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John Krebs

Jonathan Erichsen

Michael Webber

Eric Charnov

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OPTIMAL PREY SELECTION IN THE GREAT TIT (*PARUS MAJOR*)

BY JOHN R. KREBS,* JONATHAN T. ERICHSEN, MICHAEL I. WEBBER,
Animal Behaviour Research Group, Department of Zoology, University of Oxford,
AND ERIC L. CHARNOV
Department of Biology, University of Utah, Salt Lake City, Utah

Abstract. We tested the predictions of an optimal foraging model using five captive great tits as predators. The birds were presented with two prey types, profitable and unprofitable, on a moving belt. Both prey types were made out of mealworms. When the encounter rate with both prey types was low, the birds were non-selective, but at a higher encounter rate with profitable prey, the birds selectively ignored the less profitable type and did so irrespective of the encounter rate with them. These results are as predicted by the model, but the birds did not as predicted change from no selection in a single step. We suggest that this is because the birds invest time in sampling to determine the availability and profitability of different prey types.

Introduction

Do predators select prey so as to maximize their rate of food intake? In the last few years several similar models of prey choice have shown how a predator could in theory maximize its net rate of energy intake while foraging, but there have been few attempts to test the models. Essentially, all the models make the same sort of assumptions and reach similar conclusions (MacArthur & Pianka 1966; Emlen 1966; Schoener 1971; Pulliam 1974; Werner & Hall 1974; Charnov 1976). The assumptions are (a) that the predator 'tries' to maximize its net rate of energy intake (energy is taken as a convenient currency, but other components of food could be substituted), (b) that it can instantaneously recognize prey types of different profitability (reward per unit handling time) and (c) that the prey are encountered at random and not in patches (in which case different models are applicable, e.g. Royama 1970). The predictions of models of optimal prey choice have usually been treated qualitatively: if the encounter rate with profitable prey is low, the predator should be unselective, but if profitable prey are abundant the predator should ignore lower quality prey (MacArthur 1972). This is perhaps not surprising, but more interesting is the prediction that the predator's decision to ignore prey of low profitability is not dependent on how common these prey are, but only on the abundance of more profitable prey.

We can make these predictions more precise by developing the following version of the model, which we only report in outline, as it is described fully by Charnov (1973, 1976). Consider a predator foraging for a time, T, made up of time spent searching, T_s, and time spent handling the prey, T_h. While the predator searches, assume it encounters the ith prey type at a rate, λ_i, and on encounter eats it with probability P_i. We define E_i as the net energy gain and h_i as the handling time for the ith prey type. Then the total energy gain, E, in time T, will be given by:

$$E = T_s \sum_i \lambda_i E_i P_i$$

and the total handling time, T_h, by

$$T_h = T_s \sum_i \lambda_i h_i P_i$$

Then the rate of energy intake is given by

$$\frac{E}{T} = \frac{T_s \sum_i \lambda_i E_i P_i}{T_s + T_s \sum_i \lambda_i h_i P_i} = \frac{\sum_i \lambda_i E_i P_i}{1 + \sum_i \lambda_i h_i P_i} \qquad (1)$$

It can be shown that to maximize E/T, any prey type, c, should be ignored if

$$E/T > \frac{E + \lambda_c E_c P_c}{T + \lambda_c h_c P_c} \qquad (2)$$

or

$$E/T > E_c/h_c \qquad (3)$$

In other words, the addition of prey type c to the diet is independent of the encounter rate with c (which cancels out of eqn (2)), and prey type c should be eaten with a probability $P_c = 0$ or $P_c = 1$ (because (3) has to be either true or false).

