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Explaining Variation in the Effect of Floral Density on Pollinator Visitation

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ABSTRACT: Pollinator responses to floral density have important implications for plant biology. In particular, a decline in pollinator visitation at low density can cause an Allee effect (a positive relation of fitness to density) in the plant population, which heightens that population's vulnerability to extinction. Empiricists have reported a variety of relations between flower or plant density and pollinator visitation rates. Here I develop and test a model that provides explanations for this diversity. The model assumes that pollinators distribute themselves between a focal patch of flowers and the surrounding environment so as to maximize foraging success. The resulting relation of per-flower visitation rate to focal-patch floral density is nonlinear, with positive effects at low floral densities and weaker or negative effects at higher densities. The relation is influenced by floral density in the surrounding environment and traits of both the plants and their pollinators. In a field experiment, floral density of *Holocarpha virgata* ssp. *virgata* had a nonlinear effect on per-flower visitation that was largely consistent with the model's predictions. By producing testable hypotheses based on biologically reasonable assumptions, this model serves as a starting point for explaining an important facet of plant-pollinator mutualisms.

Keywords: pollination, mutualism, Allee effects, density, ideal free distribution.

Introduction

Responses of foragers to resource densities can have significant effects on the ecology of lower trophic levels (e.g., Holt and Kotler 1987; Abrams 1993; Rohani et al. 1994; Křivan 1997, 2003; Bernstein et al. 1999). In plant-pollinator interactions, increases in pollinator foraging activity with increasing floral density can generate facilitation between plant species (Feldman et al. 2004) and declines in plant fitness at low densities (Allee effects; Kunin 1997a; Ghazoul 2005). On the other hand, decreases in pollinator visitation with increasing floral density could strengthen intra- and interspecific competition among plants (Rath-

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cke 1983). Many studies have reported effects of plant density on plant reproductive success, usually positive (e.g., Kunin 1997a; Ghazoul 2005; Dauber et al. 2010). Although other mechanisms, such as changes in inbreeding rates (Karron et al. 1995) or the frequency of interspecific pollen transfer (Kunin 1993; Morales and Traveset 2008), can contribute, changes in pollinator visitation rates with increasing floral density are among the main causes of these effects (Kunin 1997a; Ghazoul 2005).

The relation of pollinator visitation to floral density is complex. Although many studies have documented increases in visitation rates with increasing plant or floral densities, others have found no effects or negative effects (e.g., Campbell and Motten 1985; Kunin 1993, 1997b; Totland and Matthews 1998; Feldman 2006; Bernhardt et al. 2008; Feldman 2008; Elliott and Irwin 2009; Jakobsson et al. 2009; Dauber et al. 2010). Some explanations offered for this variation are that density effects depend on the presence or absence of other flowering species (Kunin 1993; Feldman 2008), the spatial scale over which the relation is observed (Dauber et al. 2010), or the range of densities considered (Rathcke 1983). In this article, I explore the last of these possibilities and suggest several new ones. My goal is to identify specific, testable hypotheses that provide consistent explanations for the seemingly contradictory results of previous empirical studies.

In contrast to the large empirical literature, little theoretical attention has been devoted to the effects of plant density on pollination success. Several models predict that pollinator visitation to one plant species in a mixture should vary positively with that species' relative frequency (Bobisud and Neuhaus 1975; Goulson 1994; Kunin and Iwasa 1996). However, the effect of the absolute density of flowers on pollinator visitation has received less attention. Rathcke (1983) hypothesized that at low densities, adding flowers increases per-flower visitation by making a patch more attractive, whereas at high densities the pool of pollinators becomes saturated and flowers compete for pollinators. Rathcke provided only a brief verbal justifi-

