

Paying for nectar with wingbeats: a new model of honeybee foraging

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Honeybees acquire wing damage as they age and older foraging honeybees accept lavender inflorescences with fewer flowers. These indicate the operation of some kind of optimal response, but this cannot be based on energy because energy expenditure does not change as the wings get damaged. However, wingbeat frequency increases with wing damage. A deterministic analytical model was constructed, based on the assumptions that bees have a limited total number of wingbeats that the flight motor can perform and that they maximize lifetime energy profit by conserving the number of wingbeats used in foraging. The optimal response to wing damage is to reduce the threshold number of flowers needed to accept an inflorescence. The predicted optimal gradient between wing damage (wingbeat frequency) and acceptance threshold (number of flowers on an inflorescence) was close to the observed gradient from field data. This model demonstrates that wear and tear is a significant factor in optimal foraging strategies.

Keywords: wing damage; *Apis mellifera*; inflorescence choice

1. INTRODUCTION

Optimal foraging models typically assume a currency of either net rate (energy profit per unit time) or efficiency (energy profit per unit energy spent) (see Stephens & Krebs 1986). These models have been outstandingly successful in predicting foraging behaviour in a wide variety of animals such as honeybees (Ydenberg *et al.* 1994), starlings (Bautista *et al.* 2001), bumble-bees (Goulson 2000), squirrels (Ritchie 1990), and humans (Pietras *et al.* 2003) and form a subset of the general approach of optimality (Maynard Smith 1978; Parker & Maynard Smith 1990). Although animals probably cannot monitor rates of energy gain or use, we assume that evolution will have acted to create 'rules of thumb' that lead to behaviour similar to that expected if the animal were maximizing one of these currencies; because of this, researchers can build models using these currencies and hence predict behaviour (Ydenberg & Schmid-Hempel 1994; Vasquez & Kacelnik 2000; Ollason & Ren 2002).

More recent work on foraging bees, especially that of Schmid-Hempel and colleagues, has usually assumed efficiency to be the currency that evolution has acted to maximize. Several analyses of foraging problems have used this currency, including optimal crop load (Schmid-Hempel *et al.* 1985; Wolf & Schmid-Hempel 1989; Kacelnik *et al.* 1986) and departure rules (Schmid-Hempel 1986), although energy gain rate is typically also regarded as important (Houston *et al.* 1988; Cartar & Dill 1990; Wells *et al.* 1992) because crop load affects energy use (Wolf *et al.* 1989; Feuerbacher *et al.* 2003).

The choice of efficiency as the currency for modelling foraging honeybees is supported by work that hints at the possible mechanism. Worker longevity is related to work rate (Schmid-Hempel & Wolf 1988), and total flight performance appears to be fixed (Neukirch 1982).

Foragers usually only survive two to three weeks, whereas overwintering bees can live for months, suggesting that it is something about foraging that causes faster ageing (Seeley 1985). If honeybees die after expending a certain amount of energy, then evolution should maximize profit per unit of work done. Neukirch (1982) showed that older workers have a reduced glycogen-synthesizing ability in their flight mechanism, and suggested that 'bees exhaust their energy-supplying mechanisms after a definite total flight performance' (p. 35). This may account for the increased mortality rate as foragers age (Visscher & Dukas 1997; Hutchinson 2000).

Honeybee workers accumulate wing damage as they age, and this accumulation follows an exponential curve (Higginson & Barnard 2004). Artificially adding damage to bumble-bee wings by clipping results in reduced life expectancies (Cartar 1992). Cartar (1992) proposed two possible causes for this increased mortality. Bees with more damaged wings may be less manoeuvrable, resulting in decreased ability to avoid predators. Indeed, there is some evidence that honeybees with more damaged wings are clumsier fliers (A. D. Higginson, unpublished data). Alternatively, more damaged bees may expend more energy in flying, and so die sooner. This could be due to faster exhaustion of some aspect of flight that has a limited budget. However, Hedenström *et al.* (2001) showed that clipping bumble-bee wings does not increase the energetic cost of flight, and supposed that decreased manoeuvrability must be the cause of increased mortality in bees with more wing damage.

Crucially, Hedenström *et al.* (2001) also report that clipping wings does increase wingbeat frequency in bumble-bees. Is it possible that the actual constraint of Neukirch (1982) is that because of wear and tear the flight motor is only capable of a finite number of wingbeats? Hence, although efficiency may be the most appropriate currency in bee foraging, the data also support the use of a different currency: energy profit per wingbeat. This paper

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Table 1. The default values for the parameters and the initial values of variables that were estimated for the model.

parameter	default	basis
proportion of time spent flying while foraging	0.226	A. D. Higginson (unpublished data)
maximum life span observed	16 days	A. D. Higginson (unpublished data)
size of bout	100 inflorescences	A. D. Higginson (unpublished data)
maximum lifetime wingbeats (product of)	3600	seconds per hour
	5	hours foraging per day (A. D. Higginson, personal observation)
	16	days of life
	234	starting wingbeat frequency
	0.226	proportion of time spent flying while foraging
mean number of flowers	8.85	A. D. Higginson (unpublished data)
standard deviation of number of flowers	5.593	A. D. Higginson (unpublished data)
search time	1.121	A. D. Higginson (unpublished data)
predatory risk per visited inflorescence	2 per 100 000	Morse (1986)
increase in threshold due to learning per inflorescence	6 per 10 000	A. D. Higginson (unpublished data)

explores whether the use of this new currency can explain otherwise puzzling aspects of honeybee foraging.

