

Seasonal changes in foraging strategies of nesting blackbirds (*Turdus merula* L.)

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Summary. Blackbirds are usually multiple-prey loaders and forage mainly on the ground. We analysed the foraging behaviour of ten males in an urban park in Budapest during the breeding season from 1984 to 1986. At the end of April and in May blackbirds fed their nestlings mainly on earthworms (load type I). In this period the average searching time and route were shorter, and the territories of the pairs tended to be smaller, than in June, when males in addition brought a great variety of invertebrates per load (load type II) to the young. The average dry weight and energy content of the two load types did not differ significantly. However, the average energy delivery rate (energy content/intervisiting time) and rate of energy gain (energy content/searching time) were higher when males collected earthworms, because intervisiting and searching times were shorter. The frequency distribution of searching times for load type I suggests that the encounter with earthworms was random. For load type II birds seemed to employ a fixed-mass foraging strategy. In June, the drier conditions reduced the availability of earthworms, and blackbirds extended their foraging areas.

Introduction

The number of studies dealing with experimental tests of optimal foraging models has increased during the last ten years (Pyke 1984). However, only a few of these studies were conducted in the field (reviewed by Pyke et al. 1977; Krebs and McCleery 1984; Kamil and Sargent 1981; Pyke 1984). Moreover, there are very few studies which attempt to test the predictions of optimal foraging models without manipulation (Davies 1977; Goss-Custard 1977; Tinbergen 1981; Carlson and Moreno 1986). This study examines foraging tactics of blackbirds

(*Turdus merula*) bringing food to the nest. Blackbirds, which are very common throughout Europe, forage on the ground. In the open vegetation of urban parks they are used to the presence of man and can be observed easily.

Some aspects of the foraging behaviour of blackbirds have been previously described (Smith 1974a, b; Lawrence 1985a, b). As the food supply changes during the breeding season, so does the diet of nestlings (Davies and Snow 1965; Dyrce 1969; Török 1985). In this paper we describe different foraging strategies of blackbirds during the early and late breeding periods, focussing on relations between type of food, searching time, travel distance, load size, and energy delivery rate.

Methods

Our study was conducted in a 14-ha park in Budapest from 1984 to 1986. Most of the area is covered by lawn and scattered bushes and trees. There is a great variety of trees and shrubs. Each year about 50 pairs of blackbirds breed in this area. The earliest records of breeding are in the first half of April. There are two peaks in breeding attempts, the first at the beginning of May and the second in June. Most nests are sited between 1 and 3 m above ground-level.

Two early nests and one late nest were studied in 1984 and 1986 and three early nests and one late nest in 1985. Daily observations were made between 06.00 and 09.00 h from 20–30 m distance without obvious disturbance to the birds. While one person collected food samples from the nestlings, the other continuously recorded the foraging behaviour of blackbirds.

Food samples (loads) were collected from 5–9-day-old nestlings, using the modified neck-collar method, immediately after delivery by the parents (Kluyver 1933; Török 1981). We studied only the behaviour of males, as they supply most of the food to nestlings at this developmental stage. Samples were kept in 70% alcohol until further analysis. The length and the diameter of the items were measured in mm and the dry weight and energy content were estimated using the equations and values given in Rogers et al. (1977), Török (1981) and Gowing and Recher (1984). Since earthworms and caterpillars stored in alcohol might contract, which could have caused errors in our calculations, the length-weight regression for earthworms was determined by drying at 104° C to constant weight.

Loads containing more than 50% earthworms in dry weight (load type I, $n=63$ over 3 years) were analysed separately from loads with less than 50% earthworms (load type II, $n=40$). Loads containing artificial food (e.g. bread) or loads partly consumed by the nestlings were not included in the analysis.

