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# Influence of weather on time allocation of unpaired Pied Flycatcher *Ficedula hypoleuca* females

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Unpaired Pied Flycatcher (*Ficedula hypoleuca*) females were radio-tracked for 1–4 days in four nest box areas occupied by several singing males. Female behaviour was divided into three categories and the time spent on each one was used to construct a daily activity budget for these birds; (1) mate sampling (visiting male territories), (2) foraging, and (3) other activities (mainly moving around). On average, 14% of tracking time was used for mate sampling, while over 60% of time was devoted to foraging. When the ambient temperature of the tracking day or the day before it was high, females spent more time on visiting the territories of males. Other weather variables correlated also with sampling activity, probably because they were intercorrelated. Observed foraging time was not related to weather conditions, unless females that were moving around were actually seeking food patches. This relationship between mate sampling and air temperature indicates that during adverse weather, the females concentrated on maintenance and refrained from mate sampling. Heavier females tended to spend a greater proportion of time on visiting males than the lighter ones did, which may be due to an increasing interest for pairing when they begin to move into the reproductive phase.

## 1. Introduction

The role of weather conditions in determining the time of reproduction and reproductive traits (e.g. Perrins 1965, Järvinen 1983, Nager 1990) has been studied to a large extent, whereas its effects on daily activities, behavior and physiology of individuals have been addressed less often (however, see e.g. Grubb 1975, 1978; DeWoskin 1980). Fluctuations in temperature may affect the style of foraging (Alatalo 1982), or the amount of time devoted to it (Davies 1977, Grubb 1978). However, the time used for foraging may not increase linearly with respect to increasing temperature, and a relationship between them may be found only within a certain temperature range (Davies 1977).

Unfavourable weather often coincides with low food availability. For insectivorous birds, especially aerial feeders, low air temperature and rain diminish the available prey items (Koskimies 1950, Avery and Krebs 1984). In order to satisfy their energetic demands, birds allocate their time in foraging at the expense of other activities, such as aggression (Caraco 1979) or mate sampling. Consequently, during favourable conditions, behaviours alternative to feeding may be exhibited. There is evidence that the food intake rate solves the trade-off that exists between foraging and mating activities (Abrahams 1993; McNamara et al. 1987). Additionally, the nutritional state of an individual bird may also be an important factor affecting current time use (see Mangel and Clark 1988). The nutritional state, in turn, is affected by preceding behavior and preceding weather.

The outcome of the foraging-mating conflict may be settled by the "quality" of the individual. It may be reflected in better feeding abilities, which make the high-quality individuals resistant to short-term food deficiencies, and allows them to start mate sampling activities before the weaker individuals. Age, which has been shown to produce differences in foraging abilities (Recher and Recher 1969), is probably an important quality factor.

I studied the influence of weather conditions (air temperature and precipitation) on the time allocation of unpaired Pied Flycatcher (*Ficedula hypoleuca*) females by radio-tracking. Gottlander (1987) found that in males, temperature affects mating (= singing) activity. Therefore, I expected a similar relationship to be found also in females; they should spend more time on visiting territories of males on warm days. I intended to look for a conflict between two mutually exclusive demands, foraging and mate sampling. My aim was also to determine if there is dependence between current behavior and activity in the past.

## 2. Materials and methods

I did this study at Konnevesi Research Station in central Finland (62°36'N, 26°20'E) during May–June in 1991 and 1992. The four separate study plots (13–25 ha each) consisted mainly of coniferous forests with mosaic-like patches of deciduous vegetation. There were nest boxes at 150–200 m intervals distributed evenly across all plots. Before the tracking in both springs, six to ten singing males, each occupying one nest box, had settled in each study area.

I captured the females to be tracked from additional, remote (10 km) "reserve plots" as soon as possible after their arrival from migration, usually at the beginning of nest building. A radio transmitter (weight 0.7–0.8 g, by Biotrack) was glued with Nobecutan spray-on dressing on the back feathers between the shoulders of a female. After tagging, females were released in the center of the study plots. The females were tagged and released during a three-week period in both years, starting in mid-May. Maximum number of females released per day was five, but usually only one or two females were released at a time.

At the time of capture, I weighed the birds to the nearest 0.1 g with a Pesola spring balance. I used the weight as a measure of quality, even though the weight of females prior to breeding may be confounded by the development of follicles and eggs. This may be the case especially with the latest females, who start breeding shortly after their arrival (Lundberg and Alatalo 1992). I also aged the birds as yearlings or older by the wear in primary and outermost greater coverts (Karlsson et al. 1986).

