An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees

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Abstract. 1. A model is described that evaluates the maximum economic foraging range in central place foragers by using optimality criteria to discriminate between foraging sites at different distances from the forager's central place.

2. The basic model can be varied to suit foragers that optimise either their rate of net energy uptake or their foraging efficiency.

3. The model requires specification of the time and energy budgets of travel and foraging, and of the rewards obtainable at potential foraging sites.

4. The specific case of bumblebees, whose foraging ranges are poorly known, is considered.

5. Numerical solutions of the model for parameter values that represent bumblebees and their forage predict economic foraging ranges exceeding several kilometres. The model demonstrates that economics alone can explain extensive flight ranges in bees.

Key words. *Bombus*, central place foraging, energetics, flight range.

Introduction

Animals that forage from a single location exhibit central place foraging (Schoener, 1979). Central place foraging has been considered in optimal foraging theory with respect to the economics of territoriality (Dill, 1978), dietary choice (Orians & Pearson, 1979; Lessells & Stephens, 1983; Lifjeld, 1989), patch use (Schoener, 1979), and load size (Schmid-Hempel *et al.*, 1985). Models of home range dimensions for foragers have been proposed by Andersson (1978) and Ford (1983), but they are suited to qualitative analysis and incorporate strong, simplifying assumptions about the nature of a generalised forager and its environment that are unrealistic in specific instances. More recently, Dukas and Edelstein-Keshet (1998) used a model with more realistic assumptions to consider the optimal spatial distribution of foragers sharing a nesting site, but the economics of flight range *per se* were not a focus of their analysis. Here, a general model of foraging range in a central place forager is presented.

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Both solitary and social bees provision their broods by central place foraging from their nest, and the investigation of their flight ranges is essential to an understanding of their ecology (Bronstein, 1995; Westrich, 1996). If the reproduction of a central place forager is primarily resource limited, the ability of a landscape to sustain the animal's reproduction depends almost entirely on two factors: the density and value of suitable food in the landscape, and the foraging range of the animal. That is, animals with a small foraging range will require a greater density of resources per unit area than animals with similar needs, but greater range. The flight range of bees will determine the minimum resource density that can sustain a nest, so knowledge of flight ranges could inform the design of strategies for bee conservation when their plant resources are threatened or fragmented (Rathcke & Jules, 1993; Kearns & Inouye, 1997; Allen-Wardell *et al.*, 1998).

Flight ranges vary among bee species, and can extend up to 24 km in euglossine bees (Janzen, 1971), up to about 10 km in honey bees (von Frisch, 1967; Visscher & Seeley, 1982), and up to 5 km in *Xylocopa* spp. (Kapil & Daliwahl, 1969, cited in Roubik, 1989), although the typical distance travelled by foragers may be much less than the maximum possible range (Visscher & Seeley, 1982). Flight ranges are poorly known in certain bee taxa, such as bumblebees (*Bombus*). A few

observations suggest that bumblebees can fly over long distances (Rau, 1924, cited in Brian, 1954; Mikkola, 1984), but individuals are generally assumed to forage close to the nest, perhaps within 300 m (e.g. Heinrich, 1976; Bowers, 1985; Free, 1993; reviewed in Dramstad, 1996). In contrast, studies of bees marked at their nest have often failed to locate marked individuals in the adjacent landscape despite the presence of apparently suitable forage (Dramstad, 1996; Saville *et al.*, 1997). Moreover, a recent study that tracked bumblebees with radar found that although the mean distance from the nest of measurable outward tracks was 275 m, bees frequently flew beyond the radar horizon, which was about 500 m from their nest (Osborne *et al.*, 1999). Consequently, it would be useful to have some general principles that can explain the variation in flight range among species, and that can offer predictions about species whose flight ranges are poorly known, such as bumblebees. To this end, the model of the economics of central place foraging was solved numerically with parameter values that represented bumblebees.