2. FIELD DATA

The model reported here is based on data gathered at the Quinta de São Pedro research station (38°39' N, 9°11' W), Sobreda de Caparica, Portugal. The workers of eight hives of honeybees (*Apis mellifera*) forage for nectar and pollen (Herrera 1990; Gonzalez *et al.* 1995) on a neighbouring (10–20 m away) stand of lavender (*Lavandula stoechas*). Previous work on this system has shown that nectar-foraging bees discriminate among inflorescences on the basis of morphological cues (mainly the number of open flowers and terminal bracts), probably maximizing their energy return during foraging bouts (Duffield *et al.* 1993; Gonzalez *et al.* 1995). Choosing inflorescences, however, requires bees to inspect flower inflorescences on the wing before alighting (Duffield *et al.* 1993; Gonzalez *et al.* 1995). Recently we showed (Higginson & Barnard 2004) that honeybees accept poorer quality inflorescences as they age and accumulate wing damage, suggesting that bees may be changing their behaviour to reduce the amount of time they spend in flight.

3. THE MODEL

We assume that foragers act to maximize their lifetime energy input to the hive by maximizing the expected energy profit per wingbeat. The optimal solution is assumed to be affected by two major influences: the effects of wing damage and the mortality risk from predators. Although not inevitable, there is a substantial risk that the wings of an individual bee will become damaged as it forages because of accidental strikes against vegetation (A. D. Higginson, unpublished data). The level of predation risk determines whether bees live long enough for the wing-damage effect to become important. If they survive to acquire wing damage, their wingbeat frequency inevitably increases because of the properties of the thoracic box and wing inertia. This means they should spend less time in flight to keep their expected energy profit per wingbeat at the maximum possible. The mechanism for this is likely to be related to the lowering of a critical threshold of inflorescence quality that must be passed so that the forager alights on any given inflorescence. Lowering this

threshold, becoming less choosy, would result in a reduction in the number of wingbeats spent in foraging in any one foraging bout. A simple estimate of inflorescence quality is the number of flowers on the inflorescence.

A model was therefore constructed based on a mechanism of a quality threshold (number of flowers) for accepting an inflorescence, constrained by predation risk and the need to conserve wingbeats. The model explicitly does not include rejections of inflorescences caused by scent marking (Williams 1998; Goulson *et al.* 2001; Guirfa & Nunez 1992), which will cause rejections of apparently better-quality inflorescences.

(a) Assumptions

The parameters and initial values of variables (table 1) and relationships that comprise the model (figure 1) were estimated from observed data from Portugal and the work of other researchers.

The work of Cartar (1992) and Neukirch (1982) suggest that the flight machinery wears out after a certain number of wingbeats: this is the major constraint of the model. The mechanism may be related to muscle deterioration, wear and tear of the wing joint, deterioration of glycogen-synthesizing ability, or using up a glycogen budget. A value for the limiting number of wingbeats was estimated from the maximum observed foraging lifespan of bees in Portugal, together with an estimate of the proportion of time they spent flying. The latter came from the observed proportion of time spent flying while foraging (mean: 0.226) and the assumption that bees forage for 16 h a day but are in the hive for half that time.

For modelling purposes we used a theoretical normalized distribution of the number of flowers on 100 inflorescences, based on the observed mean and standard deviation of all inspected inflorescences (table 1; for details see Higginson & Barnard 2004). All frequencies of negative numbers of flowers in this theoretical distribution were added to the frequency of zero flowers: the resulting distribution matches the data remarkably well (figure 1a).

Measurement of the amount of nectar secreted by inflorescences with different numbers of flowers showed that the relationship between the number of flowers and the total amount of nectar (on an inflorescence) is nonlinear and best fits an increasing exponential (figure 1b; see Higginson