Searching time and intervisiting time were measured with two running stop-watches and searching routes were recorded on maps. Intervisiting time was defined as the time between two feeding visits to the nest. Searching time was defined as the total elapsed time from arrival at a foraging area until leaving it. Total searching time included both searching and handling time. Periods when the loader consumed items were subtracted from the total elapsed searching time. Handling times were measured only in the case of earthworms. The handling time of the other prey types could not be measured accurately. The total length of the searching routes was estimated from the routes plotted onto maps. To analyse the distance of searching routes from the central place we determined the frequency distribution of each route in 2-m intervals as a function of the distance from the nest. The size of the searching area was estimated by an ellipse covering all the searching routes. The boundaries of the searching area were determined mainly by the territorial behaviour of the neighbouring pairs; thus we can consider the foraging area as the territory.

In 1986 the abundance of earthworms was estimated using the extraction method (Evans and Guild 1948). Samples were taken at 2-week intervals from the end of April till mid-July. On each occasion five 0.25-m² quadrats were sampled. The earthworms were counted and total dry weight (mg) was estimated from measurements of length (mm) on the basis of a linear relationship (weight = 1.2 × length).

Results

Load types and nesting time

At the end of April and in May the nestlings' diet consisted predominantly of earthworms, while in June it contained fewer earthworms and more arthropods (*Isopoda*, *Coleoptera*, *Dermaptera*, *Homoptera*, *Diptera*, *Araneidea*; Table 1). Within the earthworms the ratio of *Allolobophora* to *Lumbricus* species also changed from 0.71 to 0.13 as the breeding season progressed. In 1986 there was a positive correlation between earthworm abundance and rainfall ($r=0.96$, $P<0.01$, $n=5$). Pooling the data of the three years, the proportion of earthworms in the nestlings' diet was also correlated with the amount of rainfall ($r=0.71$, $P<0.02$, $n=10$).

The average species diversity of the loads (calculated with the Shannon formula for each nest) tended to increase during the breeding period (Fig. 1). There was a marked difference between the loads collected in the early and late parts of the breeding season: 84% of loads were type I in April and May compared with 23% in June. Therefore the two parts of the breeding season can be characterised by the two load types (Table 2). When the birds collected mainly earthworms (load

Table 1. Energy content (J/mg) of main prey types and the food composition (percent of the total dry weight) of blackbird nestlings in the early (7 nests) and late (3 nests) periods of the breeding season (A, adult, L, larva)

Taxon	J/mg	April–May	June
Lumbricidae	20.0	77.8	42.5
Isopoda	15.9	1.2	4.3
Diplopoda	14.3	0.2	1.2
Chilopoda	20.9	10.2	1.2
Dermaptera (A/L)	26.8	0.8	13.9
Heteroptera (A/L)	26.8	0.2	0.5
Homoptera (A/L)	26.8	–	2.2
Neuroptera (L)	26.8	–	0.9
Coleoptera (A)	23.4	2.3	6.1
Coleoptera (L)	23.4	0.3	5.2
Lepidoptera (A)	21.2	0.3	2.3
Lepidoptera (L)	22.5	2.0	7.6
Diptera (A)	24.2	4.1	7.0
Diptera (L)	24.2	0.1	0.2
Hymenoptera (A)	21.3	0.2	2.0
Araneidea, Opilionea	25.1	0.2	2.6

Table 2. Foraging parameters of the two load types. Load type I means loads containing more than 50% and load type II less than 50% earthworms (dry weight). Energy delivery rate was calculated as energy content per interfeeding time and rate of energy gain as energy content per searching time for each load

Foraging parameters	Load type I		Load type II		Student's <i>t</i> test <i>P</i> <
	Mean	<i>N</i>	Mean	<i>N</i>	
Interfeeding time (min)	15.1 (9.9)	58	19.9 (7.9)	37	0.01
Searching time (min)	7.2 (3.7)	56	10.7 (5.7)	33	0.002
Searching route (m)	61.6 (48.5)	35	103.2 (63.2)	26	0.005
Dry weight of loads (mg)	116.6 (51.6)	63	110.8 (61.3)	40	NS
Energy content of loads (J)	2364 (1024)	63	2390 (1113)	40	NS
Energy delivery rate (J/min)	258.4 (301.6)	58	142.9 (99.1)	58	0.01
Rate of energy gain (J/min)	463.0 (474.4)	56	285.6 (216.3)	34	0.02
Number of food types in loads	2.7 (2.4)	63	8.7 (4.4)	40	0.001
Number of food items in loads	5.7 (6.3)	63	17.8 (12.6)	40	0.001

