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Daily foraging routines and feeding effort of a small bird feeding on a predictable resource

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According to theory, a small diurnal bird living in a predictable environment should have the highest feeding effort as late as possible in the day in order to minimize the time it carries large and costly reserves. The feeding effort should also decline with increasing food availability. We tested both these ideas with the lesser spotted woodpecker (*Dendrocopos minor*). For most of the year, this bird feeds on wood-living insects in dead tree branches. This food supply is likely to be highly predictable on a daily scale. Our results corroborated the theory. We found that the proportion of time spent actively feeding was lower in the mornings (before noon) than in the afternoons. We also found that woodpeckers spent less time feeding the higher their food availability. However, for a given food availability they spent more time feeding in the afternoons. This supports the idea that feeding is less and other activities are more valuable in the mornings given a predictable food resource. This is the first demonstration of daily routines in small birds concordant with a predictable environment. In spring, males but not females reduced their feeding time. This difference between the sexes may be related to their sex-specific reproductive effort.

Keywords: daily routines; foraging; giving-up density

1. INTRODUCTION

The optimal foraging behaviour of animals should be a trade-off between the benefits of gaining energy and the risk of being killed by predation (e.g. Lima 1986; McNamara & Houston 1990; Houston & McNamara 1993; Lilliendahl *et al.* 1996). For a small bird whose life may depend on their ability to outmanoeuvre a raptor, the risk of predation may increase severely with increasing body weight (Rogers & Smith 1993; Witter & Cuthill 1993; Metcalfe & Ure 1995).

Models of optimal daily foraging routines for birds (Bednekoff & Houston 1994; McNamara *et al.* 1994) predict that those having predictable access to food should postpone their feeding activity until late in the day. This prediction is dependent on two assumptions: (i) that birds carrying a lot of reserves suffer from a higher predation risk (Bednekoff 1996; Kullberg *et al.* 1996), and (ii) that reserves are essential in order to avoid starvation at night. In order to maximize survival, the optimal trade-off between starvation and predation will therefore be to feed late in the day and, hence, reduce the time spent carrying high reserves.

In contrast, birds with unpredictable access to food must feed early in the day. This is because they must ensure sufficient reserves by the end of the day so that they survive the night (Bednekoff & Houston 1994; McNamara *et al.* 1994). Once sufficient reserves are gained they may then spend time idle in order to reduce their predation risk.

Other models of foraging strategies (McNamara & Houston 1987; Werner & Anholt 1993; Anholt & Werner 1998; Brown 1999; Olsson & Holmgren 1999) predict that animals in rich environments should spend less time feeding than those in poor environments. The necessary assumption for generating these predictions is that the predation risk increases with feeding activity and reserve levels and the benefit from harvesting energy is a decelerating function of a cumulative harvest (Houston *et al.* 1997).

The food availability of an environment is often difficult to estimate based solely on direct sampling (Hutto 1990; Poulin & Lefebvre 1997). A more efficient means of estimating environmental quality is to consult the forager itself by the use of behavioural indicators (Brown 1988; Olsson & Holmgren 1999; Olsson *et al.* 1999). Foragers using depletable food patches should abandon these when their value to the forager corresponds to the average value of the environment (Charnov 1976; Brown 1988, 1999; Olsson & Holmgren 1998). The amount of food left in the patches at that time, the giving-up density (GUD), is one of the essential components of the behavioural indicator. By joining GUDs with data on patch residence times and a fitness measure, one has a full behavioural indicator. That is, these parameters may jointly estimate the cost of predation and the value of energy (Brown 1999; Olsson & Holmgren 1999). This can be used to determine what factors generate differences in quality between environments and to estimate that quality itself (Olsson & Holmgren 1999).