I tracked the birds daily during daylight hours by taking radio-fixes with a portable receiver and a directional antenna, at one to five minute intervals. I classified their activity in the following way: 1) Mate sampling, if the focal female was within 30 m of a nest-box of a singing male, or the female was flying straight from one male to another; 2) Foraging, if the female was clearly catching prey from air, trees or ground, or in many occasions, not in sight but moving in a tree or in a group of trees outside male territories, 3) Else, if the focal female was flying over distances of several hundred meters at a time or resting in a tree. Resting behavior was observed to occur only during the earliest hours after sunrise. Tracking was discontinued when females paired and began to build nests.

I made time budgets in order to examine the time allocation of the females. I omitted samples in which an individual was followed for less than one hour a day. From a total of 21 females, nine (43%) were tracked for one day only, seven (33%) for two days and five (24%) for three or more days. I did not, however, track all the 12 birds with multiple observation days, on successive days. Most of the tracking took place between 0600–1800 and was quite evenly distributed within this range. An average tracking bout per bird lasted for two to three hours ($\bar{x}$=142.9 minutes, range = 60–495, n = 39 bouts). Differential tracking times probably caused no bias to the results, since neither the proportion of time used for foraging versus that for mate sampling correlated with it ($r_s = 0.26$, NS, n = 21 and $r_s = -0.05$, NS, n = 21, respectively).

For statistical independence, time allocation was examined only from one day per female. I chose the representative day by selecting the day with the longest tracking time. In addition, I wanted to assess whether individual females responded to changes in temperature by changing their use of time. Therefore, I compared the two days of longest tracking time of a given female pairwise.

Weather data were recorded at Konnevesi Research Station. I used maximum and minimum temperatures and precipitation of the tracking day and the preceding day as variables explaining the foraging and mate sampling activity. When testing normally distributed (Lilliefors' test, 0.10 as a criterion level) variables, I used parametric correlations and regressions; otherwise nonparametric correlations (Spearman and Kendall) were used. The probability values for all correlations and tests are expressed as two-tailed, except where otherwise stated.

## 3. Results

On average, the females spend 61.1% of their time on foraging and 14.4% on mate sampling (visiting singing males). The rest, 24.5% consisted of rapid movements and to a minor extent, resting. Two of the females did not show any mate sampling activities. Heavier females spent proportionally more time on visiting males than the lighter ones ($r_s = 0.50$, n = 21, $P < 0.05$), but the weight did not correlate with the proportion of time for foraging ($r_s = -0.19$, n = 21, NS). There were no age differences in use of time for mate sampling (T-test T = 1.14, $n_1 = 10$, $n_2 = 11$, P = 0.27) nor foraging (Mann-Whitney U = 51.5, $n_1 = 10$, $n_2 = 11$, P = 0.81).

The proportion of time allocated to mate sampling activities was related to several different weather variables. Females spent more time on sampling mates when air temperatures were high (r = 0.53, n = 21, $P < 0.05$, Fig. 1), and, if the previous day was warm (r = 0.60, n = 21, $P < 0.01$). Also, the minimum temperature of the previous night correlated with sampling activity ($r_s = 0.49$, n = 21, $P < 0.05$). Sampling was not significantly associated with the amount of precipitation of the tracking day (r = –0.29, n = 21, NS), nor with precipitation of the previous day (r = –0.22, n = 21, NS).

The foraging activity seemed to be less affected by weather factors. The strongest correlate of foraging activity was precipitation of the preceeding day ($r_s = 0.23$, n = 21, NS), and all the rest factors had even smaller correlation coefficients. The activity category "else" did not correlate with any weather variable (all Spearman correlation coefficients between –0.32 and 0.30, n = 21, NS).

A negative relationship between mate sampling and foraging was expected, since the proportional values were obtained from the same sample and thus were likely to correlate negatively. The expected correlation coefficient was thus calculated as

$$r_{exp} = -\sqrt{p_{1j}p_{2j} / \left(1 - p_{1j}\right)\left(1 - p_{2j}\right)} = -0.51$$

where $p_{1j}$ and $p_{2j}$ are proportions of time used for mate sampling and foraging, respectively, in j individuals. Therefore, the observed correlation coefficient is compared against the null hypothesis $H_0$: $r_s = -0.51$ (Sokal & Rohlf 1981). The coefficient calculated from the data ($r_s = -0.15$) did not differ from the expected (t = 0.84, $p > 0.1$), so there was no indication that sampling and foraging correlated negatively.

The behavior data from two or more days were available from 12 females. Mate sampling activity on a given day did not correlate significantly with that on the previous tracking day (r = 0.17, n = 12, NS). Also, foraging times of two different days were independent of each other ($r_s = 0.00$, n = 12, NS).

