PROFITABILITY, RATE MAXIMIZATION, AND REWARD DELAY: A TEST OF THE SIMULTANEOUS-ENCOUNTER MODEL OF PREY CHOICE WITH *PARUS ATRICAPILLUS*

CHRISTOPHER P. L. BARKAN AND MATTHEW L. WITHIAM*

Behavioral Ecology Group, Department of Biological Sciences, State University of New York, Albany, New York 12222

The specific assumptions of a model have a crucial impact on the predictions derived from it. A case in point is the model of diet choice developed by MacArthur and Pianka (1966), in which they assumed that a forager encountered prey sequentially. As originally formulated, this model could not be used to predict the optimal strategy if more than a single prey type was encountered at one time. Recently, several authors attempted to generalize the optimal-diet model by relaxing this assumption of sequential encounter of prey (Waddington and Holden 1979; Engen and Stenseth 1984; Stephens et al. 1986). Waddington and Holden modeled the special case in which search time is zero; as soon as the predator finishes one prey, it detects the next set of prey available. In this situation the rate-maximizing strategy is always to choose the most profitable available prey (in terms of energy per handling time).

The models of Engen and Stenseth and of Stephens et al. are more general and more complex. They show that incorporating variable search times can lead to predictions different from those of Waddington and Holden's model or the classical optimal-diet model. Their generalized simultaneous-encounter models predict that under some conditions a predator trying to maximize its overall energy-intake rate should specialize on prey types other than the most profitable. A particularly interesting facet of these models is that they suggest a means of distinguishing between two possible currencies of energy maximization: one for the short term (profitability) and one for the long term (energy per total time foraging). Under some conditions these models predict that a predator attempting to maximize its long-term energy-intake rate will *not* maximize its short-term rate; this prediction is in distinct contrast to that of the sequential-encounter version of the optimal-diet model. Thus, a test of the generalized simultaneous-encounter models allows us to determine which of these two currencies is driving the predator's choice of

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* Present addresses: C.P.L.B., Environmental and Hazardous Materials Division, Research and Test Department, Association of American Railroads, 50 F Street NW, Washington, D.C. 20001; M.L.W., School of Medicine and Biomedical Sciences, 40 CFS Building, State University of New York, Buffalo, New York 14214.

foraging strategy. This was not possible in experiments designed to test the classical optimal-diet model. For an item to be included in the diet, the sequential-encounter model required that the short-term rate (profitability) of a less preferred prey be greater than the long-term rate that the forager expected to achieve if it specialized on the more preferred prey. A predator maximizing long-term intake rate was always predicted to behave so as to maximize short-term rate as well.

We conducted two experiments to test the predictions of the generalized simultaneous-encounter model in black-capped chickadees (*Parus atricapillus*, Paridae). In experiment I, we directly tested the predictions of the simultaneous-encounter models. In experiment II, we attempted to distinguish between alternative hypotheses regarding the proximate cause of the chickadees' choice behavior observed in experiment I.

TIME, ENERGY, AND PROFITABILITY

Optimality models of foraging behavior are crucially dependent on precise definitions of the terminology. We define each component of the time and energy values as follows:

s_i search time, the interval from the time of completion of ingestion of the preceding prey to the encounter with its next potential type-i prey; assuming continuous foraging, the encounter rate with prey-type i is $\lambda_i = 1/s_i$;

h_i handling time, the interval from the time of encounter with a type-i prey until completion of ingestion of that prey; handling time comprises two components, pursuit time and ingestion time ($h_i = p_i + c_i$);

p_i pursuit time, the interval from the time of encounter until the beginning of ingestion of type-i prey;

c_i ingestion time, the interval required to ingest type-i prey;

t_i total time, the total amount of time required to search for and handle a type-i prey ($t_i = s_i + h_i$);

e_i energy content of type-i prey;

e_i/h_i profitability, energy content of a type-i prey divided by its handling time.

In order to test this simple version of the model, we had to meet the following assumptions: (1) prey are always encountered in pairs; (2) a prey item not chosen first in a simultaneous encounter is lost by the predator (e.g., it escapes or is taken by a competitor); (3) searching for prey and handling prey are mutually exclusive activities; and (4) the energetic cost per unit of time is approximately equal for each component of the predator's foraging behavior.

THEORY

The generalized simultaneous-encounter model predicts that when type-1 prey has both a higher profitability and a higher energy content than type 2 ($e_1/h_1 > e_2/h_2$ and $e_1 > e_2$) the forager should always prefer the type-1 prey (fig. 1A). The most interesting prediction made by Engen and Stenseth (1984) and by Stephens et al.
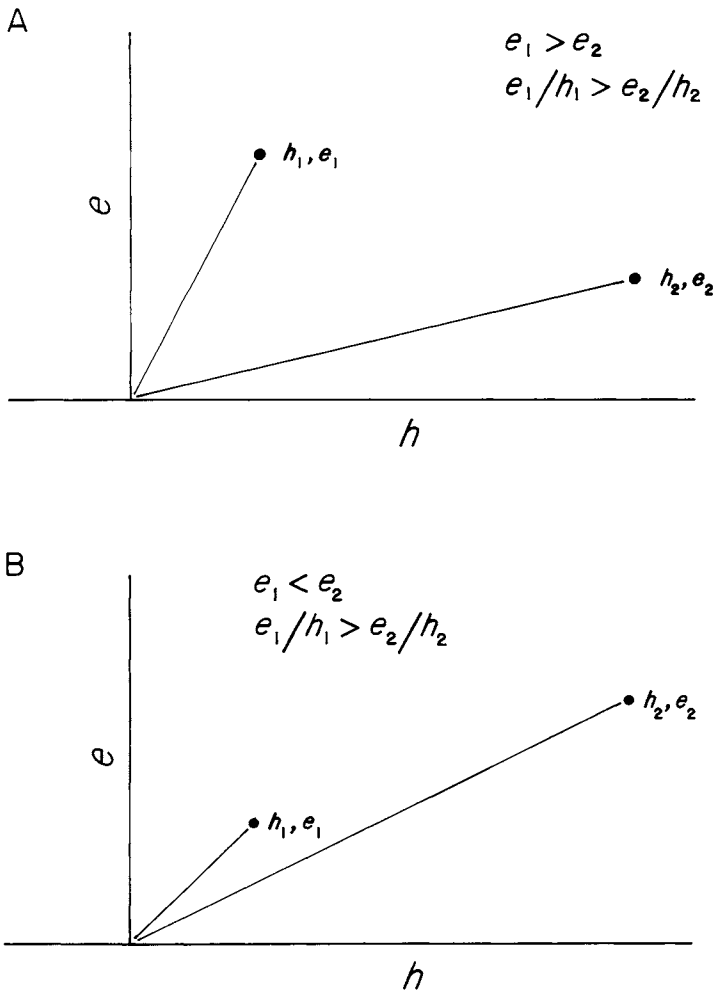
A

