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Explaining the effects of floral density on flower visitor species composition

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Abstract

Floral density often influences the species composition of flower visitors. This variation in visitor species composition could have significant effects on pollination success and plant fitness but is poorly understood, especially in the many pollination guilds dominated by non-territorial species. This paper presents a foraging model that explores how flower visitors with diverse traits should distribute themselves across resource patches differing in floral density. The model predicts that species with low flower search speeds and low flower handling costs compared to competitors will usually dominate dense flower patches. In addition, amongst flower visitors that have lower energy expenditure rates while handling flowers than while traveling, species maximizing energetic efficiency are typically associated with dense flower patches whereas those maximizing net rate of energy intake are associated with sparse patches. The model is able to predict some key aspects of a previously-observed effect of floral density on species composition of flower visitors to the yellowflower tarweed (*Holocarpa virgata*). By providing insights into how flower visitors' traits shape the effects of floral density on the species composition of flower visitors, this study makes an important step towards understanding how pollinator diversity influences relationships between plant density and plant fitness.

Keywords

Foraging behavior; optimal foraging theory; pollination; competition

Introduction

Plant-pollinator interactions are sensitive to variation in floral density: for instance, both per-flower pollinator visitation rates and seed production rates often decline at low densities (Kunin 1997; Ghazoul 2005). Shifts in flower visitor species composition with declining floral density have also been recorded in a wide variety of systems, including tropical and temperate communities and both insect and avian pollination guilds (Johnson and Hubbell 1975; Feinsinger 1976; Schaffer et al. 1979; Kwak 1987; Zorn-Arnold and Howe 2007; Essenberg 2012b). Because flower visitor taxa often vary markedly in their quality as pollinators (e.g., Wilson and Thomson 1991; Olsen 1997; Kandori 2002; Cane and Schiffhauer 2003; Ivey et al. 2003; Larsson 2005; Adler and Irwin 2006; Rader et al. 2012), these changes in flower visitor species composition can have strong effects on plant reproductive success.

Only a few attempts have been made to explain effects of floral density on pollinator species composition or to identify the traits that cause a species to exploit dense vs. sparse floral resources. In some flower visitor guilds, including many avian and some tropical insect guilds, individuals or colonies defend feeding territories. Species capable of winning a high proportion of aggressive interactions, for instance because of large body size or group foraging behaviors, often monopolize dense resource patches, leaving sparse resources to

subordinate species (Johnson and Hubbell 1974; Johnson and Hubbell 1975; Feinsinger 1976; Carstensen et al. 2011; Justino et al. 2012). However, most of the reported examples of shifts in pollinator species composition with increasing floral density have occurred amongst insect species that exhibit little or no defense of food resources.

A model by Schaffer et al. (1979) explains effects of nectar productivity on pollinator species composition based on (a) the standing crop of nectar needed for foragers to make a profit while foraging, which depends on forager body size, and (b) how productive a flower patch must be in order to support a colony, which depends on colony size. The Schaffer et al. (1979) model's predictions are roughly consistent with an observed shift from carpenter bees to bumblebees to honeybees across populations of *Agave schottii* of increasing nectar productivity. However, because the model implicitly assumes that a colony obtains all of its resources from a single resource patch, it applies only to large spatial scales: a resource "patch" must be the only significant source of floral resources within foraging range of a colony, which is commonly hundreds or thousands of meters (Greenleaf et al. 2007). By this reasoning, the resource patches in most of the cases in which floral density has been observed to influence pollinator species composition are much too small for the Schaffer et al. (1979) model to apply.

Although seldom modeled in plant-pollinator systems, shifts in the composition of forager types across resource density gradients have often been explored in other systems. Many of these theoretical studies model distributions of foragers across alternative patches within their foraging ranges and assume that foragers compete with each other only through exploitation of shared resources (e.g., continuous input models without interference, reviewed by Milinski and Parker 1991; also see Parker and Sutherland 1986; Houston and McNamara 1988; Hsieh and Grand 2003; Koops and Abrahams 2003; Jackson et al. 2004; Yates and Broom 2005). A common prediction of these models is that each forager type will be most abundant in the patch in which its food intake rate, or competitive weight, is the highest in relation to those of other foragers (Parker and Sutherland 1986; Milinski and Parker 1991). These models assume that the resources are produced continuously within foraging areas and are immediately consumed by the foragers present. In plant-pollinator systems, however, nectar and pollen accumulate in flowers to form standing crops, and foragers must expend time and energy traveling between flowers within a patch in order to harvest those standing crops. A model including these properties of plant-pollinator systems is needed to determine the extent to which the predictions of these general continuous-input foraging models apply to plant-pollinator systems.

