bias in that the pattern is deliberately chosen to resemble that of the released females. However, this concerns less than 10% of the visits and will probably not lead to great errors. Only 2 of the 294 appearances were not assigned to any of the eight naturally arriving females. One was of a female with a deformed foot which was definitely not seen more than once and did not mate in the area. The other observation was at the end of the second experiment and was separated in time and location from the other observations, and in fact the other three naturally occurring females present at that time were all mated. For the naturally occurring females the premating time is defined as the time elapsing from the first visit until the onset of nest building. This is not very different from the released females since these made their first visits only 1–92 min (median 12 min) after they were released.

Ranking of males. We ranked the males according to their attractiveness to the visiting females. We used three criteria in the following order of priority: (1) How many females were they rejected by? Rejections were defined as females leaving for other males without mating when the male was unmated. Additionally, we required that (a) there was no female in the post-search period associating with this male, i.e. there was no female that had 'decided' to settle with the male, and (b) there was no conflict with females that later mated with this particular male (conflicts are here taken as visits separated by less than 1 min). Released females that disappeared were excluded from this analysis. (2) Did the male become mated? (3) In cases of mating, how many other males did the female visit during the search period after her first visit to him? Thus, the highest-ranking male was not rejected by any females and became mated to a female that stopped searching after visiting him. The lowest-ranking male was rejected by several females and did not become mated. When using the attractiveness of the males to analyse the mate choice made by a particular female we used the male rank obtained from the behaviour of the other females to avoid pseudoreplication.

Level of competition. We estimated the level of competition experienced by each of the females by recording the time between her visit and the visits of other females (all types) visiting the same male, both before and after the visit of the female in question. A median value of these time intervals was then calculated for each female. This was estimated for (1) the whole search period, (2) for the first hour of the search period and (3) for the first visit of each female, respectively. We used the time to other females visiting the male both before and after the visit of the respective female as these were probably independent values and each value was attributed to both females in question.

Results

Extent of mate search

We released a total of 50 females in three groups into the study area. Ten of the females were not seen visiting any of the 10–12 males that were present in the study area. Compared to females that visited males, these females tended to have lower body weights at the time of release ($z = -1.63$, $P = 0.10$, Mann-Whitney U-test). Of the 40 females that were seen visiting males, 12 mated in the study area during the period of monitoring. Three females mated after we had finished videotaping, hence, we do not have complete knowledge of the mate search of these females, but they visited at least one, three and eight males, respectively. The remaining 24 females visited 1–9 different males (median 2) but did not settle. These females tended to have lower body weights than those that mated ($z = -1.41$, $P = 0.16$, Mann-Whitney U-test). Of the 35 females that did not mate in the study area, 3 returned to the areas in which they had been trapped, 1 mated in a nestbox area 8 km from the study area, and none mated in two nestbox areas 3–4 km from the study area. Here we will focus on the mate sampling behaviour of the females that mated in the study area during our experiments. We include data on eight different females that arrived spontaneously and mated during the experiments (see Methods for how we estimated their mate sampling behaviour), leaving 20 females for the subsequent analyses.

There were no differences between released females and naturally arriving females in the extent of the mate search (number of males sampled, number of visits, number of movements, total distances moved, duration of search period, duration of premating period, distances moved between subsequent males, and time elapsing between visits to different males; Mann-Whitney U-tests, $P > 0.20$ for all). The two groups are therefore pooled in subsequent analyses. However, in relation to the level of competition the duration of the search period of the naturally arriving females was shorter than for the released females (see below).

The females visited 1–10 (median 4.5, $n = 20$) different males during the mate sampling period (Table 1, Fig. 1). The males were sampled during the course of 1–46 (median 14) separate visits and the females that visited more than one male made 1–36 (median 7.5, $n = 18$) movements between males. The distance moved between subsequent visits to two males was 54–708 m (median 229 m, $n = 156$). Subsequent visits to the same male were

Table 1. Behaviour of the 20 female pied flycatchers that mated in the study area during the three experiments

Female	Female group[a]	Number of males sampled	Number of visits	Number of movements	Distance moved (km)[b]	Duration of search period (h)	Duration of premating period (h)
Experiment 1							
1	R	1	1	0	0.1	0.0	2.4
2	R	1	1	0	0.4	0.0	0.9
3	R	3	3	2	0.8	2.1	5.1
4	R	3	24	4	1.4	11.3	12.6
5	R	4	8	5	1.2	2.9	8.2
6	R	4	40	6	1.6	24.6	27.9
7	R	5	9	5	1.1	1.3	9.4
8	N	3	9	4	0.4	1.2	10.2
9	N	4	7	3	0.8	3.0	3.8
10	N	7	14	8	3.4	8.4	18.7
11	N	7	17	12	3.9	7.0	24.0
Experiment 2							
12	R	6	22	13	2.2	22.4	27.0
13	R	5	31	7	1.6	20.1	21.7
14	R	5	30	10	2.8	21.9	22.5
15	N	2	11	2	0.4	4.2	5.5
16	N	5	14	8	1.3	3.7	6.0
17	N	6	6	5	1.5	3.6	5.1
Experiment 3							
18	R	7	41	16	6.3	12.1	28.5
19	R	10	46	36	10.4	27.9	30.0
20	N	4	20	11	2.0	6.0	6.1
	All	1–10	1–46	0–36	0.1–10.4	0.0–27.9	0.9–30.0
	R	1–10	1–46	0–36	0.1–10.4	0.0–27.9	0.9–30.0
	N	2–7	6–20	2–12	0.4–3.9	1.2–8.4	3.8–24.0