In a previous study (Olsson *et al.* 1999) of lesser spotted woodpeckers (*Dendrocopos minor*), we used these behavioural indicators and determined that food availability is the main factor varying between territories. Consequently, the average GUD of an individual, $\overline{\text{GUD}}$, is a good estimate of the food availability that an individual has in its territory. Within individuals, however, GUDs may change, even at constant food availability, in response to changes in the costs and benefits associated with foraging (Brown 1988).

Here we will present data on the daily foraging routines, feeding activity and food availability (in terms

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of $\overline{\text{GUD}}$) of lesser spotted woodpeckers during both winter and spring. During this time the lesser spotted woodpecker feeds almost exclusively on wood-boring insect larvae (mainly long-horn beetles, Cerambycidae) in thin (1–5 cm) dead branches of living trees (Cramp 1985; Olsson 1998). An exception may be the moth *Argyresthia goedarthella* which occurs abundantly in the trunk bark or dead branches of Betulaceae trees (birches and alders) in the years when these tree species bloom (Agassiz 1987). The larvae usually become accessible to the woodpeckers in late March or early April, but during 1996 they appeared later than usual and also in higher abundance (Olsson 1998; Olsson *et al*. 1999).

As the woodpeckers' prey are incapable of moving distances of more than a few millimetres, we were confident that the diurnal patterns of foraging by woodpeckers do not depend on the daily routines of their prey.

During the winter, the woodpeckers live practically solitarily in vast home ranges which may partly overlap with those of other individuals (Wiktander 1998). From the end of March until mid-May they form pairs, defend territories and excavate nest holes in dead trees (Olsson 1998; Wiktander 1998). Thus, in the winter most non-foraging time is devoted to resting or preening, whereas territory defence, breeding interactions and nest excavation become more frequent in spring.

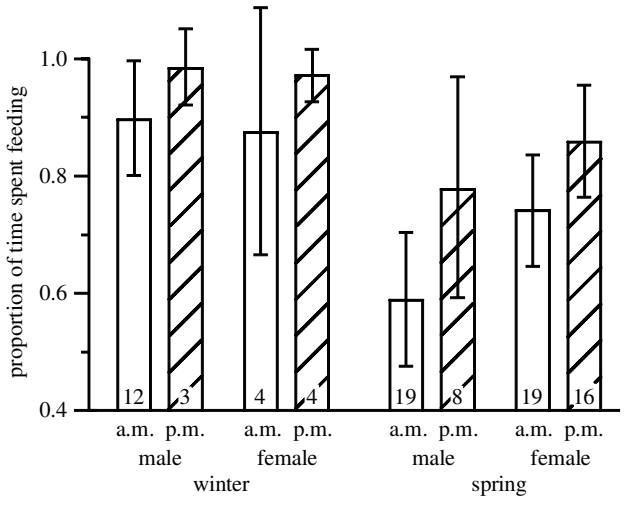

Figure 1. The proportion of the total observed time which was spent actively foraging in winter and spring in males and females: before versus after 12.00. Mean ± s.e. The number of individuals observed is shown inside each bar.

2. METHODS

The study was conducted between 1990 and 1996 in a 125 km^2 study area around Lake Möckeln in southern Sweden. The area is a mixture of open land and forest and the forests are both coniferous and deciduous. The woodpeckers mainly use the deciduous parts of the forest during spring.

We studied the woodpeckers using binoculars and noted their behaviour. In total, 85 individuals were studied and all individuals were observed for at least 15 min (range 15.2–979 min and mean 113 min). The observations were made between 1 September each year and the day when oaks came into leaf the following spring (range 3–20 May in the years studied). This study halted at leaf break because at that time new food resources, such as aphids and caterpillars, become available to the woodpeckers and the woodpeckers abandon their wood-living food resources. By ending the observations at leaf break, the behavioural observations were also not confounded by direct breeding behaviours as egg laying starts after leaf break (Wiktander *et al*. 2000). The territorial activities and nest excavation start fairly synchronously in the population at the end of March. We chose 21 March as the division between winter and spring.

