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Honeybees maximize efficiency by not filling their crop

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Summary. Honeybees often abandon non-depleting food sources with a partially filled crop. This behaviour does not maximise the net rate of energy extraction from the food sources, and thus contradicts predictions of some common models for central place foragers. We show that including the metabolic costs of transport of nectar leads to models that predict partial crop-loading. Furthermore, the observed crop loads of honeybees are less consistent with those predicted by maximization of delivery rate to the hive (net energetic gain/unit time), than with those predicted by maximization of energetic efficiency (net energetic gain/unit energy expenditure). We argue that maximization of energetic efficiency may be an adaptation to a limited flight-cost budget. This constraint is to be expected because a worker's condition seems to deteriorate as a function of the amount of flight performed.

Introduction

Foraging animals are often bound, temporarily or permanently, to a fixed place, such as a nest or a hive, to which food is carried. Workers of the honeybee (*Apis mellifera*) that collect nectar and carry the load back to the hive in their honeycrops are an example of this kind of central place foraging. It has been suggested that the foraging behaviour of nectar-gathering bees should maximize the net rate of gain of energy (e.g. Pyke 1978; Waddington and Holden 1979; Hodges 1981). For central place foragers, models based on maximization of rate of energy extraction from the food sources (equivalent to energy delivery rate to the central place if all energy costs are ignored) predict that incomplete loads should only be gathered when the animal feeds from a patch where intake rate diminishes with time (Orians and Pearson 1979).

Even in non-depleting patches, however, honeybees do not always fill their crop before returning to the hive (Nuñez 1982). Caged hummingbirds with food ad libitum were also found not to fill their crop before returning to a perch (De Benedictis et al. 1978). De Benedictis et al. showed that meals of limited size resulted in maximization of net energy gain when the cost of transporting the collected nectar was taken into account. Nuñez (1982), on the other hand, suggested that in the highly social honeybee partial crop filling may be an adaptation to the need for exchanging information between workers. Thus, a prolonged absence from the hive would result in a loss of information about alternative food sites and it would pay a worker to return sooner than with a full load. Under certain circumstances, of course, foraging bees may also have to meet other tasks, such as to collect water for cooling the hive (e.g. Lindauer 1954). We do not consider these ideas here; our goal is to investigate how much of the bees' behaviour can be accounted for by purely energetic models of nectar collecting. We present evidence supporting the view that the metabolic costs of carrying a nectar load can help to understand partial crop loading. Our discussion is restricted to only two 'currencies', energetic efficiency and net rate of energy delivery, but more complex currencies could be analyzed (see Kacelnik 1984; Cheverton et al. 1985; Houston, in preparation).

The model

Consider a worker bee which leaves the hive to forage in a patch of flowers at a given distance

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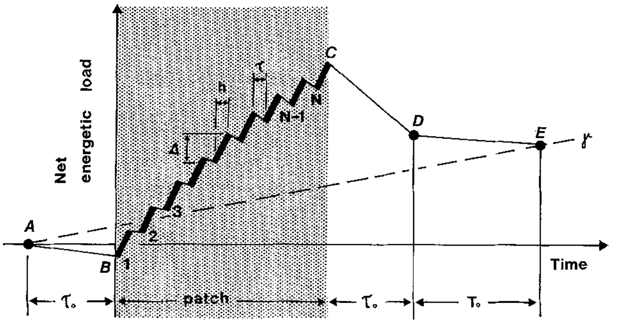

Fig. 1. The foraging cycle, shown as the net energetic load carried by a bee as a function of time. The cycle starts at *A* when the bee leaves the hive. After travel time τ_0 the first flower in the patch (*B*) is reached. In the patch (*shaded area*), the bee visits *N* flowers. Each visit increases net energy balance by an increment Δ, corresponding to the energetic equivalent of nectar reward minus energetic expenditure on flower, and takes time *h* (*heavy lines*). For *N* visits, *N*-1 inter-flower flights (duration τ, *thin lines*) are made. Because crop load is increasing, the energetic expenditure on inter-flower flights increases. The bee leaves the patch at *C* to fly back to the hive (*D*). From *D* to *E*, the bee stays in the hive for time T_0, incurring an energetic expenditure at rate a_T. The slope of γ (*broken line AE*) is the net rate at which energy is delivered to the hive. Leaving the patch after *N* flowers at *C*, rather than earlier or later, gives the steepest slope of γ (cf. Fig. 2). Hence, *N* is the optimal number (N^*) of flowers to be visited with the rate model. In a graphical representation of the efficiency model, the time axis would be replaced by an axis of energy expenditure. For further definition of parameters see text

from the hive. When the bee arrives at the first flower of the patch (Fig. 1), she has already spent a certain amount of energy in flying from the hive to the patch. If a_0 = metabolic rate of the unloaded bee during flight and τ_0 = one-way travel time, then this expenditure is $a_0 \cdot \tau_0$. With each flower visited in the patch, the animal takes up a nectar load, weight w, which is equivalent to an energy of $c \cdot w$, where c = weight-specific energetic value of the nectar. The time to gather the load from each flower is h (handling time). For simplicity, we assume flight velocity to be unaffected by load.