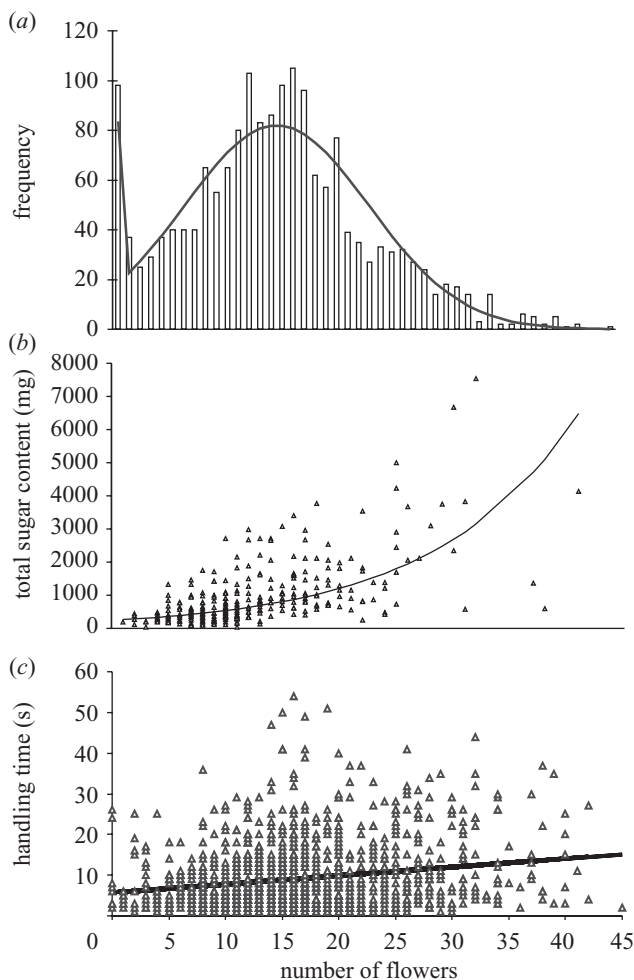


Figure 1. The observed data used by the model. (a) The fitted normal distribution (solid line). The fitted line is calculated from the mean and standard deviation of 1940 inflorescences, but the zero term is the sum of the zero and all negative frequencies. This is very similar to the actual frequencies (open bars) for the number of flowers on the inflorescences. (b) The fitted curve of the total amount of nectar against the number of flowers on the inflorescences: the fitted exponential is $\exp(5.4913 + (0.08014 \times \text{number of flowers}))$. (c) The effect of the number of flowers per inflorescence on the time spent on the inflorescence (1261 observations). The fitted line has the equation $5.66 + 0.21x$.

& Barnard 2004). Hence, each flower on inflorescences with more flowers secretes relatively more nectar.

Numerous observations of bee foraging (Higginson & Barnard 2004) show that the fitted line relating handling time to inflorescence size is linear (figure 1c), with bees spending more time on inflorescences with more flowers.

The observed accumulation of damage with bee age fits an exponential curve (Higginson & Barnard 2004), whereby damaged bees accumulate damage faster. We have used this relationship (because it is the only estimate we have) even though it is likely to be an underestimate for two reasons: first, because bees were not followed from eclosion, but rather from the time they were first seen in the field; and second, because the most-worn bees cannot fly and are therefore not detected. The net effect of such overestimation of the onset of significant wing wear, and underestimation of its eventual severity, is artificially to

broaden the period of foraging life over which decisions are made by wing-worn bees.

The model assumes that the true limit to individual life-span is set by a finite lifetime number of wingbeats, rather than age. To transform age in hours to number of wingbeats, we assume that bees forage for one-third of each 24 h period and are actually in flight for approximately a quarter of that time (table 1). We also assume that bees acquire wing damage exclusively while flying: we have some evidence that bees acquire at least some of this wing damage from brushing their wings on tough plant material while in flight (A. D. Higginson, unpublished data). Hence, the following formula was used to relate wing damage to the total number of wingbeats performed during the lifetime so for:

$$\text{wing damage (percentage wing area)} = 1.0768 \times \exp(0.0168 \times \text{lifetime wingbeats}/140400).$$

Data from bumble-bees show a 6.56% increase in wingbeat frequency caused by removal of 10% of the wing area (Hedenström *et al.* 2001). Using a wingbeat frequency of 234 Hz for honeybees (Feuerbacher *et al.* 2003) at zero wing damage, and assuming that the effect of damage on wingbeat frequency is linear, we could estimate the wingbeat frequency for a bee with any given amount of damage. For example, a honeybee with 10% wing damage has a wingbeat frequency equal to 106.56% of 234 Hz, which is 249.35 Hz. The formula that relates wing damage (percentage wing area) to wingbeat frequency (in hertz) is:

$$\text{wingbeat frequency} = 234 + (\text{wing damage} \times 0.00656 \times 234).$$

The only cause of mortality before the wingbeat limit in the model is predation. In Portugal, crab spiders (*Misumena* and *Synaema* spp.) appear to be the main honeybee predators: in a seven week season, six bees were found killed by these spiders on the lavender inflorescences of a 10 m² area (A. D. Higginson, personal observation). Using data from the crab spider *Misumena vatia* on milkweed in the eastern USA, Morse (1986) estimated that the mortality risk to insect visitors per inflorescence visit was 2–8 in 100 000. In the model, every acceptance of an inflorescence carries a constant probability of being killed. The probability that the forager is still alive is calculated from the total number of inflorescences visited in its lifetime. Each time the bee visits an inflorescence the crop taken from the inflorescence is multiplied by this ever-decreasing probability to give the average crop collected by a forager per inflorescence.

(b) Process

The model finds the optimal gradient between the acceptance threshold and wing damage (figure 2). Because the forager flies to every inflorescence and spends time deciding whether or not to alight on it, the average inter-inflorescence flight time is assumed to be constant for the whole array. The observed value is 1.12 s, but this does not include the time taken to fly to and from the hive, small in Portugal but potentially much greater in other habitats (table 1). All other costs and benefits change as the threshold changes. The proportion of inflorescences that are accepted is calculated from the threshold and the distribution of figure 1a. When the number of flowers on an inflorescence is greater than or equal to the threshold,

