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OPTIMAL FORAGING AND CRYPTIC PREY

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SUMMARY

(1) We describe an experimental test of a model of optimal choice. Captive great tits were presented with a mixture of two kinds of prey on a moving belt attached to the front of a cage.

(2) The model predicts the optimal diet when one of the two kinds of prey is cryptic. In our experiments one prey was cryptic because it closely resembled inedible ‘twigs’ which were also on the moving belt. The birds could not distinguish visually between this kind of prey and twigs without first picking up the item and inspecting it.

(3) The two kinds of prey (which were made of large and small pieces of mealworm inside short lengths of plastic drinking straws) differed approximately by a factor of 2 in their energy yield per unit handling time (profitability). Only the more profitable kind of prey was cryptic.

(4) The model predicted that the birds should switch their preference from the more profitable to the less profitable prey type as the ratio of ‘twigs’ to profitable prey increased. This predicted switch results from the time cost of picking up and rejecting twigs.

(5) All five birds switched as predicted.

(6) This contrasts with the expectation from the more familiar optimal diet model in which prey are recognized instantaneously, and a preference for less profitable prey is never predicted.

INTRODUCTION

Optimal diet models have been used to predict prey preferences of vertebrate and invertebrate predators (Werner & Hall 1974; Goss-Custard 1977; Krebs et al. 1977; Elner & Hughes 1978). However, most of this theoretical and experimental work has assumed that prey are instantly recognizable. When the predator has to spend time recognizing or discriminating different prey, the predictions of the theory may change (Charnov 1973; Hughes 1979). In this paper we describe an experiment which investigates the effect of crypsis on optimal choice.

Consider a predator feeding on two kinds of prey, ‘large’ and ‘small’ worms. Large worms are cryptic in the sense that they resemble twigs (Cott (1940) refers to this type of crypsis as ‘special protective resemblance’). Small worms are instantaneously recognizable. If the predator includes large worms in its diet, it has to spend time distinguishing between worms and twigs. The discrimination might, for example, involve inspecting or picking up twigs which look like worms. It will be advantageous to ignore the cryptic
large worms if this increases the net rate of food intake. This can be formalized in the following optimal diet equation (see also Hughes (1979)):

\[
\frac{E_2 \lambda_2}{1 + \lambda_2 I_2} > \frac{E_1 \lambda_1 + E_2 \lambda_2}{1 + \lambda_2 I_2 + \lambda_1 I_1 + \lambda R}.
\] (1)

Where \(E_1\) and \(E_2\) are the net food values of large and small worms respectively; \(I_1\) and \(I_2\) are the ‘involvement times’ for the two prey types (the time taken to detect, pick up and eat them); \(\lambda_1\), \(\lambda_2\) and \(\lambda\) are the encounter rates with large worms, small worms, and twigs, respectively; and \(R\) is the time taken to inspect and reject a twig. Equation (1) can be rearranged to give:

\[
\frac{1}{\lambda_2} < \frac{E_2}{E_1} \left( \frac{\lambda}{\lambda_1} R + I_1 \right) - I_2.
\] (2)

Calling the right-hand side of this equation \(Z_s\), the condition for specializing on small worms becomes:

\[
Z_s < \frac{1}{\lambda_2}.
\] (3)

If inequality (1) is reversed, it will pay the predator to eat both large and small worms, and by similar reasoning the condition for specializing on large worms is given by:

\[
\frac{E_1 \lambda_1}{1 + \lambda_1 I_1 + \lambda R} > \frac{E_1 \lambda_1 + E_2 \lambda_2}{1 + \lambda_2 I_2 + \lambda_1 I_1 + \lambda R}
\] (4)

which gives:

\[
\frac{1}{\lambda_1} < \frac{(E_1/E_2) I_2 - I_1}{1 + \lambda R}.
\] (5)

When there is no discrimination time (\(R = 0\)), this simplifies to the conventional optimal diet equation developed by Charnov (1976) and others. If we define the right-hand side of eqn (5) as \(Z_L\), the condition for specializing on large worms is:

\[
Z_L > \frac{1}{\lambda_1}.
\] (6)

In our experiment we measured \(E_1/E_2\), \(I_1\), \(I_2\) and \(R\) and manipulated \(\lambda_1\), \(\lambda_2\) and \(\lambda\). The predicted optimal policy was to specialize on large, cryptic worms, in one treatment (A) and in the other treatment (B) to specialize on small worms.