In our experiments, we presented the predator with only two prey types, profitable (prey type 1)

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*Reprint requests to J. R. Krebs.

and unprofitable (prey type 2), so that the model can be rewritten as:

Ignore prey type 2 only if:

$$\frac{\lambda_1 E_1}{1 + \lambda_1 h_1} > E_2/h_2 \qquad (4)$$

Let $\lambda_1/(1 + \lambda_1 h_1) = R$

and $E_1/E_2 = \alpha$

The model can now be restated as:

Ignore prey type 2 if:

$$R > 1/\alpha h_2 \qquad (5)$$

In order to control precisely the encounter rates and visibility of prey, we used an apparatus in which the predators, captive great tits, encountered prey by sitting on a perch and watching them rush past on a conveyor belt. When the bird captured a prey item, other prey continued to move past on the belt during the handling time. The prey were not arranged on the belt in a random sequence (for logistic reasons), but in a predictable order at fixed time intervals. If we assume that the bird takes this into account, a version of the model specific to our experimental set up can be developed:

Let E = the value of an unprofitable prey
$2E$ = the value of a profitable prey (the weight ratios in the experiments were 2 : 1)
t = the time interval between the current unprofitable prey and the next profitable prey on the belt
p = the probability of handling the current unprofitable prey within time t
h_1 = the handling time for a profitable prey item.

If the bird takes the unprofitable prey, its energy intake will be

$$p(3E) + (1 - p)E = (1+2p)E, \text{ in } t + h_1 \text{ seconds}$$

If the bird ignores the current prey and waits for the next profitable item, it will get

$$2E, \text{ in } t + h_1 \text{ seconds}$$

Therefore the birds should ignore the current prey if

$$(1+2p)E < 2E \qquad (6)$$

or

$$p < \tfrac{1}{2} \qquad (7)$$

This model can be extended to include longer sequences of encounters, but the prediction stays essentially the same.

Thus in our set up, with non-random encounters, the predator should ignore the unprofitable prey, if the probability of handling it before the next profitable prey arrives, is less than 0·5. It may be seen that this criterion is similar to that derived from the general model (eqn 5) in that it depends on the relative energy values and the handling times of the two prey items, but on the encounter rate with the profitable prey alone. However, the level of the criterion will differ between the models, but for the experiments we performed, the models mostly give the same predictions.

Methods

Apparatus

The experimental set up is shown in Fig. 1. It consists of a 1-m^3 cage with a conveyor belt mounted on the front. The belt is 5-cm wide, made of black rubber, and driven by a variable speed motor; it is mounted in a wooden frame. Just above the belt, in grooved runners on the wooden frame, is a cover consisting of two long narrow strips of black Perspex. These can be pushed in from either end of the wooden frame to cover the belt completely, or pulled apart to make a gap through which the bird can see a short section of belt, when sitting on a nearby perch. The gap was always closed at the end of an experiment, and only reopened at the start of the next test. The belt extends beyond the end of the cage in both directions, so that an observer, hidden from the bird, could add prey to the belt during a test, and so maintain a constant

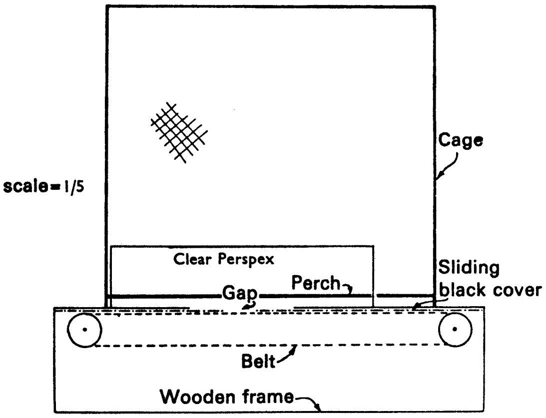

Fig. 1. A front end view of the experimental apparatus.

encounter rate. During our experiments, the belt speed was set at 12·7 cm/s, which means that the bird could see a prey item, as it moved across the 6·5-cm-long gap, for about 0·5 s. The bird could never see more than one prey at a time, so the choice was always sequential rather than simultaneous.