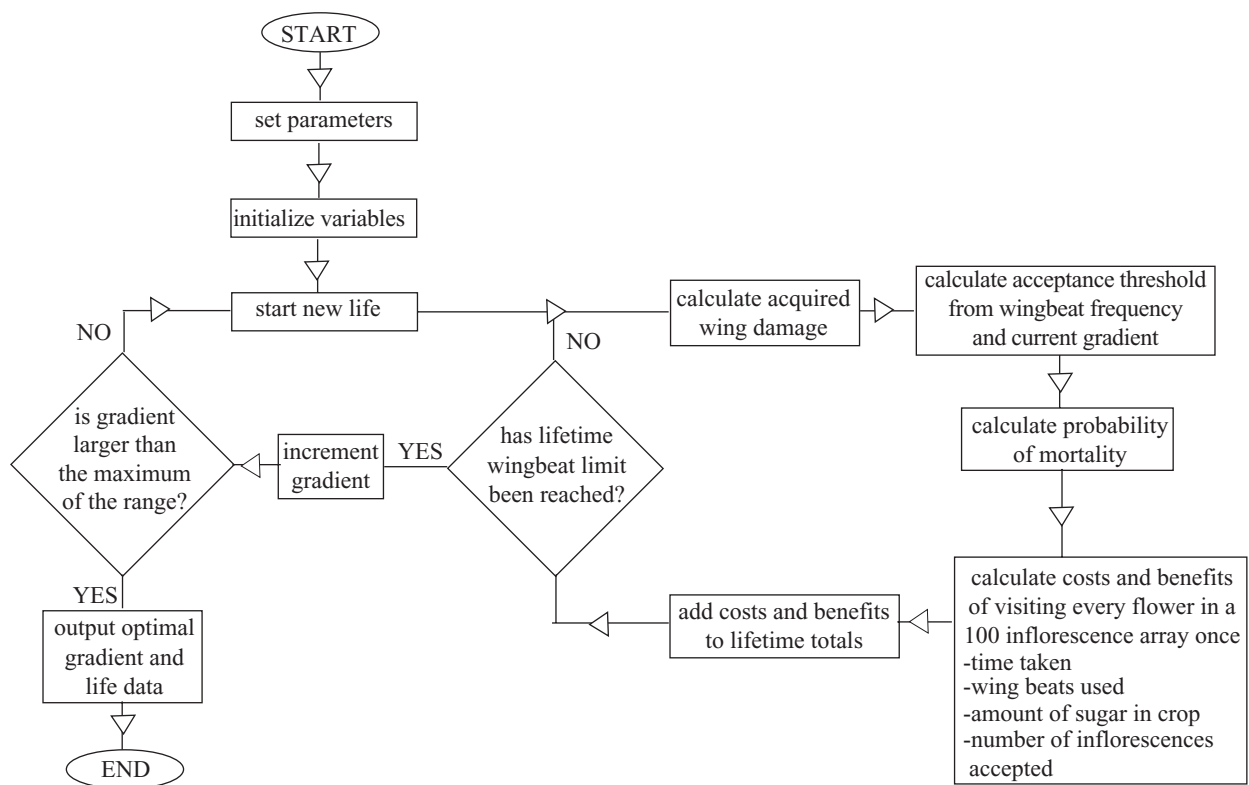


Figure 2. Flow diagram of the model process. Note the two loops, one for each foraging bout, and one for each possible level of the gradient.

the forager accepts the flower and alights; otherwise, the inflorescence is rejected. Therefore, the proportion of inflorescences that are accepted is the total frequency of inflorescences above the threshold.

The benefit to the forager is the total crop of sugar taken from the distribution of accepted inflorescences, taking into account the nonlinear relationship between sugar amount and inflorescence size (figure 1*b*). We assume that the forager probes every flower on an inflorescence, so getting all the sugar from it. Total handling time is calculated in the same way. When the bee accepts an inflorescence, the time spent on it is calculated from the number of flowers (figure 1*c*): the total handling time is then obtained via the frequency distribution of inflorescence size (figure 1*a*). In this way the rate of energy gain can be estimated for each level of the acceptance threshold (figure 3), equal to the total crop collected divided by the total time spent in foraging: the latter is simply the sum of the flying and handling times. Figure 3 clearly shows an optimal acceptance gradient in terms of the rate of sugar acquisition.

The model iterates this process. Each distribution of 100 inflorescences (figure 1*a*) is considered to be a bout of foraging in a lavender patch, in which all inflorescences are inspected once. This is the maximal situation; the forager is perfect and there are no other foragers in the patch; this is a reasonable assumption because most flowers on most inflorescences are either unvisited or only visited once per day. The bee repeats this bout as it acquires damage and its wingbeat frequency increases. Current wing damage is calculated at the start of each bout as a function of the total number of wingbeats taken so far, and wingbeat frequency is then calculated from the level of wing damage.

The acceptance threshold starts at zero in the naive forager, which accepts all inflorescences it inspects. The bee starts with no information about inflorescences and gradually learns to be a better forager (Dukas & Visscher 1994) from inflorescence profitabilities. The gradient of the increase in the mean number of flowers on accepted inflorescences for new, undamaged bees was found to be 0.081 flowers per hour by simple regression ($t_{161} = 1.992$, $p = 0.048$). This value was used to estimate the increase in the acceptance threshold per inflorescence visited by assuming a 100-inflorescence bout (including the hive visit) takes 1 h. Hence, we assume the initial 'learning rate' (i.e. initial rate of increase of the threshold) to be 8 per 10 000 inflorescences visited.