[a] R = released females, N = naturally arriving females

[b] For released females including the distance from the site of release of the first male visited

separated by 1–706 min (median 8.1, $n=178$, Fig. 2A) while 1–912 min (median 13.0, $n=156$, Fig. 2B) elapsed between subsequent visits to different males. This difference was significant ($z=-2.48$, $P=0.01$, Mann-Whitney U-test), However, there was no significant difference in the time elapsing between visits when the next male was a neighbour (median 10.0 min, range 1–912, $n=52$) as compared to when the next male was more distant (median 13.5 min, range 1–509, $n=104$; $z=-1.06$, $P=0.29$, Mann-Whitney U-test). Likewise, there was no significant correlation between the time elapsing between visits to different males and the distance between these males ($r_s=0.10$, $n=156$, $P=0.21$, Fig. 3).

The females that visited more than one male sampled males for 1.2–27.9 h (median 6.8, $n=18$). The premating period was 0.9–30.0 h (median 9.8, $n=20$). The temporal patterns of activity during the sampling period for each of the released females that mated are shown in Fig. 4. For all the seven released females that sampled males for more than 3 h (Fig. 4) the distribution of time intervals between the visits was significantly skewed to the right ($P<0.001$ for all seven females; Signed-ranks test, $P=0.008$), indicating that bouts of mate sampling activity were separated by periods of no sampling activity.

Of the 20 females, 6 visited other males after they had started nest building with one male. In one of these cases, the female eventually changed mate.

Mating options

The females visited on average less than half of the males present in the study area. However, during their mate search an increasing number of males became mated. We recorded 14 cases in which searching females visited males that were already mated, i.e. another female had started nest building. No searching females displaced already-mated females. Thus the number of mating options for the females was lower than the number of males present indicates. At the beginning of the search of each female an average of 10.2 of the males were unmated (range 2–12, $n=20$). At the end of the search period of each female some of these males had become mated, thus, an average of 8.7 of these males were still unmated (range 2–12). Of these potential mating options, the females visited an average of 4.4 during their search (range 1–10), while at the end of the search period of each female an average of 3.5 of these males were still unmated (range 1–9). This shows that the females undertook a restricted mate search in the sense that only 40–43% of the potential mating options were considered. The number of mating options may have been even lower than indicated here. In seven cases two females visited the same male at the same time (see below), and in all these cases one of the females later mated with the male. Furthermore, females often visited males that

