

Are great tits (*Parus major*) really optimal foragers?

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Abstract: In this study, we test the classical prey model of optimal-foraging theory with great tits (*Parus major*) feeding on two types of mealworms presented on a conveyor belt. Contrary to the results of some previous experiments, prey types were given to birds in random order, therefore birds could not predict their next prey item. We tested birds' diet choices at four different prey-encounter rates. Our results show that in 95% of cases great tits consumed the more profitable prey type upon encounter. On the other hand, consumption of the less profitable prey type did not differ statistically from the "always-attack" strategy in 77% of cases when the rate of encounter with the more profitable prey was below a critical value, and did differ from that strategy in 67% of cases when the rate of encounter with the more profitable prey was above that critical value. Contrary to predictions of the classical prey model of optimal-foraging theory, our birds never completely excluded the less profitable prey type from their diet. We also estimated the functional responses of individual birds with respect to the more profitable prey type; birds' diet changes occurred too slowly to make these functional responses stabilizing.

Résumé : Nous avons éprouvé le modèle classique de prédation de la théorie de la quête optimale chez des mésanges charbonnières (*Parus major*) nourries de deux types de vers de farine présentés sur une courroie de transport. Contrairement à des expériences antérieures, les proies étaient offertes ici aux oiseaux dans un ordre aléatoire, si bien que les oiseaux ne pouvaient jamais savoir quelle proie allait suivre. Nous avons examiné le choix des oiseaux dans quatre tests où les proies étaient présentées chaque fois selon un taux différent. Nos résultats montrent que les mésanges ont consommé les proies les plus profitables dans 95 % des cas. D'autre part, la consommation des proies les moins profitables ne différait pas statistiquement des résultats de la stratégie d'« attaque à tout coup » dans 77 % des cas où le taux d'exposition aux proies les plus profitables était sous un point critique, mais différait des résultats de la même stratégie dans 67 % des cas où le taux d'exposition était au-dessus de ce point critique. Contrairement aux prédictions de la théorie de la quête optimale classique, les mésanges n'ont jamais entièrement exclus de leur régime les proies moins profitables. Nous avons également estimé les réponses fonctionnelles d'individus en présence du type de proies le plus profitable; les changements dans le régime alimentaire se sont avérés trop lents pour que ces réponses fonctionnelles aient un effet stabilisant.

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Introduction

Optimal-foraging theory aims to explain animals' diet-choice behavior from the standpoint of evolutionary theory and comprises a number of specific models that are tailored to mimic specific environmental and behavioral scenarios (Stephens and Krebs 1986; Schmitz 1997). One of the simplest models is certainly the classical prey model (CPM) formulated by Charnov (1976). It assumes that in multiple-prey environments, a searching predator meets prey items sequentially and randomly and that upon each encounter it decides whether to attack and eat that item or ignore it and search for another, possibly more profitable one. This model also

assumes that a proxy for predator fitness is the average rate of net energy intake, R , during foraging:

$$R = \frac{E}{T_s + T_h}$$

Here T_s denotes time spent searching for prey, T_h is time spent handling prey items, and E is the net amount of energy gained by the predator during the total foraging time, $T_s + T_h$. To behave optimally, predators are assumed to maximize R . Searching for and handling prey are assumed to be the only predator activities and are mutually exclusive. The CPM thus assumes that predators are limited only by time: the only cost of feeding on a particular prey item is the time needed to handle it. Thus, if an encountered prey item is of a less profitable type, by feeding on it the predator loses the opportunity to search for a more profitable one. Cases where predators are limited by other constraints (e.g., digestive, nutrient, etc.) were studied by Belovsky (1978), Thompson et al. (1987), Schmitz et al. (1997, 1998), and others.

For two prey types, using the Holling disc equation (Stephens and Krebs 1986), one may express R as

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$$R = \frac{e_1 \lambda_1 p_1 a_1 + e_2 \lambda_2 p_2 a_2}{1 + h_1 \lambda_1 p_1 a_1 + h_2 \lambda_2 p_2 a_2}$$

where λ_i is the predator's encounter rate with prey type i (1 or 2), e_i is the net energy gained from ingesting prey type i , h_i is the handling time for prey type i , p_i is the probability of the encountered prey type i being attacked, and a_i is the probability of the predator's attack on prey type i being (for details see Stephens and Krebs 1986). Should the predator attack or ignore an encountered prey item? Assuming that prey type 1 is more profitable than prey type 2 (i.e., $e_1/h_1 > e_2/h_2$), the CPM predicts that the more profitable prey type, 1, will always be attacked upon each encounter ($p_1 = 1$), whereas the less profitable prey type, 2, will be attacked upon each encounter provided that, as a result, the predator's average rate of net energy intake, R , will not decrease. This occurs when the rate of encounter of a searching predator with the more profitable prey type (λ_1) falls below a critical value (Stephens and Krebs 1986):

$$\lambda_C = \frac{e_2}{a_1(e_1 h_2 - e_2 h_1)}$$

The above rules imply that predators' decisions should be independent of the rate of encounter with prey type 2 (λ_2). Note that the above predictions were derived on the basis of several simplifying assumptions: prey value can be expressed as a single quantity, predators are omniscient, and predators are perfect optimizers. Nevertheless, predictions of the CPM provide us with several hypotheses that can be tested. Despite its simplicity, this model has seemingly never been properly tested with actual observations. Stephens and Krebs (1986) surveyed 71 experimental and field studies that tested animals' foraging decisions. Despite a qualitative agreement with CPM predictions, it is difficult to fit these studies to the CPM because some assumptions of the model were often violated and (or) not all relevant parameters were measured.