The model is based on the supposition that any decrease of the threshold is due to wing damage, acting through the increased wingbeat frequency that results from a reduced wing area. We assume that the bee follows some rule that decreases its acceptance threshold as wingbeat frequency increases. The realized acceptance threshold is calculated assuming a linear relationship with wingbeat frequency, with a given intercept and gradient, the latter being the critical variable to be optimized. At the start of each 100-inflorescence bout the threshold is calculated from the number of inflorescences visited so far in the bee's lifetime, and the wingbeat frequency. The benefit for the bout is the total weight of sugar collected using the current threshold. At the same time, the total lifetime number of inflorescences accepted increases by the number of inflorescences accepted during the bout. The total lifetime number of wingbeats is incremented by the product of the total time spent in flight in the bout and the current wingbeat frequency.

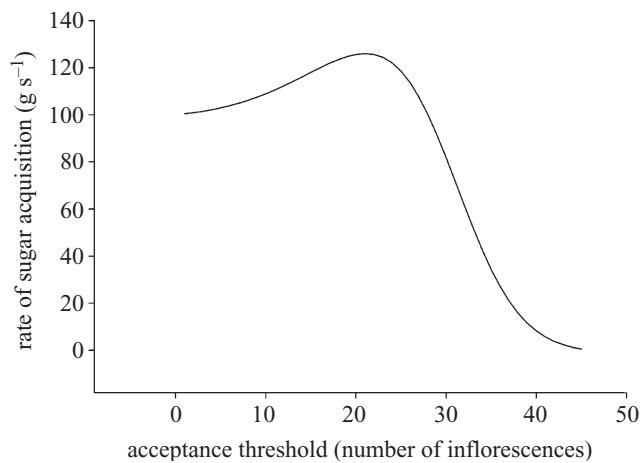


Figure 3. The relationship between the acceptance threshold (number of flowers) and the rate of sugar acquisition for each level of the threshold. This is calculated from the total amount of sugar taken in one bout divided by the total time (handling plus flying time) it takes to gather that sugar. At the default parameters, the curve shows a maximum at a threshold of 21 flowers, and hence optimal foragers should only accept inflorescences of 21 or more flowers.

The bee repeats foraging bouts until the total lifetime wingbeats exceeds the set maximum possible. Bee lifetimes are repeated for a range of values of the gradient (table 2) to find its optimal value in terms of the total lifetime sugar collected. This optimal gradient is used to predict the optimal acceptance threshold at each level of wing damage.

(c) Sensitivity to parameter values

The model is sensitive to variation in three critical parameters: search time, mortality risk and learning rate. These were systematically varied in relation to wing damage to explore the sensitivity of the model (figure 4). Variation in search time does not cause any change in the predicted optimal gradient between acceptance threshold and accumulating wing damage, whereas this gradient is predicted to change with alterations in mortality risk and learning rates.

The mean search time between inflorescences from field data was 1.12 s. If the average search time is increased merely by 0.5 s, the model predicts that a forager should accept all inflorescences by the time it has acquired just 4% wing damage. At search times lower than 1 s the forager can afford to have a higher threshold.

The model predicts no decline in the acceptance threshold with wing damage (i.e. contrary to the observed case) whenever mortality risk is greater than approximately 2.5 per 100 000 inflorescences visited (figure 4b). This is the low end of the real range estimated by Morse (1986). At higher mortality risks, the optimal acceptance threshold simply levels off because as the bee becomes choosier, it visits fewer inflorescences for every increment in wing damage. At predation risks below 1.5 the forager should accept all inflorescences it encounters, because the risk of mortality on any given one is insignificant. When there is no predation at all, the gradient will always be the largest possible, so the bee accepts all inflorescences as soon as it acquires any wing damage.

The optimal gradient increases with increasing 'learning rates' (figure 4c). When 'learning' is slow (about 4 in the

Table 2. The range of values of the variables of the model.

variable	initial	maximum	basis
wingbeat frequency	234	α wing damage	Feuerbacher <i>et al.</i> (2003)
wingbeat frequency– acceptance threshold gradient	0	20 flowers per hertz	n.a.
acceptance threshold	0	α wing damage, learning rate	n.a.

model), the optimal gradient is zero and the forager should never reduce its threshold. At the other extreme, if the forager 'learns' quickly, the forager accepts all inflorescences before it has acquired even a small amount of damage (and virtually all foragers acquire 4% damage).

4. RESULTS

(a) Comparison with observations

Figure 5 shows the best fit between the real data and the model for particular values of the parameters. Theoretically, the real acceptance threshold should follow a curve reflecting the balance between learning and accumulating wing damage on foraging (see figure 5). Several factors collude to obscure this relationship in real data. First, we cannot measure the acceptance threshold, but only its impact on the mean number of flowers on accepted inflorescences. Second, in the field bees were not captured when they left the hive for the very first time as foragers, so it is impossible to know whether new foragers are less choosy than experienced foragers with no wing damage. This uncertainty about absolute age leads to an enhanced inter-individual variation in the data recorded. Third, the initial 1% of wing damage is a very small amount, probably the result of just one random incident (or collision, A. D. Higginson, unpublished data), which then exacerbates further damage. All these factors mean that data from early ages (and hence initial phases of wing damage) are much more variable and less reliable than subsequent data, obscuring any curve in the relationship estimated from real data. We therefore used linear regression to assess the fit between the model and the data (see figure 5).