Description of the model

Consider a forager that can carry C units of provisions before it must return home. The forager travels D m in making the round trip to the foraging site and the speed of travel is $S \, \mathrm{m \, s^{-1}}$. The forager is assumed to arrive at the foraging site carrying no provisions, and to return home only when fully loaded. At the foraging site, the forager gathers its provisions as items, and each successively encountered item takes H s to locate and collect, and yields R units of resource. For convenience, the total provisioning time (HC/R) is denoted as P. The total time required by the forager to travel to and from the nest and to load to capacity is therefore $(D/S) + P$.

Suppose that a forager's rate of energy expenditure when fully laden with provisions increases $2\beta \, \mathrm{J \, s^{-1}}$ above its unladen expenditure. Assume that during provisioning the forager expends $(M - \beta) \, \mathrm{J \, s^{-1}}$ when unladen, so that it expends $(M + \beta) \, \mathrm{J \, s^{-1}}$ when fully laden, and that the rate of energy expenditure increases linearly with load. The provisioning forager will therefore have an initial expenditure rate of $(M - \beta)$ and a final rate of $(M + \beta)$, with a mean rate of M. Let δ denote the difference in mean rate of expenditure between travel and provisioning. The mean rate of expenditure during the travelling phases of the round trip will be $M + \delta$, which is the mean of the unladen outward trip (expenditure rate $= M - \beta + \delta$) and laden return trip ($M + \beta + \delta$) rates. Overall, the energetic cost of a foraging trip is $D(M + \delta)/S + PM$. If the forager's payload provides Λ units of metabolic energy per unit of resource, then the rate of net energy intake for the foraging trip, Ψ, is

$$\Psi = \frac{C\Lambda - \frac{D}{S}(M + \delta) - PM}{\frac{D}{S} + P}.$$ (1)

Next, assume that the forager has the option of travelling to either a near or a far foraging site. The parameters associated

with each site are identified by a subscript; e.g. the distances to the near and far sites are D_n and D_f respectively. Exploitation of the far site is therefore profitable when $\Psi_f \geqslant \Psi_n$. Consequently, if a unit of resource yields the same energy at both sites (i.e. $\Lambda_n = \Lambda_f = \Lambda$), then the exploitation of the far site is profitable when

$$D_f \leq \frac{SC\Lambda(P_n - P_f) + D_n(C\Lambda + P_f\delta)}{C\Lambda + P_n\delta}.$$ (2)

If the nearest foraging site is immediately adjacent to the forager's central place, then $D_n = 0$, and the exploitation of the far site is profitable when

$$D_f \leq \frac{SC\Lambda(P_n - P_f)}{C\Lambda + P_n\delta}.$$ (3)

Let T denote the maximum distance beyond the near foraging site to which the forager can profitably travel, i.e. $T = \max(D_f - D_n)$ for which inequality 2 is satisfied. T will be referred to as the *maximum economically viable travel increment*, and let T_0 denote the value of T in the special case of $D_n = 0$.

Let Φ denote the total duration of each foraging trip (i.e. travel plus foraging phases) to the most distant, economically viable foraging site, and so

$$\Phi = \frac{D_n + T}{S} + P_f.$$ (4)

Let Φ_0 denote the value of Φ in the special case of $D_n = 0$.

It is straightforward to modify the model to evaluate other optimisable currencies. For example, to analyse *efficiency-sensitive* foraging (i.e. where the optimisable currency is net benefits/energetic costs) rather than *rate-sensitive* foraging (net benefits/time), substitute $[D(M + \delta)/S + PM]$ for the denominator in eqn 1 before formulating the subsequent equations. If, as before, the nearest foraging site is immediately adjacent to the forager's central place, then $D_n = 0$, and the far site can be exploited profitably when

$$D_f \leq (P_n - P_f)\frac{MS}{(M + \delta)}.$$ (5)

An equation identical to eqn 5 is obtained when a model is formulated for *gross collection efficiency* (gross benefits/energetic costs). By equating the right hand sides of eqns 3 and 5, it can be shown that T_0 will be equal for two foragers that are, respectively, rate-sensitive and efficiency-sensitive when

$$\frac{C\Lambda}{C\Lambda + P_n\delta} = \frac{M}{M + \delta}.$$ (6)

