THE FORAGING EFFICIENCY OF GREAT TITS (PARUS MAJOR L.) IN RELATION TO LIGHT INTENSITY

By ALEJANDRO KACELNIK
Animal Behaviour Research Group, Department of Zoology, University of Oxford

Abstract. I report an experiment aimed at testing whether foraging efficiency of great tits is limited by light intensity at the time of the dawn chorus. Captive great tits hunting for prey under different luminance conditions were less successful in finding prey when foraging, hunted for a lower proportion of their time, and handled individual prey items for longer when luminance was under approximately 7 cd/m². This luminance is not reached in the field until after the time of the dawn chorus, suggesting that in the early morning foraging is limited by light intensity. I suggest that a satisfactory functional explanation of the dawn chorus must take into account the comparatively low foraging opportunity early in the morning, as well as the factors affecting the opportunity for singing and other territorial activities.

The great tit (Parus major) in Wytham Wood, Oxford, is territorial from mid January until May (Hinde 1952; Krebs 1971). Song is one of the major forms of territorial defence and advertisement (Krebs 1977), and, in common with many other species, great tits have a major period of song at dawn and a minor peak at dusk (Hinde 1952; Garson & Hunter in preparation) paralleling the bigeminus (large morning and small evening peak) pattern of activity typical of passerine birds (Aschoff 1966). The morning peak in singing activity starts when the sun is between 5° and 3° below the horizon (Kluijver 1950), that is in the middle of the morning twilight period, and lasts about 2 h (Hinde 1952, Table 8).

The dawn chorus, as it is usually called, poses a paradox. Great tits sing almost exclusively from perches not less than 5 m above the ground (Hunter, in preparation), while during winter and early spring they forage intensively on nuts and seeds on the ground (Gibb 1954; Lack 1971), so that singing and foraging are mutually exclusive activities. Since they lose between 5 and 10% of their body weight over night in winter (Owen 1954), one might expect feeding motivation to be high in early morning, to ensure that the bird does not lose even more weight. In contrast with this prediction, ‘In the early morning, however, the birds (great tits) do not in general seem to feel hungry’ (Kluijver 1950), and in fact they allocate a large proportion of time to preening and territorial activity. This apparent paradox can probably be explained by two factors: (1) the advantages of territorial defence just after dawn seem to be particularly high, due to higher intruder pressure (Krebs 1977) and to advantageous acoustic conditions (Henwood & Fabric in press); (2) the benefits of foraging at this time may be very low, if the rate of prey capture is limited by light intensity.

Foraging tendency is likely to depend both on internal state (food deficit) and incentive (food availability) (Sibly 1975), so that if foraging efficiency is limited by light intensity, foraging tendency may be very low in spite of the great food deficit, and this could ‘disinhibit’ other behavioural tendencies (McFarland 1974), explaining at least partly the great amount of singing and preening observed at the twilight.

In this paper I describe an experiment designed to test if light intensity does actually lower foraging efficiency at the time of the dawn chorus. I measured foraging efficiency of great tits in the laboratory under different light intensities, covering the range of luminance observed in the field during the first 2 h after twilight, when the dawn chorus takes place.

Methods

Subjects

I used 12 adult great tits. All were wild caught and had spent at least 45 days in captivity. They lived individually in metre cube cages provided with detachable aluminium roosting boxes (8 x 8 x 15 cm) in which the birds roosted and hid when mildly frightened. These cages were kept in a room at approximately 20°C, with light from 08.00 to 19.00 hours. Food was standard diet for insectivorous birds (modified from Krebs et al. 1972) provided ad libitum outside the experimental period, and only after 13.00 hours during this period. All tests took place between 09.00 and 13.00 hours in a room at 10°C.
Each bird was tested only once each morning, and the order was randomized to avoid circadian effects and consistent difference in deprivation between subjects. The mean body weight loss between evening and the beginning of a test was 8% which is within the normal range of body weight loss under natural conditions.