Model output best matches the data (figure 5) at parameter values slightly different from those initially assumed: the search time is slightly higher (1.421) and the learning rate is slightly slower (6 per 10 000 inflorescences). In fact, the observed rate of learning is eight over the first 2 days, but falls to 4.2 when estimated over the first 3 days, suggesting that a value of six is reasonable, in the middle of the observed range of learning rates.

At these parameter values, the model predicts that the optimal gradient between wing damage and acceptance threshold is -1.7 flowers per 1 Hz increase in wingbeat frequency. When coupled with the learning rate, the predicted decrease in the mean number of flowers on accepted inflorescences with wing damage (-0.572 in the range 2–7%) is very similar to that observed in the field (-0.58).

The magnitude of the difference between the predicted and observed lines is less than 0.5 flowers in the range 0.7–7.2% damage (see figure 5). The range below 0.7 is where the experience of the forager is uncertain

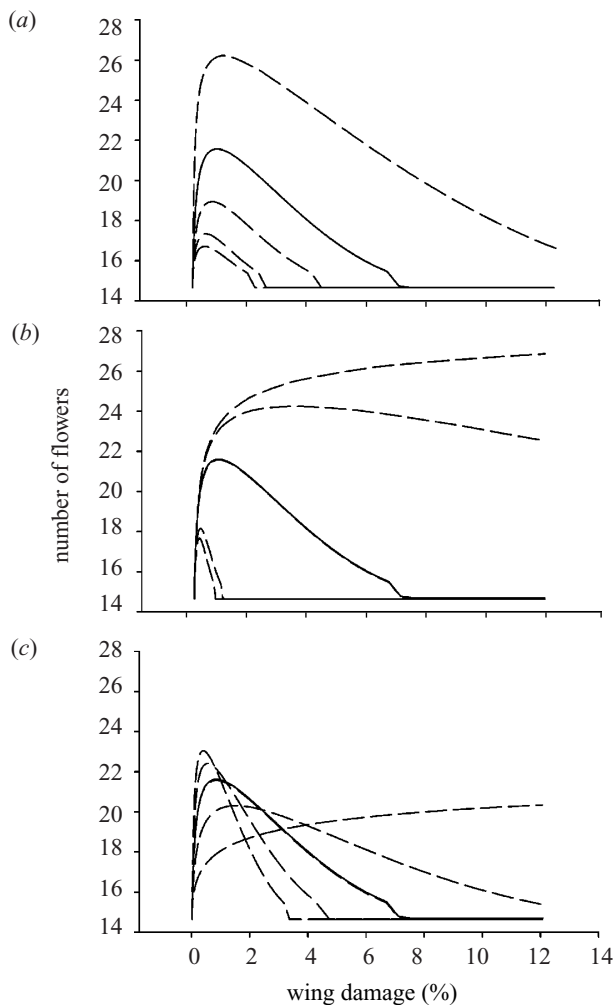


Figure 4. Relationship between wing damage (x -axis) and acceptance threshold (y -axis): sensitivity analysis of varying three parameters on the model predictions. In each case, values less and greater than the observed value were explored. In all graphs, the predicted mean number of flowers on accepted inflorescences is bounded by the value observed in the real array (= 14.5). In (b, c) the abrupt change in gradient as the line approaches the boundary of 14.5 is caused by the change in acceptance threshold from 1 to 0. (a) Search time. The mean search time between inflorescences was 1.121 s (solid line). The effect of changes of 0.5 s on the model was explored: only a single decrement was used (upper dashed line) because values lower than 0.621 are biologically unreasonable. Note that the gradient of the relationship between acceptance threshold and wing damage does not change with changing search times. (b) Mortality risk. No field estimates are available, so the lower boundary of the measured range of Morse (1986) was used (2 per 100 000 visits: solid line). This was varied in two steps of one either side of this value. Note that unlike search time, the gradient is now sensitive to the magnitude of the mortality risk, and above 3 per 100 000 (uppermost dashed line) the model predicts no reduction in the acceptance threshold with accumulating wing damage. (c) Learning rate. New undamaged bees initially accept all inflorescences, and their acceptance threshold increases by approximately 8 per 10 000 inflorescences visited (see §3b). This was varied in two steps of 2.5 either side of this value. Decreasing values cause the gradient of the approximately linear part of the curve to decrease, and the height of the line to increase (and vice versa). Very slow learning rates cause the model to predict no reduction in the acceptance threshold with accumulating wing damage.

(as discussed above in §3a). Above 7.2%, the forager has a threshold of zero and accepts all inspected inflorescences, and hence although the regression line continues below the boundary value of 14.5 (see legend to figure 4), the predicted values cannot.

(b) Comparison with other currencies

The predictions of this new currency were compared with those of the more standard currencies of rate of gain of energy and efficiency. The observation that sparked the generation of the wing-damage model is that the acceptance threshold decreases with bee age. As energy use does not change as wing damage increases (Hedenström *et al.* 2001), both standard currencies predict an optimal threshold that is constant over the lifetime of the bee. This remains the major difference between the new and the standard models. Other possible differences in predictions among the currencies lie in what happens to the optimal acceptance threshold with changing predation risk, or search time. Although we have shown the effect of changes in 'learning rate' (figure 4), this is a purely phenomenological part of our model and is not truly independent.