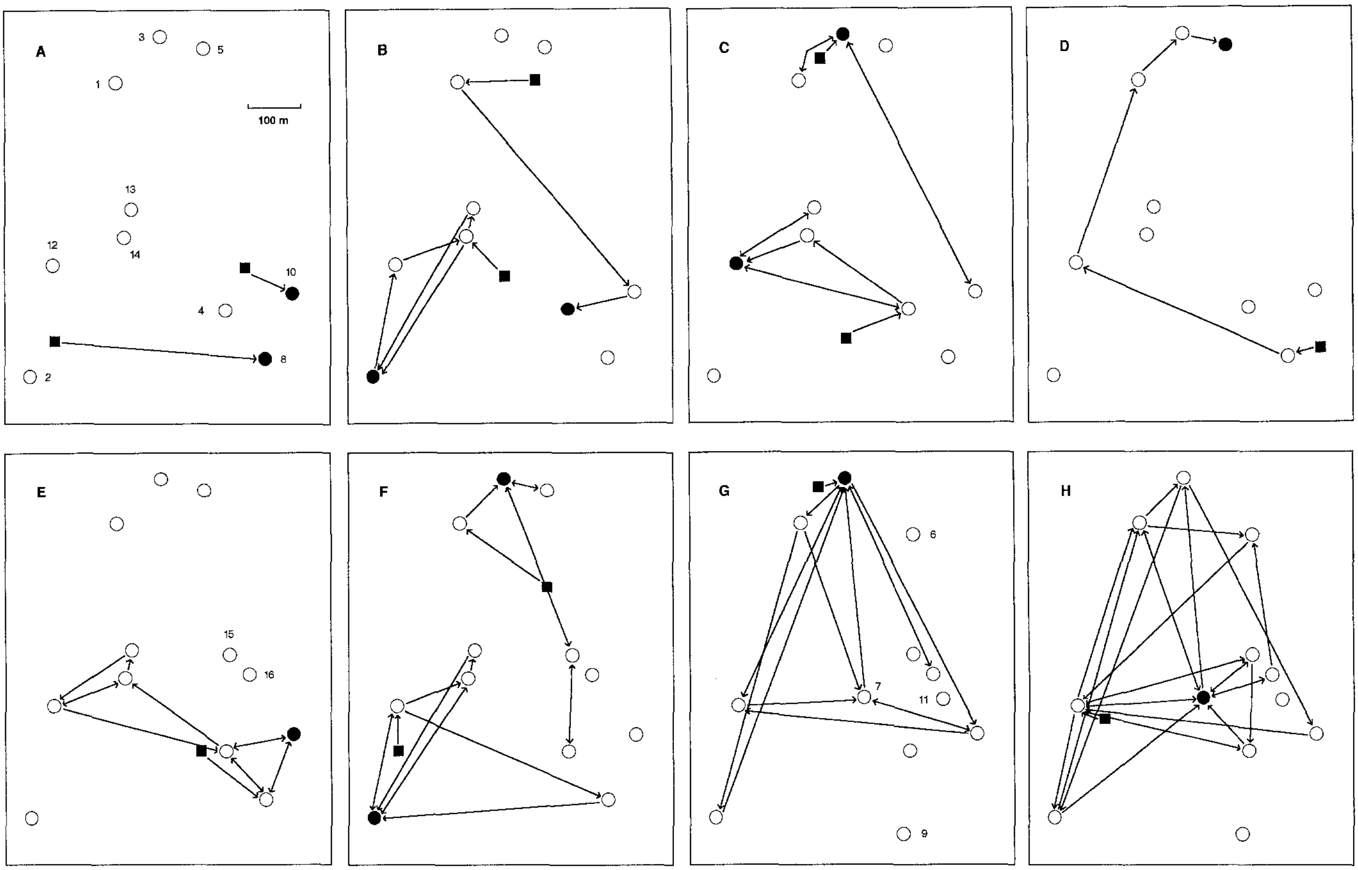

Fig. 1A–H. Movements during the sampling period of the 12 released female pied flycatchers that mated in the study during the experiments. **A** Females no. 1 and 2. **B** Females no. 3 and 5. **C** Females no. 4 and 6. **D** Female no. 7. **E** Female no. 12. **F** Females no. 13 and 14. **G** Female no. 18. **H** Female no. 19. Females are numbered as in Table 1 and Fig. 4. Males are numbered in order of their arrival times (*1* = first male etc.). *Filled squares*: sites of release of the females; *circles*: positions of the males present during each of the experiments. *Filled circles* designate the males that were chosen as mates by the respective females. *Arrows* may represent one or more movements in the direction indicated. Refer to Fig. 4 for the temporal sequence of movements

were not yet mated but that were more or less regularly visited by the female that was to be their mate, after the female had terminated her mate search. Hence, not all of these males may have been available for the searching females. With these restrictions the females considered 38–44% of the potential mating options.

Indications of restricted mate search have been found in previous studies of the pied flycatchers (Slagsvold et al. 1988; Dale et al. 1990) due to females settling closer to the sites of release than expected from random choice among all males present. There was a tendency towards this pattern in the present study also though not significant; 8 of 12 females settled with males that were closer to the site of release than the median distance for all males ($\chi^2 = 1.33$, $df = 1$, $P = 0.25$). However, the females did not choose males close to the site of release when considering only the males that were visited: relative to the median distance from the site of release, three males were closer and three were more distant, while four males were at the median distance.

Decision rules

Both the best-of-n-males rule and the threshold-criterion rule imply that females visit each male only once during the sampling period, though in the former females may return to a male after the sampling is terminated. In the following analysis we exclude the two cases in which females visited only one male, as this could be examples of any rule with $n = 1$. Of the 18 females, 7 visited each male only once before settling; these females may then have used the best-of-n-males rule. In four of the cases the chosen male was the last one of those visited which was only slightly more than expected (if females chose randomly among the n males sampled, the last one visited was expected to be chosen in 2.6 of the seven cases; $\chi^2 = 1.16$, $df = 1$, $P = 0.28$). These four cases were also the cases that may have been examples of the threshold-criterion rule since choosing the last of n males sampled can be interpreted as examples of both rules. Thus, these two rules combined applied to no more than 7 of the 18 cases in all.

The majority of the females (14 of 18) made repeated visits to one or more males. They returned to a male up to nine times (range of means: 0–3.0, median 1.5, $n = 18$) during the search, and they returned to 0–90% (median 50%) of the males visited. The chosen male was revisited by 12 of the 14 females that returned to any male (expected number under random search: 7.8; $\chi^2 = 5.06$, $df = 1$, $P = 0.03$). In the nine cases where a female

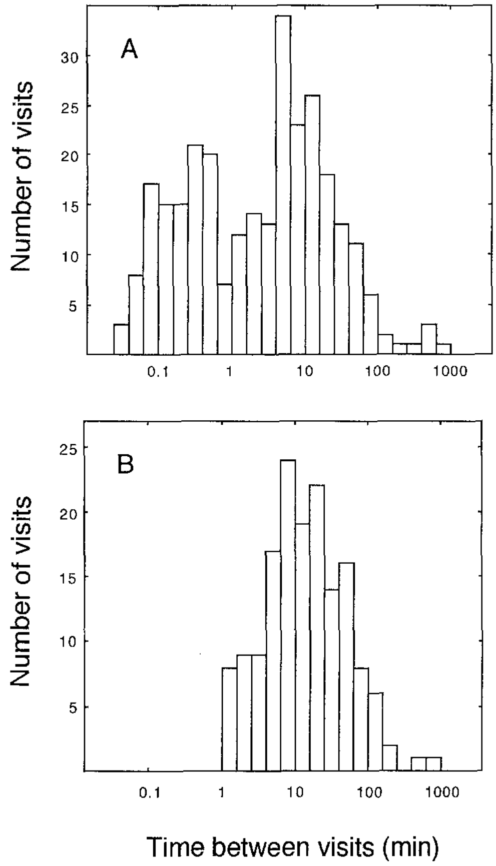

Fig. 2A–B. Frequency histograms of the times elapsing between subsequent visits of female pied flycatchers during the sampling period. **A** The cases in which subsequent visits were to the same male. **B** The cases in which subsequent visits were to different males. The *left-hand peak* in A was probably a methodological artefact and therefore appearances separated by less than 1 min are treated as one visit (see Methods)