Table 1: Symbols used in the model

Symbol	Parameter or variable
A	Area (m^2)
c	Energetic cost per unit of traveling time (J/s)
f	Floral density (flowers/m^2)
h	Handling time per flower (s/flower visit/pollinator)
k	Ratio of the energetic cost per unit of handling time to the energetic cost per unit of travel time
n	Energy, in the form of nectar or other floral rewards, produced by each flower per unit of time (J/flower/s)
p	Pollinator density in a particular area; i.e., the focal patch or background area (pollinators/m^2)
P	Total number of actively foraging pollinators in the system
r	Average energy gained per flower visit (J/flower visit, J/flower visit/pollinator)
s	"Search speed," a constant that is proportional to the pollinators' speed when traveling between flowers and also increases as flowers become more clumped (m/s)[a]
t	Average travel time per flower (s/flower visit/pollinator)
v	Visits per flower (flower visits/flower/s)

Note: Symbols with subscript "f" refer to the focal patch, whereas those with subscript "b" refer to the area with which it competes (i.e., the background). Possible units are listed in parentheses in the second column.

[a] See "Derivation of the Equation for Travel Time per Flower," available online.

cation for this hypothesis. A more rigorous approach is needed to clarify the circumstances and spatial scale(s) to which her hypothesis applies and to identify other variables that influence the relation of visitation to floral density.

In this article, I model the effect of local floral density on per-flower pollinator visitation, assuming optimally foraging, nonterritorial pollinators. I focus on situations in which flowers are all similar and are treated indiscriminately by pollinators, so that patch choice rather than flower choice drives the effect. My aim is to generate explanations for variation in the effects of local floral density.

I begin by outlining the assumptions of the model and analytically deriving predictions for a simplified version in which the rate of pollinator energy expenditure is constant. I then relax this assumption and explore numerical model results using parameter values obtained from bee-pollinated systems, which allow me to identify more specifically how each parameter will influence density effects. I also show how choice of foraging currency (net rate of energy gain vs. efficiency) influences model predictions. Finally, I present a field experiment in which I measured the shape of the relation of visitation to floral density and compare its results to model predictions.

A Model of the Effect of Floral Density on Pollinator Visitation

Pollinators commonly distribute themselves so that foraging success is the same across available resource patches (Dreisig 1995; Ohashi and Yahara 2002; Abraham 2005; Lefebvre and Pierre 2006). This distribution, known as an ideal free distribution, is expected if animals forage optimally without cognitive constraint and do not defend territories (Fretwell and Lucas 1969). Although some

flower visitors defend food resources (Johnson and Hubbell 1974; Ewald and Carpenter 1978; Kodric-Brown and Brown 1978), competition is primarily exploitative in many temperate insect pollinators (Waddington 1976; Pyke 1978; Zorn-Arnold and Howe 2007). Although flower-visiting behavior can be influenced by motivations other than maximizing foraging efficiency (e.g., Sapir et al. 2005; Ings and Chittka 2008), I do not address these issues in my model. Optimal-foraging models often successfully predict behavior of pollinators, particularly bees (Pyke 1978, 1984; Schmid-Hempel et al. 1985; Goulson 2003).

Within this context, the model is constructed as follows: flowers in a focal patch compete with those in the surrounding area for a set number of pollinators. I assume that all flowers produce identical rewards, that all pollinators are identical, and that floral density outside of the focal patch is constant and uniform. Pollinators forage for nectar and distribute themselves so that foraging success is equal inside and outside of the focal patch. I first use the net rate of energy gain as the measure of foraging success because it is the most commonly used metric and is supported by many studies (reviewed in Pyke et al. 1977; Stephens and Krebs 1986):

$$\text{net rate of energy gain} = \frac{\text{energy gain per flower} - \text{energy used per flower}}{\text{foraging time per flower}}.$$

(1)

The foraging time per flower is the sum of the handling time per flower, *h*, and the average time required to travel from one flower to the next, *t* (see table 1 for a list of symbols used in the model). The energy used per flower

is calculated from the travel and handling times and the average rates of energy expenditure during these activities:

$$\text{energy used per flower} = hkc + tc, \tag{2}$$

where c is the energetic cost per unit of traveling time. The rate of energy loss while handling flowers is assumed to be a fraction, k, of the rate during travel between flowers (although for animals that hover while feeding, such as hummingbirds, k will exceed 1; Clark and Dudley 2010).