Here, I present a model that predicts the distribution of contrasting flower visitor species across flower patches differing in floral density, assuming optimally-foraging, non-territorial flower visitors. My aim is to identify traits that cause flower visitor species to exploit dense *versus* sparse patches when in competition with other taxa. I begin by developing an analytical model that predicts the distribution of two pollinator species across a sparse and a dense flower patch, assuming that pollinators forage optimally without perceptual constraint and maximize energy intake per unit of energy expended (energetic efficiency). I then extend this model to the mathematically more complex cases in which one or both species instead maximize net rate of energy intake (NREI). Finally, I use a simulation to apply the model to a more realistic situation in which there are more than two flower densities and more than two flower visitor species and in which foragers make errors in their assessments of patch quality. I compare the resulting model predictions to observed shifts in flower visitor species composition with floral density in an annual composite, the yellowflower tarweed (Asteraceae: *Holocarpa virgata* ssp. *virgata*).

A model of two flower visitor species that maximize efficiency

Assume a system with two flower visitor species, a and b , and two flower patches, a sparse patch, S , and a dense patch, D . All individual flowers produce identical rewards, all flower visitors within a species are identical, and flower visitors interact exclusively through exploitation of shared floral resources. Foraging conditions, such as temperature and nectar secretion rates, are constant, as are the average numbers of active foragers of each species. Flower visitors forage only for nectar, and each individual forages so as to maximize its foraging success. Although other motivations can influence flower visiting behavior (e.g., Sapir et al. 2005; Ings and Chittka 2008), models assuming maximization of foraging success often successfully predict behavior of flower visiting bees (Pyke 1978; Pyke 1984; Schmid-Hempel et al. 1985; Goulson 2003).

Two currencies have commonly been used to measure foraging success in flower visitors:

$$\text{Net Rate of Energy Intake (NREI)} = \frac{\text{Net energy intake}}{\text{Time spent}} \text{ and} \\ \text{Energetic efficiency} = \frac{\text{Net energy intake}}{\text{Energy used}} \text{ or, simply, } \frac{\text{Energy intake}}{\text{Energy used}}.$$

NREI is the more commonly-used metric (Pyke et al. 1977; Stephens and Krebs 1986). However, honeybee foraging is more consistent with maximization of energetic efficiency than with maximization of NREI (Schmid-Hempel et al. 1985; Kacelnik et al. 1986; Schmid-Hempel 1987; Afik and Shafir 2007), and past data collected on bumblebee foraging can be explained equally well using either currency (Charlton and Houston 2010). Because the mathematics is simpler if both pollinator species maximize efficiency, I develop the model under this assumption before considering situations in which one or both pollinator species maximizes NREI.

Many flower visitors are central place foragers and may prefer foraging patches close to their central place (e.g., Tamm 1989; Cresswell et al. 2000; Zurbuchen et al. 2010). However, if the two patches are approximately equally distant from the flower visitors' central place, then the flower visitors' patch choice decisions should be governed by the relative energetic efficiencies obtainable while foraging within each patch. Energetic efficiency for species i foraging within patch j can be expressed as $I_j/E_{i,j}$, where I_j is average energy intake per flower visit in patch j and $E_{i,j}$ is the average energy cost per flower visit for species i in patch j (see table 1 for a list of symbols used in the model).

Average nectar volume per flower and therefore average energy intake per flower visit declines with increasing forager numbers. Suppose that the nectar in a flower is completely consumed during each flower visit and then replenishes at a constant rate, r . If the flower handling time is much smaller than the time between visits to a flower, then the average time that flowers can replenish between visits will approximately equal the inverse of the average per-flower visitation rate, V_j . Therefore, at equilibrium, r

$$I_j = \frac{r}{V_j}. \quad (1)$$

The total per-flower visitation rate is the sum of the visitation rates of the two flower visitor species:

$$V_j = V_{a,j} + V_{b,j}. \quad (2)$$

where $V_{i,j}$ is the average per-flower visitation rate by species i in patch j . $V_{i,j}$ equals the number of foragers per flower in the patch times the visitation rate per forager, which is the inverse of the average time required for each flower visit. Therefore,

$$V_{i,j} = \frac{n_i p_{i,j}}{f_j T_{i,j}}, \quad (3)$$

where n_i is the average abundance of species i across both patches, $p_{i,j}$ is the proportion of these foragers occupying patch j , f_j is the number of flowers in patch j , and $T_{i,j}$ is the average time spent per flower visit by species i in patch j . Suppose that the average time required to travel between flowers is proportional to the average distance between flowers, d_j , and inversely proportional to the flower visitors' search speed, s_i . If flower visitors do nothing other than visit flowers, then

$$T_{i,j} = h_i + \frac{d_j}{s_i}, \quad (4)$$

where h_i is the average flower handling time. Implicit in this equation is the assumption that foragers visit every flower to which they fly. Some flower visitors use scent marks to reject flowers that have been visited recently, which could increase travel time between flower visits because of wasted trips to unacceptable flowers, especially when visitation rates are high (e.g., Stout and Goulson 2002), but I do not consider the influence of this behavior here.

Suppose foragers expend energy at a constant rate, c_i , while traveling between flowers and likewise expend energy at a constant rate, $k_i c_i$, while handling flowers. Energy expenditure per flower visit for species i foraging in patch j will be:

$$E_{i,j} = c_i k_i h_i + c_i \frac{d_j}{s_i}. \quad (5)$$

For insects that land on flowers while feeding, k_i will typically be much less than 1 (Heinrich 1975; Heinrich 1979), whereas for species that hover while feeding, such as hummingbirds and hawkmoths, k_i will be equal to or greater than 1 (Ellington et al. 1990; Clark and Dudley 2010).