The energy spent flying for time τ from flower to flower increases with load, i.e. with the number of flowers already visited. We assume a linear relationship between metabolic rate during flight and the weight of the nectar load the bee carries. Such a linearity is suggested by findings of Heinrich (1975) for the bumblebee *Bombus edwardsii*, and Beutler (1937) and Heran (1962) for honeybees. An increase in metabolic rate with load while extracting nectar from a flower is probably relatively low because the bee sits on the flower rather than hovering during extraction. We therefore consider this increase only during inter-flower flights. During flower visits, the metabolic rate, a_h, thus remains constant. If the bee visits N flowers before returning to the hive, the total energy expenditure in the patch, C_p, is given by

$$\begin{aligned} C_p = {} & a_0 \cdot (N-1) \cdot \tau \\ & + a \cdot (w + 2w + 3w + \cdots + [N-1]w) \cdot \tau \\ & + a_h \cdot N \cdot h \end{aligned} \tag{1a}$$

where a = linear increment in metabolic rate as a function of load weight, and w = load increment at each flower. Equation (1a) can be written as

$$\begin{aligned} C_p = {} & a_0 \cdot (N-1) \cdot \tau \\ & + a \cdot \frac{N \cdot (N-1)}{2} \cdot w \cdot \tau + a_h \cdot N \cdot h. \end{aligned} \tag{1b}$$

The return flight to the hive will cost $a_0 + a \cdot W$ (W = total load = $N \cdot w$), and thus total expenditure during travel is

$$C_T = a_0 \cdot \tau_0 + (a_0 + a \cdot W) \cdot \tau_0. \tag{2}$$

Because nectar has to be delivered to recipient bees in the hive, we include the time and energetic expenditure while the bee is in the hive as part of the foraging cycle. If hive time is denoted by T_0 and metabolic rate while in the hive by a_T, then the total expenditure, C, per foraging cycle is

$$C = C_p + C_T + T_0 \cdot a_T. \tag{3}$$

A bee which visits N flowers in the patch accumulates a gross energy load, G, given by

$$G = N \cdot c \cdot w. \tag{4}$$

Finally, the round-trip time for an entire foraging excursion, T, is given by

$$T = 2 \cdot \tau_0 + (N-1) \cdot \tau + N \cdot h + T_0. \tag{5}$$

By combining Eqs. (1) to (5) it is possible to find the optimal load size, for both of the 'currencies' used (net rate of energy delivery, and energetic efficiency) expressed in terms of numbers of flowers to be visited (N^*). We solved the problem by numerical iteration on the number of flowers visited per trip (Fig. 2).

Methods

Individually marked workers of the honeybee (*Apis mellifera*) were trained to collect food from a feeding site (the patch), 30 m from the hive. The patch consisted of three artificial 'flowers' each containing 1 µl of 50% (weight/weight) sugar solution ("nectar"). 1 µl of 50% sugar solution contains 0.6 mg of sugar, equivalent to 10.05 J (where c = 16.7 J per mg of sugar). The bees typically took a few seconds to empty each flower before taking off to visit one of the other two. Flowers were refilled after each visit, so that they could be re-visited without depletion for an indefinite number of times. The distance between the patch and the hive was kept constant, but the inter-flower flight time, τ, within the patch was varied by controlling (with a sliding cover) the interval between leaving one flower and landing on a new one. In the field, such different interflower times would correspond to different flower densities.

Twelve individuals were tested. Each bee experienced a different average inter-flower time τ (range of means: 3.9 s to 49.9 s) during which it spent all the time in flight. Each individual was observed for 8 consecutive trips. The mean loads gathered in the patch before returning to the hive, and the mean of the time measurements (handling, hive time, one-way travel time, and inter-flower flight time) during the last four round-trips were used for the analysis. Because a bee could visit an unlimited number of nectar-filled flowers, food availability did not diminish with time.