One of the classical experiments aimed at testing the CPM is the experiment proposed by Krebs et al. (1977), using the great tit (*Parus major*) as the model organism. The results of this experiment have frequently been presented as evidence of the optimal foraging behavior of great tits (Krebs and McCleery 1984; Stephens and Krebs 1986; Begon et al. 1990). However, that study clearly suffers from three inconsistencies: (1) prey items were presented to the birds in a fixed order, i.e., the birds could predict which prey type would come next (the CPM's assumption of random prey encounters was violated), (2) predators started to forage after the first prey item was encountered (the CPM's assumption of predator omniscience was violated), and (3) relative prey preferences were tested for (CPM predictions refer to separate preferences for each prey type). To handle regularity in prey-presentation schedules, the authors developed a "non-random-encounter model", which was further elaborated by Rechten et al. (1981).

The aim of this article is to fix these inconsistencies and properly test CPM predictions using an experimental apparatus similar to the one used by Krebs et al. (1977). In addition, we wanted to study the effects of adaptive foraging on the shape of the multiple-prey Holling type II functional response.

Functional responses play an important role in ecology because they link individual behavior with predator-prey population dynamics. In their seminal paper, Murdoch and Oaten (1975) showed that the Holling type II functional response destabilizes predator-prey population dynamics if predation is the only mechanism for regulating exponential prey growth. In environments with alternative resources, the Holling type II functional response may become the Holling type III (sigmoidal) functional response provided that predators attack various prey types disproportionately to their background densities. Such predator behavior makes functional responses superlinear for certain prey densities, which is a necessary condition for stability of predator-prey population dynamics (Murdoch and Oaten 1975). In particular, van Baalen et al. (2001) showed that optimal foraging can lead to a stabilizing functional response if changes in the composition of the predator's diet are gradual. In this article we study whether the observed feeding behavior of great tits has the potential to result in a stabilizing functional response.

Methods

Experimental apparatus

The experimental apparatus (Fig. 1) was designed following the one used by Krebs et al. (1977). The conveyor belt was driven by a motor with four constant speeds. The belt side of the cage was formed by a one-way mirror with a video camera beyond it. The strips above the belt were made from plywood instead of the black Plexiglas used by Krebs et al. (1977). Below these strips was a removable sheet of transparent glass through which the perching bird could see prey items moving on the conveyor belt but could not eat them. During our experiments, the belt speed was set to 8.2 cm/s, which meant that birds could see a prey item for about 1 s as it moved across the 8 cm wide gap. To ensure sequential prey encounters, birds could never see more than one individual prey item at a time.

Predators

As the experimental predators we used five great tits, all of which were wild-caught in February and March 2001. Prior to experiments the birds were housed together in a cage similar to the experimental cage (the only difference was the absence of the conveyor belt). The normal diet consisted of sunflower, flax, and millet seeds mixed with vitamins and minerals (Roboran) and was provided ad libitum. Before the experiments were started, the birds were "trained" to search for prey on the conveyor belt, first at low speeds and then at the speed used in the experiments. This took from 2 days to 2 weeks. After the experiments were finished, the great tits were released at the site of original capture. Animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Prey

Following Krebs et al. (1977), we used two prey types, eight-segment (large, type 1) and four-segment (small, type 2) pieces of mealworm. To increase handling time and make them less profitable for predators, small prey items were partly covered with sticky transparent plastic tape. The birds had to peel off the tape before swallowing the prey item.

Fig. 1. The experimental apparatus. See the text for a detailed description.**Table 1.** Description of the four experimental tests of great tits (*Parus major*).

Test	Rate of encounter with large prey (λ_1 , items per second)	Rate of encounter with small prey (λ_2 , items per second)	Proportion of large prey items, $\lambda_1/(\lambda_1 + \lambda_2)$
A	0.033	0.233	0.124
B	0.133	0.233	0.363
C	0.333	0.233	0.588
D	0.433	0.233	0.650

Experimental procedure

During the experiments the birds were deprived of food from the time they went to sleep until 0930–1000 the next morning. Each day the birds were tested in a different order, and they were given no food until after the last bird had been tested. The birds were thus subjected to an unpredictable period of food deprivation.

The birds were tested at four different rates of encounter with large prey. The rate of encounter with small prey was the same in all experimental tests (Table 1). Individual birds were tested from February to April 2001. Each test lasted 4 weeks, from Monday to Friday every week with breaks during weekends. For bird 2, tests had to be finished earlier because of a breakdown of the conveyor belt. Table 2 shows the tests and the number of replications for individual birds.

Prior to each test replication the bird was transferred to the experimental cage. After habituation, the video camera and the belt motor were switched on and the plywood strips were removed (but not the glass). In almost all cases the birds immediately flew to the perch above the belt. Then

Table 2. Number of test replications for individual birds.

