PREFERENCE AND PROFITABILITY: THEORY AND EXPERIMENT

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Foraging theory (Krebs et al. 1983; Stephens and Krebs 1986) assumes a simple hierarchy of feeding decisions. It supposes that foragers first choose among habitats, then choose among patches within habitats, and finally choose among prey items within patches. These three decisions have usually been studied independently. In this paper we begin to integrate these problems by considering diet choice within patches both experimentally and theoretically. Our theoretical arguments follow from combining well-known ideas about diet choice (Pulliam 1974; Charnov 1976a) and patch use (Charnov 1976b; Orians and Pearson 1979). We consider patches that are nothing more than clumps of discrete prey, and we ask which prey should be attacked and in what order? Despite the simplicity of this approach, there is some confusion in the literature about how foragers should choose prey within patches.

Waddington and Holden (1979; see also Waddington 1982) pointed out that conventional diet theory (Pulliam 1974; Charnov 1976a) assumes that the forager encounters prey items one after the other (sequential encounter). Waddington and Holden argued that many foragers experience simultaneous prey encounters (e.g., a visual hunter may see many items at once) and that this fact will change the diet theory's predictions. Waddington and Holden presented a rule for choosing among simultaneously encountered items. Their rule characterizes a prey item by the quotient of its net energy value (e) divided by the amount of time (h) required to pursue and handle it. We use "pursuit" to mean the same thing as Waddington and Holden's term "travel"; like Waddington and Holden, we mean the time from encounter until the start of actual handling. This quotient (e/h) is the familiar profitability of optimal-diet theory (Pulliam 1974; Charnov 1976a). Throughout this paper we use the term "profitability" only in this restricted sense. Waddington and Holden argued that the "best" a rate-maximizing forager can do when simultaneously encountering items is to attack the item with the highest profitability (see fig. 1A). We call this the take-the-most-profitable rule. The take-the-most-profitable rule claims that the relativeprofitabilities of the items encountered

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Fig. 1.—The figure illustrates two models of prey choice when two types of prey are encountered simultaneously. Both models characterize prey types by net energy gain ($e_i$ for the $i$th type) and handling time ($h_i$). A. The take-the-most-profitable rule asserts that the prey type with the highest quotient $e_i/h_i$ (profitability) should be chosen. The slope of the line segment drawn from the origin to the point ($h_i$, $e_i$) equals the profitability ($e_i/h_i$). A forager following the take-the-most-profitable rule would always choose item 1 in the case illustrated here. B. The discrete-marginal-value theorem provides a technique for choosing the type that maximizes the long-term rate of energy intake, which specifically includes the searching time between encounters with groups. The absolute value of searching time is plotted to the left of the origin in the figure. A line drawn through the points representing both alternatives gives the critical search time $1/\lambda_c$ (see the text): for shorter search times (e.g., $1/\lambda_1$) the more profitable type 1 would be preferred by a long-term rate maximizer; for longer search times (e.g., $1/\lambda_2$) the less profitable, but larger type 2 would be preferred.

are sufficient to predict preference (Waddington and Holden 1979). Specifically, neither the absolute values of the encountered items nor the values of the forager’s options elsewhere influence preference. However, we argue that long-term rate maximizing does not predict the take-the-most-profitable rule, although it is a special case of the correct result. We also present experimental evidence that contradicts the take-the-most-profitable rule.

We present the predictions of the theory of long-term rate-maximizing foraging
when simultaneous prey encounters occur. These predictions are important because they integrate patch-use and prey-choice decisions and because they apply to dichotomous preference tests. Dichotomous preference tests are probably the most common type of experiment in the literature of feeding behavior (e.g., Kear 1962; Rachlin and Green 1972; Sorensen 1983). The problem of simultaneous encounter is also important as a way to test which rate (long-term or per-decision) foragers maximize. The predictions of foraging models can differ, if different rates are maximized. This has recently been noted in both the ecological (Templeton and Lawlor 1981; Gilliam et al. 1982; Turelli et al. 1982) and the psychological (Staddon 1983; Kagel et al. 1986) literature.

THEORY

The development of the theory proceeds in three steps. First, we use a simple model to show how the take-the-most-profitable rule may fail. Second, we generalize this model. Finally, we explain how profitability can partially determine the long-term rate-maximizing diet even if the most profitable item is not always preferred. To do this we show how diet theory predicts which patches should be entered and which should be ignored.

A Flock-Encounter Model

A simple model shows how the take-the-most-profitable rule sometimes fails to maximize the long-term rate of energy gain. Suppose that a bird of prey encounters flocks of small birds at rate \( \lambda \), so that it searches for an average of \( 1/\lambda \) s to find a flock. Also suppose that the flocks consist of two prey types. Type 1 yields \( e_1 \) net cal and takes \( h_1 \) s to pursue and handle (handling includes the time from encounter with the flock until searching resumes), and type 2 yields \( e_2 \) cal in \( h_2 \) s. Assume that type 1 is more profitable than type 2, that is, \( e_1/h_1 > e_2/h_2 \). Because an attack flushes the entire flock, only one prey item can be attacked at each flock encounter; prey choices are thus mutually exclusive. If \( r \) is the proportion of type 1’s attacked upon encounter with flocks, then the long-term average rate of energy intake is

\[
R = \frac{r e_1 + (1 - r) e_2}{\lambda^{-1} + rh_1 + (1 - r)h_2}.
\]  

(1)

It can be shown that the rate-maximizing \( r \) must be either 0 or 1 (a result analogous to the zero-one rule of diet theory; see Charnov 1976a). Thus, the take-the-most-profitable rule can be preserved only if \( e_1/(\lambda^{-1} + h_1) > e_2/(\lambda^{-1} + h_2) \) whenever \( e_1/h_1 > e_2/h_2 \). A little algebra shows that this is not always true. If \( e_2 > e_1 \) (even though \( e_1/h_1 > e_2/h_2 \)), then the take-the-most-profitable rule disagrees with long-term rate maximizing when the search time between encounters with flocks is long. A larger, but less profitable item should be preferred if

\[
1/\lambda > 1/\lambda_c = (e_1 h_2 - e_2 h_1)/(e_2 - e_1),
\]  

(2)

where \( \lambda_c \) is the critical encounter rate. At average search times longer than \( 1/\lambda_c \), the larger, less profitable item should be attacked; and at average search times
shorter than $1/\lambda_c$, the most profitable item should be attacked (fig. 1B). Two general rules can be found using expression (2): an item both less energetically rewarding and less profitable should never be preferred; and if two alternatives are equally profitable, the larger should always be preferred.

