

## Central-place foraging in honey bees: the effect of travel time and nectar flow on crop filling

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**Summary.** Crop-filling by honeybees foraging at sources of variable nectar flow at a fixed distance from the hive has been shown to maximize energetic efficiency, defined as ratio of energy gained to energy spent. Predictions based on maximisation of rate of energy gain, defined as net energy gained per unit time foraging, are significantly different from observed behaviour (Schmid-Hempel et al. 1985). In this paper we consider the effect of varying travel times in addition to flow rate. The predictions of an extended version of our theoretical model are confronted with experimental results obtained by Núñez (1982). Núñez found that bees filled their crops more fully for higher flows and longer travel times. We show that when the cost of carrying a load is considered, this trend can be predicted by maximising either energetic efficiency or net rate of gain. Figure 1 shows, however, that maximisation of net rate of gain can only produce an acceptable quantitative fit if unreasonably high costs are assumed to result from carrying the load. Energetic efficiency instead generates a good quantitative fit for acceptable assumptions about this cost (Fig. 2).

### Introduction

Optimality accounts of behavioural patterns are often too specific. Models are formulated so as to fit a given environment (Kacelnik and Cuthill in press), natural or experimental, seldom having the ability to make precise quantitative predictions beyond that environment. The serious consequence

of this limitation is that results are not commonly replicated. In this paper we test the performance of a model of crop-filling in honeybees (*Apis mellifera*) developed in one environment (Schmid-Hempel et al. 1985) when compared with data collected in a different situation. The logic of the original model is maintained, but its mathematical formulation is modified to make it applicable to a different set of results.

We reported elsewhere (Schmid-Hempel et al. 1985) on crop-filling by bees foraging in a food source at a fixed distance from the hive (30 m) and providing a range of inter-flower times approximately equivalent to sucrose flows of 0.6 to 2.4 mg/min at the source. The results were consistent with the maximisation of the ratio of energy gained per unit of energy spent. This currency is usually named “energetic efficiency”. The model used to formulate the predictions considered the energetic cost of transporting the load in the short flights between flowers while the bee was in the inflorescence (patch), and the cost of carrying the load back to the hive. Both costs were assumed to be proportional to the load, resulting in optimal loads that were for some inter-flower-times less than full crops. The effects of load on flight velocity were not included, and the model was solved by numerical iteration on the number of florets visited.

As an alternative possible currency, we tested the predictions of a model based on maximisation of energy delivered to the hive per unit time (delivery rate). The qualitative trends predicted by this model were similar to those obtained when the efficiency currency was used, but the results did not agree quantitatively with the observations. Why should honey bees maximise energetic efficiency instead of rate of energy delivered per unit of time?

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We argued that this policy might be favoured because of a combination of elements in the bees' life-history. Firstly, individual workers seem to be constrained by a limited flight budget (Neukirch 1982) so that by maximising delivery per unit of expenditure they may in fact be maximising the total amount of nectar delivered during the life of each worker. Secondly, and considering now the interest of the hive as a reproductive unit, the conversion of sugar into workers may be limited by a number of additional factors, resulting in more drones and queens being produced in a season if workers maximise foraging performance per individual than if individuals achieve greater delivery rates at the expense of shorter lives. This rationale was post-hoc, and subject to the possibility that its validity is limited to certain situations. We reasoned that the strength of the argument would be increased if the model was made more general and if it was accurate in predicting behaviour in different circumstances. In particular, our experiments did not explore the effects of both flying distance and nectar concentration, both important environmental variables for which the model can make specific predictions. Among various previous studies of crop filling in hymenoptera in relation to environmental variables the experiment reported by Núñez (1982) offered an ideal opportunity to test the predictions of our model, as it was conducted in the species for which the model was developed and for which physiological parameters are best known. The same theoretical framework can be used to explore other cases of partial crop filling in social hymenoptera (*viz* Pflumm 1971) but in this paper we restrict ourselves to the analysis of honeybees.