Bird	Test A	Test B	Test C	Test D
1	5	5	5	5
2	2	3	0	5
3	5	5	5	5
4	5	5	5	5
5	4	5	5	3

prey items were continuously put on the moving belt (equidistant prey positions were marked with chalk prior to the start of the experiment) in a computer-generated random sequence (inconsistency 1 resolved). After the bird had seen the first 10 prey items, the glass was removed from the gap in the plywood and the bird could start to forage. The ratio between the numbers of the two prey types in the first 10 prey items (which the bird could see but not eat) was approximately the same as the ratio for the whole session. Thus, the bird could estimate rates of encounter with the two prey types and the ratio between the numbers of the two prey types before it started to forage (inconsistency 2 resolved). This is an important aspect of the underlying theoretical model; unfortunately, it has been largely neglected in most empirical studies, including that of Krebs et al. (1977). The session was terminated when the bird showed any sign of satiation or when the prepared prey items (at least 100 in each case) were exhausted. The video recordings were then processed in the following way: for all test replications and for all prey items, we recorded (i) the type of prey item, (ii) whether or not it was observed by the bird, (iii) whether it was ignored, handled and lost, or handled and swallowed, and (iv) handling time.

Statistical analysis

Central to our data analysis was the “no-selection”, or “always-attack” hypothesis. This null hypothesis states that the number of prey items of a given type which are observed should equal the number of prey items of that type which are actually consumed. We used the classical Student’s *t* test to compare these numbers.

Functional response

The experimental apparatus used in the experiments is very useful for studying the effects of an alternative (less profitable) food source on the predator’s functional response. The shape of the functional response has an important bearing on the stability of predator–prey interactions. Accelerating functional responses (e.g., the Holling type III functional response) are stabilizing, while those that decelerate (e.g., the Holling type II functional response) are destabilizing. For a functional response, *F*, to be stabilizing, the following condition must be satisfied (Murdoch and Oaten 1975):

$$\frac{dF}{d\lambda_1}(\lambda_1) > \frac{F(\lambda_1)}{\lambda_1}$$

Here $dF/d\lambda_1$ stands for the derivative of *F* with respect to λ_1 . Van Baalen et al. (2001) showed that this may happen when the predator’s diet changes gradually with λ_1 and the preference for the less profitable prey type decreases fast enough. Our experimental data are appropriate to test for this condition, since the rate of encounter with the small prey type was the same throughout the tests, and changes in preference for the less profitable prey type were gradual rather than abrupt. The multiple-prey Holling type II functional response to the more profitable prey type (Krivan 1996) is

$$F(\lambda_1) = \frac{\lambda_1 p_1 a_1}{1 + h_1 \lambda_1 p_1 a_1 + h_2 \lambda_2 p_2 a_2}$$

It is a function of the rate of encounter with the more profitable prey type only, as the rate of encounter with the less profitable prey was the same for all birds tested (except bird 5; see Results).

Results

Predator preferences

Proportions of prey taken to those seen are given separately for large and small prey types in Fig. 2. The interpolation assumes that at negligible encounter rates (λ_1), both prey types are included in the predator’s diet. Table 3 presents critical encounter rates (λ_C), handling times (h_i), and probabilities of successfully attacking (a_i) large and small prey types. These data indicate that the critical encounter rates (λ_C) for birds 1, 2, and 3 lie in the range of experimentally used encounter rates (0.033–0.433 prey items/s). According to the CPM, an abrupt change in diet composition should be observed for these three birds at their critical encounter rates. Instead, Figs. 2A–2C show that the decrease in the consumption of less profitable prey is gradual and that this prey type is never excluded from birds’ diet within the range of experimentally used encounter rates. In fact, the proportion of the less profitable prey items taken to those

that a bird saw never decreased below 43%, although the model predicts 0% at high encounter rates (λ_1) (Table 4).

For bird 4 (Fig. 2D) the computed critical value, λ_C , is higher than the highest experimentally used encounter rate, λ_1 . Hence, according to the CPM, this bird should behave as a generalist, attacking each prey item encountered. However, the “always-attack” hypothesis was rejected for this bird and the less profitable prey type in tests B, C, and D (Table 4).

For bird 5, the handling time for large prey was so long compared with the handling time for small prey that the latter became more profitable for this bird ($e_2/h_2 > e_1/h_1$; Table 3). This allowed us to test another CPM prediction: the predator’s diet will not be affected by its rate of encounter with less profitable prey. Figure 3 shows the dependence of the preferences of this bird on the rate of encounter with the less profitable prey type (now prey type 1). As the CPM suggests, these preferences do not depend on the rate of encounter with the less profitable prey type, and both prey types are included in the bird’s diet because the rate of encounter with a small prey item that is more profitable (0.233 cm/s) is lower than the critical encounter rate for this bird ($\lambda_C = 0.652$).

Table 4 summarizes the observed birds’ preferences and the results of testing the “always-attack” (“no-selection”) hypothesis. Note that according to the model predictions, the number of more profitable prey taken will equal the number of more profitable prey seen, the number of less profitable prey taken will equal the number of less profitable prey seen, provided that $\lambda_1 < \lambda_C$, and no less profitable prey will be taken, provided that $\lambda_1 > \lambda_C$. The results show that consumption of the more profitable prey fits the model predictions in 18 out of 19 (94.7%) cases (the only exception is bird 2 in test D, which shows a significant difference ($P < 0.05$) between the numbers of large prey items seen and large prey items taken). For the less profitable prey type, our results correspond qualitatively to CPM predictions in 14 out of 19 (73.7%) cases, while there is a clear discrepancy in 5 cases. In two out of these five cases, birds should be selective if they are obeying the CPM (bird 2 in test B and bird 3 in test D) and in the remaining three cases they should not (bird 4 in tests B, C, and D). Consumption of the less profitable prey type did not differ statistically from the “always-attack” strategy in 10 out of 13 (76.9%) cases when the rate of encounter with the more profitable prey was below a critical value, but did differ from that strategy in 4 out of 6 (66.7%) cases when the encounter rate with the more profitable prey was above that critical value.