$e_1 > e_2$

$e_1/h_1 > e_2/h_2$

$\bullet\ h_1, e_1$

$\bullet\ h_2, e_2$

e

h

B

$e_1 < e_2$

$e_1/h_1 > e_2/h_2$

$\bullet\ h_2, e_2$

$\bullet\ h_1, e_1$

e

h

Fig. 1.—Graphic portrayal of hypothetical prey types 1 and 2. h_i, Handling time of type-i prey; e_i, energy content of type-i prey; the slopes indicate the profitability (e_i/h_i) of each prey type. A, Both energy content and profitability of type-1 prey are greater than for type-2 prey. B, Energy content of type-1 prey is less than for type 2, but profitability is greater.

(1986) arises when this is not the case, that is, when the profitability of type-1 prey exceeds that of type 2 but its energy content is less than that of type 2 ($e_1/h_1 > e_2/h_2$ and $e_1 < e_2$) (fig. 1B). The predator obtains more total energy from type-2 prey, but (by definition) the handling time required per unit of energy is greater for type-2 than for type-1 prey. When a predator simultaneously encounters prey with these characteristics, the optimal response depends on search time (s). For a predator trying to maximize its overall rate of energy intake (e/t), the average duration of search (s) determines whether it should specialize on the type-1 or type-2 prey. Note that this prediction is strikingly different from that of the classical diet

model, which predicts either specialization on the more profitable prey or generalization on both types, but never specialization on the less profitable prey type (Stephens and Krebs 1986).

A graphic model of how search time (s) affects long-term energy-intake rate when two prey types are encountered simultaneously is portrayed in figure 2. The dashed lines are the long-term rate of energy intake, which for a predator specializing on type-i prey is simply $e_i/(s_i + h_i)$, or e_i/t_i. The predator is predicted to choose prey so as to maximize the slope of the dashed lines in these figures. When the search is short, e_1/t_1 is greater than e_2/t_2 and the long-term rate-maximizing solution is to specialize on type-1 prey (fig. 2A). When the search is long, e_2/t_2 exceeds e_1/t_1 and the long-term rate-maximizing predator is now predicted to specialize on the type-2 prey (fig. 2B).

Since the predicted preferences change as a function of search time (s), it follows that there must be some critical value for s when this change in preference is predicted to occur. Intuitively, we might expect the change to occur at the search time when taking either prey type yields the same long-term rate of e/t, and indeed Stephens et al. (1986) showed this to be the case. A line drawn through the two points describing prey of types 1 and 2 (fig. 2C, *dashed line*) intersects the search (s) axis at the point where selecting either prey type results in the same intake rate. We designate this point of intersection, the critical value for search time, as s_{crit}, which equals $1/\lambda_C$ from Stephens et al. (1986), who expressed it mathematically:

$$s_{crit} = (e_1 h_2 - e_2 h_1)/(e_2 - e_1) . \tag{1}$$

The prediction is that for search times shorter than s_{crit}, the long-term rate-maximizing predator will specialize on type-1 prey, whereas for search times longer than s_{crit}, it will specialize on type-2 prey.

METHODS

We tested this generalized simultaneous-encounter model in two experiments on four captive black-capped chickadees. The birds were housed individually in chambers 49 × 58 × 66 cm and kept at a photoperiod of 10 h light and 14 h dark. Each chamber had a window with one-way glass allowing an observer to watch the bird without disturbing it. Before the experiments, sunflower seed fragments and mealworms were provided ad libitum. The food consumption and body weight of each bird was monitored daily. During an experiment, the chickadees were on a somewhat "open economy" (Hursh 1980). Each bird received a ration of food proportional to the time the bird was not in the test situation. Because a test usually lasted approximately 2 h, the post-test ration was approximately 80% of the individual bird's normal daily ration. This procedure ensured that the food ingested during the test represented an important part of the bird's total daily intake. At all times, the birds had access to water ad libitum, and they regularly received a general vitamin supplement.