If foragers maximize energetic efficiency, then the members of each species must be distributed across patches S and D so that no individual can improve its efficiency by shifting some or all of its foraging time from patch D to patch S or *vice versa*. Therefore, if a species uses both patches, then

$$\frac{I_D}{E_{i,D}} = \frac{I_S}{E_{i,S}}. \quad (6)$$

If equation 6 is not satisfied, species i will forage exclusively in the patch offering the highest foraging efficiency. Energy costs per flower visit, $E_{i,j}$, are lower in the dense than in the sparse patch because of the shorter distances between flowers in the dense patch. On the other hand, rewards per flower, I_j , must be higher in the sparse than in the dense patch. (If this were not the case, then efficiency would be greater in the dense than in the sparse patch and foragers would switch to the dense patch, causing I_D to be less than I_S .)

From Equations 1–6, one can calculate the optimal distribution of forager species *a* for any possible distribution of species *b* and vice versa (“Best response curve for a flower visitor that maximizes efficiency,” available online). These “best response curves” can be used to determine the equilibrium distribution (Grand and Dill 1999). Suppose both best response curves are plotted against $p_{a,D}$ and $p_{b,D}$, as in figure 1. Both curves are linear. The two curves overlap, and a neutrally stable equilibrium distribution of the two species is possible at any point along the shared best response curve, when the ratios of energy expended per flower visit in the dense *versus* the sparse patch are equal for the two species:

$$\frac{E_{a,D}}{E_{a,S}} = \frac{E_{b,D}}{E_{b,S}} \quad (9)$$

(“Influence of species traits on equilibrium distribution when both species maximize efficiency,” available online). However, if the ratio of energy expended per flower visit in the dense *versus* the sparse patch is less for species *a* than it is for species *b*,

$$\frac{E_{a,D}}{E_{a,S}} < \frac{E_{b,D}}{E_{b,S}}, \quad (10)$$

then the best response curve for species *a* will intercept both axes at a higher point than will the best response curve for species *b* (figure 1, “Influence of species traits on equilibrium distribution when both species maximize efficiency,” available online). Regardless of the starting distribution, the two species will approach a stable equilibrium in which species *a* fills up the dense patch, excluding species *b* from it entirely (figure 1 A), or, if species *a* is not abundant enough to exclude species *b* from the dense patch, species *a* foragers are confined to the dense patch and species *b* is found in both patches (figure 1 B). In other words, the species for which between-flower distances, and therefore floral density, have a greater influence on energy costs is predicted to forage primarily in the dense patch while the other species takes advantage of the higher per-flower rewards in the sparse patch. This result is similar to the “truncated phenotype distribution” predicted by some continuous-input models, although in those models each forager type occurs primarily at the density where its food intake rate is highest in relation to that of the other foragers rather than where its costs are lowest (Parker and Sutherland 1986; Milinski and Parker 1991).

Inequality 11 will be satisfied, and the proportion of species *a* in the dense patch will be higher than the proportion of species *b* ($p_{a,D} > p_{b,D}$), when

$$k_a h_a s_a < k_b h_b s_b \quad (11)$$

(figure 2 A, “Influence of species traits on equilibrium distribution when both species maximize efficiency,” available online). In other words, having a shorter flower handling time, slower search speed, or lower ratio of flower handling cost to flight cost compared to competitors makes a species more likely to dominate dense flower patches. This prediction makes intuitive sense. Floral density influences the costs of traveling between flowers but not the cost of handling flowers. Species with high travel costs and low flower handling costs (low s_i , h_i , and k_i) can lower their foraging costs significantly by choosing dense flower patches. However, for species whose foraging costs are dominated by the cost of handling flowers (high s_i , h_i , and k_i), the higher rewards per flower in the sparse patch may be more important than the relatively small decrease in foraging costs to be obtained by using the dense patch.

Extension of the model to species that maximize NREI

Now suppose that a flower visitor maximizes Net Rate of Energy Intake (NREI) rather than energetic efficiency. NREI for species i foraging within patch j is equal to $(I_j - E_{i,j})/T_{i,j}$, where energy intake, I_j , energy cost, $E_{i,j}$, and time cost, $T_{i,j}$, per flower visit are calculated just as they were for foragers maximizing efficiency (Equations 1–5). In this case, the mathematics is too complex for an analytical solution to be informative (see “Best response curve for a flower visitor that maximizes NREI,” available online). I instead use numerical solutions to show how forager traits influence equilibrium distributions across dense and sparse patches when both species maximize NREI and to explore how differences in foraging currency across the two species influence their equilibrium distribution.