Functional response

Figure 4 shows three functional responses for each bird (except bird 5 for which prey type 1 is less profitable). The dotted line shows the functional response of hypothetical non-adaptive generalist predators that feed on every prey item encountered ($p_1 = p_2 = 1$), the dash-dot line shows the functional response of hypothetical non-adaptive predators that specialize on the more profitable prey type only ($p_1 = 1, p_2 = 0$), and the solid line shows the functional response computed from our experimental data (prey preferences p_1 and p_2 were obtained as a piecewise linear approximation of the mean preferences shown in Fig. 2). Handling times and probabilities of successfully attacking prey are given in

Fig. 2. Prey preferences of individual great tits (*Parus major*). Both the proportion of large (solid line) and small (broken line) prey items taken to those seen (mean \pm SE) are depicted. The vertical broken line delimits the critical encounter rate, λ_C . (A) Bird 1. (B) Bird 2. (C) Bird 3. (D) Bird 4.

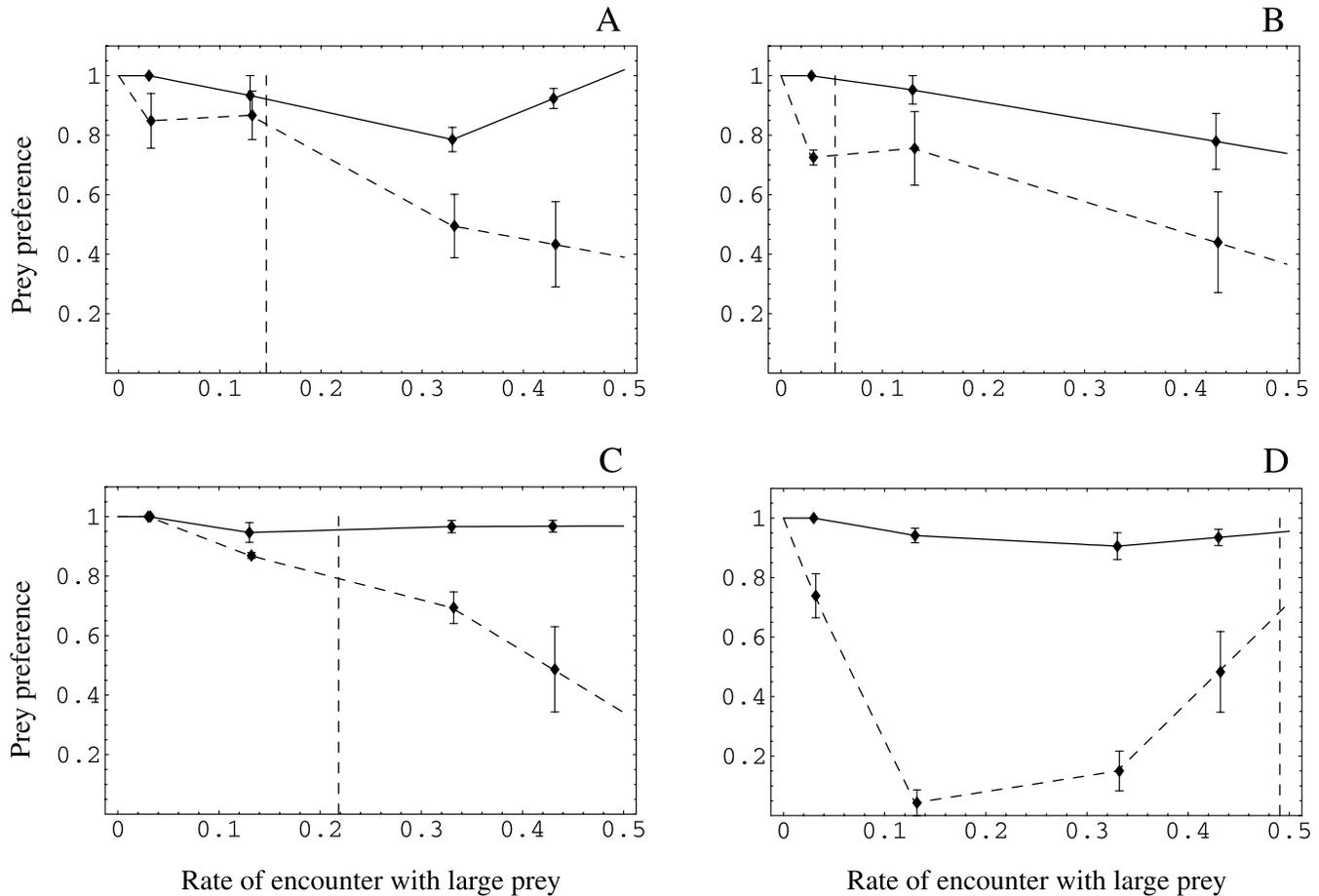


Table 3. Main characteristics of the foraging birds.