This result makes two further points about models of simultaneous encounter. First, both simultaneous and sequential encounters occur in this model; the bird of prey encounters flocks (sets of prey items) sequentially, but it encounters birds simultaneously. The restrictive assumption in conventional diet theory is that the encountered sets contain just one item, not sequential encounter. Simultaneous encounter and sequential encounter are not theoretical alternatives. They can and probably usually do occur within the same foraging bout. Second, the take-the-most-profitable rule can be the rate-maximizing rule if encounter rates are high or if the less profitable choice also provides less energy.

The Marginal-Value Theorem for Discrete Choices

This model treats the flock, a set of simultaneously encountered prey items, as if it were a patch. The result is like the marginal-value theorem (see fig. 1B; Charnov 1976b), except that the patch can be treated in only a limited number of ways: attack type 1, or attack type 2. Although in the original marginal-value theorem the forager can choose any patch-residence time in the continuous range of zero to infinity, we call our model the “discrete-marginal-value” theorem to distinguish it from the take-the-most-profitable rule. The requirement that $e_2 > e_1$ and $e_i/h_1 > e_2/h_2$ is equivalent to negative acceleration in the continuous-gain function of Charnov’s (1976b) continuous-marginal-value theorem. Similar results in the context of central-place foraging were proposed by Orians and Pearson (1979) and Lessells and Stephens (1983). Engen and Stenseth (1984) dealt with discontinuities in within-patch gains in a different but apparently equivalent way, but Real (1983) presented a strikingly different view of simultaneous encounters.

A version of the marginal-value theorem for discrete choices can be proved (see the Appendix for details). Imagine that there are $m$ mutually exclusive prey types in the flock. Because of the results above, we need consider only the subset of $k$ prey types such that $e_1/h_1 > e_2/h_2 > \ldots > e_{k-1}/h_{k-1} > e_k/h_k$ and $e_k > e_{k-1} > \ldots > e_2 > e_1 (k \leq m)$. Items are ranked by profitability (as in the conventional theory of diets), but items both less profitable and smaller than the alternatives are excluded from the ranking because they can never be the rate-maximizing choice. If $R_{\text{max}}$ is the optimal rate of energy gain in the habitat, then the following relationship must hold if the $i$th item is the rate-maximizing choice:

$$(e_i - e_{i-1})/(h_i - h_{i-1}) > R_{\text{max}} > (e_{i+1} - e_i)/(h_{i+1} - h_i).$$

The quotients that bracket $R_{\text{max}}$ are the slopes of the two line segments above and below $(h_i, e_i)$. The Appendix proves this result.

Deciding to Attack Patches

Taking the most profitable item does not necessarily maximize the long-term average rate of energy intake (even though profitability is the rate of gain measured from the time of encounter until searching resumes), since it ignores the
search time between encounters. This leads to the apparent paradox that a long-
term rate maximizer does not prefer larger profitabilities even though the model
for long-term rate-maximizing diet choice ranks items by profitability. The
paradox is resolved by realizing that conventional diet theory views prey items
unrealistically (Stephens and Krebs 1986), by assuming that all prey items of type $j$
(for example) yield $e_j$ cal and take $h_j$ s to process and that the forager has no
control over how long to handle the item or how much energy to extract. In
contrast, in patch-use theory patches are items that a forager may use in various
ways to yield various amounts of energy. The diet model tells us whether a rate
maximizer should attack an item, and the patch model (marginal-value theorem
and its successors) tells us how a rate maximizer should use the item given that it
is attacked.

The flock-encounter model presented above can be modified to illustrate the
problem. Suppose that there are two types of flocks, A and B. The forager
encounters type A flocks at rate $\lambda_A$, and they are composed of two prey types,
A1 and A2. These prey types have characteristics $e_{A1}, h_{A1}, e_{A2}, h_{A2}$. Assume that
$e_{A1}/h_{A1} > e_{A2}/h_{A2}$ and $e_{A2} > e_{A1}$. Type B flocks contain only one prey type, $e_B/h_B >
$ $e_{A1}/h_{A1}$. The forager is faced with two problems: which flocks should be attacked,
and if type A flocks are attacked, which prey type should be attacked. Type B
flocks should always be attacked because they contain the unambiguously most
profitable prey type. This follows from the "ranking by profitability" result of
conventional diet models.

However, when should flocks of type A be attacked? Type A flocks should be
attacked if excluding them yields an energy intake rate less than the maximum
profitability of A flocks ($e_{A1}/h_{A1}$). Ranking by maximum profitabilities is suggested
because diet theory (e.g., Charnov 1976a) shows that including an item whose
profitability is greater than the present rate of intake will increase the rate.
Therefore, if $e_{A1}/h_{A1}$ ($= \max[e_{A1}/h_{A1}, e_{A2}/h_{A2}]$) is greater than the rate of intake
attained by attacking only B flocks, then type A flocks should be attacked, since
taking species A1 will increase the forager's long-term rate of energy intake. It
does not follow from this argument that taking species A1 will increase the rate of
intake more than taking species A2 will. We have shown above that there are
conditions under which a long-term rate maximizer should prefer the larger but
less profitable item. The suggested generalization (see the Appendix for the proof)
is that the decision to attack can be made precisely as predicted by conventional
diet theory except that flocks (sets of simultaneously encountered items) are
ranked by their maximum profitabilities. The maximum profitability of a set of
simultaneously encountered prey items partially determines whether the set is
attacked at all; at the same time, it is not necessarily the best tactic (according to
long-term rate maximizing) to attack the most profitable item within a patch.

Three cases roughly based on the habitat rate of intake can be specified (see the
Appendix):

1. At high intake rates ignore type A flocks and attack only type B flocks ($R_{\text{max}}$
$>$ $e_{A1}/h_{A1}$).
2. At intermediate intake rates attack both A and B flocks, but take only the
more profitable type A1 prey from the A flocks ($R_{\text{max}}$ < $e_{A1}/h_{A1}$).
3. At low intake rates attack both A and B flocks, but take only the less
profitable type A2 from the A flocks \( R_{\text{max}} < e_{A2}/h_{A2} < e_{A1}/h_{A1}; \) this is a necessary but not sufficient condition for attacking A2’s instead of A1’s).