Núñez (1982) measured the patch residence time of bees collecting nectar from an artificial food source. In addition to varying the nectar flow, he varied the distance between the source and the hive, using values much closer to natural environments than those used by Schmid-Hempel et al. (1985) (see Visscher and Seeley 1982).

Qualitatively, Núñez found that the bees filled their crops more fully when the nectar flow was higher and when the travel time was longer. The correlation between load and travel time is a common finding in central place foraging (see Kacelnik and Houston 1984 and Kacelnik and Cuthill 1986). It is somewhat surprising here because the flow of nectar in this experiment did not decrease with time in the patch, *i.e.*, Núñez (and also Schmid-Hempel et al.) used non-depleting patches. Also, the results could not be explained in terms of a rigid decision rule based on overall food availabili-

ty because while higher flows increased overall rate of gain, longer travels decreased it, and yet both treatments resulted in bigger loads. Núñez called attention to the bees' need to exchange information, which results in a certain cost of long absences from the hive, and suggested how this may account for the observed qualitative trends. We find his arguments plausible, but we aim at showing that a purely energetic model that ignores information exchange can produce accurate quantitative predictions.

## Model developments

If Núñez' bees were maximizing efficiency, it ought to be possible to formulate a model based on the same principles as that of Schmid-Hempel et al. (1985) but capable of dealing with the environment offered by Núñez' experiment. In order to do this, we modified the model by describing the loading process as a continuous function instead of a discrete process based on number of florets. In addition, and because the flight distances were much greater in Núñez' experiment (100 m to 2,000 m instead of 30 m) we added the effects of loads on flight velocity. This new model makes it possible to find an expression for the optimum load as a function of time in the patch, instead of iterating on the number of florets visited as before. The predictions of this model were compared with the data previously reported by Núñez, but the process required some unorthodox numerical techniques in order to estimate parameter values. We see these innovations as a fundamental part of the content of this paper, together with our specific claim for the evidence supporting efficiency maximisation.

### *The model*

Our argument depends on the fact that metabolic rates and flight velocity are functions of crop load. The maximum capacity of a bee's crop,  $L_M$ , is approximately 60  $\mu\text{l}$ , equivalent to 36 mg of sucrose (see Appendix).

Assuming that the effects of carrying weight on both metabolic expenditure and velocity are proportional to the weight itself, we can calculate the rate of energy delivery to the hive as a function of crop filling. To do this, we shall consider the energy balance during the outward trip, the time in the inflorescence and the inward trip.

*Outward trip.* The energy spend during this stage ( $C_0$ ) is

$$C_0 = B D/v \quad (1)$$

where  $B$ : metabolic rate during unloaded flight ( $\mu\text{g sugar s}^{-1}$ );  $v$ : flight velocity during unloaded flight ( $\text{m s}^{-1}$ ) and  $D$ : Distance between hive and foraging patch (m). The bee is assumed to know beforehand how far it is going to travel, and to leave the hive with exactly  $C_0$   $\mu\text{g}$  of sugar in its crop, thus reaching the patch with an empty crop. The net balance on arrival at the patch is  $-C_0$ .

*On the patch.* The rate of change in net crop load ( $L$ ,  $\mu\text{g}$ ) while in the patch is given by

$$\dot{L} = Q - B_p - aL \quad (2)$$

where  $Q$ : solution flow in the inflorescence ( $\mu\text{l s}^{-1}$ ),  $B_p$ : metabolic rate during unloaded foraging in the patch ( $\mu\text{g sugar s}^{-1}$ ),

and  $a$  is the parameter of linear increment in foraging metabolic rate as a function of load ( $s^{-1}$ ). For simplicity we write

$$\dot{L} = F - aL \quad (3)$$

where  $F = Q - B_p$ .