The Predators

We used five great tits (four male, one female), of which four were wild caught and one (bird GBW) was hand-raised from the age of 12 days. The birds' normal diet was the mixture described in Krebs, MacRoberts & Cullen (1972), but during the experimental period, from November to December 1975, we kept the birds under continual slight deprivation. The birds were deprived of food from dusk until between 09.15 and 11.00 hours on the following day; this deprivation was sufficient to maintain the birds at an average of 1·4 g below their mean weight at 19·4 g when supplied with ad libitum food. The room in which the birds lived, and in which the experiments were done, was not heated, and the overnight minimum temperature varied between 5°C and 10°C during the period of the experiments. Each day the birds were tested in a different order, and they were not given their normal food until after the last bird had been tested. This ensured that each bird had an unpredictable deprivation time after doing the experiment; we thought this might encourage the birds to forage efficiently in the tests.

Between tests the birds were housed singly in 1-m^3 cages similar to the experimental cage, and they were transferred to the test cage in small movable aluminium roosting boxes into which they readily retreated if mildly frightened.

Before the start of the experiments the birds were familiarized with the conveyor belt and trained to hunt for prey on the moving belt at speeds far in excess of the one used in the experiments. This took as little as a few minutes for some birds, and as much as 2 or 3 days for others.

The Prey

We used two prey types, eight segment ('large') and four segment ('small') pieces of mealworm (weights from one sample of twenty-five: 0·069 ± 0·018 (SD), 0·033 ± 0·008 g respectively). The prey were obviously identical in nutrient balance and the energy ratio was approximately 2 : 1 (in two samples of twenty-five of each type the ratio was 2·1 : 1 and 1·9 : 1). The four segment prey differed from the larger prey in having a small (2 mm × 10 mm) piece of white plastic tape stuck lengthways along the top. This was primarily to increase the handling time for the small prey, so making them less profitable than the large prey (the birds had to hold the mealworm under one foot and peel off the tape before eating the prey), but it also had the effect of making the two prey types appear the same size, although of course they differed in colour. The two prey types were presented lengthways on the belt, the small prey with the tape side up.

In previous work with fish it has been found that handling time varies with hunger (Ware

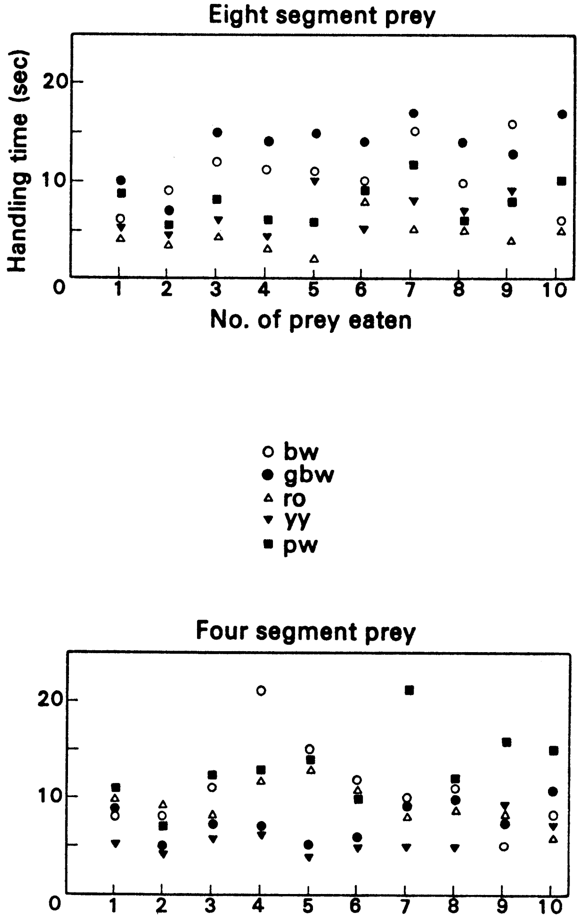

Fig. 2. Handling time (seconds) in relation to 'hunger' for large and small prey types. The regression coefficients for individual birds are shown in Table II. (For bird YY with eight segment prey, only nine captures were measured.)