**Summary of Theory**

Our theoretical analysis makes three main points. First, simultaneous and sequential encounters are not mutually exclusive alternatives; for example, foragers that encounter pairs of prey items will encounter these pairs sequentially. Second, the take-the-most-profitable rule does not maximize the long-term rate of energy intake because it ignores the time between encounters with sets of items; generally, it ignores the value of the forager’s alternatives elsewhere. Third, although maximizing profitability is not the long-term rate-maximizing tactic, the forager’s decision to attack or ignore a given set of items depends on the set’s maximum profitability.

**An Empirical Test of Rate**

Although the take-the-most-profitable rule is not consistent with long-term rate maximizing, it is a plausible alternative hypothesis. Foraging theory uses long-term rate maximizing partly because most foraging decisions are repeated many times and partly because it is a mathematically convenient assumption (for some recent controversy on this point, see Templeton and Lawlor 1981; Gilliam et al. 1982; Stephens and Charnov 1982; Turelli et al. 1982). However, psychologists have proposed a model of preference that is nearly identical to the take-the-most-profitable rule, which they call “momentary maximizing” (see Staddon 1983). The momentary-maximizing take-the-most-profitable rule might make economic sense in at least two ways. First, some authors (Staddon 1983; Kagel et al. 1986) proposed that an immediate reward is fundamentally more valuable than a delayed reward. This might make the take-the-most-profitable rule (or policies like it) the optimal behavior. Second, Staddon suggested that momentary maximization might be a cheap and effective rule of thumb for approximating long-term rate maximization, claiming that it is a “general principle of enormous simplicity” (1983, p. 233). In the remainder of this paper, we ask an experimental question: are a forager’s choices influenced only by immediate, relative payoffs, as the take-the-most-profitable rule predicts, or do the values of the forager’s options elsewhere affect preference, as the discrete-marginal-value theorem predicts? We use dichotomous preference experiments, together with the theory developed above, to distinguish between momentary rate maximizing (the take-the-most-profitable rule) and long-term average-rate maximizing (the discrete-marginal-value theorem).

**THE EXPERIMENT**

The model presented above considers only the case in which the forager chooses mutually exclusive prey items from a set of simultaneously encountered items. The alternatives analyzed must be mutually exclusive choices, but the alternatives do not have to be prey items. Imagine that a foraging honeybee encounters a pair of flowers (fig. 2). Because flowers do not run away, the close and the distant flowers can both be taken; flowers are not mutually exclusive
Fig. 2.—Every 2.44 m within the experimental apparatus the foraging honeybee encountered a patch as illustrated here. The patch was entered through a small hole, the encounter point. Behind this hole were two artificial flowers: a close but unprofitable flower and a distant but profitable flower.

choices. However, there are only a limited number of ways that this pair of flowers can be used: (1) attack only the close flower; (2) attack only the distant flower; (3) attack both flowers, the close one first; and (4) attack both, the distant one first. If at least one flower is taken and if there is no revisitation, then these four tactics are exhaustive and mutually exclusive. The results from the “flock” model presented earlier can be directly applied to these four options.

To distinguish between the take-the-most-profitable (momentary-rate-maximizing) rule and the discrete-marginal-value theorem (long-term rate maximizing), we studied the choice problem illustrated in figure 2 using foraging honeybees; in our experiments we arranged a pair of artificial flowers such that a close flower was less profitable and energetically less rewarding than a distant flower. The behavior predicted by the take-the-most-profitable rule is to pass by the close flower (since it is always the less profitable) and to attack the distant flower. In contrast, the discrete-marginal-value theorem predicts that “attacking close then distant” should occur at low habitat rates of energy intake and that “attacking only distant” should occur at high habitat rates of energy intake. (According to the discrete-marginal-value theorem, we may ignore the tactics “take close only” and “take distant then close” because these options would be less rewarding and less profitable than the other alternatives.)

The two models formulate this choice problem differently: the take-the-most-profitable rule considers only which flower should be visited first (Waddington and
Holden 1979); the discrete-marginal-value theorem considers whether one or both flowers should be visited. Despite this difference the two models make contrasting and unambiguous predictions about which flower should be visited first, although the discrete-marginal-value theorem predicts this indirectly. We can therefore use the first flower visited to distinguish between the models.

**Materials and Methods**

The experiment was conducted outdoors on a large lawn at the Smithsonian Environmental Research Center, near Edgewater, Maryland, from June 1 to August 17, 1983. The observations were made in the morning, from about 0700 to 1200 h.

*The subjects.*—The subjects were 12 worker honeybees (*Apis mellifera ligustica*). The bees were individually marked with spots of paint (Frisch 1967) and came from two different hives located about 0.5 m apart. We could not tell which bees were from which hive, although observations of marked individuals showed that we used bees from each hive.

*The alleyway.*—We trained the bees to feed in a long alleyway located 16.5 m from the hives. The alleyway was a plywood trough 11 m long, about 61 cm wide and 30.5 cm deep, painted white. Fine nylon mesh covered the alleyway to exclude unwanted bees. When a trained experimental bee arrived at the entrance to the alleyway, the experimenter could easily admit the bee to the alleyway by lifting a section of the mesh. Experimental bees always entered the alleyway at the same end and flew along it until they reached the opposite end or until they were ready to return to the hive. When a bee flew up to the mesh (anywhere along the alleyway) we lifted the mesh and released it.

*The patches.*—Four partitions blocked the alleyway at intervals of 2.44 m. Each partition contained a rectangular passage, 2.5 cm wide by 3.2 cm tall. The bottom lips of the passages were painted red to contrast with the white partition. These restrictive passages controlled the bee’s encounters with pairs of flowers, which were located immediately behind each partition. We directly observed over a thousand similar flower choices by controlling encounters in this way. We refer to the area containing the pair of flowers immediately behind each partition as a patch. The distance from the second flower to the next patch entrance represented a between-patch distance.

