

The behavioral ecology of nectar robbing: Why be tactic constant?

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Abstract

How do animals forage in environments with variable food resources? For animals foraging at flowers, the concept of floral constancy has provided a framework for understanding why organisms visit some flower species while bypassing others. Here we extend this framework to understand the various flower-handling tactics that floral visitors employ. Nectar robbers are animals that remove nectar through holes bitten in flowers, often without providing pollination service. Many foragers can switch between robbing and visiting flowers legitimately to gain access to nectar. Here we document that even though individuals can switch foraging tactics, they often do not. We explore whether, instead, individuals exhibit constancy to either robbing or visiting flowers legitimately, which we term tactic constancy. We then extend hypotheses of floral constancy to understand when and why floral visitors might exhibit tactic constancy. Recognizing tactic constancy in nectar robbing raises intriguing questions for future research into its ecological and evolutionary consequences for plants, floral visitors, and their interactions.

I. Introduction

One of the most striking behaviors that animals exhibit in variable environments is to forage consistently for a single type of food even when other, highly suitable ones are available and accessible. This is exemplified by pollinating bees' floral constancy, i.e., the tendency for individuals to persistently visit a particular species of flower even when doing so bypasses equally or more rewarding species [1] (for definitions of this and other terms used here, see Box 1). A significant body of research explores when the benefits of floral constancy would outweigh the costs of switching among species (e.g., [2]).

Here, we extend the concept of constancy to another set of puzzling behaviors that floral visitors exhibit. Many plants are subject to high rates of nectar robbing, i.e., the acquisition of nectar via holes that foragers cut in corolla tissue rather than “legitimately” via the entrance of the flower (Box 1). Robbing and legitimate foraging are not necessarily pure foraging strategies, although they have generally been studied as such. Rather, many visitors that feed legitimately can also rob that same flower type, and indeed switch back and forth between these behaviors even within a single foraging bout [3–7]. Yet, despite this flexibility, visitors often display what we here term tactic constancy, or the tendency to perform one behavior for prolonged periods (Box 1).

Why exhibit tactic constancy, given the option to switch foraging behaviors? What factors determine which tactic an individual will employ, why do foragers so often stay constant to a single tactic for prolonged periods even though they could easily switch, and what are the consequences for plants? Here, we first briefly review nectar robbing, focusing on the little-

studied aspect of intraspecific behavioral variation. We then examine why constancy to a given tactic might benefit individual foragers, and consider its broader ecological implications. In the process, we provide an important extension of the concept of constancy to a new ecological and behavioral context. Throughout, we consider whether or not individuals are tactic constant, and if they are, which tactic they employ.

II. Tactic constancy of nectar robbing: A brief review

A great deal is now known about the ecological distribution of nectar robbing, as well as its surprisingly variable fitness consequences for plants [5]. In contrast, its costs and benefits have been minimally studied from the foragers' perspective. It has become clear, however, that nectar robbing varies at several hierarchical levels [5]. At the species level, some individuals may consistently forage as primary or secondary nectar robbers (Box 1), while at the same time other individuals visit flowers legitimately [8,9] [8,9]. For social insects, some proportion of individuals within a single colony may rob while others forage legitimately. Variation can also exist at the within-individual level, both among foraging bouts (i.e., an individual might switch between robbing and foraging legitimately from one bout to the next) and within bouts [10]. Variation in foraging behaviors can also be associated with different plant species (i.e., visitors might forage legitimately on one flower species while robbing another) or with different flowers within a plant species (i.e., they may forage legitimately on shorter-corolla flowers but rob longer ones) [11–13]. Here, we focus on tactic constancy in the collection of nectar; we note, however, that floral visitors can also switch between nectar robbing and legitimate foraging for pollen (see Section IV).

Foragers that can profitably feed on a given flower species in multiple ways divide their time between alternative foraging tactics, but the rules that guide their decisions are poorly understood. Many studies simply report the proportion of floral visits of each type (e.g., [14–16]). For example, Maloof [17] reported that of the 126 visits *Bombus appositus* queens and workers made to *Corydalis caseana* flowers over the course of the flowering season at two sites, 86.5% were legitimate, and the rest involved secondary nectar robbing. This method of recording robbing is useful if the aim is to study the cumulative impacts of robbing on plants. However, this phytocentric approach reveals little with regard to which foraging strategies are adopted by individual floral visitors, and why.