Methods

I created a function in the software package R (R Development Core Team 2010) to calculate the equilibrium distribution of flower visitor species a and b across the dense and sparse patch. The function calculates the optimal distribution of species b given an arbitrary starting distribution of species a , then the optimal distribution of species a given this new distribution of species b , and so on until the distributions of both species stabilize. The outcome was not influenced by the starting distribution of species a . Formulae for optimal distributions (i.e., best response curves) of species maximizing NREI are given in “Best response curve for a flower visitor that maximizes NREI,” available online. I used this equilibrium forager distribution function along with R’s uniroot function to search for combinations of values of s_a , k_a , c_a , and h_a for which equal proportions of each flower visitor species foraged in the dense patch at equilibrium, assuming that both species maximized NREI or that one species maximized NREI and the other maximized energetic efficiency. I obtained the remaining parameter values from previous studies of bees visiting the yellowflower tarweed (Asteraceae: *Holocarpha virgata* ssp. *virgata*; table 2; Essenberg 2012a and b). The average frequency of visits per flower in this system can vary seasonally and from site to site by an order of magnitude. Therefore, I repeated these procedures after increasing and decreasing forager: flower ratios by a factor of three, which altered the average energy intake per flower visit. Results are similar for all three forager: flower ratios except where noted otherwise.

Results

Search speeds play a prominent role in determining which species will forage primarily in dense *versus* sparse flower patches regardless of which foraging currency, NREI or energetic efficiency, the flower visitors maximize (figure 2). In all cases, having a slower search speed makes a species more likely to dominate dense patches. Shorter flower handling times also make species more likely to use dense flower patches. However, flower handling times are of lesser importance than search speeds in shaping forager distributions if species maximize NREI (figure 2C–F), especially when forager: flower ratios are high (“Effects of forager to flower ratio on model predictions,” available online). The differing importance of handling time *versus* search speed is a result of their opposite effects on energy and time costs per flower. The lower rewards per flower in the dense patch compared to the sparse patch will have the greatest influence on NREI if energy and time costs per flower are low, which will be the case when flower handling times are low and search speeds are high.

When the foraging currencies of the two species differ, the species maximizing energetic efficiency is usually predicted to have the higher relative abundance in the dense patch, especially when forager: flower ratios are low (figure 2 C–D, “Effects of forager to flower ratio on model predictions,” available online). This is because, for foragers whose metabolic

rates are higher while traveling than while handling flowers ($k_f < 1$), between-flower flight distances have a stronger influence on energy costs per flower visited than on time costs, which depend more on the flower handling time. Therefore, energetic efficiency typically increases more strongly with floral density than does NREI.

If either forager species maximizes NREI, then having either a high metabolic rate, c_f , or a low energetic cost of handling flowers compared to the cost of flight, k_f , makes a species more likely to exploit dense flower patches (figure 2, “Effects of forager to flower ratio on model predictions,” available online). However, the influence of both traits is weak in comparison to the strong influence of k_f when both species maximize efficiency (figure 2 A). This difference reflects the lesser importance of energy costs compared to time costs to foragers that maximize NREI rather than efficiency. As metabolic rate increases, energy costs become increasingly important in determining NREI and foraging in dense floral patches therefore becomes increasingly advantageous for NREI-maximizers whose flight costs are greater than their flower handling costs (i.e., with $k_f < 1$).

Application to a natural system

I used a simulation to extend my model predictions to a field situation with more than two density levels and two flower visitor species, as well as to relax the assumption that foragers are omniscient about patch quality. I compared the model predictions to observed changes in the species composition of flower visitors across yellowflower tarweed (*Asteraceae*: *Holocarpha viragata* ssp. *viragata*) patches of increasing floral density. These data were recorded in a previous study and are described elsewhere (Essenberg 2012b), so I present only the most salient points here.

Methods

I recorded per-flower visitation to the yellowflower tarweed in five 2×2 m plots spanning the available range of floral densities during three sampling events at each of eight sites in the Donald and Sylvia McLaughlin Reserve in northern California (38.86°N , 122.41°W) between Aug. 8 and Sept. 22, 2010. (The flowering unit visited by pollinators in tarweeds is a flower head composed of 12–32 florets (Hickman 1993), which I refer to as a “flower” in this manuscript.) The plots were free of flowers of any species other than the yellowflower tarweed. The dominant flower visitors were three groups of bees: the long-horned bee *Melissodes lupina* (Anthophoridae), large-bodied sweat bees (Halictidae: *Halictus ligatus* and *Lasioglossum titusi*), and honeybees (Apidae: *Apis mellifera*), which together made 75% of the observed flower visits. *L. titusi* was apparently responsible for the bulk of the large sweat bee flower visits: of the 515 visits that could be assigned unambiguously to one sweat bee species or the other, 84% were by *L. titusi*. I analyzed the effect of plot floral density on the average per-flower visitation rates by each pollinator group by fitting a penalized cubic regression spline in a generalised additive mixed model (GAMM), with sampling event as a random effect (Wood 2006). In the analysis of each pollinator group, I used data only from sampling events in which at least one visit had been observed by that group. I $\log_{10}$ -transformed both visitation rates and floral densities to correct for positive skew, after adding 0.01 to visitation rates to eliminate zeroes. (The more widely-used $\log_{10}(X + 1)$ transformation failed to normalize the residuals.) To compensate for heteroscedasticity, my model allowed each sampling event to have a different variance. These analyses were carried out using the `gamm` function in the `mgcv` package in R (Wood 2006; R Development Core Team 2010).