*The flowers.*—We trained the bees to extract ‘‘nectar’’ (a solution of honey and water) from artificial flowers. The flowers were wooden disks (6 cm in diameter) painted in three different colors (blue, yellow, and red) and supported on inverted plastic cups 12 cm high. Since honeybees cannot distinguish red from gray of equivalent intensity, we used red flowers only in the training phase of the experiment. We drilled a shallow well (7 mm in diameter and about 1 mm deep) in the center of each flower to hold the nectar. The flowers were coated with transparent plastic coating to prevent the wood from absorbing the honey solution. We dispensed nectar using a Drummond dispenser (catalogue no. 105).

Preliminary experiments showed that we could not adjust the profitability (energy gained divided by time to exploit) of flowers sufficiently by varying the nectar volume. To overcome this, we placed 9-mm-thick doughnut-shaped disks
over some of the flowers. These disks resembled the flowers in every way except that they had a hole (7 mm in diameter) drilled completely through their centers. The bees learned to crawl through this hole to reach the nectar. These “doughnuts” markedly increased the time taken to extract nectar. We call these two flower types doughnut flowers and open-face flowers, respectively.

The training.—We studied individual bees in sequence. We chose an individual haphazardly from the marked bees visiting a plate of honey solution placed near the alleyway. We then trained this bee for 2–3 days to enter the alleyway, to use the small passages to enter patches (droplets of honey solution were sometimes placed on the patch thresholds), and to fly between patches to the next patch. Red flowers were used as required to shape these behaviors. Since the inside of the alleyway was painted white, these red flowers contrasted with the background. We trained each individual until it readily entered the alleyway and patches and consistently drank from both open-face and doughnut flowers (which contained equal amounts of nectar during training).

The choice problem.—Each bee encountered many identical pairs of flowers (fig. 2). All experiments offered a distant open-face flower, 16 cm from the patch entrance hole and offset to the left, with 3 μl of honey solution containing 66% sucrose equivalents. All experiments also offered a close doughnut flower, 7.5 cm from the patch entrance hole and offset to the right, with 1 μl of either 66%, 33%, or 16.5% sucrose equivalents (see “Treatments,” below). Both flowers were close enough to the patch entrance that honeybees could easily see them (see Frisch 1967). The distant flower was always a different color from the close flower. These choices were contrived so that the close 1-μl doughnut flower was always less profitable than the distant open-face 3-μl flower. The minimal expectation of the take-the-most-profitable rule was that the more profitable (distant) flower should be chosen over the less profitable (close) flower in most encounters (see Stephens 1985). The expectation of the discrete-marginal-value model is that the less profitable close flower ought to be taken when the marginal value (Δe/Δh) of doing so is greater than the rate of intake achieved by ignoring it.

Treatments.—To test the effects of both habitat richness and the relative values of the members of the flower pair, we manipulated both habitat richness and flower quality.

1. Habitat-richness manipulations. In rich-habitat manipulations, we placed five additional high-quality flowers (the same as the distant flower) in the alleyway between all patches. In poor-habitat manipulations, there were no additional flowers between patches.

2. Flower-quality manipulations. The distant flower always contained 3 μl 66% sucrose equivalents (honey solution). We manipulated the quality of the close unprofitable flower. The close flower always contained 1 μl of liquid, but the dilution of this varied. There were full (66%), half (33%), and quarter (16.5%) dilution treatments. Each experimental bee experienced only one dilution treatment (four bees in each treatment), but all bees experienced both rich and poor habitats.

Randomized variables.—Some researchers have suggested that bees may be biased in favor of flowers of different colors (for review, see Kevan 1983). To
control for this possibility we exposed an equal number of bees to "yellow-distant/blue-close" and to "blue-distant/yellow-close" flower pairs. We assigned colors at random. Because a bee's experience with the apparatus might affect its behavior (e.g., by learning; see Laverty 1980), we also randomized the order of testing in rich and poor habitats. The resulting experimental design has four "order-of-habitat-richness−flower-color" permutations. Within each dilution treatment we observed four bees (one assigned to each permutation). Statistically, individual bees were nested within dilution treatments, but crossed with respect to habitat richness.

Measurement of parameters.—Both models require a knowledge of many aspects of bee behavior, for example, rate of travel, handling times of flowers; pursuit times from the encounter hole to the distant flower. The flight time to the distant flower (for example) can only be measured if the bee does not stop at the close flower. To measure this and similar values we performed forced-choice trials, in which we offered the bee only one type of flower (close or distant). Ten trials per flower type were performed both before and after the free-choice observation trials to check for training effects. We chose the order of forced-choice trials at random. We observed no training (before vs. after) effects. Some other parameters could not be estimated from the forced-choice trials (e.g., flight time between flowers); for these we used the first 10 free-choice trials for estimates. These trials were excluded from our analysis of choice behavior. We recorded approximately 30 free choices for each bee in each treatment. We converted time and sucrose-equivalent data to energetic costs and benefits (calories) where appropriate, using Heinrich's (1983) conversion factors.

Summary of treatment.—All bees were treated in the same way. Each bee (1) was assigned to dilution, habitat-richness, and flower-color treatments; (2) performed 10 forced-choice trials each for both close and distant flower types; (3) performed 10 free-choice estimation trials; (4) performed 30 free-choice observation trials (choice data used in analyses); (5) performed 10 forced-choice trials for each of both flower types; (6) experienced a change in the habitat-richness treatment and repeated the process starting at step 2.

Observed quantities.—Two observers participated in the experiment. One experimenter cleaned and filled the flowers just ahead of the bee's position in the alleyway, and the second experimenter recorded all observations on a portable tape recorder. We decoded the tapes later using a stopwatch. We recorded the following information: (1) the return time between bouts in the alleyway (including instances in which the bee returned to the hive to empty its honey stomach and those in which the bee left the end of the alleyway and flew immediately to the beginning to start again); (2) which flower (1 μl or 3 μl) the bee chose upon arrival in a patch (the bees sometimes landed on the close 1-μl flower without drinking the nectar, so we recorded both the first flower visited and the first flower drunk); (3) all flight times; (4) the time taken to extract nectar from all flowers.