To understand behaviors from the forager's perspective, we require studies of individuals' visitation sequences, in which data on use of alternative foraging tactics are obtained both within and across bouts. The few such studies to date point to the existence of behavioral switches, but also, in most cases, to a high degree of constancy to a single tactic (e.g., [3,18]). For example, Ishii and Kadoya [10] found that individual *Bombus terrestris* showed high constancy to nectar robbing among foraging bouts on *Trifolium pratense*; when behavioral switches occurred, they involved a switch between robbing *T. pratense* and legitimately visiting flowers of another plant species, *Lotus corniculatus*. Our own research (R.E. Irwin, J.L. Bronstein, and E.M. Lichtenberg, *unpubl. data*) also lends support to the predominance of tactic constancy with occasional behavioral switches. Of 169 foraging bouts by three Colorado bumble bee species visiting *Mertensia ciliata*, we observed that only 19 bouts (11%) involved more than one tactic.

Similarly, in 386 foraging bouts to *Linaria vulgaris*, only 26 (6.7%) involved more than one tactic.

III. Why be constant to a single foraging tactic?

Ultimately, an animal should exhibit constancy to a single foraging tactic when the benefits of doing so outweigh the costs. Although the costs and benefits of tactic constancy have not been well investigated, costs and benefits of floral constancy (Box 1) have received significant attention. Four hypotheses propose that floral constancy increases the efficiency with which a forager collects nectar. This efficiency can (a) reflect greater ease in detecting one specific type of flower against a complex background (use of a search image) [19]. Floral constancy can save time that would be needed to learn or memorize (b) the appearance of alternative food types [20] or (c) how to handle (i.e., extract food from) an alternative food type [19]. Floral constancy can also (d) eliminate high time or energy costs of sampling alternative types [21].

Hypotheses (c) and (d) have the clearest relevance to understanding tactic constancy. Visiting flowers legitimately and robbing them may be equivalent to handling distinct flower types in different ways. Thus, it is reasonable to predict that tactic constancy reduces handling costs sufficiently to increase fitness (Hypothesis c). If the average volume of nectar that can be obtained differs between foraging legitimately and robbing, tactic constancy could mitigate costs arising from determining the average rewards of each tactic (Hypothesis d). Quicker recognition (Hypothesis b) could potentially boost efficiency of foragers that remain constant to one tactic, if those foragers view the flower opening versus the location that gets robbed (e.g., the nectar spur)

as separate types of food. This seems unlikely, however. Bumble bees, for example, frequently walk on various parts of flowers as they move within an inflorescence or as they search for the flower opening (E. M. Lichtenberg, *pers. obs.*).

At a mechanistic level, cognitive constraints may limit animals' abilities to efficiently switch among behaviors over short time-scales. One possibility is that foragers can only remember one handling tactic at a time, and must re-learn how to extract nectar after switching between legitimate visitation and robbing. However, several studies find that pollinators can remember at least two separate handling tactics (reviewed in [21]). A better-supported hypothesis is that floral constancy allows rapid use of short-term memory, whereas switching would entail time delays or errors as handling information is uploaded from long-term to short-term memory [20,22]. This mechanism suggests two broader hypotheses that could be investigated: (e) the probability of tactic constancy declines when a floral visitor spends several minutes not handling flowers and thus the last-used motor skill fades from short-term memory; and (f) tactic constancy may persist when floral visitors switch plant species in quick succession, thereby employing the motor task already stored in short-term memory.

Despite the efficiency gains and cognitive constraints favoring tactic constancy, there are also potential costs to being tactic constant. Again, comparison with floral constancy is informative. One of the striking features of floral constancy is that animals often bypass equally or more rewarding morphs or species [1,21]. Similarly, tactic constancy could be costly if it means ignoring one handling tactic in favor of a less rewarding one either on a given flower morph or when switching flower morphs (e.g., [18]). In particular, these costs could magnify in cases

where floral visitors are robbing-constant and robbed flowers have less nectar than unrobbed ones (e.g., [8,16]).

The net benefits of tactic constancy should be mediated by the payoffs and frequency of alternatives to the preferred tactic. Both the magnitude and predictability of these two factors are important. For example, studies of floral constancy suggest that honey bees and bumble bees are more likely to switch to different flower types if the current preferred type either provides low rewards or is not encountered frequently [2,23]. The payoffs and frequency of alternatives are influenced in part by the environment (e.g., the abundance of a plant species that can only be robbed), but there are also social influences, such as the behavior of conspecifics [24,25]. The nectar available via each tactic and the frequency of previously robbed flowers depend on the abundance, species, and tactics of other foragers (e.g., [8,16,26]).