I extended my model’s predictions to a situation with five floral density levels and three pollinator taxa, long-horned bees, large sweat bees, and honeybees, using an individual-based simulation. I assumed a constant number of foragers within each flower visitor taxon,

which were initially distributed randomly across five patches of equal flower numbers but differing densities. In each iteration of the simulation, I allowed each forager, in turn, to move to whichever patch would currently allow it to achieve the highest possible foraging success, given the patch's floral density and the per-flower visitation rates by the foragers currently in the patch, using the equations presented above (Equations 1–5). In some simulation runs, I relaxed the assumption of forager omniscience. I calculated the foraging success the animal perceived as being possible in each patch by adding a normally-distributed error, with mean equal to zero and standard deviation equal to 5% of the foraging success possible in the best patch, to the true value. The forager then moved to the patch it perceived as offering the highest foraging success. I assumed that total visitation by species other than the three focal taxa was independent of floral density, which is what I observed in my field study. I repeated this procedure, each time randomizing the order of foragers, until no forager could improve its foraging success, or, if foragers were not omniscient, until the model had completed 70 iterations. In the latter case, I averaged results from the last 20 iterations. I carried out all simulations in R (R Development Core Team 2010).

With the exception of forager energy expenditure rates, parameter values came from measurements made in the bee-tarweed system (table 2, “Measurements of parameter values in the bee-tarweed system,” available online). The handling time estimate for sweat bees appears to be close to the average handling time of the more abundant species, *L. titusi*, and lower than that of *H. ligatus*. The search speed estimate was recorded at a time when *H. ligatus* was relatively abundant and therefore is probably intermediate between the traits of the two species. I estimated flight metabolic rates, c_f , from body sizes and set k_f , the ratio of energy expenditure rate while handling flowers to energy expenditure rate while traveling, to the same value for all species. I assumed that honeybees maximize efficiency, as found in previous studies (Schmid-Hempel et al. 1985; Kacelnik et al. 1986; Schmid-Hempel 1987; Afik and Shafir 2007). Foraging currencies are not known for the other taxa, so I assumed either that both groups maximize efficiency or that both maximize NREI.

Results

Flower density was predicted to influence the species composition of flower visitors, with flowers in the densest patches receiving more honeybee visits than those in sparse-to-intermediate-density patches, which were instead visited by sweat bees and/or long-horned bees (figure 3). When foragers were assumed to be omniscient, the model predicted a truncated distribution in which each pair of species overlapped at most at a single density level (figure 3 A and B). Allowing foragers to make errors in assessing patch quality broadened their distributions so that they overlapped extensively (figure 3 C and D).

As predicted, per-flower visitation by honeybees peaked at high floral densities ($F_{2,3,56.7} = 12.6$, $p < 0.001$; figure 4). Per-flower visitation by long-horned bees was highest at low-to-intermediate floral densities, declining significantly at high densities ($F_{3,5,105.5} = 12.3$, $p < 0.001$; figure 4). Per-flower visitation by sweat bees did not respond significantly to floral density ($F_{1,113} = 0.6$, $p = 0.4$). As predicted when foragers make errors in patch assessment, all three species often overlapped across a broad range of floral densities (“Observed overlap between pollinator species distributions across floral density gradients,” available online).

Discussion

Flowers in dense patches are often visited by different animal species than flowers in sparse patches. The causes of these changes in flower visitor species composition are poorly understood, particularly where flower visitors are non-territorial. The model presented here explores how a tradeoff between relatively low travel costs in dense patches and high per-flower rewards in sparse patches can cause changes in flower visitor species composition

with changing floral density. Specifically, species with high travel costs (i.e., low search speeds and high energy expenditure rates while traveling) and low flower handling costs (i.e., short flower handling times and low energy expenditure rates while handling flowers) should use dense flower patches, whereas species with the opposite traits use sparse patches (figure 2). In addition, when foragers land on flowers rather than hovering, foraging currency can strongly influence their distributions, with species that maximize energetic efficiency foraging primarily in dense patches and those maximizing NREI foraging in sparse patches (figure 2 C and D). Observed effects of yellowflower tarweed floral density on the taxonomic composition of its flower visitors largely agree with model predictions, provided that individual foragers are allowed to make errors in their patch choices.