RESULTS

Table 1 presents the estimated handling-time and energy-gain parameters. These data confirm that the close 1-μl flower was always less profitable than the


<table>
<thead>
<tr>
<th>Parameter</th>
<th>Habitat-Richness Treatment</th>
<th>Dilution Treatments</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Full</td>
<td>Half</td>
</tr>
<tr>
<td>Handling time (s) 1-μl flower</td>
<td>Rich:</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Poor: 11.21 ± 0.45</td>
<td>10.53 ± 0.59</td>
</tr>
<tr>
<td>3-μl flower</td>
<td>Rich:</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Poor: 1.24 ± 0.45</td>
<td>1.09 ± 0.34</td>
</tr>
<tr>
<td>Net calories</td>
<td>Rich:</td>
<td>*</td>
</tr>
<tr>
<td>1-μl flower</td>
<td>Poor: 2.3</td>
<td>1.09</td>
</tr>
<tr>
<td>3-μl flower</td>
<td>Rich:</td>
<td>*</td>
</tr>
<tr>
<td>Profitability (cal/s) 1-μl flower</td>
<td>Rich:</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Poor: 0.21</td>
<td>0.10</td>
</tr>
<tr>
<td>3-μl flower</td>
<td>Rich:</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Poor: 0.58</td>
<td>*</td>
</tr>
<tr>
<td>Habitat rate of energy intake (cal/s)</td>
<td>Rich: 0.5</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>Poor: 0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>Marginal value of 1-μl flower (cal/s)</td>
<td>Rich: 0.26</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>Poor: 0.22</td>
<td>0.12</td>
</tr>
</tbody>
</table>

* No significant (5% level) differences between rich and poor treatments. Estimates of these parameters are pooled appropriately.
† No significant (5% level) differences across dilution treatments. Estimates of these parameters are pooled appropriately.

distant 3-μl flower. Because the bees did not always drink from flowers that they visited, there are four possible permutations of first flower choice: (1) visit close, drink close; (2) visit close, drink distant; (3) visit distant, drink distant; (4) visit distant, drink close. We never observed the fourth type of behavior, but we did observe all three other flower choices. The statistical results are the same regardless of whether we count the ambiguous "visit close, drink distant" choices as distant choices, close choices, or not counted. Therefore in the following we report only analyses on the proportion of "visit distant, drink distant" choices, which we call the proportion of first visits to the most profitable flower. Counting visits in this way favors the take-the-most-profitable rule, because it counts fewer visits to the less profitable flower. Figure 3 presents the proportions of first visits to distant, more profitable flowers for each of the six manipulations.

The effect of flower quality.—Both models predict (and intuition demands) that preference for the close (unprofitable) flower should decrease or stay the same as
its quality (honey concentration) is reduced. Our results confirm this prediction (fig. 3). The differences between full and half dilutions are not significant (at the 5% level, which we use throughout), but the differences between these treatments and the quarter-dilution treatments are significant.

Effect of rate: is relative value the only important variable?—The differences between rich and poor treatments are significant in every possible comparison. Moreover, they are in the direction that the discrete-marginal-value theorem predicts. The close (unprofitable) flower is less preferred in high-rate “rich” treatments. This is an important strike against the take-the-most-profitable rule as a complete description of honeybee flower choice.

The quantitative effects of quality.—Both models predict threshold behavior: preference (i.e., first choice) for the close flower below some threshold and preference for the distant flower above that threshold. Under either model it is unreasonable to expect 100% or 0% choice (so-called absolute preferences), which could only happen if one could observe the threshold with no error or variance (see Stephens 1985). Obviously, any acceptance-rejection threshold must have some variance composed of between- and within-bee variation as well as experimental error. We used probit analysis to estimate the mean and variance of the observed thresholds.
The take-the-most-profitable rule predicts that the profitabilities of distant and close flowers ought to be equal at the threshold point. Similarly, the discrete-marginal-value theorem predicts that the habitat rate of energy intake (excluding the close flower) and the marginal value of taking the close flower ought to be equal at the threshold point.

*Test of the take-the-most-profitable rule.*—The difference in profitabilities at the observed threshold is 0.43 cal/s, which lies between 0.33 and 0.53 with 95% confidence. The predicted zero difference (equal profitabilities) lies well outside the 95% confidence limits. The distant flower had to be (on the average) 5.5 times more profitable than the close flower before the bees ignored the close flower 50% of the time.

*Test of the discrete-marginal-value theorem.*—The difference between the marginal value of the close flower and the habitat rate of intake at the observed threshold is 0.26 cal/s, which lies between −0.23 and 0.75 with 95% confidence. The 95% confidence limits include the difference of zero predicted by the discrete-marginal-value theorem. The bees took the close (unprofitable) flower in somewhat richer conditions than predicted, but this difference was not statistically significant.

**DISCUSSION**

Honeybees do not simply take the most profitable flower available. The relative values (measured in time and energy) of the flowers offered affect honeybee flower choice, but flower choice is also affected by how well the bees can do elsewhere in their habitat. Our data support long-term average-rate maximization over momentary maximization. The bees sacrificed immediate gain by taking the close unprofitable flower when the habitat rate of energy gain was low, but they passed up the close unprofitable flower when the habitat rate of energy gain was high. Momentary maximizing (the take-the-most-profitable rule) failed most notably in underestimating the bees’ preference for the close unprofitable flower.

Waddington and Holden (1979) studied flower-choice behavior in honeybees, and they concluded that the take-the-most-profitable rule was well supported. However, their results are not necessarily inconsistent with ours because they gave their honeybees dense arrays of artificial flowers, and the discrete-marginal-value theorem would probably also predict taking the most profitable flower in these conditions. A thorough analysis of Waddington and Holden’s (1979) data would be complicated because they did not control the sets of flowers that their experimental bees encountered. We suspect that some of the discrepancies between Waddington and Holden’s data and the take-the-most-profitable rule occur because the bees reject all visible flowers; the take-the-most-profitable rule cannot explain these complete rejections. Waddington and Holden’s data only support the take-the-most-profitable rule indirectly, because the researchers did not directly observe the choices. Instead, they inferred support for their model by comparing the observed frequency distribution of visits to various flower types with frequencies predicted by their model. This is not strong evidence for the take-the-most-profitable rule: many models of choice would predict similar fre-
quency distributions since these predicted distributions necessarily incorporate much information about the experimental flower densities.

**Relative Value and Choice**

The most significant finding of our study is that there are both theoretical and empirical reasons to believe that the value of alternatives other than the choices immediately available affect preferences. Honeybees act like efficient shoppers in a market whose choices depend not only on what they see in that market, but also on what other markets have for sale. This finding is important for ecologists who use preference tests to draw conclusions about predator-prey relationships, habitat choice, and community ecology, because the frequency and pattern of presentation may affect preference tests. For example, an animal's preferences among items of a set presented once every hour may differ from its preferences among the same items presented once a minute. Preference is not absolute; it depends on the nature and the frequency of alternatives and on the forager's expectations of unseen alternatives.