One of the chickadee's natural foraging modes is to peck and probe at cracks and crevices in the bark of tree limbs searching for small invertebrates or cached
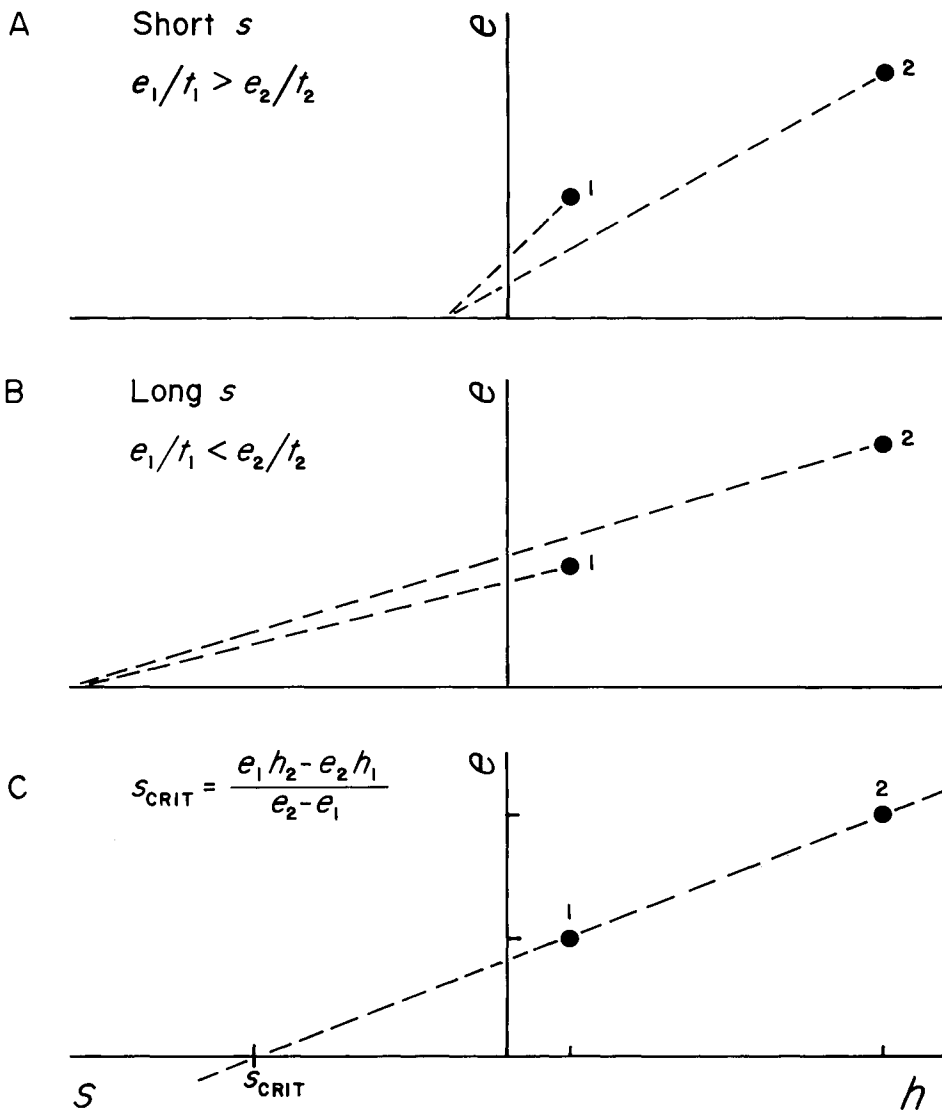
A   Short s

$e_1/t_1 > e_2/t_2$

B   Long s

$e_1/t_1 < e_2/t_2$

C $s_{CRIT} = \dfrac{e_1 h_2 - e_2 h_1}{e_2 - e_1}$

S s_{CRIT} h

FIG. 2.—Long-term energy-intake rates (e/t) for a forager specializing on different simultaneously encountered prey types as a function of search time. s, Search time (interval between encounters); h_i and e_i as in figure 1; t_i, total foraging-cycle duration of type-i prey ($t_i = s_i + h_i$). The slope of the dashed lines indicates e/t when the predator is specializing on each prey type. A, A comparison of e/t's for the two prey types when search time is short; B, a similar comparison when search time is long. C, Graphic method of calculating the critical search time; the point of intersection of the dashed line with the abscissa is s_{crit} (from Stephens et al. 1986).
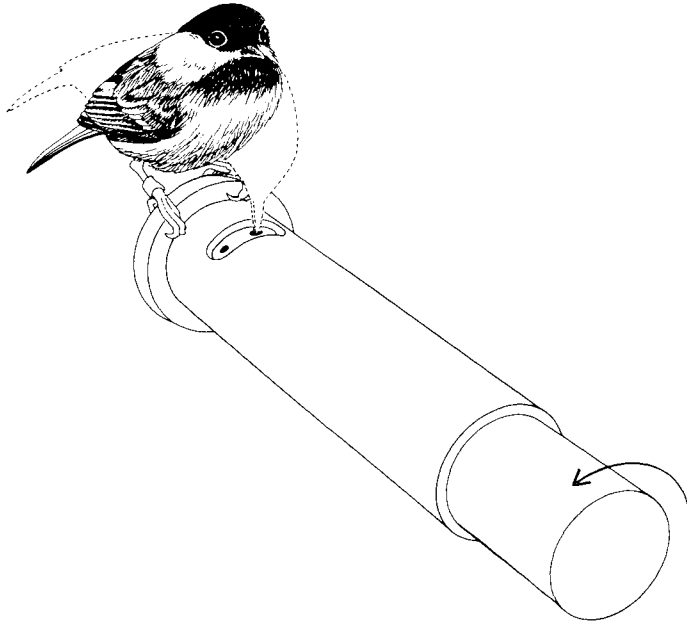
FIG. 3.—Chickadee using the experimental feeder. As depicted here, the bird has chosen the prey on its left and the observer is about to rotate the dowel counterclockwise (as indicated by the arrow), centering the chosen prey in the opening of the pipe and hiding the other prey from view.

seeds. We designed a system that mimicked the natural foraging context of chickadees and allowed us to conduct simultaneous-encounter, exclusive-choice tests. The test chamber was identical to the living chambers except that it had a metal pipe 2.5 cm in diameter, projecting horizontally through the window approximately 10 cm into the chamber (fig. 3). Near the end of the upper side of the pipe was an oblong opening (about 1.5 × 0.6 cm) perpendicular to the axis of the pipe. The chickadees were trained to perch on the end of the pipe and obtain prey through the opening. The "prey" were ground sunflower seed fragments sifted to a standard size, placed in holes drilled in wooden dowels 2.5 cm in diameter, covered with one or more layers of opaque tape, and marked with a colored dot. The dowels were inserted into the pipe from outside the chamber. Each dowel had four pairs of holes spaced at 90° intervals around one end. When the dowels were fully inserted, a pair of these colored dots was visible through the opening in the pipe. The chickadee indicated its choice by pecking at one of the two dots, and the observer then rotated the dowel until the chosen prey was centered in the opening. The other prey was then blocked from view behind the wall of the pipe, thereby ensuring exclusivity of choice.

To test the simultaneous-encounter model, it was necessary to control the three prey characteristics for each prey-type i: energetic value (e_i), handling time (h_i), and encounter rate ($1/s_i$). Prey size was controlled by varying the number of seed fragments placed in each hole, handling time was controlled by varying the

thickness of the tape covering the hole, and encounter rate was controlled by varying the interval between dowel insertions. Differently colored dots over each hole were used as cues to denote prey type.