N means number of loads; standard deviations are in parentheses; data of 3 years are combined

type I), searching time and intervisiting time were significantly shorter than for load type II. There were no significant differences between the average dry weight and energy content of the two load types (Table 2).

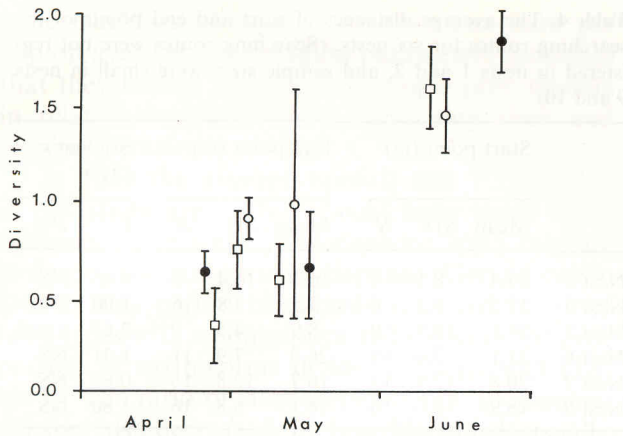


Fig. 1. Seasonal change in prey type diversity of loads in 1984 (solid circles), in 1985 (squares) and in 1986 (open circles). Diversity of each load was calculated with the Shannon formula based on the number of prey items. Each point refers to the mean ± 1 SE of loads obtained from one nest

The foraging efficiency of the males in the two periods was compared by the calculation of two rates: the energy delivery rate, defined as the energy content of loads per intervisiting time, and the rate of energy gain, defined as the energy content of loads per searching time. Both delivery rate and searching efficiency tended to be higher in April and May compared with June though the differences were not statistically significant ($t=0.70$, NS for delivery rate; $t=0.25$, NS for rate of energy gain). Both energy delivery rate and the rate of energy gain were significantly higher for load type I (Table 2).

The loading curves

To analyse the relationships between searching time and dry weight or energy content of the loads we used linear and power models. The dry weight and energy content of load type I were not related to searching time. The power model gave the better fit for both dry weight and energy content of load type II (Table 3).

The frequency distribution of searching times was calculated for 2.5-min intervals. Of 57 searching times of load type I, 2 were less than 2.5 min. These data were omitted from the analysis since the birds returned to earthworms handled during the previous trip.

The distribution of searching times for load type I is similar to an exponential distribution (Fig. 2a). This suggests that the encounters of blackbirds with earthworms tended to be random. The handling time of earthworms was much longer (103.7 ± 37.2 s, $n=16$) than that of the other prey types (approximately 0.5–10 s based on our estima-

Table 3. Correlations for searching time-dry weight and searching time-energy content regressions according to linear and power models (sample size in parentheses)

	Linear		Power	
	<i>r</i>	<i>P</i> <	<i>r</i>	<i>P</i> <
Dry weight				
Load type I (56)	0.15	NS	0.14	NS
Load type II (33)	0.49	0.01	0.67	0.001
Energy content				
Load type I (56)	0.18	NS	0.16	NS
Load type II (33)	0.54	0.01	0.66	0.001