To explore this, we calculated the lifetime energy gain per wingbeat, rate and efficiency with no wing damage at all, to compare predictions among the three currencies for the resulting (*constant*) optimal acceptance thresholds (and consequent mean number of flowers on accepted inflorescences, the variable actually measured in the field). These calculations assume that, on average, all bees inspect the same number of inflorescences. The energy use in flight was taken as 55 mW (cf. Feuerbacher *et al.* 2003). There are few data on energy use while walking on the inflorescence but, like bumble-bees, honeybees maintain flight readiness by regulating their thoracic temperature. We assumed that there was a modest saving in energy use while walking, assumed to be 30 mW. Note that if there is no saving at all (i.e. walking cost = 55 mW) then the currencies of rate and efficiency predict identical thresholds; if the saving is maximal (i.e. walking cost = 0) then wingbeat and efficiency currencies predict identical thresholds.

Variation in the predation risk had comparatively little effect on the optimal threshold when using rate or efficiency (figure 6). When using energy gain per wingbeat as a currency, the mean number of flowers on accepted inflorescences changed by 13 across the range of predation risks, more than the equivalent changes for currencies of efficiency (by 6) and energy gain rate (by 5). The gap between the predictions for the wingbeat currency versus the other two widens at low predation risks, reflecting the greater importance of the wingbeat limit as more and more bees reach it (because they are not killed by predators). One difference among currencies, therefore, is the fact that the standard currencies predict this relationship to be linear, whereas the wingbeat currency predicts it to be a curve.

The effect of varying the search time was similar, causing larger changes to the optimal threshold using the wingbeat as opposed to the other currencies (figure 7). All three show a curvilinear decrease in the mean number of flowers on accepted inflorescences as search time increases, and practically these would be hard to distinguish.

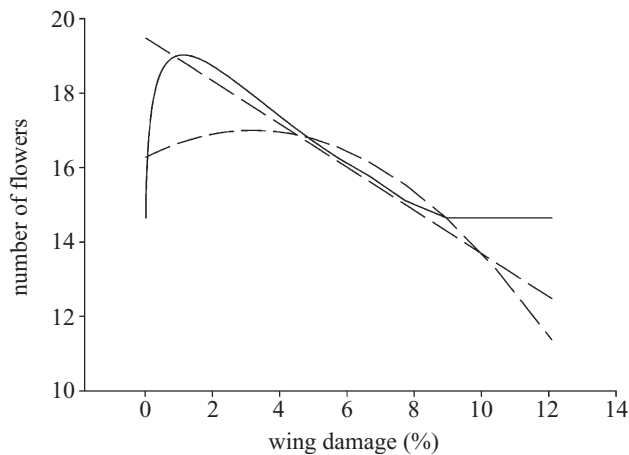


Figure 5. Observed relationship between the mean number of flowers on accepted inflorescences and accumulating wing damage in foraging honeybees. The raw data are not plotted because of the high variability among individuals, caused because of uncertainty in estimation of a worker's true age. There are two possible fits to these data: linear and quadratic (dashed lines). Theoretically, in the model the effects of learning and wing damage interact to produce a quadratic relationship: a quadratic fit is a line of form $16.27 + 0.4561x - 0.0712x^2$ ($F_{2,1258} = 2.14$, n.s.). Apart from the initial phase involving learning, the model predicts an approximately linear relationship: a fitted regression line for wing damage greater than 2% has the equation $19.49 - 0.58x$ ($t_{115} = -2.044$, $p < 0.05$). The solid line shows the predicted relationship for the following parameter values: search time = 1.42 s; predation risk = 2 per 10 000 inflorescences; learning rate = 6 per 100 000 inflorescences (see §3b).

5. DISCUSSION

The model successfully reproduces the lifetime foraging strategy of worker honeybees as observed in this system. Using the estimated parameters, it accurately mimics the decrease in choosiness of worker honeybees as they acquire wing damage (Higginson & Barnard 2004). Although the data were insufficient to get an accurate match across the entire range of wing damage, the model is incredibly accurate, considering its simplicity, for over half of the observed range of wing damage, representing the period from the end of the initial learning curve for the forager until a level of damage that very few bees actually survive long enough to acquire.

The increased accuracy that results when search time is increased from the observed mean (1.12 s) by 0.3 s could represent the flight time to and from the hive. The increase is merely 30 s per 100-inflorescence foraging bout. Because neighbouring hives in the field are *ca.* 20 m from the lavender, with many intervening trees, 15 s is a perfectly plausible flight time, especially when the initial spiral locating flight is taken into account. When the search time is increased further, the threshold should stay lower to maximize lifetime energy input to the hive. A test of the model would be to manipulate travel time to and from the hive: the model predicts that the mean number of flowers accepted by foragers will be lower as travel times become shorter.