In experiment I the type-1 prey always had 2 seeds per hole and a single layer of masking tape. Throughout the tests with the first bird, LW, the type-2 prey had 3 seeds per hole and a double layer of masking tape. To ensure a substantial difference in the quality of the two prey types, all of the other birds were tested with type-2 prey with 4 seeds per hole and a double layer of masking tape. These characteristics resulted in simultaneous encounters of prey with the properties illustrated in figure 1B. In experiment II, all four birds were given type-1 prey with 2 seeds per hole and a single layer of masking tape plus a single layer of adhesive cellophane tape (Scotch Brand Magic Tape) and type-2 prey with 16 seeds per hole and a double layer of masking tape. This resulted in prey with the relative characteristics illustrated in figure 1A.

<center>DATA COLLECTION</center>

<center>*Training Tests*</center>

Before the experimental preference tests, the chickadees were trained to use the choice apparatus. Each day the birds were deprived of food for 1 h and then given 40 forced-choice training trials in which the birds were given 20 of each prey type alternately. The bird pecked at the dot marking the hole until it broke through the tape, extracted the seed fragments therein, and ingested them. When the bird finished, it either left the perch or engaged in some activity other than feeding, and the dowel was removed from the pipe. Together, these 40 trials constituted a "test."

Several events were recorded in each foraging-choice cycle: (1) Choice, the time when the bird first pecked at one or the other prey; (2) First seed, the time when the bird obtained its first seed fragment from under the tape; (3) Seeds, the time when each subsequent seed was obtained; and (4) Done, the time when the bird finished eating and the dowel was removed. An observer using an event-recording program on a Radio Shack Model 100 portable computer recorded the time (to the nearest second) when each of these events occurred, as well as the prey type chosen. The event-recording program also included a timer, which began when the Done key was depressed. After a fixed interval, the computer signaled the observer when the next prey choice was to be given to the bird. The duration of this interval was set at the beginning of each run and allowed the observer to control the chickadee's encounter rate with a fair degree of accuracy. Search time and handling time were mutually exclusive using this protocol.

The data were analyzed to determine the average interval between each of the above events for each bird using both prey types. The most important of these was handling time (h_i), which was defined as the interval from Choice until Done. Also important was pursuit time (p_i), which we termed "pecking time"; this was defined as the interval from Choice until First seed. The chickadees were given forced-choice tests until their behavior with regard to handling time and the

other parameters approached an asymptote. Asymptotic behavior was defined as a 3-day sequence of 40 trials per day, during which the bird's performance remained relatively static.

Choice Tests

The choice tests were conducted using the same protocol as the training tests except that instead of 20 forced choices of each prey, the chickadees were allowed to choose spontaneously between the two prey types 40 times. The data on handling time and prey size (number of seed fragments taken) from the last three training tests and the choice tests were combined, and the mean values were used in equation (1) to estimate each bird's s_{crit}. Each bird's prey preferences were tested using search times (s) less than and greater than that individual's estimated s_{crit}. Each bird was tested at least once at four different encounter rates. The color cues were then reversed and the birds were retested at the same four rates, thereby providing a control for color bias. The data for the first day of exposure to a new association of color cue and prey type were not included in the analyses of preferences because they included a certain amount of sampling as the bird learned the new cues. We controlled for a position bias within each test by alternating the sides on which the two prey types were found. The sequence of the different encounter rates was arbitrary except that the first test of each association of color cue and prey type was always conducted at one of the two lowest encounter rates (search time of 90 or 120 s). This meant that the first exposure to each association occurred under conditions favoring a preference for the larger but less profitable type-2 prey. We used the binomial test (Siegel 1956) with a null hypothesis of indifference to determine if the birds demonstrated a significant preference ($\alpha = 0.05$) for either prey type in each day's choice test.

The design of experiment II used the same apparatus and basic protocol as experiment I. Each bird was given approximately 30 trials, which together made up a single day's choice test. The birds were tested twice for each association of color cue and prey type; the color cues were then reversed, and the tests were repeated for a total of four choice tests per bird (five for chickadee LW). As in experiment I, the data from the first day of exposure to a new association were not included in the analyses to reduce the effect of sampling on our measure of the chickadees' preferences.

RESULTS

Training Trials

All the chickadees showed strong consistent differences in several foraging parameters, especially handling time (h) and pursuit time (p) (tables 1, 2). Since the type-2 prey were twice as large (50% larger in the case of LW) and on the average took 3.9 times as long to handle (2.7 times for LW), they were about one-half as profitable as the type-1 prey. The data on handling time (h_i) and prey size (e_i) allowed us to calculate each individual chickadee's hypothetical long-term rate of intake (e_i/t_i) if it specialized on either prey type as a function of search time

TABLE 1

s_{crit}, Handling Time (h), and the Number of Seeds Obtained Using Type-1 and Type-2 Prey

Bird	s_{crit}	Prey Type	h*	Seeds*	N†
LW	28.6	1	12.32 ± 0.44	2.00 ± 0.04	275
		2	32.97 ± 3.23	3.01 ± 0.12	96
YB	15.7	1	10.02 ± 0.38	1.91 ± 0.04	360
		2	35.48 ± 2.70	3.80 ± 0.16	91
L	20.8	1	9.29 ± 0.37	1.94 ± 0.04	296
		2	36.89 ± 3.23	3.72 ± 0.25	71
GB	20.7	1	8.90 ± 0.38	1.93 ± 0.04	392
		2	37.24 ± 2.59	3.78 ± 0.13	158
$\bar{x}$		1	10.13 ± 1.53	1.95 ± 0.04	4
		2	36.54 ± 1.08	3.77 ± 0.05	3

* Values are the means ± 2 standard errors.
† N, The combined number of each prey type taken during both training and choice tests.

TABLE 2

Pursuit Time (p) and Profitability (e/h) of Prey Types 1 and 2 in Experiment I

Bird	Prey	p*	e/h*	N†
LW	1	3.93 ± 0.25	0.176 ± 0.006	275
	2	16.20 ± 2.11	0.111 ± 0.008	96
YB	1	4.79 ± 0.28	0.213 ± 0.008	360
	2	21.49 ± 2.16	0.127 ± 0.010	91
L	1	4.37 ± 0.27	0.248 ± 0.019	297
	2	21.65 ± 2.61	0.115 ± 0.013	71
GB	1	3.93 ± 0.30	0.246 ± 0.009	392
	2	20.49 ± 2.05	0.119 ± 0.009	158
$\bar{x}$	1	4.26 ± 0.41	0.221 ± 0.034	4
	2	21.21 ± 0.73	0.120 ± 0.007	3

* Values are the means ± 2 standard errors.
† N, The combined number of each prey type taken during both training and choice tests.