revisited more than one male (range 2–9 males) and the chosen male was among them, he was revisited more often than the other males that were revisited ($\chi^2 = 8.99$, $df = 2$, $P = 0.01$).

Females visiting more than one male chose the last one visited in eight cases, the first one in five cases and an intermediate male in five cases. The last one was chosen slightly more often than expected from random choice (expected number of first, intermediate and last males chosen: 4.58, 8.85 and 4.58, respectively, $\chi^2 = 4.27$, $df = 2$, $P = 0.12$).

Choice relative to male rank

To analyse whether the females made optimal choices we used the attractiveness rank of the males (see Methods). We excluded the last experiment in which only three females settled since this would not provide good estimates of male attractiveness. Most females (13 of 17) mated with a male of median or above-median rank while four mated with a male of below-median rank ($\chi^2 = 1.83$, $df = 1$, $P = 0.18$). Of the 15 females that sampled more than one male, 9 mated with the highest ranked unmated male encountered (expected number under random choice: 6.19; $\chi^2 = 2.17$, $df = 1$, $P = 0.14$). If the females chose among only the unmated males at the end of the search period (best-of-*n*-males rule), 11 of 14 females that had more than one male to choose among mated with the highest ranked male (expected number under random choice: 5.38; $\chi^2 = 9.54$, $df = 1$, $P = 0.002$).

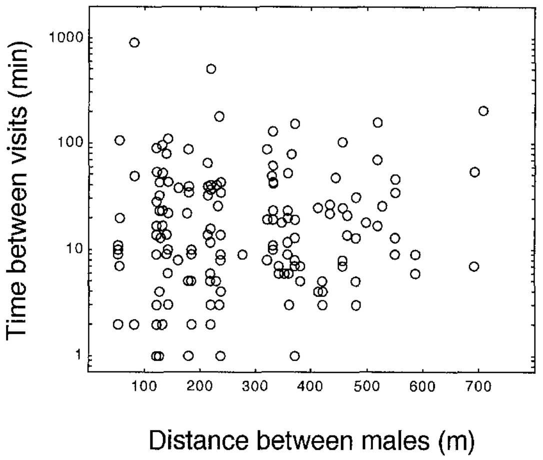

Fig. 3. The time elapsing between subsequent visits of released female pied flycatchers to different males as a function of the distance between the males

This seems to indicate that the females benefited from sampling. However, we also compared their choices with what they would have obtained if they had not sampled males at all, i.e. settled with the first male encountered. Of the 12 females that did not settle with the first mating option, 6 ended up with males of higher rank, 4 with males of lower rank and 2 with males of equal rank. Thus, the females did not obtain a significantly higher-ranking male by continuing their search ($\chi^2 = 0.40$, $df = 1$, $P = 0.53$). Note that in all the four cases in which the females obtained lower-ranking males by leaving the first unmated male visited, this male had become occupied when the females ended their search.

Search costs

The mate sampling period lasted for a median of 5.1 h ($n = 20$, Table 1). At the most, females visited 1–7 (median 3) different males within 1 h which accounted for 43–100% (median 68%) of all the males sampled. The median duration of the visits at the males' nestboxes for individual females was 27–124 s (median 52 s, $n = 20$) while the single longest visit lasted nearly 16 min. During the whole sampling period each female spent 2.3–43.3 min (median 14.3 min, $n = 18$) at the males' nestboxes, which was 1–15% (median 4%) of the whole sampling period. Hence, the time cost involved in the search of the females in this study was probably low. This was also supported by the fact that the time elapsing between visits to different males was not or only weakly correlated with the distance between the males, as shown above.

During their search the females frequently moved from one male to another. When they left a male, the