**Apparatus**

The experimental set-up consisted of two similar aviaries, a waiting compartment and a searching arena, measuring 90 x 90 x 60 cm and separated by a wooden wall. The birds could cross from one to the other through a passage which could be opened or closed by a remotely controlled sliding door. Illumination was the same on both sides, provided by a pair of 150-W reflector lamps on each side. The four lamps were connected in parallel to a single dimmer which was used to vary light intensity between treatments. The waiting compartment had three perches, and the searching arena was filled up with leafless branches and twigs in which the prey were hidden. The branches were rearranged every day so that the birds could not get familiar with the searching environment. When a test was due to start the subject bird was caught in its roosting box which was then attached to the waiting compartment.

**The Prey**

Fifty artificial prey were distributed in the searching arena before each test. They consisted of a piece of mealworm (mean weight 14 mg) enclosed in a pastry cocoon made of flour and a water solution of food dyes in a proportion of two to one in volume. The water solution was of 8 ml of green, 4 ml of red, and 2 ml of yellow ‘Boots food colouring, with water up to 100 ml. The birds handled the prey by pecking open the cocoon and eating the mealworm piece. They did not eat the cocoon, the purpose of which was make the the prey match the background.

**Training and Testing**

The birds were trained to hunt for prey in the searching arena under intermediate luminance (0-10 cd/m²) until they reached a constant latency to search and capture rate. Each test consisted of two 15 min blocks. In the first block, the birds were released in the waiting compartment and allowed to accommodate visually to the current level of illumination for 15 min. The passage was then opened and the birds crossed to the searching arena where they hunted for prey for the next 15 min. Searching, handling and non-foraging times were recorded on a computer compatible event recorder. After finding a prey, a bird usually took it to an horizontal branch, where it held the cocoon with one or both feet while hammering with its bill. Once a hole was made, it cleanly pulled out the piece of mealworm and swallowed it. After this, birds sometimes discarded the cocoon while others continued with it, searching for remaining bits of food. Handling time is defined as the period between the first contact with a prey until discarding the empty cocoon.

I will discuss this point further when analysing the effect of light on handling strategy.

Each bird was subject to ten different treatments, each one consisting of a test at a given luminance. Figure 1 shows the actual values of luminance used in the ten treatments. Since both prey and background are secondary luminous sources of low reflection factor, I included in the same figure luminance as measured on a white matt sheet of paper in the same situation.

![Fig. 1. Luminance at prey, background and matt white paper surfaces for the 10 different treatments. The values for the white surface are shown to facilitate comparison with other experimental situations.](image-url)
to facilitate comparisons with different experimental situations. The experimental range was from 0.01 to 10.0 cd/m², which covers the full range of luminance as measured on the same prey in the natural feeding grounds during the first 2 h after twilight (see Fig. 5). I assume that if the prey has the same luminance in the field and laboratory situations, and the two backgrounds are similar, the subjective brightness will be the same and so will be its detectability (Walsh 1958).

All luminance measurements were made with a S.E.I. photometer.

**Results**

Figure 2 shows the effect of luminance on two measures of foraging success. The first measure, profitability, is defined as prey caught per second foraging (searching + handling). The second measure, searching efficiency, is defined as prey captured per second of searching time. While profitability increases up to a maximum at a luminance of 1 cd/m², searching efficiency increased with luminance throughout the whole experimental range. This second measure rises more steeply with light because it ignores handling time: at high light intensity the birds caught more prey and therefore spent more time handling (Holling 1965), and this sets an upper limit to profitability. This effect is complicated by the fact that handling time is inversely related to light intensity (Fig. 3), which reduces apparent profitability at low light intensity. The reason for the decrease in handling time with increasing light is that the birds extracted food from the cocoons more thoroughly when light intensity was low, spending additional time gleaning the open cocoon for extra pieces of mealworm. Most of the cocoons recovered after experiments with high light intensity had a clean hole through which the piece of mealworm had been extracted, while cocoons recovered after low light tests were fully opened as a conse-
quence of this extra attention. Table I shows that the birds actually found more food when they had fully opened the cocoons. It is interesting to note that the decrease in handling time with decrease in inter-catch interval is what would be expected from optimal foraging theory (Cook & Cockrell 1978).