Beyond assessing the benefits of constancy to any one particular tactic (rather than to another tactic), it is also important to explore the benefits of tactic constancy (rather than behavioral switches) in general. To do so, it would be informative to study variation among individuals in a single population. If all individuals are tactic-constant, but some are constant to one tactic and some to another, it is likely to be constancy *per se* that is beneficial. To our knowledge, no studies have attempted to quantify those potential benefits. However, studies reporting multiple foraging behaviors employed by a diverse floral visitor assemblage often describe species employing both constant and flexible foraging strategies, suggesting that trade-offs between the benefits and costs of constancy vary among species and contexts [18,27]. Closer study would provide insight into which costs, benefits, and constraints are at play. For example, in terms of

constraints, tactic constancy within but not among foraging bouts would suggest the role of short-term but not long-term memory limitations. The drivers of differences in the benefits of tactic constancy across species will be more difficult to identify, as species differences in morphology, cognition, and ecology may all play a role.

IV. Future directions in the study of tactic constancy

We have described here a poorly understood but common set of behaviors of certain nectar-feeding insects, which we term tactic constancy. Researchers have only just begun to explore its implications for plants, floral visitors, or the mutualisms they sometimes form. Here we point to specific gaps in our understanding of tactic constancy, as well as the kinds of studies that are needed to fill them.

Implications for floral visitors – Our current understanding emerges from studies of a handful of insect species, primarily bumble bees, almost all of them studied during a single season. A deeper understanding of tactic constancy requires comparing populations across ecologically disparate sites and years, as well as documenting these behaviors in a wider variety of taxa. For example, several species of Lepidoptera and Diptera, as well as a variety of halictid, megachilid, and apid bees, employ multiple foraging tactics on *Arctostaphylos pungens* flowers in Arizona [27]; it will be exciting to examine whether they too show tactic constancy. Moving beyond insects, it is important to explore tactic constancy in the many bird species noted in the literature to forage both legitimately and as nectar robbers [5]. As we point out in Section III, comparative studies would also help generate hypotheses regarding the fitness consequences of tactic

constancy. Finally, it is important to extend the study of tactic constancy to include pollen foraging. Visitors commonly combine nectar robbing with legitimate foraging for pollen (rather than nectar), as noted among visitors to *A. pungens* [27]. More generally, how pollen and nectar resource acquisition are combined is surprisingly poorly understood from the perspective of either foragers or the plants they visit [28].

Implications for plants - Although floral constancy is clearly tied to pollen flow and plant fitness, the link between tactic constancy and plant fitness is less clear and is in need of further investigation. The effects of nectar robbing range from negative to positive [5]. It is possible that this wide variation in effects is related to whether or not individual robbers are constant to that tactic. The inconsistent use of tactics within a foraging bout could reduce geitonogamy (deposition of self-pollen) and increase pollen flow distances as the number of flowers between two legitimate foraging tactics increases. It should also be noted that some of the strongest negative effects of robbing are known from systems in which legitimate visitors and robbers are separate species and robbing results in pollinator avoidance of robbed plants and flowers [29]. Alternatively, variable effects of robbing may primarily reflect the total amount of robbing a plant receives, regardless of whether individual robbers are constant. The latter may especially be the case when robbing directly damages reproductive structures or causes flower abortion [30].

Implications for pollination mutualisms – Finally, we envision that tactic constancy could hold insights for understanding the evolution and persistence of pollination mutualisms. Mutualism theory proposes that if mutualists are offered a “temptation to cheat” and if cheating goes

unchecked, mutualistic behaviors and hence mutualism will erode ([31]; but see [32]).

Legitimate nectar foragers able to switch to robbing may provide an example of mutualists faced with this temptation. However, if tactic constancy to legitimate visitation carries a fitness advantage to an individual forager, that individual would be expected to pursue this behavior despite the availability of a cheating alternative. If legitimate foraging results in successful pollen transfer, mutualism would then be reinforced. In this way, tactic constancy offers a potential solution to one of the most persistent mysteries surrounding mutualism: why cooperate, when there are options not to do so?