Given an ideal free distribution, foraging success is equal in the focal patch and the surrounding, or background, area, so

$$\frac{r_f - (hkc + t_f c)}{h + t_f} = \frac{r_b - (hkc + t_b c)}{h + t_b}. \tag{3}$$

Here, r is the energy gain per flower and the subscripts "f" and "b" refer to the focal patch and the background, respectively.

Increased pollinator numbers elevate per-flower visitation rates and decrease per-flower rewards. Suppose that the nectar in a flower is completely consumed during each visit and then is replenished at a constant rate, n. The time since the last visit will approximately equal the inverse of the average per-flower visitation rate, v, if the flower-handling time is much shorter than the time between visits. Therefore,

$$r = \frac{n}{v}, \tag{4}$$

where r is the average reward per flower.

The per-flower visitation rate equals the density of pollinators in the patch, p, times the visitation rate per pollinator, divided by the floral density, f. If a pollinator does nothing other than visit flowers, its visitation rate equals the inverse of its travel and handling times per flower, $h + t$. Therefore,

$$v = \frac{p}{f(h + t)}, \tag{5}$$

where v is the per-flower visitation rate (Pleasants and Zimmerman 1983).

If the energetic cost of handling flowers equals the cost of flight (i.e., $k = 1$), then the net rate of energy gain in the focal patch equals that in the background area when

$$\frac{f_f}{p_f} = \frac{f_b}{p_b} \tag{6}$$

("Model Assuming That Flight and Handling Flowers Are Equally Costly," available online). This matching rule, whereby the ratio of resource inputs to foragers is constant across patches, is typical of ideal free distributions (Milin-

ski and Parker 1991; Tregenza 1994). The assumption that handling flowers and traveling between them have equal energetic costs is usually false, especially for animals that land on flowers to feed (Heinrich 1979a; Abrol 1992). Nonetheless, this assumption greatly simplifies the mathematics. Therefore, I continue model development under this assumption before returning to the more realistic scenario in which costs differ for handling flowers and traveling.

If pollinators always fly between neighboring flowers, if flight time increases linearly with the distance between flowers, and if floral dispersion does not change with floral density, then

$$t = \frac{1}{s\sqrt{f}}, \tag{7}$$

where t is the flight time, f is floral density, and s, the "search speed," is a constant proportional to the pollinators' velocity that also increases as floral dispersion becomes more clumped (Pielou 1977; Kunin and Iwasa 1996; "Derivation of the Equation for Travel Time per Flower," available online). Also implicit in this equation is the assumption that pollinators visit every flower to which they fly. Some pollinators use scent marks to reject flowers that have been visited recently (e.g., Stout and Goulson 2002). However, incorporating this behavior into the model has only modest effects on model predictions ("Model Assuming That Pollinators Use Scent Marks to Reject Flowers That Have Recently Been Visited," available online).

Finally, I assume that flowers in the focal patch and background area compete for a fixed number of actively foraging pollinators, P. Specifically,

$$P = p_f A_f + p_b A_b, \tag{8}$$

where A_f is the area of the focal patch and A_b is the area of the background, which is the area around the focal patch that is within the pollinators' foraging range. Equations (5)–(8) imply

$$v_f = \frac{P}{(A_f f_f + A_b f_b)[h + (1/s\sqrt{f_f})]}, \tag{9}$$

which states that the per-flower visitation rate, v_f, equals the overall pollinator : flower ratio divided by the average time required to travel to and handle each flower in the focal patch. Increased focal-patch density can influence per-flower visitation in two different ways. Because the average distance between flowers declines with density, increasing floral density reduces the time required to travel between flowers, increasing the per-flower visitation rate. On the other hand, the pollinator : flower ratio within the pollinators' foraging range declines as focal-patch floral density increases, causing a reduction in visitation. The

relative importance of these two effects changes with density: adding flowers causes a much stronger reduction in the spacing between flowers, and therefore in flight times, at low than at high densities. As a result, the effect of density on visitation is positive at low densities and negative at high densities, as suggested by Rathcke (1983; fig. 1*A*).