Metabolic rates of bees in flight have repeatedly been measured (e.g. Jongbloed and Wiersma 1934; Beutler 1937; Sotavolta 1954; Scholze et al. 1964; Bastian and Esch 1970; Heinrich 1979; Withers 1981; Rothe 1983). We assume that the metabolic rate during flight by an unloaded bee (70 mg) is 82 ml O_2/g/h (at average ambient temperatures during the experiment of 30° C, Heinrich 1979) which gives $a_0 = 3.34 \cdot 10^{-2}$ W. This value is close to figures provided by Bastian and Esch (1970), Withers (1981), and Rothe (1983) and takes into account that the bees spent most of their time in a more expensive manoeuvring flight, rather than in straight flight. The linear increase in metabolic rate with load, $a = 5 \cdot 10^{-5}$ W J^{-1} was estimated from findings of Beutler (1937), Heran (1962), Nuñez (1974), and Heinrich (1975): an increase of approximately 1% of the unloaded rate per mg of additional load.

It is assumed that the metabolic rate while in the hive, a_T, or handling a flower, a_h, is similar to that experienced by an actively moving bee which is not in flight. Where metabolic rates for this type of activity have been measured, the values given range widely (e.g. Kosmin et al. 1932; Bastian and Esch 1970; Rothe 1983 and references therein). Here, we will assume $a_T = a_h = 0.42 \cdot 10^{-2}$ W. This value amounts to 1/8 of the consumption of the unloaded bee in flight, and is close to figures suggested by Bastian and Esch (1970) for pre-flight activity, and Rothe (1983) for walking bees.

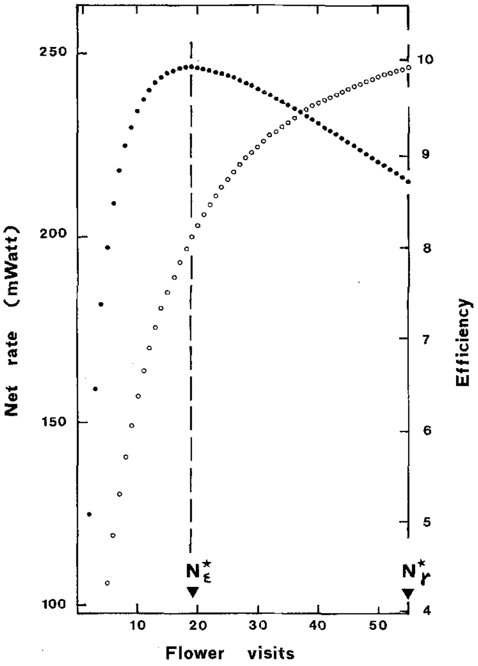

Fig. 2. *Ordinate: net rate* (o), and *efficiency* (•) that can be achieved by a bee which leaves the patch to return to the hive after 1, 2, 3...flower visits (*abscissa*). Net rate and efficiency are scaled such that the maximum has the same ordinate. The average parameter values for all individuals tested were used to generate this example ($\tau_0 = 22.8$ s, $h = 12.0$ s, $T_0 = 235.0$ s). Interflower flight time is $\tau = 20$ s. When maximising the net rate, the bee should leave the patch after $N^*_\gamma = 55$ flower visits, yielding a net rate of energy delivery to the hive of $\gamma = 245.5$ mW. For maximising efficiency, the bee should leave earlier, after $N^*_\varepsilon = 19$ visits (efficiency = 9.93)

Results

Equations (1) to (5) were used to find the optimal load size for two different models of foraging behaviour: maximizing the *net rate* of energy delivery to the hive $= (G - C)/T$, or maximizing the *efficiency*, i.e. energetic gain per unit of energy spent $= (G - C)/C$. The net rate or efficiency that can be achieved in a foraging cycle is, everything else kept constant, a function of the number of flowers visited before returning to the hive (Fig. 2). Repeated numerical evaluation of Eqs. (1) to (5) will thus lead to the number of flowers which results in the highest value for a chosen currency.

Both models predict that for large inter-flower times, the optimal number of flowers to be visited, N^*, is less than maximal crop capacity. The effect is more marked with the efficiency model, whereas the rate model would predict full loads for nearly all of the experimental conditions. As Fig. 3 shows, the observed numbers of flowers visited is indeed close to the numbers predicted by the efficiency model. For long inter-flower times, observations and predictions seem to be less consistent than for short inter-flower times.

The predictions in Fig. 3 are calculated with the average parameter values for all individuals. Yet, the individuals differed in their foraging parameters (τ_0, h, T_0) due to, for example, somewhat different flight paths to and from the hive. We therefore made a prediction for each bee separately by inserting the appropriate values into the model. The values of N observed and predicted in this manner are shown for both models in Fig. 4. As this figure shows, the predictions from the efficiency model do not differ significantly from the observations, but the rate model cannot account for the observations.