Selection of parameter values to represent bumblebees

The model considers a forager that collects provisions in the form of resource items. Bumblebees are floral foragers, and it is possible to view flowers, inflorescences, or entire plants as
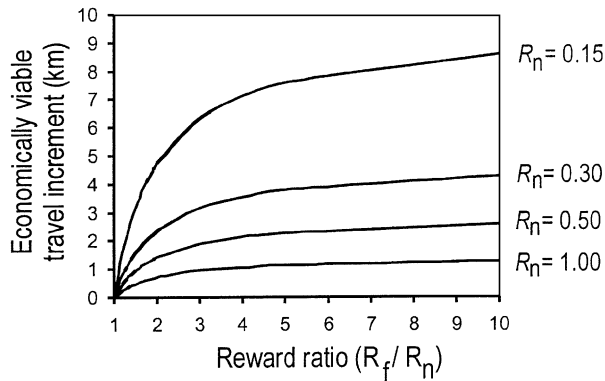
Fig. 1. Predicted relationships between the maximum economically viable travel increment and the ratio of the volumes of nectar rewards at far vs. near sites. If the near foraging site is adjacent to the bees' nest, the maximum economically viable travel increment can be interpreted as the maximum viable foraging range T_0. Curves are shown for four mean nectar volumes (μl) in flowers of the near site.

discrete items containing nectar and/or pollen. To simplify the parametrisation of the model, an item is here defined as the nectar obtained from an individual flower. Therefore, R represents the mean volume of nectar per flower in μl, and H amalgamates the mean time taken to fly between successively probed flowers with the mean handling time per flower. Clearly, H depends on the spatial distribution of flowers, and on their morphology and ease of handling for the bee. To solve the model, the flowers at both foraging sites are assumed to require the same handling time, $H = 5$ s, which is based on studies of fireweed (*Epilobium angustifolium*: $H \approx 2.5$ s; Heinrich, 1979), monkshood (*Aconitum columbianum*: $H = 6.5$; Pyke, 1979), Nelson's larkspur (*Delphinium nelsoni*: $H = 2.8$; Hodges, 1981), foxglove (*Digitalis purpurea*: $H \approx 14.0$; Best & Bierzychudek, 1981), borage (*Borago officinalis*: $H \approx 4.0$; Osborne, 1994), and oil-seed rape (*Brassica napus*: $H \approx 2.0$; Cresswell, 1999).

Allen *et al.* (1978) reported that many bumblebee workers return to their nest with a honey crop filled approximately to capacity. Heinrich (1979) estimated the maximum capacity of a worker's honey crop at 100 μl, but Allen *et al.* (1978) reported the net sugar gain per trip in *B. vosnesenskii* to be 0.025 g, which is about 60 μl of a typical 40% w/v nectar (Proctor *et al.*, 1996). To solve the model for a worker bumblebee, C is set at 80 μl.

With respect to flight speed, some studies have reported estimates of 5 m s^{-1} (Demoll, 1918, cited in Ellington *et al.*, 1990; Heinrich, 1979), but a recent study that tracked free-flying bumblebees (*Bombus terrestris*) with radar recorded mean airspeeds in calm conditions of 7.1 m s^{-1} (Riley *et al.*, 1999), so $S = 7.1$ is used here.

In the model, it is assumed that bumblebees' flight expenditure averages M during both travel and provisioning, so $\delta = 0$. In reality, flights between flowers may be slower than the flights between nest and foraging site, but the energy expenditure of bumblebees appears to be insensitive to flight

speed (Ellington *et al.*, 1990), at least at the lower speeds (< 4 m s^{-1}). Consequently, M cancels from eqns 2 and 4, and there is no need to specify values of M. Additionally, equality holds in eqn 6, so identical solutions apply to both rate-sensitive and efficiency-sensitive bumblebees.

An upper limit to flight range can be calculated, and this is determined by the requirement for each foraging trip to yield a net energy gain by the colony. To calculate this maximal range, it was assumed that the metabolism of nectar sugars yields 16.7 kJ g^{-1} (Heinrich, 1979) and that a flying bee expends 1.2 kJ h^{-1} while flying (Ellington *et al.*, 1990). If a bumblebee metabolised all the sugars in a full honey crop (80 μl of nectar equivalent in concentration to 1 M sucrose) during a single, uninterrupted flight back to its nest, then, given the previous estimate of flight speed, the upper limit to flight range is ≈ 10 km.