The majority of all non-foraging activities were either nest building or perching. We defined perching as either resting or actively preening, as both activities provide ample possibilities for predator scanning. Perching did not include the 'freezing' behaviour which the woodpeckers performed in the presence of avian predators. During perching, resting and preening were often mixed within short time-periods and were sometimes ambiguous to separate. Several activities, such as drumming, territorial interactions and mating, were also recorded, but the duration of these activities was too short for productive analysis.

All observations were grouped as being made in the mornings (before 12.00) or in the afternoons (after 12.00). Preliminary analyses showed that moving the division by an hour in either direction did not alter the conclusions. The observations were made throughout the woodpeckers' active time, i.e. from approximately 30 min after sunrise until 30 min before sunset (Wiktander 1998), although, in any given day, a single woodpecker was only followed for several hours.

We used the proportion of time engaged in foraging, nest excavation and perching for analysis of the behavioural data. The proportion of time spent foraging is the ratio of the total time spent foraging to the total time observed during the given period of a day (i.e. not per foraging patch). The statistical distribution of this proportion was normalized by arcsine transformation. However, the proportions of time spent on non-foraging activities included many observations of zero value and, hence, could not be normalized. We therefore first used the frequencies of individuals observed performing these activities in Fisher's exact tests for the analyses. For the individuals engaged in these activities, we also analysed the respective proportions using ANOVAs.

The GUDs were measured in the thin dead branches which the woodpeckers had foraged on. They were calculated as the number of prey remaining in the branches per square decimetre of surface. The measure was achieved by cutting down the branches and using X-rays to count the numbers of remaining larvae (see Olsson *et al*. (1999) for a complete description of the method). We log transformed the GUD values before analysis to normalize the distribution. Data on the GUDs were collected from 1993 to 1996 from a total of 35 individuals with at least two branches sampled per individual.

Each individual occurs only once in each analysis. In the cases where individuals were observed in more than one period, one of these periods was selected for analysis at random.

3. RESULTS

The lesser spotted woodpeckers foraged more actively in the afternoons than in the mornings ($F_{1,80} = 11.22$ and $p = 0.001$) (figure 1). Furthermore, they spent less time actively foraging during the spring than during the winter period ($F_{1,80} = 18.52$ and $p < 0.0005$). The males

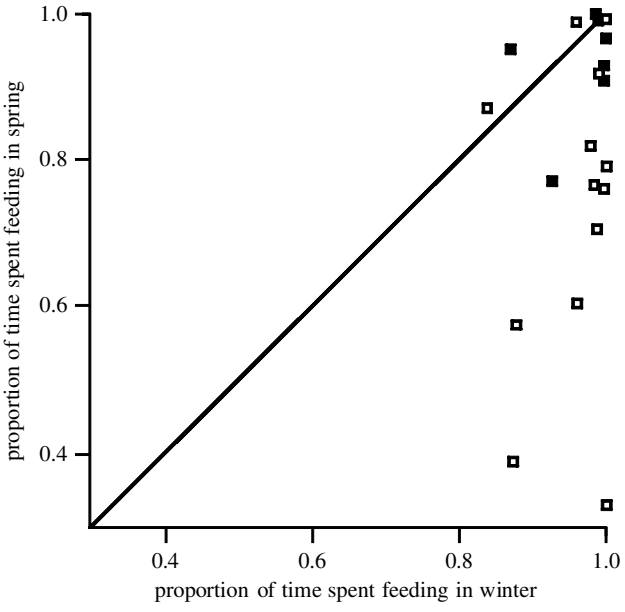

Figure 2. The proportion of time spent feeding by 20 individual woodpeckers during winter (horizontal axis) and spring (vertical axis). Open symbols are males and filled symbols are females. The diagonal line indicates the 1:1 line, i.e. where the points would be expected to be if the feeding times were equal in the two seasons.