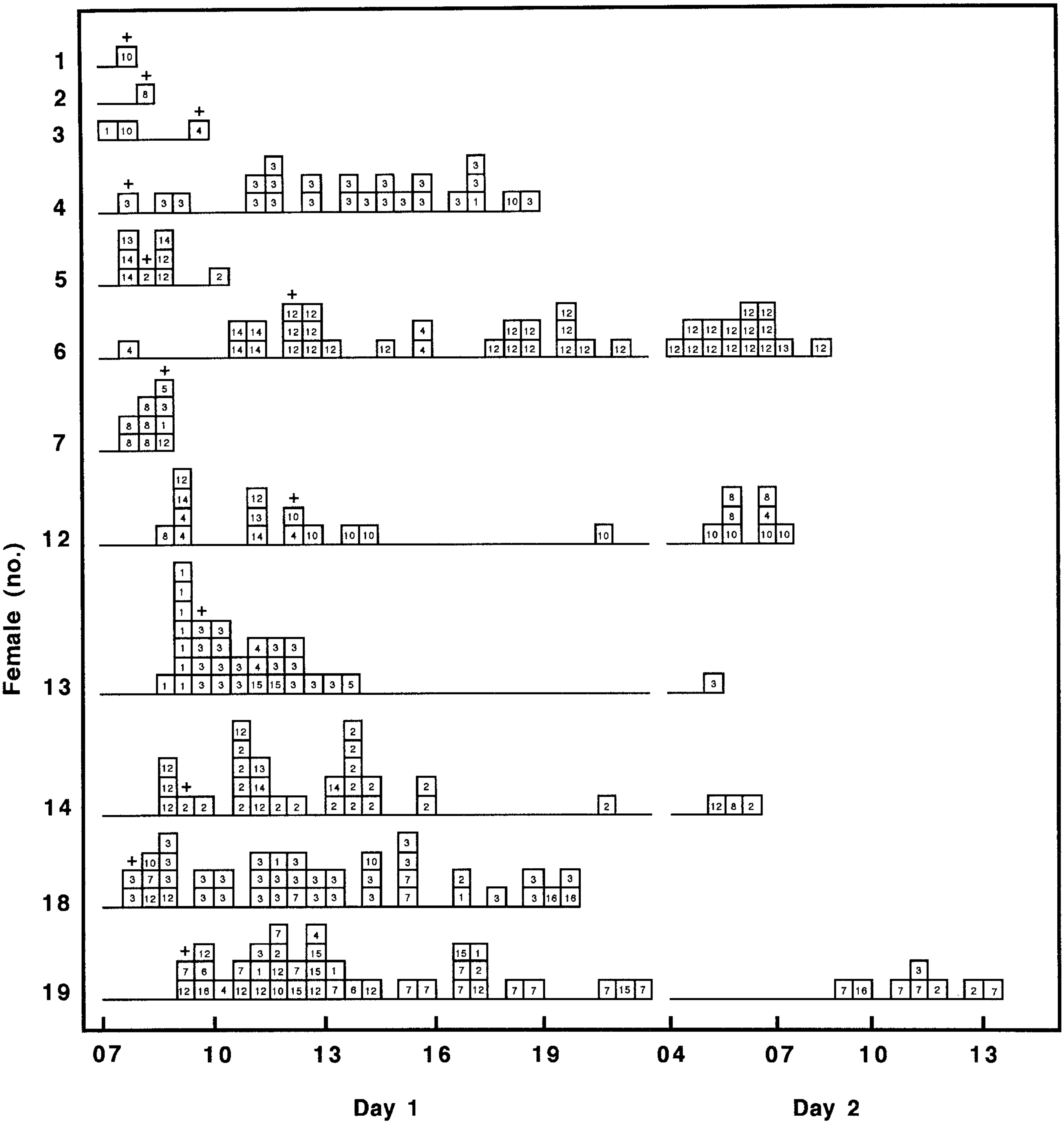

Fig. 4. The temporal pattern of visits during the sampling period made by the 12 released female pied flycatchers that mated in the study area during the experiments. Each *square* represents a visit. In the cases in which a female made several visits during one half-hour period the first visit is shown at the *bottom* and the last visit at the *top* of the *stack of squares*. Females are numbered as in Table 1 and Fig. 1. *Numbers* in the squares refer to the males which were numbered in order of their arrival times (*1* = first male etc.). *Crosses* above squares indicate the first visit to the male that was later chosen as mate

next visit was to a neighbouring male in 52 cases, while in 104 cases the next male was more distant. This is significantly different from random (expected number of movements to neighbours versus other males under random search: 23.8 and 132.2, respectively; $\chi^2 = 39.3$, $df = 1$, $P = 0.0001$). Thus, the minimum distance moved by the females during the whole sampling period was only 0.1–10.5 km (median 1.4 km, Table 1). However, females probably did not move in straight lines between males and the speed of flight inside the forest was probably not very high; even so the average female probably spent less than 20 min moving between the males (given that they travelled 3 times as long as our estimates indicate at a flight speed of 15 km/h). Hence, the energy costs of searching by the females were probably also low in our study area.

Competition between females

In seven cases two unmated females visited the same nestbox at the same time. At least one of these cases involved a physical fight. The loser continued her search and finally settled with another male. This suggests that competition influenced the mate search of the females. We therefore compared the extent of the mate search (the number of males sampled and the duration of the search period) with the level of competition experienced by the females (Table 2). The analysis revealed that competition had an effect, in particular the level of competition experienced during the first hour of the search. Thus, females that experienced a high level of competition had a more restricted mate search than females that experienced a low level of competition (Fig. 5). In addition, further analyses showed that the number of unmated males visited during the search was also significantly correlated with the level of competition during the first hour of the search ($r_s = 0.56$, $n = 20$, $P = 0.01$), as was the number of mating options in the strictest sense (excluding mated males, males with a female in the post-search period and direct conflicts; $r_s = 0.61$, $n = 20$, $P = 0.01$).