(s) (fig. 4). As expected, when search (s) was short, long-term rate (e/t) was higher if the chickadee specialized on the type-1 prey. With longer search time, long-term rate (e_1/t_1) declines until at s_{crit} the lines intersect, and for search times greater than s_{crit}, e_2/t_2 is higher. If the chickadees were maximizing long-term rate (e/t), as generally assumed in most foraging-behavior models, they should switch from specializing on type-1 prey to specializing on type-2 prey as search (s) increased from less than s_{crit} to greater than s_{crit}.

CHOICE TESTS

Experiment I

The development of the chickadees' preferences was usually fairly rapid. On the first day of exposure to a new association of color cue and prey type, the
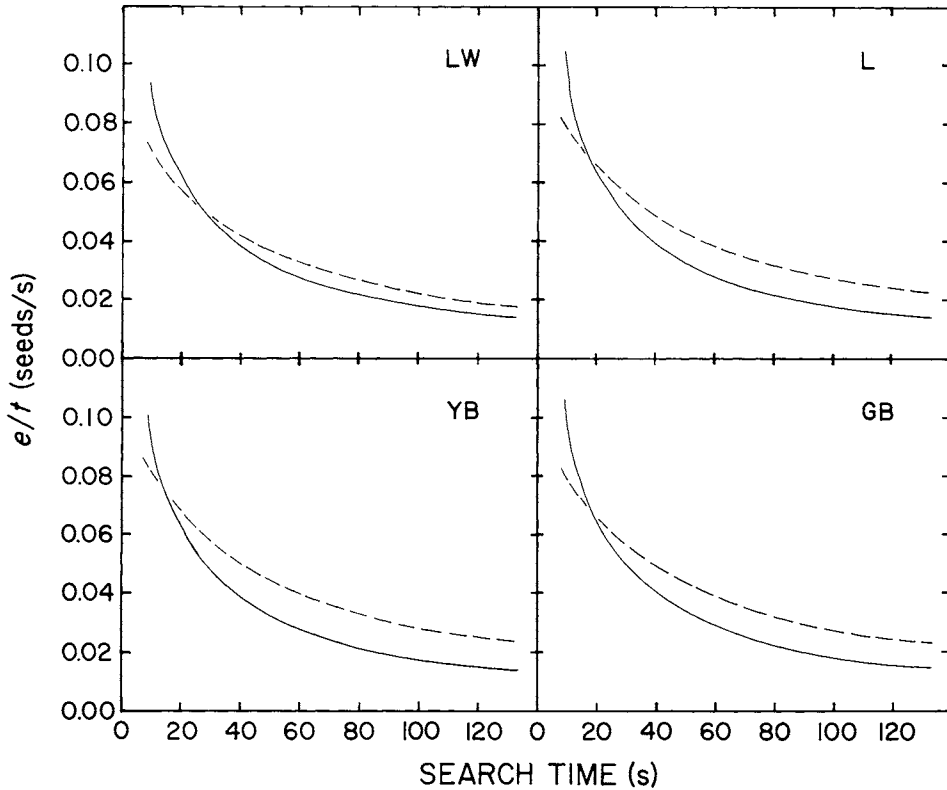
Fig. 4.—The estimated long-term intake rates (e/t), as a function of search time, of four black-capped chickadees when specializing on smaller, more profitable prey (*solid lines*) versus the larger, less profitable prey (*dashed lines*). These functions are calculated using each individual chickadee's achieved seed intake and handling-time values during the pre-experimental and experimental periods. The two lines intersect at each individual chickadee's s_{crit}.

chickadees generally sampled each type about 10 times and then began to show a preference. The data for these initial tests are not included in figure 5; however, even on these days the preference by the end of the test was often significant.

The four chickadees' preferences for the two prey types as a function of the difference between s and each bird's s_{crit} are shown in figure 5. The dashed line indicates the birds' predicted preference according to the generalized simultaneous-encounter model. The points are the chickadees' actual preferences expressed as a proportion of their total choices. When $s - s_{crit} < 0$, the birds were predicted to specialize on type-1 prey; and when $s - s_{crit} > 0$, they were expected to specialize on type 2. It is evident that their behavior did not agree with the prediction of the generalized simultaneous-encounter model. The chickadees showed a strong, consistent, and significant preference for the type-1 prey, regardless of search time.
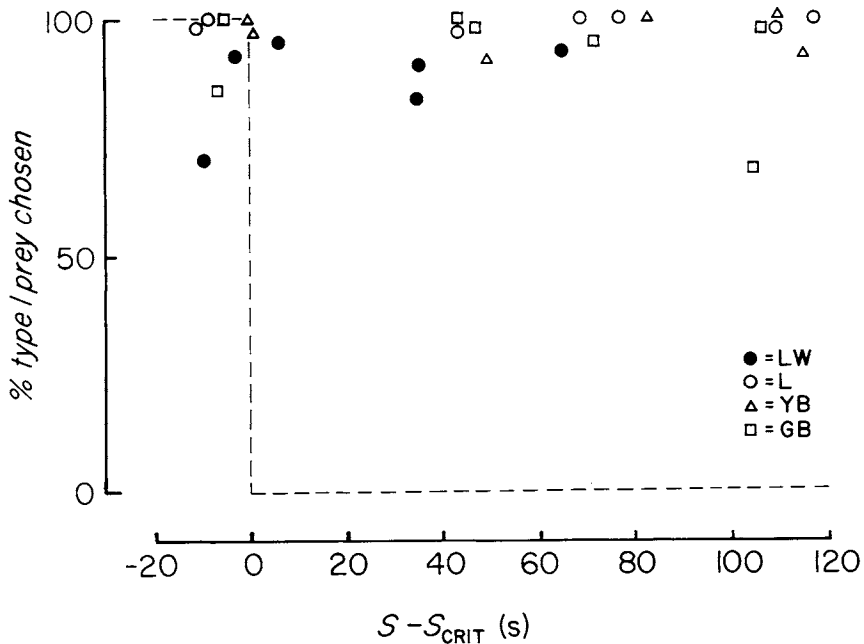
Fig. 5.—The percentage of type-1 prey taken by four chickadees as a function of the observed search time minus s_{crit}. Each point represents the results of one choice test comprising 40 trials. *Dashed line*, The predicted preferences according to the generalized simultaneous-encounter model.