Bird No.	λ_C	h_1 (mean \pm SE)	h_2 (mean \pm SE)	a_1	a_2
1	0.146	6.1 \pm 0.28 ($n = 85$)	6.94 \pm 0.44 ($n = 99$)	0.87	0.85
2	0.053	21.36 \pm 1.44 ($n = 43$)	21.07 \pm 2.54 ($n = 25$)	0.9	0.86
3	0.217	9.17 \pm 0.29 ($n = 139$)	7.2 \pm 0.22 ($n = 160$)	0.88	0.89
4	0.487	7.55 \pm 0.36 ($n = 108$)	5.09 \pm 0.35 ($n = 15$)	0.78	0.67
5	0.652	30.44 \pm 2.15 ($n = 40$)	13.53 \pm 0.87 ($n = 77$)	0.85	0.87

Note: λ_C , critical encounter rate; h_i , mean handling time of prey i (in seconds); a_i , mean probability that the attack on prey i was successful (averages are taken over all tests and replications). Large prey: $i = 1$; small prey: $i = 2$; n is the sample size.

Table 3 and encounter rates in Table 1. The vertical broken line in Fig. 4 denotes the critical encounter rate, λ_C (Table 3), for the optimal foragers; the functional response corresponding to the optimally foraging predators ($p_1 = 1$, $p_2 = 1$ if $\lambda_1 < \lambda_C$, and $p_2 = 0$ if $\lambda_1 > \lambda_C$) is then obtained as a composition of the functional response for the generalist predators (dotted line) for encounter rates $\lambda_1 < \lambda_C$ and the functional response for the specialist predators (dash-dot line) for encounter rates $\lambda_1 > \lambda_C$ (van Baalen et al. 2001). We observe that the functional response computed from the observed data lies between the two extreme cases of the non-adaptive predators. To determine whether it satisfies the stability condition (1), we plotted

derivative $\frac{dF}{d\lambda_1}(\lambda_1)$ of this data-based functional response together with $\frac{F(\lambda_1)}{\lambda_1}$ (Fig. 5). Stability requires that the former be above the latter. However, this is never the case and we conclude that the birds change their diet too slowly to make their functional responses stabilizing.

Discussion

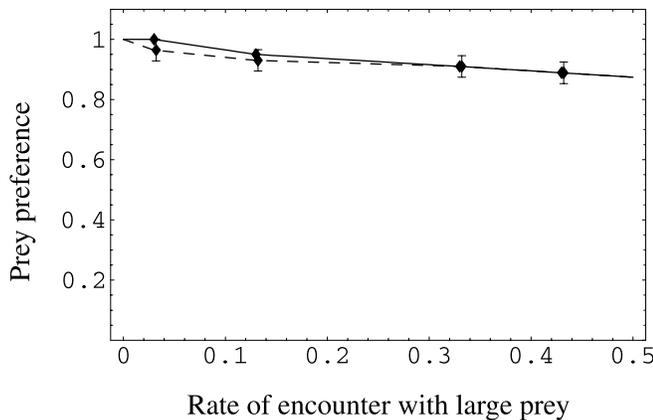
Although a large number of studies aim to test the predictions of optimal-foraging theory, not one seems to have

Table 4. Mean proportions of large and small prey items in the predators' diet and the predicted proportion of small prey items in the diet, for every combination of birds and encounter rates.

Bird and treatment	Percentage of large prey items (mean ± SE)	Percentage of small prey items (mean ± SE)	Predicted percentage of small prey items
Bird 1 in test A	100.0 ± 0	84.8 ± 18.4	100
Bird 2 in test A	100.0 ± 0	72.5 ± 2.5	100
Bird 3 in test A	100.0 ± 0	100.0 ± 0	100
Bird 4 in test A	100.0 ± 0	73.9 ± 14.8	100
Bird 5 in test A	100.0 ± 0	96.4 ± 6.2	100
Bird 1 in test B	93.3 ± 16.3	86.7 ± 13.3	100
Bird 2 in test B	95.2 ± 6.7	75.6 ± 17.5	0
Bird 3 in test B	94.6 ± 6.6	86.9 ± 1.9	100
Bird 4 in test B	94.1 ± 4.8	4.3 ± 8.7**	100
Bird 5 in test B	95.0 ± 10	93.0 ± 8.5	100
Bird 1 in test C	78.5 ± 21.3	49.5 ± 19.5**	0
Bird 3 in test C	96.6 ± 4.1	69.4 ± 10.7*	0
Bird 4 in test C	90.5 ± 9.1	15.0 ± 13.3**	100
Bird 5 in test C	91.0 ± 11.1	91.0 ± 11.1	100
Bird 1 in test D	92.3 ± 28.6	43.3 ± 25.8*	0
Bird 2 in test D	77.9 ± 18.7*	44.0 ± 33.8*	0
Bird 3 in test D	96.8 ± 4	48.7 ± 28.7	0
Bird 4 in test D	93.5 ± 5.4	48.3 ± 27.1**	100
Bird 5 in test D	88.9 ± 15.7	88.9 ± 15.7	100

Note: The percentage is averaged over all tests and replications and computed as the ratio of the number of prey items consumed to the number of prey items observed for each prey type separately. Preferences that conform to the model predictions are in boldface type. Statistical differences from the "no-selection" hypothesis were tested by Student's *t* test: *, *P* < 0.05; **, *P* < 0.01.