However, we must ascertain that this important result is not due to differences between different types of females. We have included both naturally arriving females and released females. The released females were of two types; some were captured during the nest-building stage and some during the incubation stage. We therefore looked at the relation between the level of competition and the number of males sampled for these groups separately. Considering only the released females, the correlation was significant ($r_s = 0.62$, $n = 12$, $P = 0.04$, Table 2), and the correlation coefficient was about the same when considering only the naturally arriving females ($r_s = 0.58$, $n = 8$, $P = 0.13$, Table 2). The correlation coefficient was also about the same when considering only the released females in the first experiment which were all captured during the nest-building stage ($r_s = 0.66$, $n = 7$, $P = 0.11$, Table 2). For the relation between the duration of the search period and the level of competition during the first hour of the search the correlations were significant for the released females but were non-significant for the naturally arriving females (Table 2). The naturally arriving females also had a more restricted mate search than released females experiencing a compa-

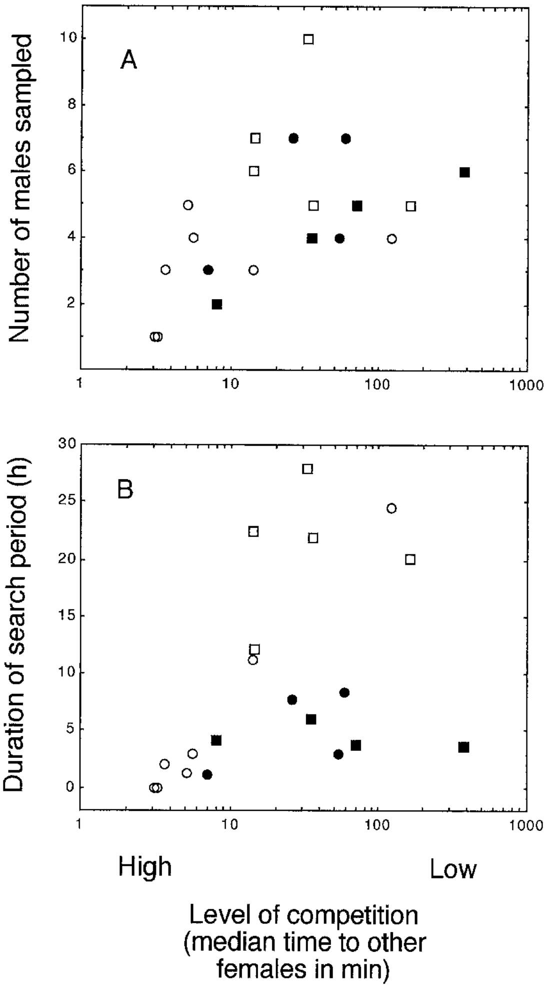

Fig. 5 A, B. The relationship between the level of competition experienced during the first hour of the search of each female pied flycatcher, and the extent of the mate search. **A** Number of males sampled. **B** Duration of the search period. *Open symbols*: released females; *closed symbols*: naturally arriving females; *circles*: females in the first experiment; *squares*: females in the second and third experiments. Tests are given in Table 2

Table 2. Spearman rank correlations between the level of competition and the extent of the mate search (number of males sampled and the duration of the search period) of female pied flycatchers

Level of competition	Experiment 1		Experiments 1–3					
	Released females $n = 7$		Released females $n = 12$		Naturally arriving females $n = 8$		All females $n = 20$	
	Males	Duration	Males	Duration	Males	Duration	Males	Duration
First visit	0.50	0.58	0.37	0.42	0.69[1]	0.33	0.36	0.39[1]
First hour	0.66	0.96*	0.62*	0.85**	0.58	0.10	0.55*	0.60**
Whole search	0.46	0.67	0.60*	0.65*	0.75*	0.36	0.64**	0.37

[1] $P < 0.10$; * $P < 0.05$; ** $P < 0.01$

rable level of competition (Fig. 5). However, the naturally arriving females were probably in better condition than the released females since 49 of 50 released females lost weight during captivity. There was a negative correlation between the condition of the released females and the duration of the search period, although not significant ($r_s = -0.52$, $n=11$, $P=0.10$). Such a relationship may explain why the naturally arriving females settled more quickly. We conclude that the relation between the level of competition and the extent of the mate search was probably not an artefact of differences between different kinds of females.

Discussion

Based on the behaviour of 12 individually marked females and 8 naturally occurring females we found that:

(1) The females undertook a restricted mate search; they sampled less than half of the males available even though the study area was rather small. This conclusion must be evaluated with some possible sources of bias in mind. (a) The nestboxes were not monitored 24 h a day. However, nearly all daylight hours were covered while the peak sampling period was several hours after sunrise. Thus, we believe that only few visits may have been missed. (b) Three females mated after we had finished videotaping. These females may have had a more extensive search than other females. (c) The females may have visited males outside the study area before mating with a male inside the study area. This is not very likely because of the isolation of the study area; other nestbox areas were at least 3 km away and there were few pied flycatchers in between (see also below). (d) Females that did not mate in the study area may have mated elsewhere. Of the 35 released females that did not mate in the study area only 1 was later found nesting in other nestbox areas 3, 4, and 8 km away, respectively (3 returned to their former nesting areas). We probably have very good control over the local population of pied flycatchers as shown by our unusually high return of males (Slagsvold and Lifjeld 1990). This suggests that many of the disappearing females did not mate at all. In addition, there was a trend for the females that did not mate in the study area to have lower body weights than those that mated, although this was not significant. However, this trend has been significant in another study (Slagsvold et al. 1988). Therefore, we believe that many of these females did not mate at all because of their poor condition. (e) The study was made late in the season. It is possible that late-arriving females have a less extensive search than early-arriving females as has been suggested by Dale and Slagsvold (1990). However, this may be due to differences in the level of competition rather than a direct effect of the time of the season (see below).