**MATERIALS AND METHODS**

We presented captive great tits (*Parus major L.*) with a choice of two different prey. These were large and small pieces of mealworm *Tenebrio molitor* (four and two segments respectively) inside 15 mm lengths of plastic drinking straw. The large worms weighed about twice as much as the small worms (mean weights of 55 and 26 mg respectively), so that the ratio \(E_1/E_2\) in eqn (5) was taken as 2. The small worms were inside clear straws and could therefore be easily distinguished from the large worms which were in white opaque straws. The large worms, however, were indistinguishable by weight or appearance from ‘twigs’, which consisted of white opaque straws containing a small piece of brown string. The birds could only discriminate between twigs and large worms by picking up the item and inspecting it closely on a nearby perch.
The birds were presented with prey on a moving conveyor belt attached to the front of a 1 m cube cage (for diagram see Krebs et al. 1977). The prey were presented in a pseudo-random sequence (Fellows 1967) and the birds could see one prey at a time as it passed a 7 cm gap in a black Perspex cover on top of the belt. The belt speed was 15 cm/s so that each prey was visible for 0.5 s. The birds readily learned (usually in less than 10 min) to pick prey off the moving belt and take them to a nearby perch to eat them.

We used five wild caught, adult great tits (three females and two males, referred to subsequently as Betty, Martha, Olivia, Greg and Doug), some of which had been used in previous foraging experiments involving choice of prey types. All the birds had been in captivity for at least 12 months before the experiments, which were run in November and December 1978.

Before the start of the experiments the birds were familiarized with the prey and conveyor belt every day for several weeks. During this familiarization period and during the experiments the birds were deprived of their normal food (‘Aleckwa’ Mischung I) last thing at night, and tested the following morning. This deprivation was sufficient to maintain the birds at about 2 gm below their mean ad lib. weight of 19.6 gm.

The birds were housed in 1 m cube cages similar to the test cage (but without the conveyor belt) and each individual was transferred just before testing by chasing it into an aluminium roosting box (‘Kacelnik Box’) in which it could be carried from one cage to another. During the period in which the experiments were run the range of minimum temperatures in the bird room was 5 to 16 °C.

Each bird was tested in two conditions (Table 1). In treatment A, twigs were four times as common as large worms and in B this ratio was reversed. The encounter rate with small worms remained unaltered. Within each treatment the birds were given short tests on five consecutive mornings, and a test lasted until the bird had eaten about fifteen items. Prey and twigs were continuously replenished during an experiment to maintain constant encounter rates. Three birds were given treatment A first and B second; the other two were tested in reverse order.

Table 1. Inter-prey intervals (s) in treatments A and B. In both treatments, there were fifteen items on the belt, which made a complete revolution every 16 s. Five of these items were always small prey. In treatment A there were eight twigs and two large worms, and in B there were two twigs and eight large worms. The order of these items on the belt was determined by a pseudo random sequence

<table>
<thead>
<tr>
<th>Prey</th>
<th>Treatment A</th>
<th>Treatment B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large (1/λ₁)</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Small (1/λ₂)</td>
<td>3.2</td>
<td>3.2</td>
</tr>
<tr>
<td>‘Twigs’ (1/λ₃)</td>
<td>2</td>
<td>8</td>
</tr>
</tbody>
</table>

We recorded the data from a video screen, measuring the following. (a) Type of prey taken. (b) Involvement time: the time taken to pick a prey item off the belt and finish eating it. The end of eating was almost always signalled by bill-wiping, but occasionally a bird flew directly back to the belt. The birds always ate prey on a perch near the belt. They held the straw under one foot, pulled out the worm with the beak and swallowed it. (c) Discrimination time: the time between picking a twig off the belt and dropping it uneaten. The usual method of rejection was to fly with the twig to a perch, peer or peck into the end of the straw, and immediately drop the item.
RESULTS

Table 2 shows the measurements of involvement time \((I)\) and discrimination time \((R)\) made during the experiments. The involvement times for large and small worms are similar because the major component for both times was flying to a perch and extracting the worm from the straw. As a result of the similarity of involvement times, large worms are roughly twice as profitable as small worms (mean value = 1.98), where profitability is defined as the ratio \((E/I)\). Thus conventional optimal diet theory would not predict a preference for small worms. Table 3 shows the calculated values of \(Z_S\) and \(Z_L\) necessary to test the predictions of eqns (3) and (6). In addition it also contains a value \(Z_{L0}\), which is equivalent to \(Z_L\) when discrimination time is zero. We include this value simply to show how our predictions contrast with those of the conventional model with no discrimination time.

TABLE 2. Involvement and discrimination times (s). Involvement time \((I)\) was measured from the moment the bird picked up the prey item until it wiped its beak after eating the worm. Discrimination time \((R)\) started when the bird picked up a ‘twig’ and ended when the straw was dropped

<table>
<thead>
<tr>
<th>Birds</th>
<th>(I_1)</th>
<th>(I_2)</th>
<th>(R)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Doug</td>
<td>9.08 ± 0.50 (56)</td>
<td>8.89 ± 0.54 (90)</td>
<td>3.68 ± 0.33 (27)</td>
</tr>
<tr>
<td>Greg</td>
<td>9.21 ± 0.54 (59)</td>
<td>9.37 ± 1.00 (81)</td>
<td>4.99 ± 0.31 (27)</td>
</tr>
<tr>
<td>Martha</td>
<td>9.73 ± 0.35 (60)</td>
<td>10.29 ± 0.68 (80)</td>
<td>4.67 ± 0.85 (11)</td>
</tr>
<tr>
<td>Olivia</td>
<td>10.02 ± 0.39 (85)</td>
<td>8.69 ± 0.43 (70)</td>
<td>4.18 ± 0.16 (71)</td>
</tr>
<tr>
<td>Betty</td>
<td>8.01 ± 0.29 (75)</td>
<td>6.09 ± 0.19 (64)</td>
<td>3.43 ± 0.19 (42)</td>
</tr>
</tbody>
</table>