Sensitivity to parameter values. In order to study the sensitivity of our models to variations in the parameter values, the following modifications were made and their effect on our predictions evaluated numerically. The values of the parameters standing for the metabolic rates of bees (a_0, a, a_h, a_T) were

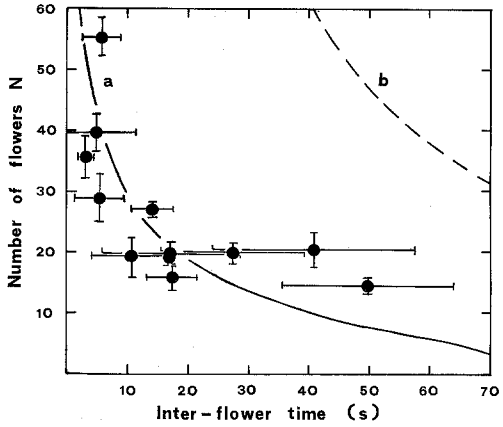

Fig. 3. The number of flowers visited, N (*ordinate*), as a function of inter-flower time τ (*abscissa*). The numbers predicted by the two models (curves in graph) correspond to the behaviour that maximises energetic efficiency (net energetic gain/energy expenditure, *solid line* (*a*), or maximises delivery rate to the hive (net energetic gain/time, *broken line* (*b*). With both models, partial crop loads are predicted for long inter-flower times. The observations for twelve different individuals are shown (●: mean; bars equal standard deviation). Observations were averaged over four consecutive foraging trips. As in Fig. 2 the predictions *a* and *b* were calculated with the average parameter values for all individuals tested. A full crop load corresponds to approximately 55 flowers

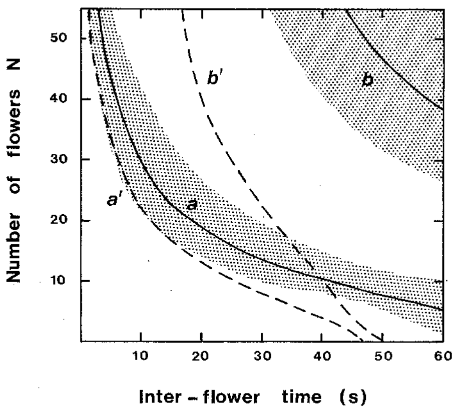

Fig. 5. Sensitivity of model predictions to variations in parameter values. *Ordinate, abscissa*, and predictions of the efficiency model (*solid line a*) or rate model (*solid line b*) as in Fig. 3. The *shaded areas* around *a* or *b* show the range of predictions (number of flower visits as a function of inter-flower time) if the following parameter values are doubled or halved: a_0, a, a_h, a_T (see text for definitions). If a decrease in load weight proportional to sugar consumption in flight is taken into account, the predictions are also within the shaded area. The *broken line a'* is predicted if either energetic expenditure while in the hive (a_T), or hive time (T_0) is omitted from the efficiency model. *Broken line b'* is predicted if hive time is omitted from the rate model

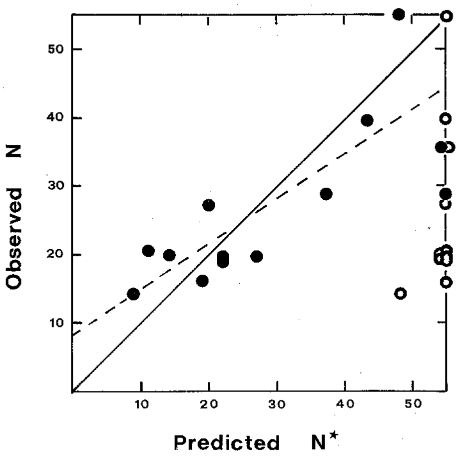

Fig. 4. *Ordinate:* the observed number, N, of flowers visited in the patch by individual bees before returning to the hive. *Abscissa:* number, N^*, of flowers to be visited, as predicted for the same individual, if either the net rate of energy delivered to the hive is to be maximized (rate model, o), or energetic efficiency is maximized (efficiency model, ●). The predictions are based on foraging parameters (τ, τ_0, h, T_0) as measured for each of the individuals separately. *Each circle* represents the observation as compared to the prediction of the particular model for a given individual. The mean inter-flower times (τ) range from 3.2 s to 49.9 s. The rate model cannot account for the results when observations and predictions are compared pairwise ($t = 8.54$, $P < 0.001$, $n = 12$). For the efficiency model, no significant difference is found (pairwise $t = 0.43$, $P > 0.1$, $n = 12$). The regression relating predictions of the efficiency model to observations is $n = 0.66 \cdot N^* + 8.30$ ($r = 0.831$, $P = 0.008$, $n = 12$)