(2) The search patterns and the decision rules of most of the females were more complex than suggested by current models of mate choice, and involved repeated visits to about half of the males sampled.

(3) Sampling of several males did not give any obvious benefit compared to random settlement.

(4) The search costs in terms of time and energy were probably low; the sampling period was only a matter of hours, and visits to males lasted for only about 1 min indicating easy assessment of nest site quality.

(5) Competition between females reduced the extent of the mate search; females that experienced a high level of competition had a more restricted mate search than females that experienced a low level of competition. There remains the question of whether competition also has an effect under natural conditions. One could argue that the level of competition was artificially high because females were released into the area. However, since the study was done late in the season there were relatively few naturally arriving females. Thus, the total number of searching females may not have been particularly high. The number of females mating per day during the three experiments was 5.5, 3 and 1.5, respectively, while up to four females mated per day earlier in the season. As a comparison, up to 12 females mated per day in the same study area during the 1987 season, though there were more males present in that year. In conclusion, we believe that the levels of competition produced in our experiments are within the natural range in this area.

There is some uncertainty associated with the data on the search patterns of the naturally arriving females. We may have made mistakes when reconstructing their search patterns and it is possible that they visited males before the start of our monitoring with videocameras. However, our conclusions do not depend on these data. All the above points were supported by the behaviour of the released females, but the behaviour of the released females did not seem to be very different from that of the naturally arriving females.

The present study is the best so far of the mate sampling behaviour of female pied flycatchers. Dale and Slagsvold (1990) suggested that many females settled randomly, i.e. after sampling only one male. This was based on indirect evidence and the actual behaviour of the females was not observed. Dale et al. (1990) observed the behaviour of the females but did not obtain a complete knowledge of the search pattern of individual females as about two-thirds of the visits were by unidentified females. The present study has documented a wide range in the behaviour of the females and shows that competition is an important factor causing the variation. However, only 10% of the females sampled only one male which may seem to contradict our earlier conclusion of random settlement of females (Dale and Slagsvold 1990). However, there was a large number of females arriving in the study area during that year and because of this the level of competition may have been higher than in the present study. Thus, we still think it is possible that random settlement may be an important strategy under some circumstances.

Decision rules

Janetos (1980) compared different decision rules and concluded that the best-of-*n*-males rule yielded the highest expectation of fitness for the females. Some support for this rule has been found in lek species such as the Guianan cock-of-the-rock, *Rupicola rupicola* (Trail and Adams 1989), Lawes' parotia, *Parotia lawesii*, a bird of paradise (Pruett-Jones and Pruett-Jones 1990) and peafowl, *Pavo cristatus* (Petrie et al. 1991). However, the models of Janetos did not incorporate any costs of choice. Real (1990) has shown that a threshold-criterion rule will be superior to the best-of-*n*-males rule if costs are involved. However, search costs are probably low for females sampling males on a lek. There is some evidence that other species use a threshold-criterion rule (Moore and Moore 1988; Zuk et al. 1990). According to Real (1990) competition can be viewed as a cost; the cost of leaving a male when there is a risk that the male will be occupied by another female if the female decides to return to him later on. In our study, half of the females mated with the last male visited but only 6 of the 20 females might have used a pure threshold-criterion rule. Thus, the prediction from the model of Real (1990) does not receive clear support from our data. In addition, the search pattern of seven of the females fitted the best-of-*n*-males rule. However, most of the females made repeated visits to many of the males during the search. This is not expected from either of these two rules. It is a more or less unspecified assumption of the best-of-*n*-males rule that the males should not be revisited. Only if the females returned to *all* males could the pattern be considered a best-of-*n* rule. Otherwise it would be more appropriate to call the behaviour an elimination tactic which is almost the opposite of a pool-comparison tactic. However, our observations suggested that the behaviour of the females was even more complex in that the revisitations were highly irregular. Repeated visits were also observed in the studies of Trail and Adams (1989) and Petrie et al. (1991).

Why did the females return to males during the search? One possibility is that there are limitations on the memory of the females. Females that sample more than one male need to remember the assessed quality of previously encountered males when deciding which male to choose, both if they are using the best-of-*n*-males rule or a threshold-criterion rule with a relative threshold (i.e. the threshold may change depending on the quality of those males already encountered). Females using a threshold-criterion rule with an absolute threshold should not need to return to males. The need to reassess males will depend on the variation in quality among males. In our study, all nestboxes were similar and the habitat was fairly homogeneous. Nest site quality is known to have a profound influence on the mate choice of the females (Alatalo et al. 1986; Slagsvold 1986; Alatalo and Lundberg 1990). Hence, the low variability among males in important mate choice cues may have imposed great strains on the memory of the females, leading to extensive revisitation to compare males. Therefore, it is possible that studies of natural populations or of nestbox populations with greater variation in nest site quality may show that females have simpler search patterns and use more clear-cut rules.