Integrating (3) gives

$$L(t) = F/a + k_1 e^{-at} \quad (4)$$

where  $k_1$  is the constant of integration. Since the bee arrives with an empty crop (i.e.  $L(0) = 0$ ), it follows that  $k_1 = -F/a$ , so that

$$L(t) = (F/a) (1 - e^{-at}) \quad (5)$$

*Inward flight.* Metabolic rate is assumed to be a function of carried load, but load changes during flight due to consumption. The rate of change in  $L$  is given by

$$\dot{L} = -B - kL \quad (6)$$

where  $k$  ( $s^{-1}$ ) is the factor expressing the linear increment in flight metabolic rate due to the carried load. To calculate the net load at the end of an inward trip that starts at  $x=0$  and ends at  $x=T$  we integrate (6), which gives

$$L(x) = k_2 e^{-kx} - B/k \quad (7)$$

where  $k_2$  is the constant of integration. We find  $k_2$  by considering the load at the start of the inward flight. Calling this load  $L_0$ , for  $x=0$  we get  $L_0 = k_2 - B/k$ , i.e.,  $k_2 = L_0 + B/k$  and thus,

$$L(T) = (L_0 + B/k) e^{-kT} - B/k \quad (8)$$

where  $L_0 = (F/a) (1 - e^{-aT})$  and  $T = D (1/v + zL_0)$ , with  $z$  ( $s m^{-1} \mu g^{-1}$ ) expressing the drop in velocity as a function of crop load. Notice that we ignore the effect on velocity of the change in load during flight. This is because doing otherwise would unduly complicate the equations without introducing almost any change in the predictions.

Finally, let  $t_H$  denote the time in the hive during which the metabolic rate is  $B_H$ . The energy expenditure in the hive is therefore  $B_H t_H$ . We can now find the payoff corresponding to a given time in the patch for each of the two currencies, rate of energy delivery,  $R(t)$ , and energetic efficiency,  $E(t)$ .

#### Net energy delivery rate, $R(t)$

This currency is defined as the net energy gained per unit of time. From the above equations,

$$R(t) = (L(T) - B D/v - B_H t_H) / (t + D/v + T + t_H). \quad (9)$$

#### Energetic efficiency

This currency is the energy gained per unit of energy spent. From the previous definitions,

$$E(t) = Qt / (Qt - L(T) + B D/v + B_H t_H). \quad (10)$$

#### Finding the optimum $t$

We can now seek the value of  $t$  that maximises  $R(t)$  and  $E(t)$ . It is possible to differentiate the equations for  $R(t)$  and  $E(t)$  with respect to  $t$  and set the result equal to zero, but the resulting equations are complicated and have to be solved numerically. It is more straightforward to find the optimum numerically from the equations for  $R$  and  $E$  (Eqs. 9 and 10).

Corresponding crop loads can be found by the equation:

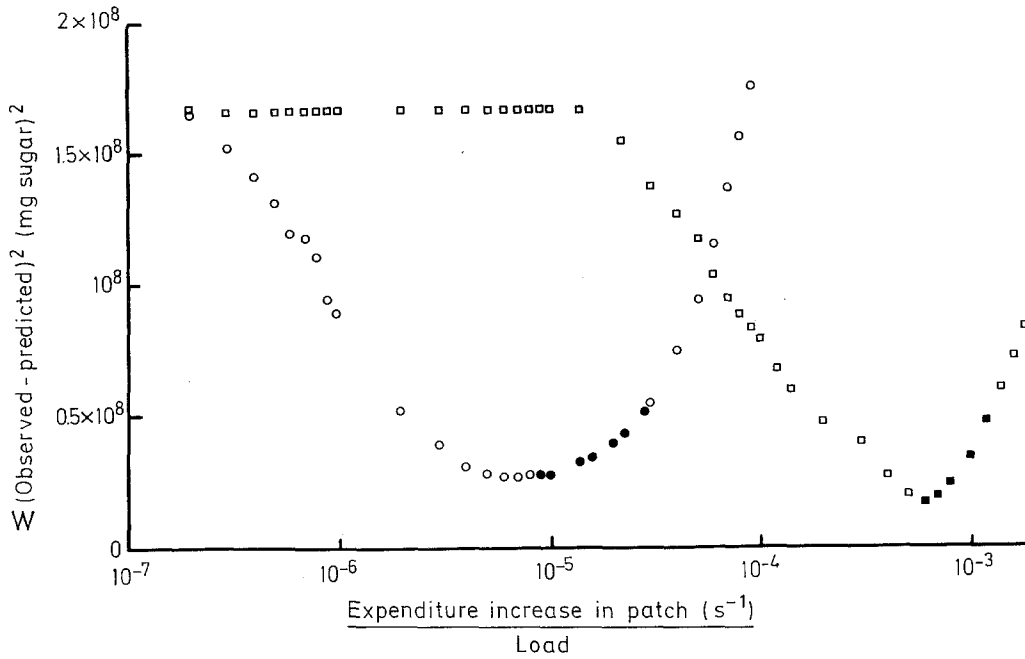
$$L^* = Qt^*. \quad (11)$$

## Results

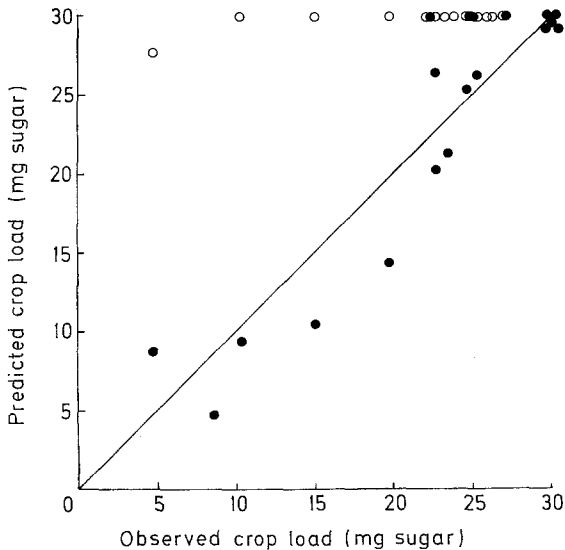
Both currencies predict successfully the trend in Núñez' results: optimal loads under either model are decelerating positive functions of both flow and travel time. The quantitative predictions however are widely apart.

As discussed in the previous section, the quantitative predictions depend on a number of physiological parameters, but most notably on the assumed costs (in terms of metabolic rate and flight velocity) of carrying the load. In general, the lower these costs, the larger the predicted optimal loads, so that when the load-related costs are assumed to be low, predicted loads are larger than anatomical constraints allow for, and one expects to see the bees filling their crops. Nevertheless, as the assumed costs are increased, the two currencies behave very differently in quantitative terms. Because of this difference, it is possible to separate the currencies by their performance in terms of quantitative fitting of the experimental results. We can do this by iterating on the value of the fundamental parameter  $a$  (metabolic increase due to carrying the load, see Appendix) in order to find the range of values for which each of the currencies results in a good quantitative fit to the behavioural data. Once these values are known, it is possible to test the two currencies in two respects: a) How good is the fit when predictions for each currency are based on its most favourable parameter assumption? and b) Do the required values of metabolic cost fall within possible physiological values? This technique is a variant of "inverse optimality" (McFarland 1977; Kacelnik et al. 1981).

Figure 1 shows the goodness of fit of both versions of our model for an extended range of values of the parameter  $a$ , the increase in metabolism per mass of load transported. For both currencies there is a range in values of  $a$ , extending roughly for a third of a logarithmic cycle, where the sum of the squares of the deviations between predictions and results is minimum, and where there is no significant difference between predicted and observed loads ( $P < 0.05$ ,  $t$ -test). As discussed in the previous section, and in the Appendix, the true value of  $a$  must be below  $3 \times 10^{-5}$  (units:  $s^{-1}$ ), that is below the range in values of  $a$  where the rate model behaves satisfactorily but above the range where efficiency fits the data. On this basis it is possible to exclude rate maximisation but maintain efficiency maximisation as consistent with the bees' behaviour. The observed crop loads are shown plotted against predicted loads using the "best guess" for the value of  $a$  in Fig. 2.