Fig. 3. Prey preferences of bird 5. Both the proportion of large (solid line) and small (broken line) prey items taken to those seen (mean ± SE) are depicted. The vertical broken line delimits the critical encounter rate, λ_c . Large prey are less profitable than small prey in this case, owing to long handling times for the former.



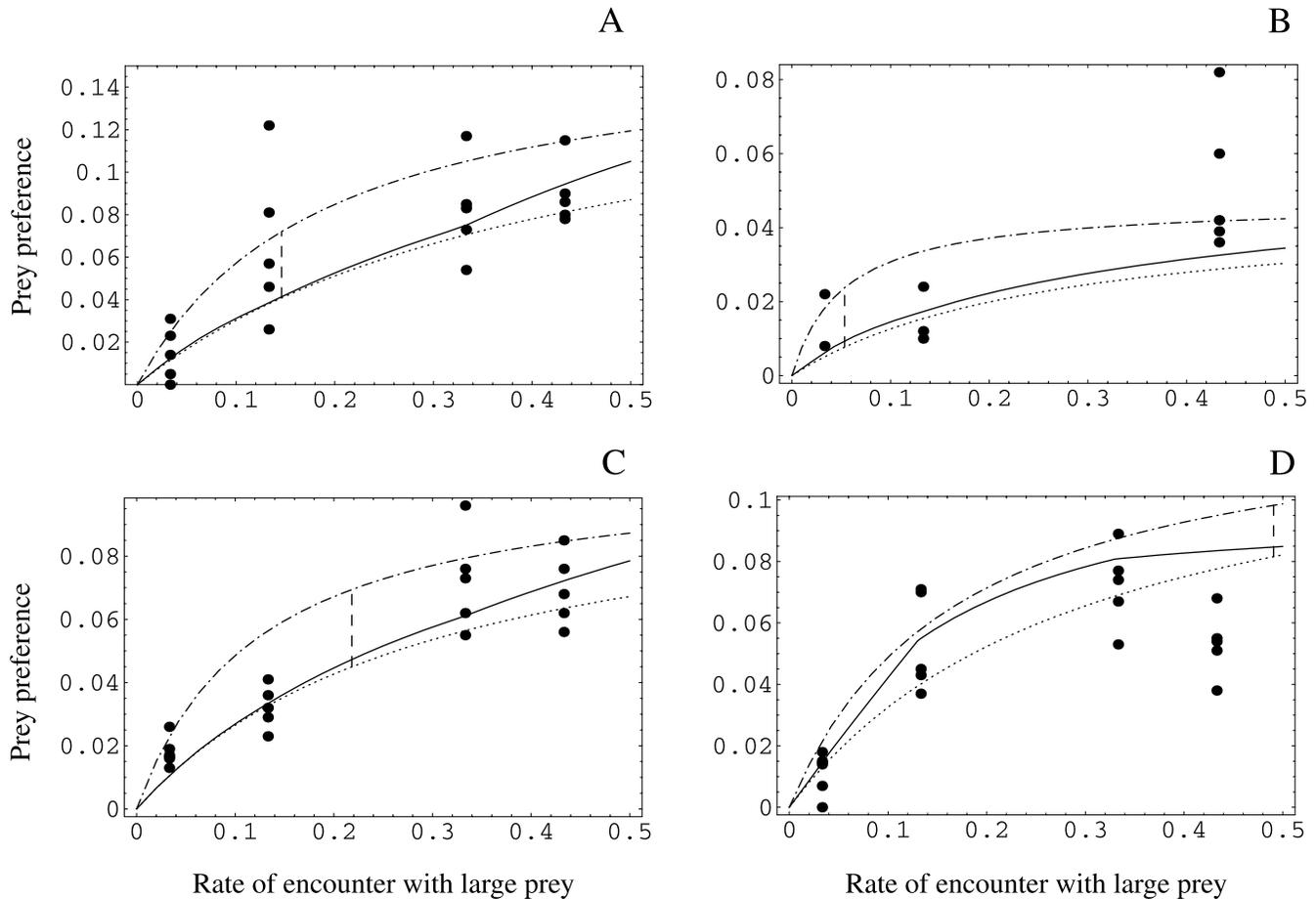
properly tested the predictions of the CPM, one of the simplest models upon which the theory is built. The experimental framework of Krebs et al. (1977) is one of the closest to the assumptions of the CPM, but it still suffers from a number of inconsistencies. In particular, prey items were presented to birds in a predictable order so that the birds could predict which prey type would come next. Also, the birds were given no opportunity to estimate rates of encounter

with prey a priori, and thus to be (more or less) omniscient as the CPM assumes. Last but not least, Krebs et al. (1977) tested for relative prey preferences instead of separate preferences for each prey type, yet the CPM makes predictions about the latter. Despite these inconsistencies and the fact that Krebs et al. (1977) and later also Rechten et al. (1981) modified the CPM to account for nonrandomness in prey encounters, the study of Krebs et al. (1977) is still largely cited as evidence of the validity of the CPM (Krebs and McCleery 1984; Stephens and Krebs 1986; Begon et al. 1990).