The derivative of visitation rate with respect to focal-patch floral density shows that the relation of visitation to floral density will be hump shaped regardless of the parameter values, as long as density varies over a sufficiently wide range ("Model Assuming That Flight and Handling Flowers Are Equally Costly," available online). As density approaches 0, this derivative approaches positive infinity. Therefore, visitation should always depend strongly and positively on floral density at very low densities. As floral density increases, the derivative declines until it becomes negative. Specifically, the effect becomes negative when

$$\frac{1}{1 + 2hs\sqrt{f_f}} < \frac{f_f A_f}{f_b A_b} \quad (10)$$

("Model Assuming That Flight and Handling Flowers Are Equally Costly," available online), which occurs when the focal patch contains a large number of flowers compared to the background and therefore strongly influences the overall pollinator : flower ratio. Negative effects of density are therefore more likely when the background floral density, f_b, is low and the pollinators' foraging range (which affects A_b) is small with respect to the size of the focal patch, A_f. The likelihood of negative effects also depends on the search speed, s, the handling time, h, and the floral density within the focal patch, f_f. All three parameters act by changing the strength of the effect of floral density on time spent per flower, the first two by altering the fraction of time that is spent traveling between flowers and the third for reasons discussed above. The effect of density on foraging time per flower is weaker, and the probability of a positive relation of visitation to density lower, when the focal-patch floral density or travel speed is high, the handling time is long, or the flowers have a clumped distribution (which increases s).

Predictions for Realistic Parameter Values

Although the simple model developed above provides insights about the shape of the relation of visitation to floral density and identifies variables that could influence it, the model cannot by itself reveal how often detectable positive or negative effects should be expected in nature or which parameters vary enough to have a noticeable influence. To explore these questions, I ran the model with plausible parameter values for bee-pollinated systems. For these model runs, I relaxed the assumption that the energetic costs of travel and handling flowers are equivalent (i.e., that $k = 1$), using instead the more realistic assumption that $k = 0.1$ (Heinrich 1975). Actual values of k vary, both between bees and with ambient temperature (Heinrich 1975, 1979*a*; Abrol 1992), but model predictions proved relatively insensitive to this variation, provided that $k < 1$.
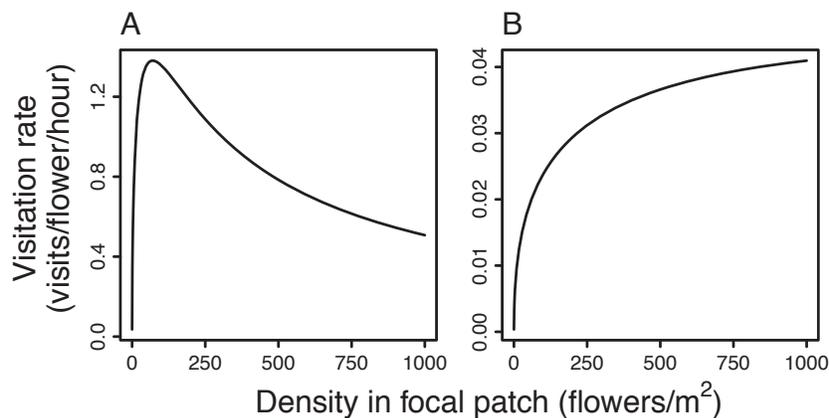