**Fig. 1.** The sum of the squared deviations between the predictions and the Núñez' observations plotted as a function of the parameter  $a$ . This parameter determines the increase in metabolism as a function of load while the bee is in the patch. The circles represent the efficiency model and the squares the rate model. In each case the filled symbols indicate values for which a  $t$ -test indicates no significant difference between observations and predictions at the 0.05 level. Since the estimated upper limit of the parameter  $a$  is  $3 \times 10^{-5}$ , only the efficiency model produces accurate predictions in the acceptable range of physiological assumptions



**Fig. 2.** Predicted versus observed crop loads. The predictions are based on the value of the parameter  $a$  that generates the smallest  $t$  value between predictions and results for the efficiency model ( $t=0.888$ ). Empty circles represent the efficiency model and filled circles represent the rate model

Notice that at travel times beyond that for which complete crop filling is predicted, no correlation between travel time and observed load is possible. This travel time is of course a function of flow, but for intermediate flows in Núñez' experiment, the efficiency model with its best parameters predicts full loading slightly above 1,000 m, so that one ought to expect that the effect of travel time on load would be only noticeable below this distance. This is indeed what Núñez reported: loads increased in the range between 100 and 1,000 m but did not vary between 1,000 and 2,000 m. One interesting discrepancy between our predictions and the observed results is that according to the model high flows would favour filling of the crop at all the experimental distances, but this was not observed in the data. Instead, at and below 600 m crop load increased with flow but reached a plateau below the maximum.

## Discussion

Our main conclusion is that honey bees foraging for nectar fill their crops to an extent consistent with the maximisation of the ratio between energy

delivered to the hive and energy spent by the individual worker.

This result is the same as reported previously (Schmid-Hempel et al. 1985), and is consistent with the hypothesis that individual honey bee workers may be limited in the amount of work they can perform in their life span.

There is additional independent evidence consistent with efficiency maximisation: Waddington (1985) reported that the attractive value of a food source as evaluated by the recruiting dance is affected positively by its rate of food delivery and negatively by energy expenditure, but that the effects were not additive on an energetic scale: costs had greater effect than intake. This is consistent with an utility function in which the value of each food source is proportional to the energy obtained and to the reciprocal of the cost, rather than to cost with negative sign. Efficiency has this property, while rate maximisation does not.

Our study underlines the necessity of formulating optimality models in precise quantitative form. Here, two versions of a model agree with the qualitative trend observed in the data, but one of them requires unreasonable values of a crucial physiological parameter in order to fit the results quantitatively. Used in this way, optimal foraging models have the additional advantage of highlighting physiological properties that may have been overlooked and that have ecological significance, providing a framework for the integration of physiological and behavioural ecology.

As an example of this advantage, it is interesting to note that Seeley (1985) in his detailed analysis of the strategy of honey bee foraging calculated that the gross rate of energy intake is a close approximation of the net rate of intake (his Fig. 5), and concluded that it is fair to characterize patches by the gross energy obtained by a bee that filled its crop fully. This is not our conclusion. The modal distance of foraging trips in a variety of habitats is around 600 m (Seeley 1985) and both the data collected by Núñez and our theoretical calculations indicate that bees do not (and should not) fill their crops at those distances. Thus, for most foraging trips the behaviour of the bees is consistent with a rather precise effect of energy costs, i.e. with the analysis in terms of net rather than gross estimates of energy gain.

Our emphasis has been on the performance of two alternative energetic hypotheses, and we showed that our current knowledge allows us to reject one of them (rate maximisation) but not the other (efficiency maximisation). In the current controversial climate surrounding the application of

optimality to animal behaviour it is perhaps worth pointing out the obvious: while the rejection of one model is an unambiguous step forward, being unable to reject another model is not equivalent to prove it to be right. A good quantitative fit ought instead to be considered good inductive evidence in favour of the interpretation of the biological phenomena embodied in the model. We are not as yet in a position to make claims about the uniqueness of our interpretation.

## Appendix

### *Parameter values used in the model*

The experimental situation from which our present data set is derived (Núñez 1982) is different in important details from the situation described earlier (Schmid-Hempel et al. 1985). In choosing the numerical values for our model parameters we took account of these differences, although using the same set of measurements as available from the literature.

