How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamot *Monarda fistulosa* (Lamiaceae)?

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Summary. By experimental manipulation of the nectar in flowers, I characterized the decision-making process used by nectar-gathering bumblebees for initiating movements between inflorescences of wild bergamot. The decision-making process has these characteristics: departure from an inflorescence is less likely as nectar rewards increase; departure decisions are based on the amount of nectar in the last flower probed and are not influenced by the nectar rewards in either the previously probed flower or the previously visited inflorescence; the number of flowers already probed at an inflorescence influences departure decisions weakly; a bees' response (to stay or to depart) to a given size of nectar reward is variable. Since previously proposed foraging rules do not accord with this description, I propose a new rule. I show by experiment that the movements made by bumblebees enhance foraging success.

Key words: Bumblebees - Bergamot - Foraging - Nectar - Optimal foraging theory

In this paper, I address 5 related subjects. First, I suggest that realistic characterization of decision-making processes are essential for the most fruitful optimal foraging models. Second, I describe the behavior of nectar-gathering bumblebees foraging among inflorescences of wild bergamot and, by experiment, show that the frequent movements made by bees between inflorescences enhance foraging success. Third, by experimental manipulation of nectar rewards, I attempt to characterize the decision-making process governing the movements of the bumblebees that I studied. Fourth, I use data from the experiments to test for the applicability of some previously proposed decision-making rules to the bees. Since the pre-existing rules do not describe the observed behavior well, I propose a novel model. Finally, I suggest that an understanding of bumblebees' response to the nectar rewards that they encounter will direct speculation about the adaptiveness of nectar production strategies exhibited by plants pollinated by bumblebees. In particular, I use data from my experiments to address the possible effect of variability in nectar rewards on the pollination success of the plants.

The value of realism in optimal foraging models

Presumably, animals have undergone natural selection for the adoption of foraging behaviors that maximize gain in a currency that ultimately translates into fitness (Schoener 1971). Often, it is assumed that the currency that is maximized is the net rate of energy intake (Emlen 1966; Schoener 1971; Stephens and Krebs 1986). What foraging behavior should the animal adopt to maximize its currency gain? Decision problems such as this have been addressed in models derived from optimal foraging theory. I suggest that a fruitful optimality analysis results from models that include a realistic characterization of the decision-making process of the animal as it operates in the wild because then the interaction between natural selection and behavior can be elucidated.

Optimality analysis of a model of foraging behavior leads to identification of the particular variant of a foraging strategy that gives the maximum possible rate of energy intake. Comparison of the success of the strategy adopted by the animal with that identified by the model can be used to determine whether there is the potential for selection for improved foraging behavior to operate. If, in the model, the forager is given perfect information for decision making [perfect sensory and cognitive abilities, i.e. a ‘literal optimality’ model (Mazur 1983)] then a difference between the rate of energy uptake of the animal and the model can indicate the potential for selection to improve sensory and cognitive capabilities of the animal because the difference indicates how much the foraging success (hence fitness) of the animal would be enhanced by improved capabilities. Similarly, if, in the
model, the forager is given realistic information for decision making [realistic sensory and cognitive abilities, i.e. a ‘constrained optimality’ model (Maynard Smith 1978; Staddon and Hinson 1983)] then a difference between the rate of energy intake between the animal and the model indicates the potential for selection to improve the use of the present sensory and cognitive abilities of the animal. If the potential for selection is indicated as a result of optimality analyses, then it raises the question of why selection has not acted previously to improve foraging performance. Possible answers include the opposition of selection for improved foraging by other pressures through trade-offs, or the failure of the assumption that more food equals higher fitness. Therefore, much can be inferred about the likely action of selection on behavior and its interaction with other aspects of an animal’s life history through including in foraging models both idealized and realistic characterizations of an animal’s sensory and cognitive capabilities and the decision process that it uses.

Despite the importance to optimality analyses of discovering realistic decision-making mechanisms, it has been recognized repeatedly that little work has been directed towards identifying them (Ollason 1980; McNair 1985). Typically, investigations involving the construction of models of foraging behavior have emphasized testing the hypothesis that the animal attains literal optimality (e.g. Lima 1984, 1985). However, discrepancies between the performance of the animal and model may be because of the inaccuracy of the model and not indicative of the potential for selection.

Some authors have recommended using comparisons with optimality models to infer the sensory and cognitive capabilities of animals (Cheverton et al. 1985). However, to the extent that one wishes to use optimality analyses to address evolutionary questions about the interaction between natural selection and foraging behavior, then it is important to derive the characterization of the animal independently from the formulation of a model, as is done here. [An optimality analysis of models of bumblebee foraging incorporating the findings of this paper is in Cresswell (1989)].

Bumblebees as suitable experimental subjects

Many animals forage for food items that are spatially distributed into discrete clumps or patches (MacArthur and Pianka 1966). Having begun to forage in a patch, an animal must decide how long to remain before moving to a new patch (Cowie 1977). Since the quality of patches varies, a prudent forager might make an assessment of the patch it is in, compare it with patches it has previously encountered, and decide whether it might be more profitable to move to a new patch. This type of problem has been addressed in optimal foraging models of patch departure (e.g. Charnov 1976; Cowie 1977). Bumblebees are well suited for optimality analyses of patch departure behavior because bumblebees often exploit food items (nectar rewards in flowers) that are distributed in patches (inflorescences). Furthermore, models of foraging can be relatively simple since bumblebees’ decisions may be focused entirely on net energy intake since foraging behavior is unlikely to be influenced by predation or searching for mates or nests, at least for the worker caste (Pyke 1979).

What kinds of ‘rules’ might bumblebees use?

Although useful qualitative investigations into inflorescence departure decisions by bumblebees have been made (Pyke 1982, 1979), only 1 potentially predictive, quantitative mechanism has been proposed; the ‘threshold departure rule’ for bumblebees foraging on Delphinium nelsonii (Hodges 1981, 1985a, b). The decision mechanism has a single parameter, the threshold; the bumblebee leaves an inflorescence after receiving a subthreshold nectar reward. This rule can be efficient when the amounts of nectar in adjacent flowers are related, i.e. when a subthreshold reward is predictive of little nectar in the next flower also (Hodges 1985b). The rule was formulated to explain the behavior of bees foraging systematically on vertical inflorescences of 3 flowers. I test the generality of the rule for bumblebees in different circumstances since, on wild bergamot, bumblebees forage systematically on radially arranged inflorescences with usually 10–15 flowers. I also test the applicability of various models that were not intended specifically for bumblebees.

Contemporary mechanistic models are often formulated from the premise that animals make foraging decisions by a simple ‘rule-of-thumb’ (McNamara and Houston 1980; Janets and Cole 1981). Decision making rules-of-thumb that have been investigated and that might be used in solution to the problem of when to move between inflorescences faced by bumblebees foraging on bergamot include giving-up-time rules where the forager leaves a patch after some interval without capturing a prey (Krebs et al. 1974; Iwasa et al. 1981) and counting rules where the forager leaves a patch after some number of trials and/or captures (Green 1980; Iwasa et al. 1981; Lima 1984, 1985). For the bumblebee-bergamot system, fixed giving-up-time rules can be translated into fixed numbers of flowers searched without reward. The counting rule as stated by Green is inapplicable because it depends on the number of equally sized prey items captured in a patch, while the amount of nectar in flowers is a continuous variable. However, an analogous formulation might base movement decisions on the sum of the amount of nectar gathered at previous flowers.

The role of nectar in pollination

Bumblebees serve as pollinators for many plants. For these plants, reproductive success is, in part, determined by pollen flow that is mediated by bumblebees’ move-