Explanations for density effects on flower visitor species composition

Search speed—My model predicts that search speed, the ratio of the distance between flowers to the time required to travel from one flower to the next, plays an important role in determining which species forage in dense *versus* sparse flower patches, with species having low search speeds being most likely to favor dense flower patches (figure 2). Variation in search speeds across flower visitor taxa (e.g., table 2) is probably attributable to differences in both flight and sensory capabilities. Optimal flight speeds are predicted to increase with increasing body size, and small wings are predicted to increase both agility and optimal flight speed (Lighthill 1978; Dudley 2002). However, flower visitors may also adjust their flight speeds in response to how readily they can detect flowers. Spaethe et al. (2001) found that bumblebees flew faster when flowers were large than when they were small and that flower search time decreased strongly with both increasing floral size and increasing color contrast with the background. These results suggest that visual abilities can limit flower search speeds in insect pollinators. In general, larger eyes are capable of higher resolution and sensitivity than smaller eyes (Land and Nilsson 2002). As a result, visual capacities should increase with body size, and indeed, large worker bumblebees do have better visual abilities than small ones (Spaethe and Chittka 2003). Different eye designs can also lead to differences in visual capabilities. For instance, the superposition eyes of many moths and skippers give these taxa better eyesight in low light conditions than taxa with apposition eyes, such as bees (Land and Nilsson 2002). The simple eyes of vertebrates are also typically capable of much higher resolution than the compound eyes of insects (Land and Nilsson 2002). Abilities in other sensory modalities, such as olfaction, could also influence search speeds, particularly in nocturnal pollinators. Finally, adaptations for exploiting flowers of particular plant taxa could increase search speeds, perhaps by aiding detection of those flowers: Strickler (1979) found that a specialist bee spent less time traveling between flowers of its host than did any of several generalist bee species.

Flower handling time—Having a short flower handling time is predicted to make a species more likely to use dense flower patches, particularly when species maximize energetic efficiency (figure 2). Flower handling times on a given plant species can vary greatly across flower visitor taxa (e.g., Strickler 1979; Inouye 1980, this study). Part of this variation is due to differences in the length of the structure used to access floral nectar. For instance, bumblebees with long tongues often handle flowers, particularly flowers with deep corollas, more quickly than short-tongued bees (Inouye 1980; Harder 1983; Graham and Jones 1996). On the other hand, on shallow flowers short-tongued bumblebees sometimes have faster handling times than long-tongued bees (Inouye 1980; Dohzono et al. 2011). Large individuals can at least sometimes consume nectar and/or collect pollen more quickly than small individuals, and therefore may require less time to empty a flower if species are similarly adept at accessing the floral rewards (Hainsworth 1973; Strickler 1979; Harder 1983). Finally, limited evidence suggests that specialists can handle their host flowers more

quickly than generalists can (Strickler 1979) and likewise that flower-constant foragers are faster than inconstant foragers (Chittka and Thomson 1997).

Foraging currency—Where foraging currencies vary and energy expenditure rates are higher while traveling between flowers than while handling them, the species maximizing efficiency should usually dominate in dense flower patches, whereas those maximizing NREI should be more abundant in sparse patches (figure 2 C and D). Unfortunately, data on foraging currencies are available for only a few pollinator taxa. As mentioned above, honeybee foraging behavior is more consistent with maximizing efficiency than with maximizing NREI (Schmid-Hempel et al. 1985; Kacelnik et al. 1986; Schmid-Hempel 1987; Afik and Shafir 2007). In bumblebees, the available data on nectar foraging behaviors appear equally consistent with maximization of either NREI or energetic efficiency (Charlton and Houston 2010). Bumblebees foraging for pollen behave as though maximizing the amount of pollen collected per unit of energy expended (Rasheed and Harder 1997), which is analogous to energetic efficiency. In hummingbirds, behavior consistent with both currencies has been found in different individuals (Tamm 1989).

One hypothesis to explain why some foragers appear to maximize energetic efficiency rather than NREI is that foraging activity in these individuals is more strongly limited by their maximum daily rates of energy assimilation and use than by available foraging time (McNamara and Houston 1997; Ydenberg and Hurd 1998). A similar hypothesis can be applied at the scale of a forager's lifetime: energy use can accelerate senescence, and therefore lifetime foraging performance in some species may be limited by the amount of energy a forager can expend over its lifespan (Schmid-Hempel et al. 1985; Tolkamp et al. 2002). In insects, wing wear during flight can also contribute to senescence (Cartar 1992; Dukas and Dukas 2011). As a result, insect foragers may maximize a currency such as energy acquired per wingbeat, which could resemble maximization of energetic efficiency.

Unfortunately, neither available data nor theoretical considerations indicate clearly how foraging currencies might vary across flower visitor taxa. Variation in the predation rates experienced by different pollinator species could influence foraging currency by affecting the probability that foragers survive to senescence, and hence the importance of lifetime limits on energy expenditure or flight. By this reasoning, species that experienced low predation rates, for instance because of defenses such as the stings of many bee and wasp species, would be more likely to maximize efficiency whereas species that experienced high predation rates would be more likely to maximize NREI. The demands of other fitness-enhancing activities for energy or time could also influence foraging currency. For instance, minimizing time away from the nest may be less important to foragers in social taxa, such as honeybees and bumblebees, in which other workers are always present in the nest, than to solitary taxa, whose nests are frequently parasitized in their absence (Weislo and Cane 1996). Finally, foraging currency can be condition-dependent: Cartar and Dill (1990) found that bumblebees from nectar-deprived colonies foraged as though they valued energetic costs less in relation to nectar harvest rates than did bees from colonies with abundant nectar reserves.

Energy expenditure rates—If flower visitors maximize NREI and have higher energy expenditure rates while traveling than while handling flowers, my model predicts that having a high metabolic rate during flight will make a species more likely to exploit dense rather than sparse flower patches. Flight metabolic rates correlate strongly and positively with body size in both vertebrates and insects (Darveau et al. 2005; Niven and Scharlemann 2005). Amongst species of similar size, flight metabolic rates are typically lower in taxa with longer or larger wings and lower wingbeat frequencies (Full 1997; Darveau et al. 2005).