The carbohydrate concentration of nectar rewards determines the minimum mean nectar volume per flower that renders a site profitable. If the nectar rewards are carbohydrate with a concentration of 40% w/v (i.e. ≈ 1 M sucrose or equivalent), Ellington *et al.*'s (1990) information on flight metabolism implies that the flying bumblebee must take up ≈ 0.06 μl s^{-1} to balance its energy expenditure. Therefore, if $H = 5$ s, the minimum economic nectar reward is ≈ 0.3 μl. If, instead, the nectar rewards have carbohydrate at 60% w/v (i.e. ≈ 2 M sucrose or equivalent), the minimum economic reward is ≈ 0.15 μl.

Results

Some general conclusions

Equations 2 and 3 expose several conclusions about the maximum economically viable travel increment T. Clearly, a far site is economically viable only when $T > 0$. A positive, non-zero economically viable travel increment is possible only when resources at the far site allow faster provisioning (i.e. $P_f < P_n$), and T increases with a forager's capacity to carry provisions C and its speed of travel S. T therefore increases with factors that diminish either travel time or its contribution relative to that of provisioning in the total duration of foraging. Conversely, T decreases with the amount by which the metabolic costs of travel exceed those of foraging, δ. It also emerges from eqn 2 that T increases linearly with the distance to the near foraging site D_n.

Numerical solution of the model when specified for bumblebees

If floral rewards adjacent to the nest are rich (e.g. ≈ 1 μl per flower), $T_0 < 1$ km unless floral rewards at the far site approach 10 μl (Fig. 1). If, in contrast, nectar rewards adjacent to the bumblebees' nest provide minimal profit, T_0 can extend over several kilometres and T increases with nectar concentration. For example, if nectar comprises 40% w/v sugar, the minimum viable floral reward is $R_n = 0.3$ μl, and when the distant site
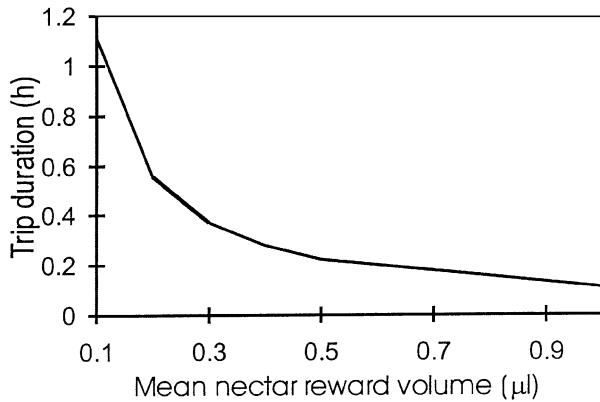
Fig. 2. The predicted effect of the mean nectar reward volume at the near site on the duration of a foraging trip to the most distant, economically viable foraging site.

offers nectar rewards of $2R_n$, $T_0 \approx 2.4$ km (Fig. 1). If nectar concentrations are 60% w/v, the minimum viable floral reward is $R_n = 0.15 \mu l$, and when the distant site offers nectar rewards of $2R_n$, $T_0 \approx 4.7$ km (Fig. 1).

These predictions of relatively extensive flight ranges depend on equal metabolic costs for travel and foraging (i.e. $\delta = 0$). If the rate of metabolic expenditure during travel exceeds that during foraging by even 10% (i.e. $\delta = 0.1$), T_0 will be cut by 10% for efficiency-sensitive foragers, and by about one-third for rate-sensitive foragers.

When the near site is immediately adjacent to the bumblebees' nest (i.e. $D_{n=0}$), the duration of foraging trips to the farthest economically viable site Φ_0 declines with the size of the nearest rewards per flower (Fig. 2). Given the minimum economic nectar reward at 40% w/v carbohydrate (0.3 μl), $\Phi_0 \approx 22$ min, and for 60% carbohydrate (0.15 μl), $\Phi_0 \approx 44$ min.