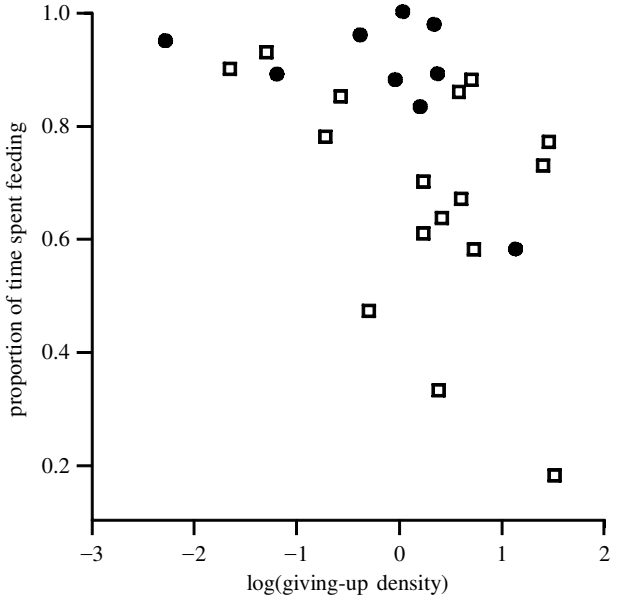

Figure 3. The proportion of time spent foraging as a function of the mean giving-up density of prey in patches which the same individuals were observed on. Squares indicate individuals observed in the mornings and circles those observed in the afternoons.

and females spent similar proportions of their time feeding ($F_{1,80} = 0.015$ and $p = 0.6$). However, there was a tendency for the males to decrease their feeding times more in spring than did the females (interaction term $F_{1,80} = 3.36$ and $p = 0.070$) (figure 1). All other interaction terms were removed from this ANOVA as they were non-significant ($p > 0.6$ in all cases).

We made a repeated-measures ANOVA within individuals across seasons in order to further investigate the seasonal change in foraging between the sexes. Only 20 individuals were observed during both seasons and, hence, the analysis has to be confined to these. As in the former analysis, the individuals fed less in spring than in winter ($F_{1,18} = 22.20$ and $p < 0.0005$). However, the males reduced their feeding time significantly more than did the females ($F_{1,18} = 6.48$ and $p = 0.020$) (figure 2). As in the previous analysis, when combining seasons the males and females fed for similar proportions of time ($F_{1,18} = 2.61$ and $p = 0.12$).

During the spring period, the proportion of time spent foraging was negatively correlated with the $\overline{\text{GUD}}$ (figure 3). This relationship was influenced by the time of day such that, in the mornings, the time devoted to foraging was lower than in the afternoon for a given $\overline{\text{GUD}}$ (figure 3). In an ANCOVA of the proportion of foraging time using the $\overline{\text{GUD}}$ as the covariate and time of day as a factor, both were significant ($F_{1,22} = 5.64$ and $p = 0.027$, and $F_{1,22} = 7.71$ and $p = 0.011$, respectively and $r^2 = 0.45$), whereas their interaction was not (partial $r = 0.10$ and $p = 0.3$). During the winter period the $\overline{\text{GUD}}$ was measured on too few individuals for productively making the same analysis.

During the *Argyresthia* presence in 1996, the $\overline{\text{GUD}}$ was higher than during previous periods (Olsson *et al.* 1999).