Still, the fact that the search patterns of the females in this study did not fit well with any of the simple models of mate search indicates that the females may use more complex decision rules or that they may be flexible regarding which rule they use under specific circumstances, or both. Female behaviour may change depending on physical condition, time of season, habitat, weather conditions, number of competitors, density of males, quality of males and quality of nest sites (cf. Real 1990).

Among the mating options at the end of the search period the females chose males of higher ranks than average. This would be expected if the females were using the best-of-*n*-males rule and were making optimal choices. However, compared with a hypothetical female that mated with the first male encountered the females did only slightly better. The reason for this was that males became occupied during the search of the females that sampled several males and these males were often those of highest rank. This illustrates one of the costs of sampling whenever there is competition between females; the best males are most likely to become occupied by competing females. Under such conditions the threshold-criterion rule will be favoured over the best-of-*n*-males rule, and there will be selection for females with a low threshold (Real 1990), and under very intense competition, random settlement will be favoured.

Search costs

We found that the females undertook a restricted mate search. This is expected if females incur costs while searching (Daly 1978; Parker 1983; Pomiankowski 1987; Real 1990; Slagsvold and Dale 1991). In the pied flycatcher it is known that the breeding success declines with the time of season at an average rate of about 1% per day (Alatalo and Lundberg 1984). Given the short duration of the search period, it is unlikely that the time cost was important to the females in this study. The density of males in our study area was as high as in the best natural habitats. Hence, in most natural situations search costs may be higher. But the benefits of searching for mates may still outweigh the time costs in natural populations due to the large and predictable effect nest site quality has on breeding success (Alatalo and Lundberg 1990). Energetic costs during the search were probably also low in this study. The distances moved during the search were short and the females probably also had the opportunity to forage while searching because of the low proportion of the time spent at the nestboxes of the males. In addition, females usually did not spend more time moving between distant males than between neighbouring males.

In other species the mate search may be costly because of harassment by males (Trail and Adams 1989). In the pied flycatcher we have made occasional observations of males following the females in pursuit flights when they leave their nestboxes but the males usually return shortly afterwards (Dale et al. 1990). The risk of predation during the sampling period is another potential cost. We do not have any data on this for the pied flycatcher, but generally the predation rate during the whole breeding season is low (pers. obs.), so it is unlikely that predation during the short sampling period is a significant selective factor. The females are alert during the visits and leave the males if disturbed (pers. obs.). The visits were of short duration and much of the time was spent inside the nestbox (Dale et al. 1990; S. Dale unpublished). Thus, the cost of assessing nest site quality also seemed to be low.

In conclusion, none of the costs discussed above provide an explanation for the restricted mate search of female pied flycatchers found in this study. Instead, we suggest that competition had a major influence.

Competition between females

We found indications that the restricted mate search of the female pied flycatchers was due to competition between the females. The number of males sampled and several other aspects of the extent of the mate search were correlated with the level of competition experienced during the whole search and during the first hour of the search. Even the level of competition at the first visit seemed to have some influence on the extent of the mate search. Encounter rates with other females may provide a cue for the females to modify the extent of their search.

The level of competition under natural conditions may vary according to the time of the season, weather and habitat. Females that arrive early in the year may have more unmated males to choose among than late-arriving females. The number of females arriving may depend on the weather conditions. Females arriving after a night with good conditions for migration may face more competition from other females than those arriving under more unfavourable conditions. Females searching for a mate in preferred habitats may have more competitors and fewer mating options than females searching in other habitats. Data are now needed to test if these variations are also reflected in the extent of the mate search. Circumstantial evidence for the effect of the time of the season was found by Dale and Slagsvold (1990); a greater proportion of the late-arriving females seemed to settle with the first male encountered.

How can the females assess the level of competition? When different females visit the same males only a few minutes apart it is reasonable to believe that they can know of each other. The fact that females generally moved between neighbouring males suggests that the females were present somewhere in between in the meantime. When females visit males, the males change from the normal song type to an excited song type and utter enticing calls (Dale et al. 1990). This can be heard by a human from a distance of up to at least 50 m. Thus, females may hear whether other females are visiting males they themselves have visited or are going to visit.

The effect of competition has not been included in any of the current models of mate choice. However, the evolutionary consequences of the phenomenon are important. First, it provides a general explanation for restricted mate search and rapid settlement even in highly mobile animals like birds. Second, it may affect the search tactics of females. In the presence of competition the females may have to sacrifice some of the benefits of continued search to safeguard mating opportunities. One solution to this problem may be to associate with one male to achieve superiority in future conflicts with other females due to uncorrelated owner-intruder asymmetries (Davies 1978) or asymmetries in pay-off (Krebs 1982). A female may after some time search for other males and still be able to evict intruders if she returns. Our data indicate that this may be so. Several females visited other males after they had started nest building with one male, and one female changed mate as a consequence of this. Some females also associated with one male for a long time during the search but thereafter visited other males before settling. Third, competition between females for a mate provides an explanation for the evolution of polygyny in the pied flycatcher and other species. Even if females that mate with already-mated males suffer a reduction in breeding success due to reduced male parental care, this is still better than not mating at all. Many pied flycatchers are prevented from breeding each year, probably because of a shortage of breeding sites (e.g. Sternberg 1989).

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