Discussion

The model presented here can be used to analyse the economics of foraging range in any central place forager provided that the parameter values can be quantified. The model adopts the standard economic perspective that has proved insightful in many studies of foraging behaviour (reviewed in Stephens & Krebs, 1986; Perry & Pianka, 1997), and all its aspects are amenable to testing by standard, manipulative approaches. Additionally, even if it proves impossible to parametrise the model in certain instances, it may prove possible to examine its qualitative predictions, such as the existence of a linear relationship between the distance to the nearest foraging site and the maximum economically viable foraging range.

There are three fundamental requirements for testing the model: foraging range must be measured, reward availability at potential foraging sites must be quantified, and the forager's currency of economic optimisation must be known. With respect to the last, the assumption that individual foragers are

energy-rate maximisers has been applied widely and successfully (see reviews in Stephens & Krebs, 1986; Krebs & Davies, 1993) but it may not hold invariably. Houston *et al.* (1988) demonstrated theoretically that an animal that forages to provision its offspring will have been selected to maximise its net foraging efficiency (net benefits/energetic costs). In addition, some foragers may maximise gross collection efficiency (benefits/energetic cost) (Rasheed & Harder, 1997a,b). It has been shown, however, that it is straightforward to modify the basic model to encompass these various optimisable currencies.

Critique of the model's assumptions

The model's formulation assumes that metabolic rate increases linearly with load from $(M - \beta)$ to $(M + \beta)$ during provisioning, such that the mean rate $= M$. This assumption is unlikely to be entirely realistic (e.g. Cooper, 1993), and a nonlinear relationship will result in an alteration in the mean costs of provisioning at the foraging site. In the model of rate-sensitive foraging, the maximum economically viable travel increment T does not depend on metabolic rate. In contrast, metabolic rate does affect T for efficiency-sensitive foragers and, all else being equal, eqn 5 indicates that T will increase with the mean rate of energy expenditure during provisioning. The mean rate of energy expenditure during provisioning will exceed M when the rate of increase in metabolic expenditure decelerates with load from $(M - \beta)$ to $(M + \beta)$. When necessary, it will be straightforward to incorporate nonlinear relationships between load and travel speed into the model.

The model also assumes that the forager loads with provisions to capacity. Sometimes, central place foragers do not load to capacity (e.g. Kacelnik, 1984; Kacelnik *et al.*, 1986), and, under some circumstances, this may be profitable (Schmid-Hempel *et al.*, 1985). In eqns 3 and 5, provisioning time appears in the numerator, which implies that failure to load to capacity, and decreased provisioning time per round trip, would lead to decreases in the maximum economically viable travel increment T, all else being equal. Variability in loading could, however, be incorporated into revised versions of the model.

The model's applicability to a given forager relies on the forager's energy budget being the sole determinant of the optimal foraging range. In nature, the economics of energy are likely to be the major determinant of foraging range but a complex of other factors may also have influence. For example, the risk of mortality can alter predicted optimal behaviour (Milinski & Heller, 1978; Lima *et al.*, 1985; Sih, 1992; Dukas & Edelstein-Keshet, 1998). When an individual's lifespan depends on the amount of travelling or labour that it undertakes (e.g. Schmid-Hempel & Wolf, 1988; Cartar, 1992a), animals may have been selected either to forage within the maximum economically viable range or to collect less than a full load (Kacelnik, 1984). Nevertheless, the extent to which resource economics determine foraging range can be evaluated by testing the predictions of the model. Additionally, the potential effects

of other factors, such as predation risk, can be isolated experimentally and tested (Cartar, 1992a,b).

Application of the model to bumblebees

Influenced by the qualitative predictions of optimal foraging theory, many authors have assumed that the foraging range of bumblebees tends to be short (<300 m) because of the cost of travel in either energy or time (reviewed in Dramstad, 1996). The extent of flight ranges by foraging bumblebees has yet to be quantified but various observations (Dramstad, 1996; Saville *et al.*, 1997; Osborne *et al.*, 1999) do not support the assertion that bumblebees are economically constrained to short range travel. These observations have prompted the proposal of adaptive, non-economic explanations for extended flight distances, such as the avoidance of parasites and predators (Dramstad, 1996). An important result of the proposed model therefore is the conclusion that, for bumblebees, flight ranges in the order of kilometres can be economically viable. Note that this result does not depend on whether the bumblebees' foraging is *rate-sensitive* or *efficiency-sensitive* because if the metabolic costs of flight are equal during the bee's trip to the foraging site and during flower visits (i.e. $\delta = 0$), eqn 6 yields an equality. Similarly, Dukas and Edelstein-Keshet's (1998) model of social foraging predicted an economic viable flight range of 5.4 km for bumblebees.