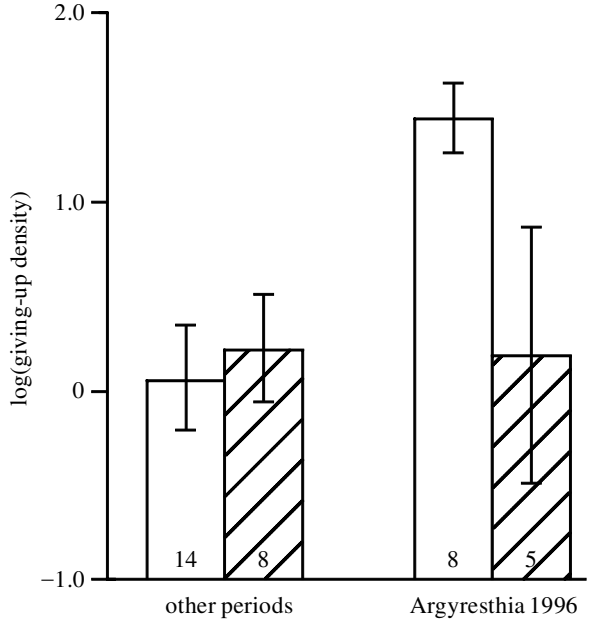

Figure 4. The mean (± s.e.) giving-up density (log transformed) of prey in patches before and during the peak occurrence of *Argyresthia* in 1996. All years before 1996 and 1996 before the *Argyresthia* appeared are thus included in the 'other periods'. Open bars are mornings and hatched bars are afternoons. The number of individuals observed is shown inside each bar.

Separating the mornings and afternoons, it appears that most of this difference was due to an exceptionally high $\overline{\text{GUD}}$ in the mornings during the *Argyresthia* presence (figure 4). This was formally shown by an ANOVA with the season, time of day and sex as factors. Only the season and the interaction between the season and time of day were close to significance (before versus during

Argyresthia in 1996, $F_{1,31} = 3.53$ and $p = 0.070$, mornings versus afternoons, $F_{1,31} = 2.44$ and $p = 0.13$, and interaction, $F_{1,31} = 4.01$ and $p = 0.054$). All other terms had *p*-values above 0.15. When testing mornings and afternoons separately, the difference between seasons was strong in the mornings ($F_{1,20} = 12.1$ and $p = 0.002$) but not in the afternoons ($F_{1,11} = 0.005$ and $p = 0.9$).

The woodpeckers spent a similar proportion of time foraging during the *Argyresthia* presence and the other period of spring ($F_{1,81} = 1.29$ and $p = 0.26$). The feeding effort depended on the time of day and sex of the individuals only ($F_{1,81} = 8.62$ and $p = 0.004$, and $F_{1,81} = 6.55$ and $p = 0.012$).

The proportion of perching individuals did not differ between winter and spring: 15 out of 23 versus 43 out of 62 (Fisher's exact $p = 0.8$).

There was a similar proportion of individuals observed perching in the mornings and afternoons in both seasons combined (Fisher's exact $p = 0.15$) and the proportion of individuals observed perching did not differ between males and females (Fisher's exact $p = 0.6$). However, among these perching individuals the time spent perching was higher in the mornings ($F_{1,55} = 5.37$ and $p = 0.026$), but similar between the sexes (two-way ANOVA, $F_{1,55} = 0.024$ and $p = 0.9$).

Out of the 23 individuals observed during the winter period, only one spent some time excavating a nesting hole, whereas during the spring period 36 out of the 62 observed did so (Fisher's exact $p < 0.0005$).

Excavation of nest holes was predominantly performed during mornings in the spring (Fisher's exact $p = 0.035$). In total, the frequency of excavation was approximately the same across the sexes (Fisher's exact $p = 0.17$). However, out of the 36 individuals observed to build nests, males spent significantly more time at this activity, but there was no difference between mornings and afternoons ($F_{1,33} = 6.01$ and $p = 0.020$, and $F_{1,33} = 0.00$ and $p = 1.00$).

4. DISCUSSION

Our major and novel findings were that lesser spotted woodpeckers feed less actively in the mornings than in the afternoons, that individuals in territories with high food availability feed less than those with low food availability and that females feed more than males during spring.