doubled or halved in turn. As Fig. 5 clearly shows, under these modifications the efficiency model maintained a better fit than the rate model. The rate model proved to be generally more sensitive to variations in parameter values, as reflected in the wider range of predictions when values were doubled or halved (shaded area around b in Fig. 5). If hive time is not included in the foraging cycle, the rate model predicts values of N^* which are closer to observations (Fig. 5). Even in this case, however, efficiency yields a significantly better fit than rate when *deviations* (observed minus predicted) are compared pairwise for the two models (Wilcoxon's matched pairs signed rank test, $P = 0.01$, $n = 12$). A proportional decrease in load weight due to sugar consumption in flight was also taken into account, but proved to have little impact on the predictions (Fig. 5).

Discussion

We conclude that the crop-loading of bees can be predicted by assuming that the workers maximize energetic efficiency per foraging trip and incur increasing foraging costs due to the weight of their load. For both models considered here including additional energetic expenditure due to load weight results in smaller rather than larger loads (as in the case of De Benedictis et al. 1978). This finding differs from earlier theoretical claims that the effect of including energy costs should be an increase in load size (Orians and Pearson 1979, see also critique in Kacelnik and Houston 1984).

Whether or not time and energetic expenditure in the hive is included in the foraging cycle has an effect on the quantitative predictions (whereas the qualitative conclusions remain essentially the same in the present case). There is no a priori reason to exclude this period from a complete cycle. However, we would like to point out the importance of the social habit of the honeybee in deciding this question. A worker returning from a foraging trip will typically transfer its load to recipient bees in the hive. If the load is desirable relative to what is delivered by other workers at that time, the forager can unload very quickly and will also convey information about the food source by performing the bee's dance (von Frisch 1965, p. 30ff; Michener 1974, p. 182ff). Eventually, the worker will beg for food from others and leave the hive again (von Frisch 1965; Nuñez 1970). Only if a forager is unable to deliver the crop load, or takes a very long time to do so, will she remain in the hive or fly to a different patch (Michener 1974). This would show up in the experiment as the end of a foraging bout, but this was never observed – all bouts were terminated by the experimenter. A worker while in the hive between foraging trips will therefore typically not participate in activities unrelated to the foraging process itself (activities that should be excluded from the cycle or impose constraints on foraging time available, Lucas 1983), such as brood care or cleaning the comb. Rather, an individual adopts the role of a foraging bee late in her life (Lindauer 1952), and there seems to be a relatively sharp distinction between the activities of house bees and field bees in the case of *Apis* (Michener 1974). This temporal division of labour among workers of the honeybee, which is a typical feature of social insect colonies (Oster and Wilson 1978), could thus have profound consequences for how the foraging process should be analyzed theoretically.

The present study is restricted to a situation where workers have to collect food from very close to the hive. In a companion paper (Kacelnik et al., in preparation), we show that the same kind of analysis leads to similar predictions in a situation where food sources are available at different distances from the hive (up to 2000 m). In both cases, partial crop loads are to be expected for short distances and patches with low nectar yield. The question is not merely of theoretical interest, as partial crop-filling is observed under quite realistic conditions (Boch 1956; Nuñez 1982). In contrast, Seeley (1985) suggests that the concentration of nectar brought back from the various food patches within a colony's foraging range is the proximate cue that a bee colony could use to assess the profitability of different food sources, since (the similarly sized) workers usually return to the hive with full loads. This view is not supported by our analysis.

But why should bees, when foraging, maximize energetic efficiency rather than delivery rate to the hive? The rationale underlying the use of models of net rate maximization is the assumption that each calorie spent in foraging is compensated by an extra calorie gained through foraging. This assumption, however, is not necessarily true for animals such as the honeybee. Workers seem to be constrained not by a fixed (life) time available for foraging, but instead by a limited amount of flight performance. As this budget is used, the flight metabolism degenerates and the workers become unable to forage (Neukirch 1982). Therefore, each calorie spent is essentially a non-renewable loss of foraging capacity. If the hive is limited by the number of individuals that can be produced in a given season, as it is likely to be the case, a hive would therefore accumulate more resources if its workers maximize efficiency in foraging rather than if they gathered energy at the greatest instantaneous rate. We therefore suggest that such constraints, set by physiology or population mortality schedules, should be included in the functional analysis of foraging behaviour.

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