The results of experiment I were inconsistent with the hypothesis that the chickadees were foraging so as to maximize long-term rate (e/t). For instance, examination of figure 4 indicates that by choosing the type-1 prey at a search time of 120 s, chickadees L, YB, and GB suffered an approximately 40%–50% reduction in long-term rate compared with their rate had they chosen the type-2 prey. However, we still had some doubt regarding the proximate factor affecting the birds' foraging choice. Two hypotheses could explain their behavior. The birds consistently chose higher profitability. In so doing, however, they pecked through only a single layer of tape; hence, pursuit time (p), the interval between choice and reward, was shorter for the type-1 prey than for type 2 (table 2). Thus, the chickadees might have been choosing to maximize profitability or to minimize pursuit time (Fantino and Abarca 1985). In order to distinguish between these two hypotheses, we conducted a second experiment on the same four chickadees.

Experiment II

In this experiment, we wanted to come as close as possible to reversing the profitabilities of the two prey types while maintaining the same relative differences in reward delay. The number of seed fragments for the type-2 prey (double-thickness masking tape) was increased to 16 and the handling time of the type-1 prey was increased approximately 60% by adding a single layer of cellophane tape

TABLE 3

Pursuit Time (p) and Profitability (e/h) of Prey Types 1 and 2 in Experiment II

Bird	Prey	p^*	e/h^*	N†
LW	1	9.49 ± 1.55	0.127 ± 0.015	59
	2	26.33 ± 2.73	0.224 ± 0.011	125
YB	1	12.02 ± 2.00	0.120 ± 0.014	49
	2	33.91 ± 3.04	0.241 ± 0.012	130
L	1	8.27 ± 1.24	0.155 ± 0.016	64
	2	18.50 ± 1.56	0.257 ± 0.011	140
GB	1	7.44 ± 2.01	0.152 ± 0.019	43
	2	12.78 ± 1.36	0.334 ± 0.015	140
$\bar{x}$	1	9.30 ± 2.00	0.139 ± 0.018	4
	2	22.88 ± 9.21	0.264 ± 0.049	4

* Values are the means ± 2 standard errors.
† N, The combined number of each prey type taken during both training and choice tests.

over the masking tape. The type-2 prey were then larger and more profitable than type 1, but they still had a p almost 2.5 times that of the type-1 prey (table 3). The chickadees could choose type 2, maximizing their profitability, or type 1, minimizing their pursuit time (p). Note that the results of this test do not have a direct bearing on the simultaneous-encounter model because the relative characteristics of these prey were illustrated in figure 1A. Recall that under these circumstances the simultaneous-encounter model predicts that the forager will choose the more profitable prey no matter what the encounter rate. This design permitted us to determine whether pursuit time (reward delay) or profitability was the primary factor affecting the choice behavior we observed in experiment I. The results of experiment II were clear. Bird LW chose 11 prey of type 1 and 79 of type 2; bird YB, 2 of type 1 and 57 of type 2; bird L, 4 of type 1 and 58 of type 2; and bird GB, 2 and 60, respectively. All four chickadees strongly preferred the type-2 (more profitable) prey, even though they had to endure a longer pursuit time (p).

DISCUSSION

Experiment I indicated that the chickadees were choosing prey on the basis of profitability rather than long-term rate. These results are important because by choosing to maximize short-term rate (profitability) the chickadees often experienced a substantially lower long-term rate, the usual currency of maximization in optimality models of foraging. Experiment II showed that the proximate cause of the birds' preference for type-1 prey was indeed its higher profitability and not its shorter pursuit time (fig. 6).

Other Tests of Simultaneous-Encounter Models

The only previous explicit test of the generalized simultaneous-encounter model is that of Stephens et al. (1986). They trained free-living honey bees (*Apis mellifera*) to use a series of artificial flowers located near the hive. Stephens et al. manipulated resource quality (energy, *e*, and handling time, *h*) and habitat rich-
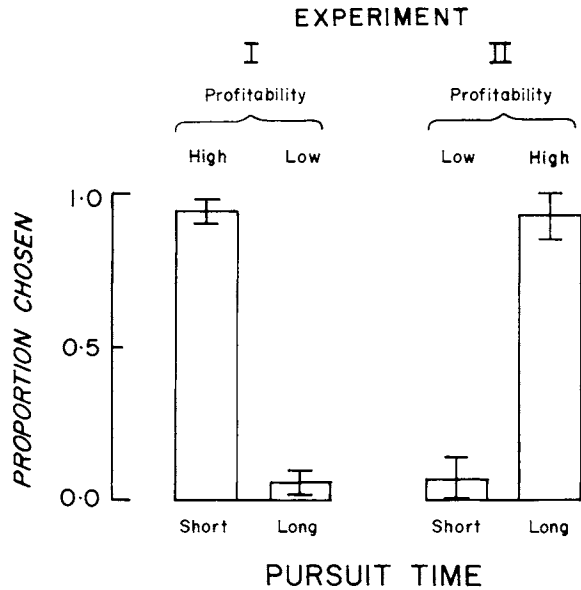
EXPERIMENT

FIG. 6.—A comparison of the proportion of each prey type chosen by four chickadees in experiments I and II. In experiment I, the more profitable prey had the shorter pursuit time (interval between choice and ingestion). In experiment II, the more profitable prey had the longer pursuit time. Error bars indicate ± 2 standard errors.

ness. Their design differed from ours in that the bees' choices were not mutually exclusive. As in our experiment, the bees simultaneously encountered a pair of flowers, one highly profitable and one low in profitability. In their experiment, unlike ours, the bees were permitted to visit both flowers. There were two "sensible" strategies that the bees could adopt in each encounter with a pair of flowers. The bees could take only the more profitable flower, or they could visit both the more profitable and the less profitable flower. Visiting only the more profitable flower was analogous to choosing the type-1 prey in our experiment, and visiting both flowers was analogous to taking the larger but less profitable type-2 prey. The situations are analogous because the amount of nectar obtained from both flowers combined was greater but the resulting short-term intake rate was lower. There was qualitative agreement between the bees' behavior and the prediction of the model. The bees were more likely to specialize on the more profitable flower when there was a large difference in profitability, and more significantly, they were more likely to visit both flowers in a poor habitat (low encounter rate) than in a rich one (high encounter rate).