Operant psychologists (e.g., Fantino and Abarca 1985) have concluded that the immediate consequences of choice are more important than the long-term consequences of choice in determining preference, although they concede that long-term consequences sometimes have an effect. This conclusion may seem at odds with our results, but the model we present predicts that changes in the long-term rate of gain need not always affect preference. For example, if one of the forager's two alternatives is both larger and more profitable, then it should be preferred regardless of the net habitat rate of energy gain. This interpretation is different from the view that immediate consequences are most important because it identifies conditions under which immediate consequences (i.e., profitability) are enough to determine the best long-term foraging tactics. Viewed in this way, results showing the importance of immediate consequences are not necessarily inconsistent with the general importance of long-term rate.

**Patches and Diet**

Our results show how the floral diet may be influenced by the patchiness of the habitat. Our theoretical and empirical results show how a patch-use model can determine prey (or flower) choice; diet choice is sometimes a patch-use problem (cf. Engen and Stenseth 1984).

This confusion between patch and diet models has appeared in the literature at least twice. In part, Waddington and Holden seem to have proposed the take-the-most-profitable rule because of the prominence of profitability in the conventional diet model. A more subtle confusion has arisen between Schoener's (1979) and Orians and Pearson's (1979) central-place-foraging models. Schoener asserted that both models "can be broadly applied to many of the same data" (1979, p. 912). However, these models are not alternatives; they can apply simultaneously and in complementary fashion. Schoener's model deals with the effects of distance on profitability, and hence on the diet or "whether to attack at all" problem. The Orians and Pearson single-prey-loader model deals with the effects of distance on patch use.
Schoener’s model might be called an encounter-at-a-distance model. The central idea is that a prey item encountered at 4 m away is less profitable than the same item encountered at 4 cm. Schoener studies the effects of ‘‘encounter distances’’ on profitability, whether an item that is attacked when it is close ought to be attacked when it is farther away. In contrast, Orians and Pearson’s single-prey-loader model assumes that a forager is repeatedly exploiting the same item (patch), and deals with the question of how this item should be exploited. The flock-attacking bird of prey we discussed earlier faces Schoener’s and Orians and Pearson’s problems simultaneously. Schoener’s model tells us whether a rate-maximizing raptor should attack a flock encountered half a kilometer away, but Orians and Pearson's (and more specifically our model) tells us which members of the flock should be taken, given that the flock is attacked.

Limitations of the Model

Some have criticized foraging theory for only treating patches that have discrete and well-defined limits (e.g., Bond 1980). These critics argue that many natural patches are little more than loose clumps of discrete prey items. Our results show how basic theory can be applied to clumps of discrete prey, by a hierarchical use of the prey-choice and patch-use models (for different views of similar problems, see Heller 1980 and McNair 1979). The main limitation of our approach is that we must assume that the whole clump is encountered (e.g., seen) simultaneously. Suppose that a honeybee encountered a group of three flowers and chose to attack the closest one. What should it do, if when flying toward this flower it encounters a previously unseen flower? Neither our model, nor any other model, treats this situation. These considerations suggest that lumping pursuit time with actual handling time (as is usually done) may be unreasonable because pursuit requires less commitment (i.e., less loss of opportunity) than does actual handling of prey.

Like other forms of the marginal-value theorem, our patch-use model says little about the tactics an animal can use. Our technique cannot even be applied until all the ways that the patch (clump, flock, etc.) can be used have been listed, and plotted as \((h_i, e_i)\) points. Our experimental situation was especially simple because it was easy to make an exhaustive list of possible tactics. The marginal-value theorem (including our discrete version and others) is not a decision rule, but a technique for choosing among a set of possible decision rules. The view that the marginal-value theorem is itself a decision rule is the source of much controversy (Oaten 1977; Green 1980; McNamara 1982).

Momentary Maximizing, Self-Control, and Rules of Thumb

Animal psychologists have studied a broad class of problems under the general heading of ‘‘self-control’’ experiments. In these experiments, animals (rats or pigeons) using an operant device choose between keys. Associated with each key is a food value (a period of access to food) and a delay. These quantities are comparable to the \(e\) and \(h\) of our model, so that a profitability \((e/h)\) can be associated with each choice. Between each choice is a fixed inter-trial interval. This experimental set-up is analogous to a two-species mixed-flock version of our patch-use model. Psychologists have traditionally been interested in the effects of
delay on choice (will animals delay gratification for a proportionately larger reward?), and they have performed many manipulations of absolute and relative delays (handling times) of the two choices. The basic trend observed in these experiments is consistent with our empirical and theoretical results. Increasing absolute delay (for both alternatives) increases the preference for the larger (more energetically rewarding) alternative (Rachlin and Green 1972; Navarick and Fantino 1976; Staddon 1983).

The results of our experiment, although consistent with the general trends shown in self-control experiments, differed in many ways. We manipulated relative value rather than handling time (delay), and we explicitly manipulated the richness of the habitat. We found that overall habitat richness (an ecological analogue of inter-trial interval) affects bee choice behavior, as a long-term rate-maximizing model would predict. Many (but not all) self-control results can be explained by momentary maximizing because at fixed inter-trial intervals the qualitative effects of changing delays (i.e., handling times) are the same under both momentary and long-term maximizing models. Our experiment should help to illustrate the kind of natural situation to which self-control results from the operant laboratory may be relevant. It is a significant and hopeful sign that animals as different as pigeons and bees have similar behavioral patterns.

As we noted, many, but not all, self-control data can be interpreted according to momentary maximizing (the take-the-most-profitable rule). Staddon (1983) concluded that animals are momentary maximizers, but that they sometimes take account of the long-term rate of gain. However, we show theoretically that taking the most profitable is sometimes the long-term rate-maximizing behavior. Our experiments show that when taking the most profitable item does not maximize the long-term rate of energy gain, then foragers do not take the most profitable item. We conclude, contrary to Staddon’s view, that momentary maximizing cannot be a complete description of behavior. At best it requires a supplementary decision rule to decide between long-term rate maximizing and momentary maximizing, since animals do both.