1974; Werner 1974). We tested for this effect by depriving the birds overnight in the usual way and measuring the handling time for each of the first 10 prey eaten, repeating this on 3 days with large, and 3 days with small prey. Figure 2 and Table I show that there is no significant effect of hunger on handling time over the range we measured. Although there is a slight increase in handling time with satiation with the eight-segment prey, only one of the individual bird regressions is significant. In our subsequent test of the model, we treated handling time as a constant, and used a cut-off point of 10 prey items eaten to end any particular test. Smith & Dawkins (1971) found a slight increase in handling time with satiation, but they were using larger prey items. They also found that the variability in handling time increased with satiation, an effect which seems to be apparent in Fig. 2. If a bird showed any sign of satiation before the cut-off point, we ended the test at once. The individual tests lasted between 150 and 300 s. The handling times and relative profitabilities of the two prey types are shown in Table II.

Table I. Regressions of Median Handling Time in Seconds (Three Trials) Against 'Hunger', Measured by Number of Mealworms (One to Ten) Eaten After Standard Overnight Deprivation

	Regression coefficient ± SE	
Bird	Eight-segment prey	Four-segment prey
BW	0·248 ± 0·39	−0·345 ± 0·51
RO	0·12 ± 0·19	−0·26 ± 0·23
PW	0·33 ± 0·25	0·68 ± 0·35
GBW	0·75 ± 0·29*	0·41 ± 0·20
YY	0·50 ± 0·235	0·218 ± 0·15

*$P < 0·05$, none of the others differs significantly from 0.

Table II. Median Handling Times ± SE (based on About Thirty Observations Per Bird)

Bird	Four-segment prey	Eight-segment prey	$\frac{(E_1/h_1)}{(E_2/h_2)}$
BW	10·5 ± 1·36	10·5 ± 1·27	2·0
RO	9·0 ± 1·61	5·0 ± 0·80	3·6
PW	12·5 ± 1·65	8·5 ± 1·39	2·94
GBW	8·0 ± 0·95	14·5 ± 2·37	1·10
YY	5·0 ± 0·54	6·0 ± 0·99	1·70

Experimental Procedure

Table III summarizes the experimental design. We used five different treatments, ranging from low encounter rates with both prey types (*A* and *B*) to high encounter rates with the good prey and varying proportions of good and poor prey (*C*, *D* and *E*). Each bird received the treatments in a different order. A treatment consisted of five trials, one on each of five successive mornings, so each bird was only tested once per day, and the whole experiment lasted 25 days. As we discussed above, we used a cut-off point of 10 prey for an individual test, which means that a bird chose about 50 prey items in each treatment.

The procedure in actually running the experiment was as follows: we translated the chosen encounter rates with the two preys types into interprey distances on the belt, and the prey positions were indicated with chalk marks. As the belt moved around and the bird took prey, one observer replenished the empty chalk marks by dropping the appropriate prey type onto the belt with forceps, while the second observer recorded the data by watching the bird on a video monitor. Both observers were out of sight of the bird. As we have discussed earlier, the prey were not presented in a random sequence but in a fixed order according to the chalk marks on the belt. In treatments *A*, *B* and *D*, the order was L, S, L, S, . . . (L = large, S = small); in treatment *C* it was L, L, L, S, L, L, L, S, . . .; and in treatment *E* it was L, S, S, L, S, S, . . .

Table III. The Experimental Design: Encounter Rates (= Prey per Second)

Treatment	Encounter rate with large prey	Encounter rate with small prey	Proportion of large and small
A	0·025	0·025	50 : 50
B	0·05	0·05	50 : 50
C	0·15	0·05	75 : 75
D	0·15	0·15	50 : 50
E	0·15	0·30	33 : 67

N.B. Each individual was given the five tests in a different order.