We modified the experimental framework of Krebs et al. (1977) in order to handle the above inconsistencies. In particular, we used computer-randomized sequences of prey types, which should have eliminated the effects of the birds' memory and learning (Hughes 1979; Real 1979). Also, we provided birds with an introductory prey sequence during which they could observe a prey item but not eat it. Five birds were subjected to four experimental tests, each consisting of about five replications. Following Charnov (1976) and Krebs et al. (1977), we assumed that birds optimize *R*, the average rate of net energy intake, during foraging. *R* is the most common proxy for animal fitness (for a review see Stephens and Krebs 1986), although some works suggest optimization of other food components, such as size (Barnard and Brown 1981; Hughes and Seed 1981; Jaeger and Barnard 1981), protein-to-fiber ratio (Milton 1979), nutrients (Thompson et al. 1987), or even shape of the prey item (Pulliainen 1986).

In general, our results suggest that great tits showed a

Fig. 4. Functional responses of individual birds. Solid lines depict the functional response based on actual prey preferences. The functional response of a hypothetical non-adaptive generalist predator is marked by a dotted line and that of a hypothetical non-adaptive specialist predator by a dash-dot line. The functional response of the optimally foraging predator coincides with that of a generalist predator below the critical value, λ_C (marked by a segment of the vertical broken line), and that for a specialist predator above the critical value (there is a gap in the functional response of predators that behave optimally). (A) Bird 1. (B) Bird 2. (C) Bird 3. (D) Bird 4.



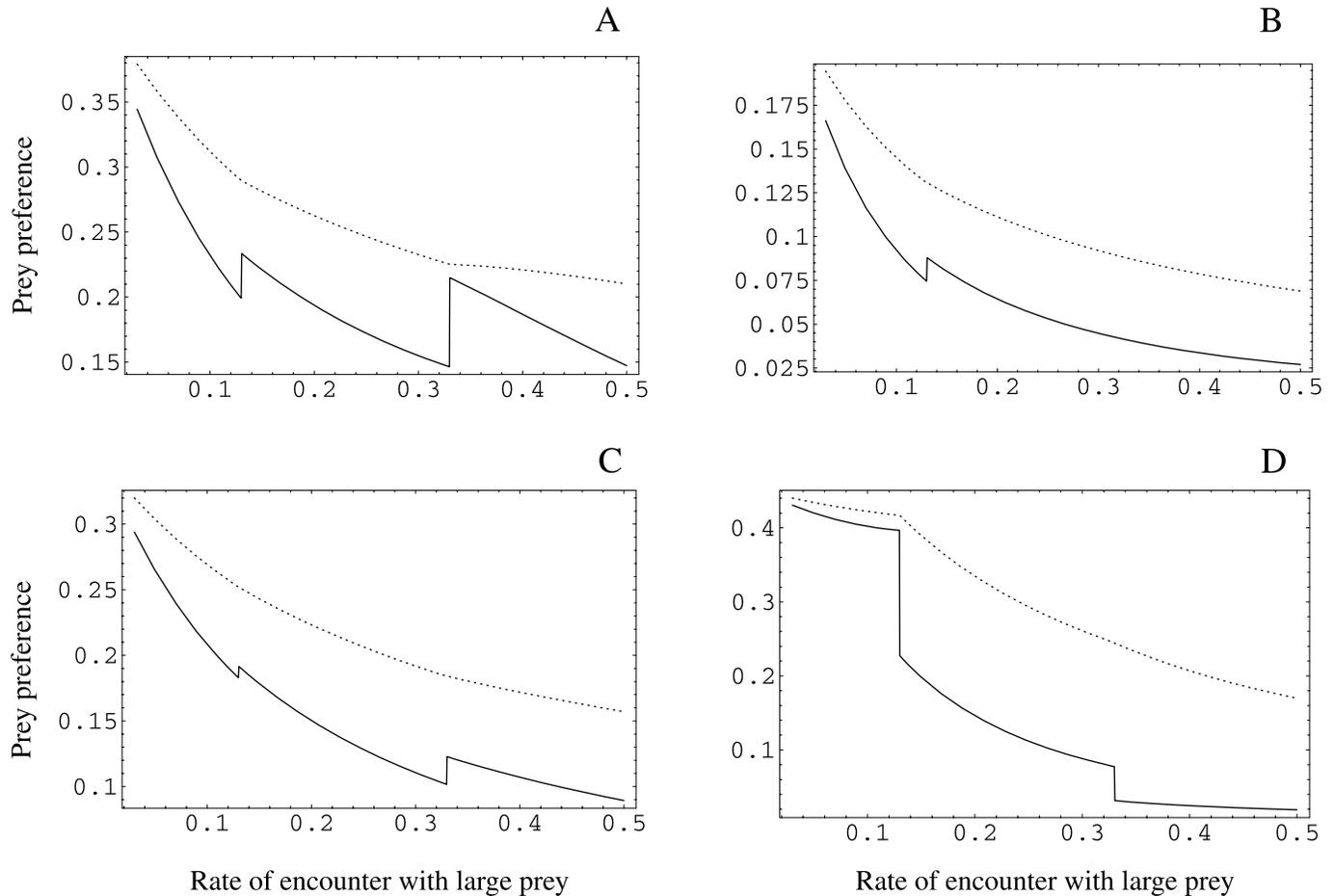
strong preference for the more profitable prey type, their diet changed gradually and slowly with the rate of encounter with the more profitable prey type, the less profitable prey was not excluded from the birds' diet even at high rates of encounter with more profitable prey, and the birds' preferences did not seem to depend on the rate of encounter with the less profitable prey type. Because the diet change was too slow, it did not transform the multiple-prey Holling type II functional response into a sigmoidal and thus stabilizing form.