Staddon was impressed by the general applicability and apparent simplicity of momentary maximizing as a so-called “rule of thumb.” Many other authors have suggested that the mechanisms required to achieve long-term rate maximization are too complicated or expensive for animals to implement (e.g., Janetos and Cole 1981; Myers 1983). In their collective haste to find simple and cheap rules, many authors have ignored the possibility that the rules required to approximate long-term rate maximization need not be complicated or expensive. For example, a decision rule based on continually updated achieved rates associated with various activities may be all that is required. A running tally might be simple and cheap to operate and maintain. The chief problem is that the intuition of biologists about which rules are simple and cheap has been unreliable. Animals can often perform more-subtle tasks than an intuitive view of their simplicity allows (a prominent example is the discrimination of prey by planktivorous fish simply on the basis of apparent size, O’Brien et al. 1976; real fish can do better than hypothetically limited ones, Gibson 1980).


**Time Discounting**

Although long-term rate maximization is generally well supported, there are reasons to think that it does not completely account for food-choice patterns. Consider the following thought experiment: a forager is offered two alternatives, which may be characterized by \((h_i, e_i)\) pairs, \(i = 1, 2\) (handling times/delays and energy gain). Assume that \(h_1\) and \(h_2\) are fixed. By making \(e_2\) sufficiently large there will always be some point where it is preferred to the smaller \(e_1\) choice regardless of the values of \(h_1\) and \(h_2\). Now suppose that \(h_2\) is increased to an extraordinarily large value (say, longer than the forager expects to live). According to long-term rate maximizing we could still make \(e_2\) the preferred choice by increasing \(e_2\) to infinity. Should a forager prefer to wait for something it has little hope of living to obtain? The point is that long-term rate maximization is in danger of ignoring the pattern of energy gain (see Caraco 1980; Real 1980; Stephens and Charnov 1982). A more sophisticated (and realistic) view would discount the future food value \(e_2\) to reflect not only the forager’s mortality schedule, but also its short-term energy requirements. It has been suggested that foragers ought to discount the future (Staddon 1983; Kagel et al. 1986) because rewards now are fundamentally more valuable than rewards in the future. If time discounting is sufficiently drastic, momentary maximizing may be a sensible strategy. Our bee’s tendency to take the unprofitable flower in richer than predicted conditions may reflect a form of time discounting.

**Summary**

We attempt to integrate the related problems of patch choice and prey choice within patches. Two models of prey choice within patches are discussed. One based on momentary rate maximizing (the take-the-most-profitable rule) has been presented previously. We develop an alternative long-term rate-maximizing rule, the discrete-marginal-value theorem. We present an experimental test of these two alternatives using honeybee flower-choice behavior. These empirical results strongly favor the discrete-marginal-value theorem. The relative values of flowers affect honeybee flower choice as both models predict, but the overall richness of the habitat also affects flower choice as the discrete-marginal-value theorem predicts. Our experimental result is consistent with existing data on the so-called “problem of self-control” in animal psychology. We consider the generality of momentary rate maximizing versus long-term rate maximizing, and attempt to clarify some of the literature’s confusion about when the diet and patch-use models apply.

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APPENDIX

Although the mathematical assertions made in the text may be obvious to many readers familiar with the subject, we include a brief mathematical appendix for thoroughness and clarity.

DEFINITIONS AND REQUIRED RESULTS

Consider a case in which pairs of items are encountered and only one item may be attacked. Call the items 1 and 2.

\( \lambda \) is the encounter rate with pairs.

\( h_i \) is the time required to attack, eat, and leave the patch if type \( i \) is chosen.

\( e_i \) is the net energy gain if \( i \) is chosen. It will always be possible to rename the two items such that \( h_2 \geq h_1 \), that is, type 2 has a longer handling time than type 1.

\( \Delta e/\Delta h \) is the slope of the line segment with endpoints \((h_2, e_2)\) and \((h_1, e_1)\); that is,

\[
\Delta e/\Delta h = (e_2 - e_1)/(h_2 - h_1). \tag{A1}
\]

Suppose that when the pair is encountered the forager attacks type \( i \). The long-term rate of gain is

\[
R_i = \left( \frac{\sum_{j=1}^{n} \lambda_j e_j}{1 + \lambda h_j} \right) + \lambda h_i. \tag{A2a}
\]

The terms in brackets represent the gains and time expenditures from encounters with other patch types. However, because we are interested in a particular patch type, we summarize these terms using nonnegative constants. Thus,

\[
R_i = (c_i + \lambda e_i)/(k_i + \lambda h_i). \tag{A2b}
\]

The subscript in \( c_i \) and \( k_i \) shows that the way other patches are treated may depend on whether item 1 or item 2 is chosen from the patch type of interest. Specifically, we suppose that \( c_i \) and \( k_i \) are chosen to maximize the long-term rate of gain \( R_i \), given that type \( i \) items are chosen from the patch type of interest. It follows that

\[
(c_i + \lambda e_i)/(k_i + \lambda h_i) \geq (c_j + \lambda e_i)/(k_j + \lambda h_j), \tag{A3}
\]

for any feasible \((c_j, k_j)\) pair.

From elementary algebra,

\[
e_i/k_i > e_i/h_i \quad \text{and then} \quad c_i/k_i > (c_i + \lambda e_i)/(k_i + \lambda h_i). \tag{A4}
\]

In words, no item such that \( c_i/k_i > e_i/h_i \) can be in the long-term rate-maximizing diet, because the alternatives, represented by \( c_i \) and \( k_i \), give a higher rate of energy gain without this item.
The following expressions are algebraically equivalent for any \( c \geq 0, k \geq 0, \) and \( h_2 > h_1 \).

\[
\begin{align*}
\Delta e/\Delta h & \equiv (c + \lambda e_2)/(k + \lambda h_2) \quad \text{(A5a)} \\
\Delta e/\Delta h & \equiv (c + \lambda e_1)/(k + \lambda h_1) \quad \text{(A5b)} \\
(c + \lambda e_2)/(k + \lambda h_2) & \equiv (c + \lambda e_1)/(k + \lambda h_1). \quad \text{(A5c)}
\end{align*}
\]

**Proof of the Discrete-Marginal-Value Theorem**

Consider two arbitrarily chosen items 1 and 2. The discrete-marginal-value theorem consists of the following three statements.