Results

Selection and Encounter Rates

Table IV shows the percentage of large prey eaten in the different treatments, and Table V gives the values of R and $1/\alpha h_2$ (eqn (5)), which can be used to predict whether or not a bird should select large prey. In treatments A and B, R is less than $1/\alpha h_2$ for all five birds, so the general model correctly predicts no selection. The encounter rate with large prey is constant in tests C, D and E, so the predictions of the model for a particular bird are the same for all three treatments. For birds, RO, BW and PW the model predicts selection, and all three selected large prey (although PW in test C did not deviate significantly from chance, the trend was in the right direction). The random encounter model also correctly predicted that GBW would not select prey in tests C to E. In both this instance and for the previous results the non-random encounter model (eqn (7)) makes the same predictions.

It is only in tests C to E for YY that the two versions of the model differ in their predictions. From eqn (5) we predict no selection in these tests (Table V), but eqn (7) predicts that YY should select large prey in D and E, and that the strategies of selection and no selection are equally profitable in treatment C. The results conform to the predictions of the non-random version of the optimal foraging model: YY preferred large prey in tests D and E, and showed no selection in C. The reason that YY is the only bird for which the two versions of

Table IV. Percentage of Profitable Prey in the Diet in the Five Different Experiments. For each Experiment the Total Number of Prey Eaten was about Fifty

		Percentage profitable prey in the diet					
Test	λ	Encounter frequency	BW	RO	PW	GBW	YY
A	0·025	50	52	54	52	56	50
B	0·05	50	50	52	44	58	56
C	0·15	75	86*	94*	82†	82	78
D	0·15	50	98*	86*	80*	48	78*
E	0·15	33·3	64*	91*	78*	40	70*

*Percentage good prey in diet differs significantly from no selection (χ^2 test).
†No significant selection observed, but selection predicted by the model. All the other results are consistent with the optimal foraging model. In the case of YY, the strategy of selection is equally profitable with no selection for test C.

Table V. Median values of R ($= \lambda_1/1 + \lambda_1 h_1$) and $1/\alpha h_2$ with SE

	Value of R			
Bird	$\lambda_1 = 0{\cdot}025$	$\lambda_1 = 0{\cdot}05$	$\lambda_1 = 0{\cdot}15$	$1/\alpha h_2$
BW	0·020 ± 0·001	0·033 ± 0·002	0·062 ± 0·003*	0·047 ± 0·004
RO	0·022 ± 0·001	0·039 ± 0·002	0·086 ± 0·003*	0·055 ± 0·008
PW	0·021 ± 0·001	0·035 ± 0·002	0·067 ± 0·004*	0·040 ± 0·003
GBW	0·018 ± 0·001	0·029 ± 0·002	0·050 ± 0·003	0·063 ± 0·007
YY	0·022 ± 0·008	0·038 ± 0·002	0·079 ± 0·004†	0·100 ± 0·007

*The model predicts selection at these encounter rates.
†The model predicts no difference in profitability of selective and non-selective strategy in test C, selection in D and E (see text).

the model make different predictions, is that this individual had a very short handling time for small prey (Table II). In treatment *C* the time from the small prey to the next large is 5 s, the same as the median handling time, so in eqn 7, $P = \frac{1}{2}$. In tests *D* and *E* the interval between a small prey and the next large is less than 5 s, so eqn (7) predicts selection.

Figure 3 represents the results from Table IV in a different way. Tests *C* to *E* are combined to give an average value of 'percentage selection' at the high encounter rate with large prey: the degree of selection for large prey shown by an individual is a function of the relative profitabilities of the two prey types. (The method of calculating 'percentage selection' is detailed in the caption of Fig. 3. It is the deviation from the encounter frequency in the proportion of large prey in the diet, expressed as a percentage of the maximum possible deviation.) The most selective bird, RO, has a profitability ratio of 3·6 while the least selective, GBW, has a ratio of 1·1.