Given the parameter values used, the model does not predict the extended duration in foraging trips exhibited by some bumblebees. J. L. Osborne (unpublished) has recorded a mean trip duration of 108 min (SD = 78, $n = 722$) in a study of *Bombus terrestris*, and other studies report bumblebee trip durations of 20–120 min (Brian, 1954; Free, 1955; Alford, 1975; Thomson *et al.*, 1987). The numerical solution to the model produces trip durations of 108 min for bumblebees only when average nectar rewards at nearby sites, R_n, approximate 0.05 µl of 40% w/v sugar. Nectar rewards of this size fall at the lower end of the range reported from natural systems (Hodges, 1981; Opler, 1983; Zimmerman & Pyke, 1986; Cresswell, 1990; Real & Rathcke, 1991) but could not be exploited profitably given the parameter values used to solve the model.

The duration of foraging trips may exceed the model's predictions for several reasons. First, the number of flowers that a bumblebee visits before filling its crop may be underestimated if bees concentrate collected nectar in flight, and this would extend predicted duration of flights. Second, the model has not been parametrised for pollen-collecting bees. If pollen collectors either visit more flowers during a foraging trip or experience longer handling times per flower than nectar collectors, pollen collectors would forage for longer than the predictions based on nectar collection would suggest (Free, 1955). Third, the model does not include parameters for bees that collect both nectar and pollen. If, during pollen collecting, bees periodically collect nectar to extend their flight while success is measured in terms only of pollen gain, longer trips could result than for nectar collection alone.

Testing the model's applicability to bumblebees

The three fundamental requirements for testing the model are not yet met for bumblebees. It has proved difficult to quantify the flight range of bumblebees although the continuing development of radar technology may offer a solution (Riley *et al.*, 1996, 1999; Osborne *et al.*, 1997, 1999). Whether bees are to be located visually or by radar, the results from the model imply that observers may need to be prepared to search far from bees' nests, i.e. several kilometres or more. Once the flight ranges of individuals are quantified, it will be possible to use (or to impose) variation among bees, for example with respect to load capacity and flight speed, to test specific predictions about flight range.

Similarly, reward availability at potential foraging sites of bumblebees is yet to be quantified at the landscape scale. To solve the model numerically, similar handling times, nectar concentrations, etc. were assumed for all plants, and the landscape was simplified in that only a pair of potential foraging sites was considered. Clearly, nature is more complicated but the time and energy budgets for a broader set of foraging options could be constructed by techniques that are already standard in pollination studies (e.g. Dafni, 1992) and compared by the principles used here.

Finally, the currency of economic optimisation must be established for bumblebees. Either rate of net energy intake (e.g. Pyke, 1979, 1982; Hodges, 1985; Cresswell, 1989; Pleasants, 1989) or foraging efficiency (Schmid-Hempel *et al.*, 1985; Rasheed & Harder, 1997a,b) is likely to be a large determinant of the foraging behaviour of bees. Here, calculations in both currencies have yielded identical predictions about foraging range. Other factors, however, may modify the bees' response to the availability and location of resources, such as risk sensitivity (Real, 1981), the relationship between labour and lifespan (Schmid-Hempel, 1987; Cartar, 1992a), and the energy status of the colony (Cartar, 1992b). Additionally, it is necessary to identify the resource whose collection is being optimised. Rasheed and Harder (1997a,b) showed that pollen collecting, like nectar collecting, may be economically motivated. In principle, it would be straightforward to evaluate a reward budget that comprised either nectar or pollen but it is not yet clear how to unify these commodities in a single economic model. In the meantime, it will be easiest to study systems where the foragers concentrate on nectar or pollen exclusively.

Acknowledgements

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