Previous studies have shown routines expected for unpredictable feeding conditions in several bird species (great tits *Parus major*, Lilliendahl *et al.* 1996; blackbirds *Turdus merula*, Cresswell 1998). That is, most of the mass increase took place in the mornings, but was also dynamic such that previous mass loss could be rapidly regained. The species studied spent a large fraction of their time in winter feeding on the ground. Therefore, the weather conditions may often make their feeding gains unpredictable (Rogers & Smith 1993).

Our study is the first to show the opposite pattern, i.e. more feeding in the afternoon. This is the predicted optimal daily routine for birds with predictable food resources (Bednekoff & Houston 1994; McNamara *et al.* 1994), i.e. when their starvation risk is negligible. It seems justifiable to argue that this is the case for woodpeckers. During the course of a year, their prey density distribution does not vary stochastically over time (except for the rapid increase in the *Argyresthia* density). The accessibility of the wood-living prey should also not be severely influenced by weather conditions, etc. The physical properties of the branches and also the activity of the prey may to an extent vary with factors such as temperature and humidity. However, as these factors vary much more between days than within days, we find it unlikely that they will influence diurnal foraging patterns. Furthermore, the woodpeckers visited over 100 branches (patches) per hour (arithmetic mean 116) (Olsson 1998; O. Olsson and U. Wiktander, personal observations). Thus, although their gain from single patch visits is clearly stochastic and should have a large standard deviation, the standard error of the expectation over a few hours or a whole day will be small. Hence, our study together with previous studies (Lilliendahl *et al.* 1996; Cresswell 1998) fit the patterns predicted by theory.

The lesser spotted woodpeckers' propensity to engage in activities other than gaining energy was influenced by the availability of food in the environment, as measured by the $\overline{\text{GUD}}$. This result in itself indicates the existence of trade-offs between energetic gain and other factors which may enhance fitness, as assumed in a number of theoretical models (McNamara & Houston 1987; Werner & Anholt 1993; Anholt & Werner 1998; Brown 1999). Results in accordance with such models have been shown in the wild in only a few cases (e.g. Davies & Lundberg 1985). Woodpeckers with abundant food spend much of their time keeping their plumage in good condition and being vigilant against predators and they can afford to invest more into excavating high-quality nests. All of these activities may obviously have a positive influence on fitness without increasing their energy gain.

During the peak occurrence of *Argyresthia* in 1996, the $\overline{\text{GUD}}$ was higher in the mornings, both compared to the previous period and compared to the afternoons in the same period. This higher intake rate (during the active foraging time) in the mornings is obviously chosen by the woodpeckers as their food availability does not change (so dramatically) between mornings and afternoons. As such, this strongly indicates that the woodpeckers' foraging is dynamic and possibly state dependent, as has also been demonstrated, for example, in great tits (Lilliendahl *et al.* 1996). Having higher GUDs but shorter feeding times in the mornings than in the afternoons implies that the woodpeckers found activities alternative to feeding more valuable in the mornings than in the afternoons (Brown 1988). Such a conclusion is in complete agreement with models of daily routines (Bednekoff & Houston 1994; McNamara *et al.* 1994), although it is only implicit in them.

The total time that woodpeckers are outside their roosting hole in spring is much longer than during the winter (O. Olsson and U. Wiktander, personal observations). This factor alone may be responsible for why the woodpeckers fed for a lesser proportion of their time during spring than in winter. It is interesting though that males and females respond differently to seasonal change. Males reduce their feeding effort in order to invest more time into nest excavation instead. Females do not. This is probably related to the fact that the approaching breeding

may present different challenges and opportunities for females than for males (e.g. Askenmo *et al*. 1992). The most obvious difference is of course that the female is the one to produce the eggs which may be energetically rather costly (see the review by Monaghan & Nager 1997). Females may therefore value energy higher than males. Our result that males and females spent similar proportions of time feeding in winter but that females fed more in spring supports this idea. Given that foraging is the most dangerous activity this may explain the observation (Wiktander 1998) that females suffer higher mortality prior to egg laying than do males. The females may thus pay a high cost for their increased energy gains.

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