As predicted by the optimal foraging model, the birds that selected large prey at the high encounter rate did so even when the encounter rate with small prey was varied sixfold (treatments *C* to *E*). For RO, PW and YY, the percentage large prey eaten was fairly constant through tests *C* to *E*, and in the case of BW, the percentage dropped in treatment *E*.

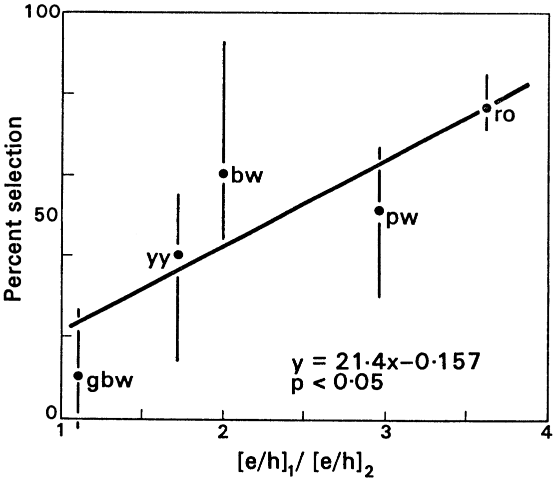

Fig. 3. Percentage selection for large prey plotted as a function of the profitability ratio of the two prey types. Percentage selection is calculated as follows:

$$\frac{\text{Observed per cent} - \text{Expected per cent}}{\text{100 per cent} - \text{Expected per cent}}$$

The reason for dividing by (100 per cent — Expected per cent) is so that data from tests, *C, D, E*, in which the expected percentages were 75, 50 and 33·3 respectively, could be combined. Vertical bars are ranges.

In summary, all twenty-five results in Table IV are consistent with the hypothesis of optimal foraging (many are, of course, also compatible with a null hypothesis of no selection). Although bird PW did not show statistically significant selection in test C, it is much more difficult to show a significant deviation in excess of 75 per cent encounter frequency of this treatment, than it is in *D* and *E*, where the expected proportion is 50 per cent and 33·3 per cent respectively.

All or Nothing Selection

Although the model is successful in predicting when individuals should select large prey, it is

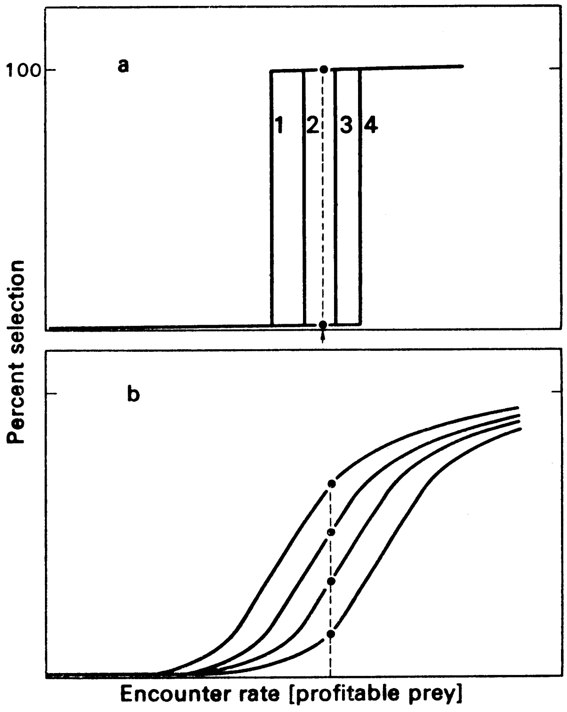

Fig. 4. Two graphical models of prey selection. (a) The upper model is that predicted by the optimal foraging model, with a step change from no selection to 100 per cent selection. The four lines represent four individuals with different profitability ratios $(E_1/h_1)/(E_2/h_2)$ and the vertical dotted line represents a cross-section at one particular encounter rate. (b) An alternative model which takes into account the role of sampling.