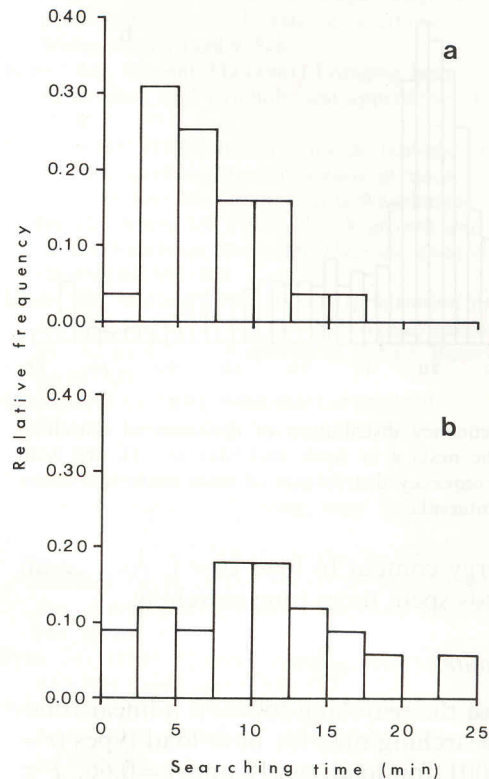


Fig. 2a, b. Frequency distribution of searching times in **a** load type I and **b** load type II. The ordinate is the frequency of searching times of different duration as the proportion of the total number of searching times measured. **a** Summarizes 56 data points and **b** 33 data points obtained from 10 individual males

tion). The handling time was included in searching time in our calculation, which explains why the distributions begins in the second interval, except for the two cases mentioned above.

The distribution of searching times for load type II resembles a normal distribution (Fig. 2b). In June, when the availability of earthworms was low, the birds collected a large number of items of the smaller food types, resulting in a similar

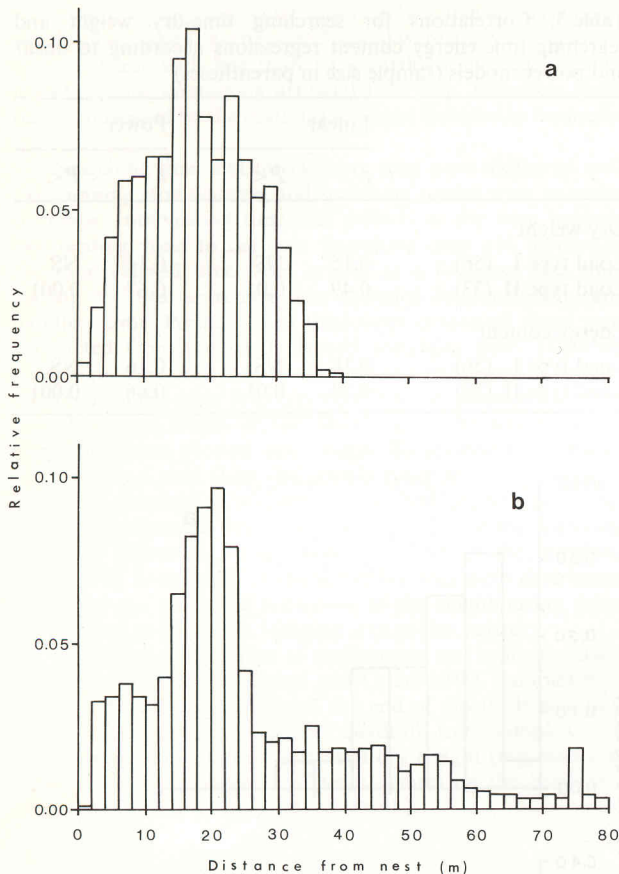


Fig. 3a, b. Frequency distribution of distances of searching routes from the nests **a** in April and May ($n=4$), and **b** in June ($n=2$). Frequency distribution of each route was determined at 2-m intervals

average energy content to load type I. As a result the blackbirds spent more time searching.

Searching routes

The length of the searching routes is a linear function of the searching time for both load types ($r=0.52$, $P<0.001$ for load type I and $r=0.66$, $P<0.001$ for load type II). The average length of the routes differed significantly between the two load types (Table 2). In June blackbirds collected a great number of small prey types over a longer route. This is reflected in a positive correlation between the number of prey types in the loads and the length of the searching routes ($r=0.47$, $P<0.001$). The longer searching routes in June appeared to cause a seasonal increase in territory size. The average territory size in April and May was 0.18 ha ($n=6$) compared with 0.34 ha in June ($n=2$). The frequency distribution of the searching routes as a function of the distance from the nest extended to the longer distances in June (Fig. 3).