1. If \( \Delta e/\Delta h > R_{\text{max}} \), then item 2 is the long-term rate-maximizing choice, that is, \( R_2 > R_1 \).
   
   **Proof.**—\( \Delta e/\Delta h > R_{\text{max}} \) implies that \( \Delta e/\Delta h > (c_2 + \lambda e_2)/(k_2 + \lambda h_2) \geq (c_1 + \lambda e_2)/(k_1 + \lambda h_2) \).

   Application of equation (A5) yields
   
   \[
   R_2 = \frac{c_2 + \lambda e_2}{k_2 + \lambda h_2} \geq \frac{c_1 + \lambda e_2}{k_1 + \lambda h_2} > \frac{c_1 + \lambda e_1}{k_1 + \lambda h_1} = R_1;
   \]
   
   that is, \( R_2 > R_1 \) by transitivity, as required.

2. If \( \Delta e/\Delta h < R_{\text{max}} \), then item 1 is the long-term rate-maximizing choice; that is, \( R_1 > R_2 \).
   
   **Proof.**—The proof is by contradiction. Assume that \( \Delta e/\Delta h < R_{\text{max}} \), but \( R_2 > R_1 \). This requires that \( \Delta e/\Delta h < R_2 \). Applying (A4) and (A5) gives
   
   \[
   R_2 = \frac{c_2 + \lambda e_2}{k_2 + \lambda h_2} < \frac{c_2 + \lambda e_1}{k_2 + \lambda h_1} \leq \frac{c_1 + \lambda e_1}{k_1 + \lambda h_1} = R_1,
   \]
   
   which implies that \( R_2 < R_1 \) and this contradicts the stated assumptions.

3. If \( \Delta e/\Delta h = R_{\text{max}} \), then the long-term rate-maximizing forager is indifferent between items 1 and 2; that is, \( R_1 = R_2 \).
   
   **Proof.**—There are two cases. Case 1. Assume that \( R_2 \geq R_1 \). This implies that \( \Delta e/\Delta h = R_2 \), which in turn requires that
   
   \[
   R_2 = \frac{c_2 + \lambda e_2}{k_2 + \lambda h_2} = \frac{c_2 + \lambda e_1}{k_2 + \lambda h_1} \leq \frac{c_1 + \lambda e_1}{k_1 + \lambda h_1} = R_1;
   \]
   
   that is, given that \( \Delta e/\Delta h = R_{\text{max}} \), if \( R_2 \geq R_1 \), then \( R_1 \geq R_2 \). Both inequalities can hold only if \( R_1 = R_2 \).
   
   Case 2. Similarly, if \( R_1 \geq R_2 \), then this implies that \( R_1 = R_2 \), as required.

**Extension of the Discrete-Marginal-Value Theorem to the Many-Prey Case**

The discrete-marginal-value theorem can be extended to include an arbitrary number of feasible (within-patch) prey by induction. The crucial assertion is that if prey item \( x \) is the long-term rate-maximizing choice among a set of \( m \) prey items, then an \( m + 1 \) item can be the long-term rate-maximizing choice only if choosing the \( m + 1 \) item produces a larger rate of intake than choosing \( x \) does. The addition of the \( m + 1 \) item to the feasible set cannot make a previously suboptimal choice optimal.

Since we have shown that the discrete-marginal-value theorem applies for pairs, it follows by induction that it is correct for an arbitrary number of prey in the feasible set. Explicitly, it is obvious that if the discrete-marginal-value theorem holds for \( m \) prey, then it holds for \( m + 1 \) prey, because this addition only requires a pairwise comparison.

**Patch Choice**

In this section we present a symbolic argument to support the claim in the text that the long-term rate-maximizing patch choice can be made according to the same rules as the long-term rate-maximizing diet choice in the conventional prey model except that patches must be ranked by their maximum profitabilities.
We use symbols modified from Charnov (1976a).

$C_i$ is the vector describing the way the forager exploits patch type $i$. $C_i$ may be complicated, possibly including information about the order of prey attack, methods of hunting, and all conceivable aspects of within-patch tactics.

$g_i(C_i)$ is the gain function, specifying energy gain as a function of within-patch tactics $C_i$.

$t_i(C_i)$ is the time spent in patches of type $i$ given that the forager adopts tactics $C_i$.

We wish to show that the following rule is the long-term rate-maximizing patch-choice rule.

Step 1. Rank the patches such that

$$\max_{C_i} \frac{g_i(C_i)}{t_i(C_i)} > \max_{C_i} \frac{g_i(C_i)}{t_i(C_2)} > \ldots > \max_{C_i} \frac{g_i(C_i)}{t_i(C_k)}.$$

Step 2. Add patch types to the “patch diet” in the order of their rank until satisfying

$$\max_{C_1, C_2, \ldots, C_m} \left[ \left( \sum_{i=1}^{m} \lambda_i g_i(C_i) \right) \left/ \left( 1 + \sum_{i=1}^{m} \lambda_i t_i(C_i) \right) \right. \right] > \max_{C_{m+1}} \frac{g_{m+1}(C_{m+1})}{t_{m+1}(C_{m+1})}.$$  \hspace{1cm} (A6)

We call the right side of equation (A6) the maximum profitability of patch type $m + 1$. The maximization of the left side must satisfy the discrete-marginal-value theorem.

**Proof.**—It is a claim of conventional diet theory (see Pulliam 1974; Charnov 1976a) that an $m + 1$ type should be ignored when encountered if and only if

$$\max_{C_1, C_2, \ldots, C_m} \left[ \left( \sum_{i=1}^{m} \lambda_i g_i(C_i) \right) \left/ \left( 1 + \sum_{i=1}^{m} \lambda_i t_i(C_i) \right) \right. \right] > \frac{g_{m+1}(C_{m+1})}{t_{m+1}(C_{m+1})}. \hspace{1cm} (A7)$$

Our only problem is the interpretation of the right side of this expression. In the conventional model this “profitability” is unique, since the forager is supposed to have no control over $e$ and $h$. If inequality (A7) is false for any choice of $C_{m+1}$, say $C'_{m+1}$, then the long-term rate of energy intake can be increased by taking $m + 1$ type patches and using tactic $C'_{m+1}$.

Clearly, (A7) can be false for some $C_{m+1}$ only if it is also false for the $C_{m+1}$ that maximizes profitability.

**LITERATURE CITED**