Figure 4 shows that the proportion of experimental time spent foraging increased with light intensity up to an asymptote of 100%. At low light intensity the birds spent as much as 50% of their time preening, resting or bathing.

In order to relate the laboratory results to the levels of light intensity in the field, I combined the laboratory results with measures of luminance at the surface of the artificial prey in the field (Fig. 5).

From Fig. 5 I conclude that:

(a) Searching efficiency is light limited for over 1 1/2 h after the onset of great tits’ activity on sunny days and more than 2 h on overcast days, which are more typical in Oxfordshire.
(b) Profitability for birds hunting for prey requiring a handling time similar to the experimental prey would be limited by light for 40 min on sunny days and over 1 h on overcast days.
(c) The proportion of time allocated to foraging matched profitability under the experimental conditions, i.e. the birds foraged nearly all the time when luminance was above 1 cd/m², the luminance at which profitability reached its asymptotic value.

**Discussion**

My results show that part of the explanation of the dawn chorus in the great tit may be that light intensity limits foraging efficiency in the early morning. Birds in the wild may, to some extent, compensate for the effect of light intensity by exploiting each item more thoroughly, as they did in my experiments, and by switching to normally less preferred but more conspicuous sorts of prey. Nevertheless, in both cases, the overall pay-off for foraging would be lower than at other times of the day.

The poor profitability of foraging at dawn and dusk would itself favour the concentration of other incompatible activities at these times, provided that the birds expect to have enough profitable foraging time during the rest of the day. Singing and preening are two examples of such activities: they are partly incompatible with foraging because great tits in late winter sing and preen in the canopy (Garson & Hunter, in preparation) while they feed mainly on nuts which they find on the ground (Gibb 1954). The evening peak of song may be smaller than the morning one because of the rate of change of light intensity. While early in the morning profitability is improving, at dusk the bird has to gather enough food to survive overnight even if profitability is low.

In addition to poor profitability there is evidence that there are special advantages for territorial activity at the time of the dawn chorus. In the first place, activity of potential invaders is higher early in the morning than at any other time, making territorial advertisement by song more important as a deterrent at that time. This has been shown by J. Krebs (in preparation, quoted in Krebs & Perrins 1977) who removed territory holders from a piece of mixed wood and replaced some of them by broadcasting their

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**Table I.** Sixty Fully Open and 60 Perforated Cocoons Were Classified According to the Presence or Absence of Traces of Food. More Fully Open Cocoons Were Totally Empty ($\chi^2 = 5.40, P < 0.05$)

<table>
<thead>
<tr>
<th></th>
<th>Some food left</th>
<th>No food left</th>
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</thead>
<tbody>
<tr>
<td>Fully open</td>
<td>10</td>
<td>50</td>
</tr>
<tr>
<td>Perforated</td>
<td>21</td>
<td>39</td>
</tr>
</tbody>
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![Fig. 5.](image-url)
own songs, recording the rate of arrival of new birds at different times. The rate of arrival was higher during the first 4 h of the morning, regardless of whether song was being broadcast or not. This result may be a consequence of the fact that it pays non-territorial birds to seek territories at the time of low foraging efficiency.

Secondly, there seems to be an intrinsic advantage for acoustic communication at dawn. Sounds in the frequency range of the great tit song are likely to be less attenuated (i.e. reach greater distances) when produced around sunrise than later on (Henwood & Fabrick in press; Roberts et al. in preparation).

These are not, of course, alternative explanations but rather different elements of the intricate set of factors that must be governing the temporal organization of great tits' behaviour.

It is possible that the relative importance of the different factors will ultimately be resolved by further quantification of the risks and advantages of performing different activities at certain times of the day and by analysing how these risks and advantages are reflected in the animal's motivational system (Sibly & McFarland 1976). It may develop instead, that further quantification may prove insufficient until a more workable theory of the functional determinants of temporal organization of behaviour is available.

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References

Garson, P. J. & Hunter, M. L. In preparation. The singing behaviour of wrens (Troglodytes troglodytes L.) and great tits (Parus major L.): effects of temperature and time of year.


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