The variation in search time in the model can be altered to make other predictions that are experimentally testable in the field. The search cost, in terms of wingbeats spent

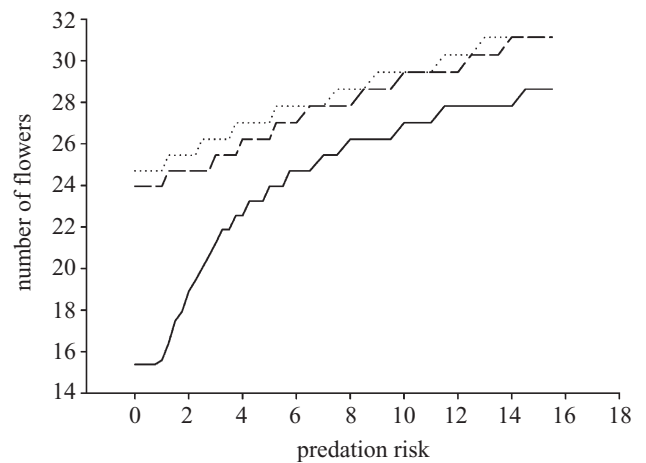


Figure 6. The predicted mean number of flowers on accepted inflorescences as predation risk varies for the three different currencies. The means for currencies of efficiency (dashed line) and energy gain rate (dotted line) change less than those for energy gain per wingbeat (solid line). The lines increase in steps because only integer thresholds were tested.

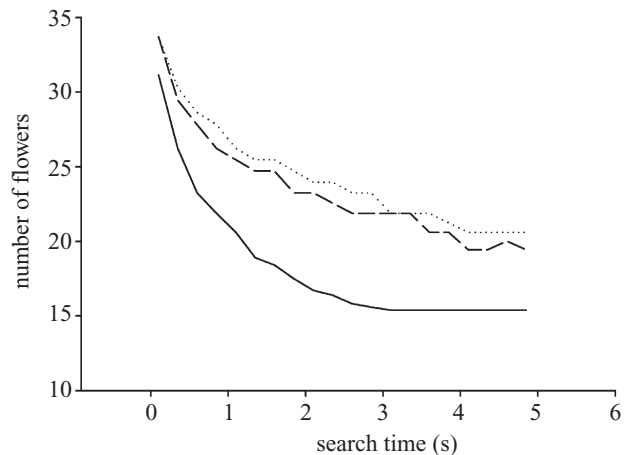


Figure 7. The predicted mean number of flowers on accepted inflorescences with varying search time for the three different currencies. The means for efficiency (dashed line) and energy gain rate (dotted line) change less than those for energy gain per wingbeat (solid line).

between inflorescences, can be increased by experimentally reducing the density of inflorescences in the flower patch. Increasing flight time between inflorescences would be expected to cause a reduction in the mean number of flowers accepted by foragers.

An alternative method of testing the model would be to alter experimentally the mortality risk to foragers. From matching the model to real data, the density of crab spiders in the lavender system should correspond to the lower end of the range found by Morse (1986). Because predator density will depend on prey availability, the number of crab spiders in any system is likely to be restricted by how many insects are foraging there, and hence these risks may be fairly similar for flower visitors in any habitat. Once the density of predators exceeds a certain value, there is no point in bees conserving wingbeats, because a forager is too likely to be captured.

The success of the model in explaining the decrease in the quality of accepted inflorescences suggests that foragers can be treated as though they are maximizing their energy intake per wingbeat spent. The new currency ties together the work of Neukirch (1982) and Cartar (1992) by providing an explanation why bees with clipped wings experienced increased mortality. It could help to solve many of the debates over the correct foraging currency in honeybees, such as departure rules (Goulson 2000), the effect of distance from the hive (Gary *et al.* 1981) and an apparent inconsistency in currencies (Cartar & Dill 1990). It could provide an explanation for many aspects of honeybee foraging because under many conditions it approximates both rate and efficiency. It is likely that in many cases the number of wingbeats taken during a foraging bout is linearly related to both the time taken (rate) and energy used (efficiency). This currency is compatible with the finding that bees forced into inactivity in the hive have an increased lifespan (Wolf & Schmid-Hempel 1989), because bees would 'spend' their wingbeats at a slower rate.

The new currency does not seem to explain the increased mortality of workers permanently carrying extra weight (Wolf & Schmid-Hempel 1989). The number of wingbeats would not be affected by load weight because an increased weight apparently does not require an increase in wingbeat frequency (Feuerbacher *et al.* 2003). However, Wolf and Schmid-Hempel only observed reduced lifespan in the most heavily loaded individuals (mean extra weight of 38.6 mg), whereas the mean nectar load observed by Feuerbacher *et al.* (2003) was approximately one-third of this (13.2 mg). The bees with a mean extra weight of 16.1 mg in Wolf and Schmid-Hempel's study lived as long as controls (10.2 and 10.8 days, respectively, *s.e.m.* > 0.5). Feuerbacher *et al.* actually report very small increases in metabolic rate with increasing nectar loads and in one case (bumble-bees with a load equal to 18% of body mass), there was an increase in metabolic rate of 15% and a 5% increase in wingbeat frequency. Thus, under normal nectar loads, there may be no increase in mortality rates.

The most powerful test of the model is the prediction that artificial wing damage will decrease acceptance thresholds: we now know that this does happen (Higginson & Barnard 2004). A further test would be for a curved relationship between the threshold and predation risk: mortality risk can be manipulated in field experiments using flower spiders (A. D. Higginson, C. Barnard and F. Gilbert, in preparation).

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