My model also predicts that species that have high energy expenditure rates while handling flowers in relation to their metabolic rates while traveling (that is, high values of k_f) will be more likely to dominate sparse flower patches whereas species with low values of k_f will be more likely to dominate dense patches, especially if both species maximize efficiency. Values of k_f differ sharply between species that hover at flowers, such as hummingbirds and hawkmoths, and species that land on flowers, such as most bees. Hovering is typically at least as expensive as forward flight (Ellington et al. 1990; Clark and Dudley 2010), so $k_f \approx 1$ in species that hover at flowers. For species that land on flowers, k_f will usually be much less than 1 (Heinrich 1975; Heinrich 1979). Amongst the latter species, values of k_f will depend on air temperatures and thermoregulatory efficiency. When air temperatures are low, many flower visitors, including insects such as bees, may expend substantial energy maintaining high muscle temperatures between flights (Heinrich 1975; Heinrich 1979). Adaptations for efficient thermoregulation, such as dark coloration and insulating structures, should therefore reduce the value of k_f during cool weather.

Are the model's predictions realistic?

Observed effects of floral density on the species composition of visitors to the yellowflower tarweed are reasonably consistent with model predictions. The model correctly predicts that visitation by honeybees should be highest in the densest flower patches and that long-horned bees should, on average, be found in sparser patches than were honeybees. However, per-flower visitation by sweat bees was nearly independent of floral density, rather than exhibiting a peak at low or intermediate floral densities as predicted. Relaxing the model's assumption that foragers are omniscient about patch quality broadens their distributions, blurring the distinctions between the species' density preferences (figure 3 C and D). These broader, more overlapping distributions are much more consistent with observed bee species distributions in the bee-tarweed system than is the truncated distribution predicted if foragers are omniscient (figure 3 A and B).

Several factors ignored by my model could have contributed to the patterns I observed. Information sharing in social flower visitors such as honeybees could provide these foragers with better information about resources than is available to relatively solitary taxa such as longhorned bees and the sweat bee *L. titusi* (e.g., Seeley 1995). A model by Spencer et al. (1996) predicts that foragers with superior perceptual abilities will usually be most abundant in patches with high resource input rates while foragers with inferior perceptual abilities are more abundant in low-input patches. Honeybees also recruit nestmates to rewarding patches (Dyer 2002), making high-density patches, which can be shared with many nestmates, especially profitable to them. Changing conditions, particularly changing ambient temperatures, could cause deviations from the predicted distributions. For example, species able to forage at lower temperatures than their competitors could achieve high densities in the densest flower patches before competitors became active in the morning and then be slow to abandon those patches, even if later-arriving competitors had strong preferences for dense patches. However, no obvious temperature-related shifts in flower visitor species composition occurred in the tarweed system. Finally, differences between the scale at which foragers perceive resources and the scale observed, such as the 4-m² plots in my study, could cause deviations between observations and model predictions, such as the sweat bees' apparent failure to respond to floral density. Furthermore, species may vary in the scale at which they perceive resource density, which could cause their distributions to overlap more than expected.

My model includes only a single plant species. Often, however, multiple plant species flower together, and some foragers will visit multiple species within a foraging bout. Although the main predictions of my model should still apply to these systems, plant species diversity introduces some new complexities. For example, flower visitor taxa vary in their

willingness to switch between plant species. A patch composed of two flower species may appear dense to a forager willing to visit both species but sparse to a forager that is constant to only one species.

Conclusion

Effects of floral density on flower visitor species composition have often been observed but are poorly understood, especially in the absence of aggressive interactions between flower visitors. My model provides an explanation for these density-related shifts in flower visitor species composition and identifies traits that will predispose species to exploit dense or sparse flower patches when in competition with other taxa. I hope that this paper will inspire further investigation of how floral density influences flower visitor species composition and of the implications of these effects for plant fitness.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Best response curves for two pollinator species, a (solid line) and b (dashed line), foraging in a dense and a sparse patch. Black dots indicate the stable equilibrium distribution in each case. The ratios of species abundances, $n_a:n_b$, in these plots are: 1:2 (A) and 3:1 (B). Other parameter values are constant across the two panels: $k_a = 0.1$, $k_b = 1$, $s_a = s_b = 0.1$ m/s, $h_a = h_b = 5$ s, $c_a = c_b = 10$ J/s, $n_b = 20$ foragers, $d_D = 0.1$ m, $d_S = 0.2$ m, $q_D = 0.5$.

Figure 2.