The central place foraging model (Orians and

Table 4. The average distances of start and end points of the searching routes for six nests. (Searching routes were not registered in nests 1 and 2, and sample sizes were small in nests 9 and 10)

	Start point (m)			End point (m)			Student's <i>t</i> test	
	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>	<i>t</i>	<i>P</i> <
Nest 3	24.4	8.1	9	16.2	14.4	9	0.85	NS
Nest 4	17.5	8.1	6	9.5	3.8	6	1.90	0.05
Nest 5	19.1	10.5	9	8.9	4.5	9	2.67	0.005
Nest 6	21.1	7.6	11	26.0	7.9	11	1.41	NS
Nest 7	20.8	12.8	15	16.7	12.8	15	0.85	NS
Nest 8	18.9	6.0	16	14.1	8.8	16	1.80	NS

Pearson 1979) predicts that optimal foragers should show centripetal searching routes. This prediction was tested in six nests. Two male blackbirds showed a trend consistent with the model, three males showed a weak tendency to initiate foraging at the periphery, while one male showed the reverse trend (Table 4). These differences between individuals were probably determined by the microhabitat of their territories. Male blackbirds behaved as predicted on lawn areas, but where the territories contained bushes and larger patches without grass, there was no significant difference between the distances of the starting and ending points from the nest.

Discussion

Blackbirds modify their foraging strategy on a seasonal basis when feeding their nestlings. In April and May the average searching time was significantly shorter than in June, although the dry weight and energy content of loads did not differ in the two periods. Early in the breeding season birds specialized on earthworms as the availability of this prey type was probably high due to the high soil moisture (2.9 mm/day precipitation on average in this period). The numbers and distribution of earthworms show a seasonal change as a function of the amount of rainfall (Evans and Guild 1948; Davies and Snow 1965; Gerard 1967). We found a similar tendency in 1986. More precipitation resulted in a higher proportion of earthworms in the nestlings' diet as well. Although earthworms provide much energy per prey captured, blackbirds do not specialize exclusively on this food type in April and May, possibly due to nutrient constraints (Tinbergen 1981; Krebs and Avery 1984).

In the early part of the breeding season blackbirds often encountered earthworms. Although

male blackbirds loaded more than one item per trip on average, the foraging parameters indicated that they tended to behave as single prey loaders in relation to earthworms: searching time and searching routes were short.

In June the average rainfall was 1.5 mm/day in our study area, which could have made some earthworms (mainly *Allolobophora* spp.) migrate to deeper soil and go into diapause (Gerard 1967). During this period blackbirds switched to other food types with a consequent reduction in the proportion of earthworms in the nestlings' diet (Table 1). The ratio of *Allolobophora* spp. to *Lumbricus* spp. also decreased. In June blackbirds usually carried large loads to the nest. The searching routes did not concentrate on particular patches. However, small dipteran species, aphids, and ants occurred in large numbers in some loads and were missing from others, possibly because they are distributed patchily. As the sizes of these patches are very small (e.g. the area of a leaf) compared with the length of the searching routes, the patches of these food types could be interpreted as "single food items".

The power model gave a better fit than the linear function of searching time for both dry weight and energy content per load (Table 3). The most probable reason for the diminishing rate of food gain with increasing searching time is the loading effect (Carlson and Moreno 1982).

The average energy content of the loads did not differ in May and June. In the latter period blackbirds had to collect a lot of items from the small food types (arthropods) to reach the energy content in May. This could explain why the average searching time and length of the searching routes increased. For many species of birds there is a pronounced reduction in territory size when food is abundant (Andersson 1981). This appeared to be true for the blackbirds, too. In June the abundance of earthworms decreased, probably causing the extension of territories.

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