To separate the effects of several intercorrelated variables, I performed a multiple regression analysis (SYSTAT Statistical Package) for four normally distributed variables (Table 1). I first forced all four variables into the model. None of the factors had a significant main effect

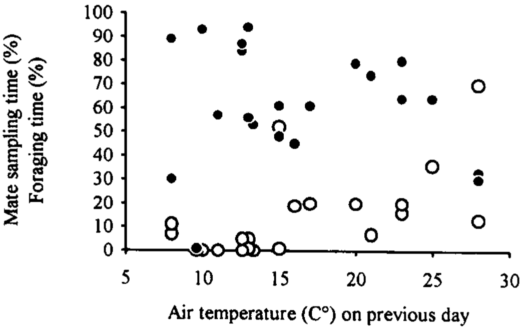

Fig. 1. Proportion of time spent on visiting male territories (= mate sampling time, open markers), and on foraging (filled markers) in relation to the maximum temperature of the day preceding the tracking day. Each individual female is represented by both markers.

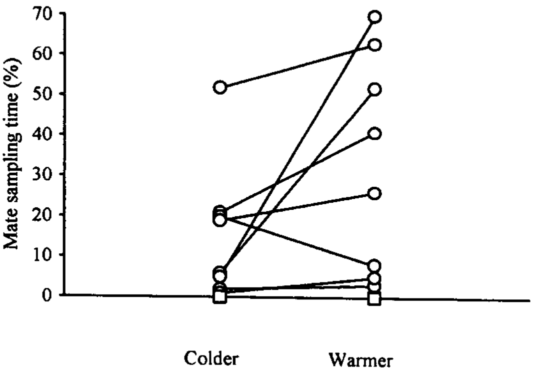

Fig. 2. Paired comparison of proportions of time spent on visiting territories of males (=mate sampling time) for ten females. Squares indicate two multiple observations. Each female was tracked on two days (colder and warmer, difference in temperature 2°C). Seven females devoted more time for mate sampling on the warmer day.

on mate sampling (Table 1). However, when each variable was tested alone, maximum temperature of the previous day ($b = 1.77$, $F = 10.61$, $P = 0.004$) and maximum temperature of the tracking day ($b = 1.73$, $F = 7.35$, $P = 0.014$) were significant, but the two rain variables were not.

Controlling for the previous day temperature, the mate sampling activity tended to be related to the weight of the female (Kendall's partial $T = 0.27$, $n = 21$, $P < 0.1$). Corrected with the same variable, minimum temperature of the previous night had no effect ($T = -0.03$, $n = 21$, NS).

Next, I assessed whether individual females responded to changes in temperature by changing their use of time. I evaluated the effect of maximum air temperature on mate sampling activity female-wise, i.e., considering each female as an independent observation, and looking if more time was used for sampling on warmer (at least 2°C difference between days, $\bar{x} = 3.9°$) days (Fig. 2). Seven females (58.3%) spent more time on sampling on warmer days, four (33.3%) were neutral (due to no difference in activity or temperature between days), and one (8.3%) showed a negative relationship. Omitting cases of no difference (Sokal and Rohlf 1981) gives a significant difference with the sign test (7 versus 1, $P = 0.035$, 1-tailed). This effect could arise, for instance, if females were more likely to sample mates during the latter part of the tracking period, since date and daily maximum temperature were positively correlated ($r_s = 0.69$, $n = 21$, $P < 0.01$). However, only six females devoted more time to sampling on the latter day of tracking, whereas four did the opposite, and two females had no mate sampling activities on either day (sign test, 6 versus 4, NS).

## 4. Discussion

The pied flycatcher females spent more time visiting males when the air temperatures were high. This has already been cautiously suggested by Hovi and Rätti in their earlier analysis (1994), and corresponds with Gottlander's (1987) result of male singing activity. There seemed to be a delayed response to favourable weather, since the tempera-

Table 1. A multiple regression model, where the dependent variable is the proportion of time used for visiting territories of males (= mate sampling). All four variables are forced in the model. Day 0=tracking day, day −1=the day preceding the tracking. $R^2=0.385$.

| | Coefficient (b) | SE | P |
|---|---|---|---|
| Max. temp. of day −1 | 2.458 | 1.541 | 0.130 |
| Max. temp. of day 0 | −0.628 | 0.171 | 0.700 |
| Precip. of day −1 | −0.063 | 1.591 | 0.716 |
| Precip. of day 0 | 0.164 | 0.247 | 0.516 |

ture of the day before observations had the strongest effect. This suggests state-dependency in the time allocation decision. Effects of the activities of the previous day of tracking, however, were not observed. With a larger data set, it would be possible to assess the length of the past period that is important for time allocation.