*Metabolic rate while in the hive  $B_H$ .* No measurements of this rate in the literature are known to us. As in Schmid-Hempel et al. (1985), we assume this value can be approximated by the rate of a walking bee, thus  $B_H = 0.25 \mu\text{g s}^{-1}$  ( $10 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) at a hive temperature in the range of  $30^\circ\text{--}35^\circ \text{C}$ .

*Travel between hive and food source.* In his experiments, Núñez (1982) does not report the actual time spent in flight between hive and source, but rather the time the bee was absent from the source until return. We derive the flight time by assuming a constant velocity  $v$  of  $8 \text{ m s}^{-1}$  for the unloaded bee, similar to Boch (1956), von Frisch (1965, p. 195), and Levchenko (in Núñez 1982), together with taking into account distance. The average weight of the unloaded bee is 70 mg, and a full crop load is taken to be 36 mg of sugar (i.e.  $60 \mu\text{l}$  of 50% w/w sugar solution), as suggested by the observed average maximal crop load in the experiments (Fig. 3, Núñez 1982). To calculate the flight time for the loaded bee on her way back to the hive, we assume that flight velocity decreases linearly with the weight of the crop load, with slope  $z = 2.1 \times 10^{-6} \text{ s m}^{-1} \mu\text{g}^{-1}$ . A fully loaded bee thus has an average flight speed of  $5 \text{ m s}^{-1}$ , in broad agreement with the findings of Boch (1956) and Heran (1962). Scholze et al. (1964) measured the energy consumption of freely flying bees. These figures have to be corrected to account for the extra load (a piece of wire) their experimental bees permanently carried with them. When this is done, Scholze et al.'s rates are very close to the ones reported by Sotavolta (1954) and Rothe (1983). We used  $B = 1.50 \mu\text{g s}^{-1}$  which corresponds to Rothe's value of  $62 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ). This value is lower than the one used in Schmid-Hempel et al. (1985), since in the latter case, the bees spent virtually all of their flight time in a presumably more expensive manoeuvring flight. As justified in our earlier study, the increase in metabolic rate of flying is roughly 1% per mg of crop load, therefore  $k = 3 \times 10^{-5} \text{ s}^{-1}$  (1 mg of load = 0.5 mg of sugar).

*At the food source.* The food source used by Núñez (1982) mimicked the natural situation of a dense array of flowers in that the bees had to fly frequently from one flower to the next in order to collect "nectar". Thus, the patch residence time reported by Núñez is composed of periods of extracting nectar,

while sitting on flowers, interrupted by short bouts of flights between "flowers". Though Núñez did not report the durations of these different activities, the flower visitation rates given by him (7 to 10 flowers  $\text{min}^{-1}$ ), together with the physical dimensions of the feeding apparatus, allow one to estimate the relative proportion of total patch time that is spent in flight or sitting on flowers. Given that the change-over time, i.e. flying between two flowers, is in the order of 2 s, we estimate that 30% of the patch residence time is actually spent in flight. Thus the metabolic rate in the patch before taking into account the load is  $B_p = 0.45 \mu\text{g s}^{-1}$  (30% of  $B$ ). The numerical value of  $a$  – increase in metabolic rate with load in patch – is the least known among any of the parameters needed for the model. In addition, we found that the model is quite sensitive to variation of this value. The magnitude of  $a$  is influenced by assumptions about the magnitude of metabolic rate of the unloaded bee ( $B$ ), the proportion of the time in the patch that the bee is in flight, and the increase in rate with crop load during flight ( $k$ ). A reasonable upper limit results from assuming that  $a$  equals  $k$ , i.e. that the bee spends all its time in the patch flying. Under this assumption  $a = 3 \times 10^{-5} \text{ s}^{-1}$ . A more likely value of  $a$  results from assuming that only about 30% of the patch time is spent in flight, in which case  $a = 0.90 \times 10^{-5} \text{ s}^{-1}$ . In spite of this three-fold possible variation in the value of a crucial parameter, the range of possible values is narrow enough to separate the predictions of the two models (see Fig. 1).

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