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Papers of particular interest, published within the period of review, have been highlighted as:

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- Queen bumble bees foraged legitimately at the outset of flowering, but switched their foraging tactics to nectar robbing later in the season. This allowed honey bees and other legitimate nectar foragers to switch to secondary nectar robbing. Nectar robbing bumble bees were the most

efficient pollinators, and honey bees' switches to secondary robbing had little negative effect on seed set.

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●●Secondary nectar robbing is common in nature, often occurring when legitimate nectar foragers switch behaviors following primary robbing. In the first study to examine the fitness consequences of secondary robbing for plants, the authors experimentally manipulated robbing status of flowers, and found that those experiencing both primary and secondary robbing had lower estimates of female fitness (pollen receipt and fruit and seed production) than flowers that had only experienced primary robbing and unrobbed controls. Primary robbing alone reduced only some of these reproductive success measures, suggesting that secondary robbing is an important driver of overall outcomes of nectar robbing.

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●● In experiments with two or three plant species, bumble bees foraging for pollen and nectar both legitimately and illegitimately exhibited a high degree of tactic constancy. Behavioral

switches were only observed between a fraction of possible plant-tactic combinations, suggesting that handling skills required by one tactic constrain short-term options for behavioral switches.

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- The authors document variability in floral traits within one plant species, and report that nectar robbing frequency was a function of corolla length, lip size, and nectar volume. Bumble bee and carpenter bee nectar robbers may opportunistically switch to robbing in response to these traits. Outcomes of robbing and these tactic switches resulted in two floral trait optima for plant reproduction: flowers with long corollas and little nectar, and those with short corollas and abundant nectar.

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- The authors make a plant community-level survey of nectar robbing across disparate ecosystems, identifying two distinct topologies in patterns of primary robbing: communities where opportunistic robbers exploit a few, highly rewarding plant species, and those in which robbing is evenly spread across multiple species of plants, and nectar robber species richness may be high. A variety of plant traits were associated with nectar robbing, especially corolla morphology and nectar reward quantity, but this varied among community types.

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- Bumble bees and honey bees were usually tactic-constant to legitimate nectar and pollen foraging, but in about 10% of foraging bouts, switched between legitimate behavior and one or more forms of nectar robbing. Nectar robbing changed nectar reward dynamics, causing changes in pollinator behavior and increases in male plant fitness.
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●● Bees must harvest both nectar and pollen from flowers, yet the energetic cost of switching between these foraging tasks may favor tactic constancy, and may be a function of relative floral rewards. The authors manipulated bumble bee colonies' access to pollen, then allowed workers to forage on arrays of artificial flowers with low, medium, or high nectar:pollen reward ratios. These treatments interacted to affect individual bee foraging strategy, with bees from pollen-starved colonies showing greater constancy to pollen foraging regardless of reward ratios, and those from pollen-satiated colonies adopting high pollen constancy only when nectar resources were highest. This context-dependent behavioral constancy may thus play key roles in outcomes of plant reproduction and the evolution of relative reward ratios.

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● In a chapter within a comprehensive treatment of mutualism, the author presents a broad review of the exploitation of mutualisms, including legume-rhizobium symbiosis, invertebrate-algal symbiosis, and pollination. Nectar robbers often exploit pollination mutualisms by removing floral resources without pollinating; similar to exploiters of other forms of mutualism,

robbers may be third species ‘parasites of mutualisms,’ or may be ‘cheater mutant’ individuals of species that also function as pollinators.

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Box 1. Terminology used in this review to describe the behavior of floral visitors. Additional detail may be found in Inouye [33] and Irwin et al. [5].

Constancy	Short-term fidelity of foragers to one plant species (floral constancy) or foraging behavior (tactic constancy)
Efficiency	Degree to which a behavior maximizes benefits and minimizes costs per unit time
Legitimate forager	A forager that obtains nectar in a manner for which the floral morphology appears adapted, usually resulting in minimal flower damage
Pollinator	An animal that transfers pollen from one flower to another, regardless of its floral handling behavior
Nectar robber	A forager that perforates a flower's corolla (primary nectar robber or 'primary robber') or uses a perforation made by another forager (secondary nectar robber or 'secondary robber') to access nectar, often without contacting anthers or stigmas, or pollinating
Strategy	A behavioral rule employed by a forager that can include a single tactic (pure strategy) or multiple tactics (mixed strategy)
Tactic	A behavior adopted as part of a strategy