incorrect in predicting that the birds should switch in a step function from no selection to 100 per cent selection. Figure 4(a) shows graphically the behaviour of a bird as predicted by the model: a stepwise change in selection at a threshold rate of encountering large prey. Fig. 4(b) shows an alternative model with a gradual increase in selection, which fits the data more closely. Figure 3 suggests that the transition from no selection to selection is a gradual one. In this figure we have, in effect, taken a 'cross-section' of Fig. 4 at an encounter rate of 0·15 large prey per second. A cross-section through Fig. 4(a) (indicated by dotted line) would show the birds either at 100 per cent selection or at no selection according to their individual profitability ratio, while a similar cross-section through 4(b) would show the birds arranged on a slope, as in Fig. 3: the regression of Fig. 3 is an estimate of the slope of Fig. 4(b).

All the versions of the optimal diet model, both stochastic and deterministic, predict all or nothing selection (with the exception of Pulliam's (1975) model based on qualitative difference between prey types, which does not apply here). This may well be because the models do not include the effect of sampling: a predator has to invest time in estimating the encounter rates and profitability of different prey types, and thus puts a constraint on the extent to which it can select the optimal diet in a given bout of foraging. (Royama (1970) developed the same idea in the context of foraging in a patchy environment.) The difference between Figs 4(a) and 4(b) can be viewed as the price the predator is willing to pay in sampling. At extremely high encounter rates with large prey the predator invests little in sampling so that 4(b) approaches 100 per cent selection, but at encounter rates near the threshold of 4(a) the predator invests an increasing amount of time in sampling less profitable prey.

The data in Table VI show how sampling experience plays a role in determining the degree of selection for large prey. The table shows the percentage change in selection between the first and last test of a particular treatment (as we described earlier, each treatment consists of five tests on successive mornings). The left-hand part of the table contains data from tests in which no selection was predicted and the 'selection' treatments are on the right-hand side. If the birds base their selection on accumulated experience, we would predict an increase in selection in the latter group but not in the former. In the 'selection' group there is a mean increase of 29 per cent in selection for large prey, but this is not significantly larger than the 3 per cent increase in 'no-selection' treatments. A more telling comparison is to contrast those selection tests which immediately followed a no-selection treatment (for example, treatment *E* following *A*), with the remaining selection tests (e.g. *E* following *D*). If the bird makes a decision about selection on the basis of recent experience, we would predict a lag in switching to selection immediately after the transition from low to high encounter rates, and therefore a large increase in selection during the five trials. Table VI shows that in the four such transitions there was a large increase in selection for large prey during the five tests and the difference between the percentage change in these and in the remaining high encounter rate treatments is significant. It is not surprising that the reverse transition, from high to low encounter rates, does not produce a lag (left-hand side, Table VI), since the new low encounter rate must become apparent immediately: the bird simply does not find a large prey item for, say, 20 s.

One could view these results as showing that the birds make mistakes rather than that they follow a deliberate sampling strategy. We allowed the birds such a short time each day (about 4 min) to assess the encounter rates that we may well have been operating near the limit of their capabilities. In practice, it will be impossible to distinguish between 'mistakes' and 'deliberate sampling' until we have devised a specific predictive sampling model. One other possibility should be mentioned: that the failure to optimize could result from discrimination mistakes. This is most unlikely to be of importance in our experiments because the prey were quite distinct in appearance, and each prey was visible for approximately 0·5 s. Other tests have shown that great tits are capable of discriminating finer differences between prey types at much higher belt speeds (J. T. Erichsen, unpublished data).

Discussion

Our results show that great tits can select prey on the basis of reward per unit handling time, and that the degree of selection depends on the encounter rate with profitable prey, rather than with unprofitable prey. The optimal foraging model was successful in predicting for each individual the encounter rates at which selection occurred, but it was incorrect in predicting a stepwise increase in selectivity.