Effects of flower visitor traits on equilibrium distributions if (A–B) both flower visitor species maximize foraging efficiency, (C–D) species *a* maximizes NREI and species *b* maximizes efficiency, or (E–F) both species maximize NREI. Curves indicate trait combinations for which the species can have identical distributions. Below and to the left of each curve, species *a* is predicted to have a higher relative density in the dense patch compared to species *b* ($p_{a,D} > p_{b,D}$), whereas the opposite is predicted above and to the right of each curve. Where multiple lines are present, they show predictions for different relative values of k_i (A, C, and E) or c_i (B, D, and F). Solid line: $k_a = k_b$ and $c_a = c_b$; Dotted line: k_a/k_b or $c_a/c_b = 0.1$; Dashed line: $k_a/k_b = 10$. (Predictions for $c_a/c_b = 10$ are not shown in plots B, D, and F because when $c_a/c_b = 10$, one or both flower visitor species is unable to achieve positive foraging success for every combination of the remaining parameter values. In (B), the predictions for $c_a = c_b$ and $c_a/c_b = 0.1$ are identical.) Parameter values are: $h_b = 4$ s, $s_b = 0.1$ m/s, $k_b = 0.1$, $c_b = 0.03$ J/s, $r = 0.00004$ J/s, $n_a = n_b = 750$ insects, $f_{Tot} = 1,000,000$ flowers, $d_D = 0.05$ m, $d_S = 0.1$ m, $q_D = 0.5$ (Table 2). Predictions for other forager: flower ratios are given in “Effects of forager to flower ratio on model predictions,” available online.

Figure 3.

Predicted effects of floral density on species composition of flower visitors to the yellowflower tarweed if (A and C) all species maximize energetic efficiency or (B and D) honeybees maximize efficiency and the other taxa maximize NREI. In panels A and B, foragers are omniscient whereas in panels C and D foragers make errors in assessing patch quality. Black = large sweat bees, striped = long-horned bees, white = honeybees. Parameter values are listed in Table 2.

Figure 4.

Observed effects of floral density on per-flower visitation rates by (A) honeybees and (B) long-horned bees on yellowflower tarweed. The solid lines are penalized cubic regression splines, the dotted lines show the bounds of 95% confidence bands (Bayesian critical intervals), and the points are partial residuals. Both visitation and floral density are $\log_{10}$ -transformed. Residuals are estimated by: (observed visitation rate) – (sampling event term (random effect)).

Table 1

Symbols used in the models

Symbol*	Parameter or variable†
c_i	Rate of energy expenditure by flower visitor species i while traveling between flowers (J/s)
d_j	Average distance between flowers in patch j (m)
$E_{i,j}$	Average energy expended per flower visit by flower visitor species i in patch j (J/visit)
f_j	Number of flowers in patch j
f_{Tot}	Total number of flowers across both patches
h_i	Flower handling time for flower visitor species i (s/visit)
I_j	Average gross energy intake per flower visit in patch j (J/visit)
k_i	(Energetic expenditure rate while handling flowers): (energetic expenditure rate while traveling between flowers) for flower visitor species i
n_i	Number of foragers of flower visitor species i
$p_{i,j}$	Proportion of total foragers of flower visitor species i foraging in patch j
q_j	Fraction of total flowers that are in patch j
r	Nectar secretion rate (J/s)
s_i	(Distance between flowers): (time required to travel between them), or search speed, for flower visitor species i (m/s)
$T_{i,j}$	Average time spent per flower visit by flower visitor species i in patch j (s/visit)
$V_{i,j}$	Average per-flower visitation rate for flower visitor species i in patch j (visits/flower/s)
V_j	Average per-flower visitation rate across all flower visitor species in patch j (visits/flower/s)

* The subscript i refers to the flower visitor species, a or b , and the subscript j refers to the patch, D (“dense”) or S (“sparse”). Lower-case letters refer to parameters and upper-case letters to quantities calculated within the model.

† Possible units are listed in parentheses.

Table 2

Parameter values for simulation of bees visiting yellowflower tarweed (*Holocarpha virgata*).

A.				
Parameter	Value(s)			
Patch floral densities	5, 20, 45, 95, and 205 flowers/m ² *			
Per-flower visitation rates by taxa other than the three focal groups	0.3 visits/flower/hour *			
Number of flowers per patch (f_j)	1,000,000			
Nectar secretion rate per flower (r)	0.00004 J/s *			
Energy expenditure rate while handling flowers: energy expenditure rate while traveling (k_i)	0.1 †			

B.				
Pollinator taxon	Number of foragers (n_i) *	Flower handling time (h_i), in s *	Search speed (s_i), in m/s *	Flight metabolic rate (c_i), in J/s §
Sweat bees (<i>Halictus ligatus</i> and <i>Lasioglossum titusi</i>)	560	4.9 (297) ‡	0.11 (51) ‡	0.01
Long-horned bee (<i>Melissodes lupina</i>)	330	2.1 (200)	0.17 (14)	0.02
Honeybee (<i>Apis mellifera</i>)	130	3.7 (93)	0.09 (31)	0.04

* Measured in the bee-yellowflower tarweed system as described in "Measurements of parameter values in the bee-tarweed system," available online.

† Based on a bumblebee at 30° C (Heinrich 1975).

‡ Numbers in parentheses indicate the number of individual foragers upon which the estimate is based.

§ Estimated from body size as described in "Measurements of parameter values in the bee-tarweed system," available online (Cane 1987; Niven and Scharlemann 2005).