Considering treatment A first, Table 3 shows that all five birds specialized on small worms (see column three). According to eqn (3), the optimal policy for four out of the five birds was to specialize on small worms \((Z_S > 1/\lambda_2)\), and the fifth bird, Doug, was very close to the threshold \((Z_S = 3.01, 1/\lambda_2 = 3.2\), see column one). In contrast, the conventional optimal diet equation with no discrimination time predicts that three birds should specialize on large worms \((Z_{L0} > 1/\lambda_2)\) and that two should generalize.

TABLE 3. Values for testing eqns (3) and (6) derived from the measurements in Table 2. The column \(Z_{L0}\) refers to the optimal diet equation for \(R = 0\). In this case, the threshold for specialization on large worms is given by \(Z_{L0} > 1/\lambda_1\) where \(Z_{L0} = (E_1/E_2)I_1 - I_1\). The threshold depends only on \(\lambda_1\) which is why the value \(1/\lambda_1\) is given under \(Z_{L0}\) in both treatments

<table>
<thead>
<tr>
<th>(Z_S)</th>
<th>(Z_{L0})</th>
<th>% small taken</th>
<th>(Z_L)</th>
<th>(Z_{L0})</th>
<th>% small taken</th>
</tr>
</thead>
<tbody>
<tr>
<td>1/\lambda_2 = 3.2</td>
<td>1/\lambda_1 = 8</td>
<td>Chance = 33%</td>
<td>1/\lambda_1 = 2</td>
<td>1/\lambda_1 = 2</td>
<td>Chance = 33%</td>
</tr>
<tr>
<td>Doug</td>
<td>3.01</td>
<td>8.70</td>
<td>76.5***</td>
<td>5.96</td>
<td>8.70</td>
</tr>
<tr>
<td>Greg</td>
<td>5.22</td>
<td>9.53</td>
<td>82.1***</td>
<td>5.87</td>
<td>9.53</td>
</tr>
<tr>
<td>Martha</td>
<td>3.92</td>
<td>10.85</td>
<td>98.2***</td>
<td>6.85</td>
<td>10.85</td>
</tr>
<tr>
<td>Olivia</td>
<td>4.68</td>
<td>7.36</td>
<td>49.5**</td>
<td>4.83</td>
<td>7.36</td>
</tr>
<tr>
<td>Betty</td>
<td>4.78</td>
<td>4.17</td>
<td>56.8***</td>
<td>2.92</td>
<td>4.17</td>
</tr>
</tbody>
</table>

*** \(P < 0.001\)  
** \(P < 0.01\) deviation from chance (\(\chi^2\) test)
(Z\textsubscript{L0} < 1/\lambda) as shown in column two of Table 3. Thus the effect of crypsis is to dramatically alter the predictions, and our results demonstrate that the birds actually tend to ignore the more profitable prey.

In treatment B, twigs were much less abundant than large worms (Table 1), and eqn (6) predicts that all five birds should specialize on large worms (Table 3, column four). Four out of the five birds showed clear specialization (Table 3, column six). The fifth bird (Doug again!) was the only individual to show a significant change in preference through the 5 days of testing. His preference for large worms increased through time (regression coefficient = 5-73, P < 0-02) so that on the fifth day he showed a strong preference for large worms (only 13% of items eaten were small). Thus Doug appeared to be slow to change his preference, and he showed a ‘transition effect’ similar to that described by Krebs et al. (1977). In treatment B, the equation with no discrimination times makes predictions similar to those of eqn (6) (Table 3, column five).

DISCUSSION

The simple optimal diet equation with no discrimination time predicts that a predator should either specialize on the more profitable of two prey types (i.e. the one with a higher E/I ratio) or eat both. The conditions for specialization depend on the encounter rate with profitable but not with less profitable prey. In contrast, the equations we have tested in this paper can predict specialization on profitable or unprofitable prey, depending on the encounter rates with the two types. It is an essential feature of these equations that the discrimination time is associated with only one of the two prey types. An alternative model with symmetric discrimination costs is tested by Houston, Krebs & Erichsen (1980).

In conclusion, our experiments show that when a predator eats cryptic prey, it must spend time discriminating them from the background. This discrimination cost can be incorporated into optimal diet equations and used to make successful predictions. The results suggest that a predator will actually stop looking for an otherwise profitable prey which has become sufficiently cryptic to be excluded from the optimal diet.

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REFERENCES


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