Several studies have shown that predators can select prey of high profitability (e.g. Kear 1962; Smith 1970; Menge & Menge 1974; Davies 1977), and Partridge (1976) showed that captive great tits can learn to forage preferentially at feeding sites, analogous to prey types, with high profitabilities. Kear (1962) also found that chaffinches ranked six seed types in an order of preference roughly equivalent to the rank order of profitability. Charnov (1976) has recently taken this type of observation a step further by showing that mantids (*Hierodula crassa*) can rank 'prey types' (flies at different distances) in order of profitability and that with increasing hunger, less profitable types are added to the diet in rank order.

Four recent studies have been designed more specifically to test the optimal foraging model. Werner & Hall (1974) found that bluegill sunfish became more selective as the encounter rate with profitable prey (large *Daphnia*) increased, and further, that smaller size *Daphnia* were selectively ignored at the predicted density of large prey. Werner & Hall did not test whether the degree of selection was independent of the availability of small prey. This prediction is important because it is less likely to be compatible with an alternative model. For example, it might be possible to explain Werner & Hall's results by postulating that the fish always scan for the next visible prey. If large prey are more abundant and more conspicuous, one would expect selection.

Emlen & Emlen (1975) tried to test the optimal diet model using laboratory mice supplied with ad libitum food. Their results did not support the model, but by incorporating a 'mistake' factor, they could adjust the results to fit. It is possible that the 'mistakes' they proposed are analogous to what we have called sampling in discussing our results.

In a field study of sunbirds foraging on mistletoe flowers, Gill & Wolf (1975) found no evidence of a preference for profitable (unopened) flowers. They concluded that their results supported the optimal diet model because the encounter rate with profitable prey was low enough to expect no selection, but their results do not distinguish between this explanation, and a null hypothesis. Goss-Custard (1976) has provided the best evidence to date for optimal prey choice. In a field study he found that redshank preferred the size classes of *Nereis diversicolor* and *Nephthys hombergi* with the highest reward per unit

Table VI. The Percentage Change in 'Per Cent' Selection (Defined in Fig. 3) Between Trials One and Five of a Treatment*
(Italicized scores are transitions)

	Prediction							
	No selection†				Selection‡			
	A	*B*	*C*	*D*	*E*	*C*	*D*	*E*
BW	*0*	+20				*+120*	0	−15
RO	−10	0				0	*+120*	+15
PW	*−20*	−20				*+80*	+40	−15
GBW	+20	+40	+80	−40	−15			
YY	*−20*	0	*0*				*+20*	−45

*The left-hand part of the table shows treatments in which no selection was predicted and the right-hand part refers to the other treatments. Although there was a tendency for selection to increase more in the right-hand group than in the left-hand, the difference is not significant. However, there is a significant difference within the right-hand group, between transition (see text) trials and others. This shows that the birds accumulate experience during the five trials.

†No selection: ($\bar{x} = 2{\cdot}5$) versus selection ($\bar{x} = 29{\cdot}1$): $P > 0{\cdot}10$.

‡Selection: transition ($\bar{x} = 85$) versus others ($\bar{x} = -2{\cdot}14$): $P < 0{\cdot}01$.

handling time (large prey), and that this preference was dependent on the encounter rate with large, but not with small prey. He incorporated the observed preference relationships in a simulation model and was able to show that redshank select the optimal diet.

None of the studies we have discussed has reported a step change from no selection to selection for profitable prey, so it seems that our failure to find this in our experiment is likely to be a general result.

Do our laboratory results have any relevance for the field situation? In the real world prey selection will be influenced by factors such as crypsis, defence mechanisms, and patchiness of distribution (Tinbergen 1960; Royama 1970). The point of the laboratory work is that it shows that great tits have the machinery for making decisions about optimal prey choice, and they could only have acquired this machinery through the action of natural selection in the wild.

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