The suitability of least square estimation in regression analysis for this data was weakened by a multicollinearity problem and the resulting predictors of mate sampling activity should not be taken as the only true factors. It would be more realistic to regard all weather factors as essential, because they apparently work in concert, and possibly interact with each other.

There was no negative correlation between foraging and mate sampling activities, which might suggest that there was no trade-off between them. The proportion of time allocated to foraging was independent of weather. However, the activity category "else", that consisted almost solely of flights, was apparently overestimated, since during quick flights of several hundred meters I could not track the birds very closely. They may have stopped for feeding for a few minutes and then kept on flying. It would be realistic to interpret them as searching for better food patches, since the females did not visit territories of males at all during coldest days. But, even if females were looking for food when moving around, the prediction that birds should use more time feeding when the temperature is low, is not supported, because "else" was not related to weather. Additionally, it is nearly impossible to find out the real motivation for the flights included in "else".

A potential overestimate is also "mate sampling", since the females may well have been doing something else within 30 m of a nest box, even though foraging was never observed in the male territories prior to pair formation (pers. obs).

Food availability was presumably lower on cold or rainy days (e.g. Koskimies 1950, Avery and Krebs 1984), and, as a consequence, it could have forced the females to spend much of their time searching for food. However, since the proportion of time used for foraging did not decrease with increasing temperature, it could be argued that a certain feeding effort is maintained even at times of higher food availability. In these conditions also mate searching takes place. This does not fully agree with the hypothesis of two competing demands, feeding and mating (Abrahams 1993). It is unclear whether the trade-off exists in males, who face the problem of allocating time to feeding and singing (McNamara et al. 1987).

For a small passerine, it takes about 1.4 times the basal metabolic rate to produce an egg (Walsberg 1983). Thus, because of demands for reproduction, the threshold for switching from "foraging" mode to "mating - foraging" mode may be higher in females than in males. One could also expect a relationship between a female's mate searching ability and her quality. In this study, heavy females were slightly more active than light females in sampling mates. However, the result must be treated with caution, since weight alone may not be a proper measure of phenotypic quality. Heaviness may be related to physiological state and indicate readiness for breeding, since prelaying females may accumulate energy and nutrients (Murphy and Haukioja 1986). Thus, the correlation between weight and mate sampling activity could be explained by a motivation to pair. However, female weight did not correlate with mate sampling activity, in terms of the number of males visited (Hovi and Rätti 1994). Also, the time delay between capture and pair formation was not related to the weight at capture ($r_s = -0.22$, $n = 12$, NS).

To conclude, there did not seem to be any trade-off between foraging and mate searching in pied flycatcher females. The allocation of time was affected indirectly by weather conditions, the direct mechanism being, assumingly, food availability. During adverse conditions, activities related to pairing were suppressed, as predicted by McNamara et al. (1987), and probably more energy was allocated to maintenance metabolism. More detailed information on the responses of individuals to changing weather would be of interest. This would demand intense and long-term monitoring of individuals.

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## Selostus: Säätilan vaikutus pariutumattomien kirjosiepponaaraiden ajankäyttöön

Neljällä pöntötysalueella seurattiin radiolähettimillä varustettujen kirjosiepponaaraiden ajankäyttöä. Käyttäytyminen jaettiin ruokailuun, pariutumattomien koiraiden reviireillä vierailuun ja muuhun käyttäytymiseen. Naarat käyttivät keskimäärin 61,1% kokonaisajasta ruokailuun, ja 14.4% koiraiden reviireillä vierailuihin. Jälkimmäinen käyttäytymisaktiivisuus korreloi positiivisesti seurantapäivän ja sitä edeltäneen päivän maksimilämpötilan kanssa. Naarat käyttivät enemmän aikaa reviireillä vierailuun lämpiminä päivinä. Ruokailun osuus kokonaisajasta oli sitävastoin riippumaton säätekijöistä. Ruokailuun ja koirasvisiitteihin käytetyn ajan välillä ei ollut myöskään tilastollisesti merkitsevää yhteyttä. Tulokset viittaavat siihen, että kirjosiepponaarart joutuvat epäsuotuisa sään vallitessa tinkimään parinvalintaan liittyvistä toiminnoista. Mahdollinen yhteys naaran painon ja koirasaktiivisuuden välillä saattaa merkitä fysiologisen lisääntymisvalmiuden vaikutusta naaraan motivaatioon pariutua.

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