   At first glance, the results of Stephens et al., which are consistent with the prediction of the generalized simultaneous-encounter model, might seem contrary to our own. However, because the bees' choices were not exclusive, they were not asked to pass up the more profitable prey to benefit long-term intake rate. Instead, the experiment asked under what conditions the bees would include the less profitable flowers in their diet. The varying results could be due to this

difference in experimental protocol or some difference in the time scale over which bees and chickadees evaluate intake rate. It would be worthwhile to conduct a test on either of these species using the experimental protocol by which the other has been tested.

Carlson (1983) modified Orians and Pearson's (1979) central-place foraging model to allow for simultaneous encounter of a pair of prey. In Carlson's model, increasing the distance from the central place is analogous to increasing search time in the generalized simultaneous-encounter model. Carlson tested the model by varying the distance from the nest at which breeding red-backed shrikes (*Lanius collurio*) encountered a pair of prey with the relative characteristics of the type-1 and type-2 prey in figure 1*B*. In agreement with Carlson's model, the shrikes preferred the smaller, more profitable prey when they were presented close to the nest and switched to the larger, less profitable prey at a more distant site.

Using honey bees, Waddington and Holden (1979) tested a special case of the simultaneous-encounter model, in which search time was assumed to be zero. Their basic experimental design differed from ours and that of Stephens et al. (1986). They tested bees on a large, open "bee board" upon which 400 artificial flowers were simultaneously present. Under these conditions, the investigators could measure visitation sequence, frequency, and rate for each flower type, but it is difficult to know what the bees' perceived encounter rate was since it undoubtedly included flowers they detected but did not visit. Waddington and Holden did not manipulate profitability per se; instead, they varied the proportion of flowers within each flower type that yielded a reward. This meant that the two flower types had different variances as well as different expected values. Finally, their definition of handling time differs from the conventional usage (MacArthur and Pianka 1966; Krebs et al. 1983) in that they did not include pursuit time as a component. Taken together, these differences in terminology and experimental design make it difficult to compare their results directly with our own. In general, Waddington and Holden found that when the proportion of flowers containing nectar within each type was equal, the bees were indifferent. When there was a difference in the proportion containing nectar, the bees preferred the flower type with the higher expected reward. The strength of this preference appeared to be correlated with the degree of difference in the expected value.

Alternative Explanations

One might be tempted to conclude that our results are consistent with the prediction of Waddington and Holden's (1979) simultaneous-encounter model: when prey are encountered simultaneously, the optimal strategy always is to choose the more profitable prey. However, this prediction is based on the assumption of zero search time. It would be true only if the chickadees did not perceive the interval we called search time as a part of the foraging cycle. Although we cannot rule out this possibility, the behavior of the birds during the tests suggests otherwise. Between presentations, they often alighted on the feeding perch and looked into the holes as if they really were searching for prey.

An interpretation that could be used to salvage the generalized simultaneous-

encounter model is that one of our four stated assumptions was invalid. Our design ensured that prey were encountered in pairs, that choices were exclusive, and that searching and handling were mutually exclusive activities. Our fourth assumption, that the energetic cost of all the components of the foraging cycle were equal, was almost certainly false. If handling time was sufficiently more costly than search time, the effect would have been an increase in s_{crit}. If this was the case, then we might have underestimated s_{crit} and never tested the chickadees at a search time long enough for them to have preferred the type-2 prey. We are disinclined to accept this explanation. For the prey sizes used in our experiment, the energetic cost of handling would have had to be roughly three to four times that of searching for the s_{crit} value to exceed the maximum duration of 120 s used in our tests. This alone seems unlikely; and the fact that the chickadees flew about the chamber during the search phase further erodes the credibility of this argument, since flight is generally considered one of the more energetically costly activities.

Self-Control and Reward Delay

Although our results may be somewhat surprising to many behavioral ecologists, they should be less so to many comparative psychologists. Investigators in that discipline have been studying a phenomenon they refer to as "self-control behavior" for some time (for discussion of this work, see Staddon 1983). The usual protocol of experiments investigating self-control has been to give animals a choice between a small, immediately delivered reward and a larger, delayed reward. Depending on the parameters used in such a test, either one may yield the greater long-term reward rate, but the interesting case is when the delayed reward is the higher. The animals often prefer an immediate, small reward, even when their overall rate is lower than if they had chosen the larger, but delayed, alternative (Green et al. 1981). Thus, the animals fail to demonstrate "self-control." This effect can be overridden by various experimental manipulations, such as increasing the time between choice and reward or sufficiently increasing the size of the delayed reward, as we did in our own experiment II. These experiments are part of an attempt to understand the effect of reward delay on food choice (recently reviewed in the context of optimal-foraging theory in Fantino and Abarca 1985). Snyderman (1983) specifically addressed the optimal-diet model in an operant paradigm and showed that reward delay affected prey choice. These results indicate that reward delay should not be overlooked in ecologically motivated studies of foraging behavior.

The Pigeon Study by Green et al.

Although not intended as a test of the generalized simultaneous-encounter model, Green et al. (1981) conducted a study complementary to our own. They manipulated variables that we held constant, and vice versa. In our experiment I, we held the profitability of each prey type constant and manipulated search time, consequently varying the e/t for each type. Green et al. held e/t for each prey type constant by keeping the overall foraging-cycle duration the same but varied the

proportion of time within each cycle allocated to searching and handling. As in our experiment I, the size of each prey type remained the same, but in contrast, the pursuit portion of handling time was manipulated. Green et al. gave their pigeons a choice of two prey types, a small reward after a short delay versus a larger reward after a longer delay. Within each 40-s foraging cycle, they manipulated when the choice of the two alternatives could be made. The period before choice is analogous to search time, and the interval from choice until reward is analogous to pursuit. By varying the portion of the cycle allocated to pursuit, Green et al. could reverse the relative profitabilities of the two prey types while holding overall e/t constant for each type.