As Krebs et al. (1977) evaluated and tested relative prey preferences instead of separate preferences for each prey type, no direct comparison of their results with our own is possible. The observation that nearly all birds followed the prediction that the more profitable prey type will always be included in their diet, irrespective of the rate of encounter with this prey type, is consistent with the observations of Houston et al. (1980) and Rechten et al. (1983). Preferences for the less profitable prey type were much less consistent with the CPM. When data for all tested birds were pooled, however, at least a qualitative agreement was obtained: as the encounter rate with the more profitable prey increased, birds seemed to be more selective with respect to the less profitable prey type. On the other hand, average preferences

for the less profitable prey type never fell below 43% at high rates of encounter with the more profitable prey type (here the CPM predicts 0% preference). This is a striking difference from the observations of Krebs et al. (1977) and treatment A of Houston et al. (1980), where in many cases the less profitable prey type was completely or nearly completely excluded from the predator's diet. The difference probably results from the elimination of the effect of memory in our experimental setup. Because of the regularity with which prey items were presented in the experiments of Krebs et al. (1977) and Rechten et al. (1983), their birds could remember the order of individual prey types in a relatively short time (one of Krebs et al.'s (1977) cycles consisted of four prey items at most, while that used by Rechten et al. (1983) consisted of only two prey items). In contrast, no regular pattern of prey presentation was used in our experiments, and the birds could only estimate the ratio between prey types presented, never the exact position of each prey item (our cycle involved about 100 prey items, though this number was reached only occasionally in the test replications).

The type of behavior in which some but not all prey items that are encountered are attacked is called partial preferences, and many mechanisms have been proposed to explain

Fig. 5. Graphical representation of the condition (1) under which the data-based functional response is stabilizing. For a functional response to be stabilizing, the solid line ($\frac{dF}{d\lambda_1}(\lambda_1)$) must lie above the dotted line ($\frac{F(\lambda_1)}{\lambda_1}$). (A) Bird 1. (B) Bird 2. (C) Bird 3. (D) Bird 4.



it (McNamara and Houston 1987). Both Krebs et al. (1977) and Rechten et al. (1983) found that partial preferences occurred regularly in their experiments, and suggested misidentification of prey items or sampling of presentation schedules as possible sources. In addition, Rechten et al. (1983) found differences in such preferences between hungry and satiated birds. In their experiments, hungry birds followed predictions of energetic efficiency more closely than partially satiated ones did. Unfortunately, this result is hardly comparable with our findings because Rechten et al. (1983) also used regular sequences of prey items.

Bird 4 clearly specialized on the more profitable prey type despite the fact that all four experimental rates of encounter with that prey were below the predicted critical value. In some test replications the bird completely ignored items of the small prey type. This behavior is inconsistent with CPM predictions. Houston et al. (1980) observed similar behavior: three birds showed absolute preferences for the more profitable prey type and two others were close to absolute preferences, although those authors were logically not able to evaluate rates of encounter with prey at the start of the foraging experiment. This sort of behavior could be due to a bad estimate of the rate of encounter with large prey, search image (Lawrence 1986; Guilford and Dawkins 1989), long-term memory (higher rates of encounter with the more profit-

able prey presented in training sessions), or an insufficient period of food deprivation, which did not force the bird to optimize its R . We can probably reject the bad-estimate hypothesis: the introductory sequence from which all birds could assess rates of encounter with both prey types prior to the start of foraging should lead to a lower variance in estimated encounter rates. However, we are short of data that would allow us to discern between the other suggested hypotheses.

Bird 5 showed unexpectedly long handling times for large prey, and this resulted in reversed prey profitabilities. This allowed us to test whether the birds' preferences depended on the rate of encounter with the less profitable prey. We observed no dependence, which is consistent with CPM predictions; an analogous observation was also made by Krebs et al. (1977), Erichsen et al. (1980), Barnard and Brown (1981), and Jaeger and Barnard (1981).

Direct measurement of functional responses necessitates keeping prey density at a constant level. Experimentally, this means that prey must be replaced as soon as they are captured by predators. Thus, the experimental setup with a moving conveyor belt is a perfect apparatus for estimating functional responses because the assumption of fixed prey density is automatically satisfied. Consequently, our data allowed us to estimate a functional response for all birds except bird 5. As the

theory suggests, the shape of the functional response has an important bearing on the stability of predator–prey interactions. Accelerating functional responses (e.g., the Holling type III functional response) are stabilizing, while those that decelerate (e.g., the Holling type II functional response) are destabilizing (Murdoch and Oaten 1975). Van Baalen et al. (2001) showed that a functional response can be stabilizing for adaptive foragers provided that they change their diet gradually and their preference for the less profitable prey type decreases fast enough. We could see that the stability condition was never fulfilled by our experimental birds, and we conclude that their diet changes were too slow to make the functional response stabilizing.

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