When the search was long and pursuit short, the pigeons preferred the immediate, small reward; as search time decreased and pursuit correspondingly increased, the pigeons completely reversed their preference and chose the delayed, larger reward. A foraging model based on a currency of maximizing e/t cannot explain these results. If the pigeons were simply maximizing intake rate, they should have always preferred the larger, delayed reward because overall cycle length was held constant, and when the pigeons specialized on the larger prey, e/t was three times what it was when the pigeons specialized on the smaller prey.

Profitability Maximization

An alternative hypothesis not explicitly considered by Green et al. is that the pigeons were choosing prey on the basis of profitability. By manipulating the time in the cycle when the pigeons encountered the two prey, Green et al. were varying the pursuit time and hence profitability. Using an approach comparable to the one used to calculate the critical search time, one can determine the critical value for pursuit time, at which point the profitability for the two prey types reverses. For the values used in the experiment of Green et al., the critical pursuit time is 2 s. When pursuit time was less than 2 s, the small, immediate reward was more profitable, whereas when pursuit time was longer, the larger, delayed reward was more profitable.

The pigeons switched their preferences as a function of pursuit time, but not at the value of 2 s predicted by the profitability-maximization model. Instead, all four pigeons switched at somewhat longer pursuit times; the average of the four birds was approximately 10 s. The pigeons' preferences lagged behind the profitability in that they did not switch from the smaller, more immediate reward to the larger, more delayed reward until the latter was nearly twice as profitable as the former. In contrast to a model that maximizes e/t, a simple profitability-maximization model does predict a reversal in the pigeons' preference. However, it fails to predict accurately when that switch occurred.

Although Green et al. did not consider the profitability-maximization model, they did suggest an additional factor that could explain the disparity between the predicted and observed switching points according to the profitability-maximization model. Their idea was elaborated upon by Kagel et al. (1986), who developed a formal model of "future discounting." Kagel et al. proposed that,

because of uncertainty about future prey captures, foragers may devalue or "discount" the value of these prey relative to an otherwise equivalent, immediately captured prey. Among the possible ecological sources for this uncertainty are competitors, predators, and energetic condition of the forager. Kagel et al. suggested that the extent to which these and other factors are operating affects the shape of the functional relation between delay and the perceived value of the prey; they refer to this as the discounting function.

A profitability-maximization model incorporating discounted future rewards can explain both the pigeon and the chickadee data. The pigeons could have discounted the value of the delayed reward relative to the more immediate one. When the more delayed prey became so much more profitable than the less delayed prey that it offset the discounting effect, the pigeons switched their preference. The results of our experiments are not inconsistent with this hypothesis. In experiment I, the chickadees might have sufficiently discounted the value of the type-2 prey such that they considered them lower in value. Since we did not manipulate profitability in this experiment, we would not expect any change in preference as a result of our manipulation of search time. In experiment II, we substantially increased the size of the type-2 prey, thereby increasing its profitability, and this might have overridden the discounting effect.

Such a model is not necessarily inconsistent with the results of previous tests of the conventional sequential-encounter diet model. In experiments testing this model, foragers became more general in their choice of prey as the abundance of the preferred types declined. This translates into a longer interval before an encounter with a preferred prey is expected. If the forager were discounting future rewards, then its perception of the value of the preferred prey would be diminished. As a consequence, its estimation of the difference in value between the two types would decline, thereby leading to increasingly generalized prey choice.

It would be premature to suggest that discounted profitability maximization is anything more than a plausible alternative hypothesis of prey choice. The viability of the hypothesis is difficult to assess in the context of most previous studies since it was not explicitly considered an alternative. The shape of the discounting function is critical regarding the switch in prey preference, and as yet, no one has measured one in a foraging animal. Indeed, there are only rather minimal data supporting the existence of future discounting in nonhuman animals. Furthermore, it is not clear that discounting can explain the empirically supported relation between traveling time and patch-residence time (Stephens and Krebs 1986).

However, we do think that, in the context of prey choice, the hypothesis of discounted profitability maximization is a reasonable alternative, one that is worthy of theoretical and empirical consideration in future studies of animal foraging behavior. Before its importance as a possible new paradigm in foraging theory can be assessed, experiments are needed in which the variables that have been proposed to affect the discounting function are manipulated. Our data suggest that a simple currency of long-term rate maximization provides an inadequate basis for optimality models of foraging. Future theoretical attempts to describe foraging behavior should incorporate possible alternative currencies.

SUMMARY

Recently, several authors attempted to generalize the optimal-diet model by relaxing the assumption of the sequential encounter of prey. Engen and Stenseth (1984) and Stephens et al. (1986) showed that, for some prey characteristics, diet models incorporating the simultaneous encounter of different prey types make strikingly different predictions from those of the traditional diet model. In particular, when the less profitable prey is larger than the more profitable prey, a long-term rate-maximizing predator is predicted to specialize on the larger but less profitable prey if the encounter rate is sufficiently low.

We tested this prediction with captive black-capped chickadees. The results were inconsistent with the prediction of the model. The chickadees always preferred the higher-profitability prey, regardless of encounter rate. A second experiment was designed to determine the proximate factor affecting the chickadees' choice in experiment I. The chickadees could have been choosing prey so as to minimize pursuit time or to maximize profitability; the results indicated the latter.

We suggest that, contrary to what has previously been assumed, foragers often choose prey to maximize profitability rather than long-term intake rate, the traditional currency of optimality models of foraging. This might have been obscured by the empirical emphasis on testing the sequential-encounter diet model. The sequential-encounter case does not present foragers with a clearly dichotomous choice between maximization of short-term and long-term intake rates, whereas the simultaneous-encounter case does.

Factors previously thought to affect foraging choice need closer examination. We think that the most parsimonious explanation of our results is to reject a diet model based solely on a currency of long-term rate maximization. We consider several alternatives, concluding that a model of prey choice based on maximizing profitability that incorporates discounted future rewards can explain a variety of empirical results, including our own.

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