Figure 1: Hump-shaped (*A*) and saturating (*B*) relations of visitation to floral density predicted by the model. Hump-shaped curves are always predicted if focal-patch floral density varies over a sufficiently wide range. However, for most combinations of the parameter values shown in table 2 (excluding parameter combinations that produce negative net rates of energy gain), the peak of the curve occurs at an unrealistically high focal-patch floral density. Therefore, for realistic parameter values, the relation is usually predicted to be saturating (*B*). The parameter values used to produce these curves were: $f_b = 0.1$ flowers/m^2 for *A* and 10 flowers/m^2 for *B*, $A_f = 100$ m^2, $A_b = 1.3 \times 10^5$ m^2, $P = 13$ pollinators, $h = 0.5$ s, $s = 0.1$ m/s, and $k = 1$.

Table 2: Parameter values used to assess general patterns in the relation of pollinator visitation to floral density

Parameter	Values
Focal-patch floral density (f_f; flowers/m^2)	.5, 50, 5,000
Background floral density (f_b; flowers/m^2)	.1, 10, 100
Focal-patch size (A_f; m^2)	1, 10, 100
Pollinator density (bees/m^2)[a]	.0001, .01, 1
Foraging range (m)[b]	100, 1,000, 10,000
Handling time (h; s/flower)	.5, 5, 50
Search speed (s; m/s)	.01, .1, 1
Flight cost/nectar secretion rate (c/n)	.001, 1, 1,000

Note: Values are based on parameter estimates from published studies and my study system (see supplementary table, available online). I use 1,000 as the maximum value of c/n because the net rate of energy gain is usually predicted to be negative at substantially higher values of this parameter.

[a] Pollinator density is used to calculate pollinator abundance, as follows: P = pollinator density $\times$ ($A_f + A_b$).

[b] Foraging range is used to calculate the area with which the focal patch competes, as follows: $A_b = \pi(\text{foraging range} \times 2)^2 - A_f$.

Methods

The parameter estimates I used, shown in table 2, span the range of values reported from a variety of bee-pollinated systems (supplementary table, available online). To see whether setting $k < 1$ altered the shape of the relation, I estimated the slope of the curve at 0.1, 10, 100, or 1,000 flowers/m^2 when $k = 0.1$ for all 1,782 combinations of the remaining parameter values that produced nonnegative net rates of energy gain for all focal-patch floral densities. I estimated slope by calculating the change in visitation rate predicted when focal-patch floral density increased by 0.01 flowers/m^2.

I explored how often strongly positive or negative effects might be expected by running the model with every possible combination of the parameter values in table 2, again omitting parameter combinations that produced a negative net rate of energy gain. I defined effects as "strongly" positive or negative if visitation changed by more than 10% with a doubling of floral density. To determine how each model parameter influences the relation of visitation to floral density, I calculated the number of combinations of the other parameters that produced strongly positive or negative effects for the highest and lowest value of each parameter, omitting any parameter combinations that produced negative net rates of energy gain for either value of the focal parameter. I carried out these and all other calculations in R (R Development Core Team 2010).

Results

Within a realistic range of focal-patch floral densities, the shape of the relation of visitation to floral density was usually predicted to be saturating rather than hump shaped (fig. 1*B*). Indeed, visitation was still increasing with density at 1,000 flowers/m^2 for 81% of the parameter combinations. As predicted for the simpler model in which $k = 1$, positive effects were always strongest at the lowest focal-patch floral densities.

Both weak and strongly positive effects of increasing floral density on visitation were predicted for many parameter combinations, whereas strongly negative effects were seldom predicted (table 3). At low focal-patch floral densities, effects were usually strongly positive, whereas at high densities, effects were usually weak (fig. 2). A low background floral density, a small pollinator foraging range, or a large focal-patch size made strongly negative effects more likely. Strongly positive effects of increasing floral density on visitation were much more likely when handling times were short and search speeds slow. A high ratio of flight cost to nectar secretion rate also made strongly positive effects slightly more likely. Pollinator density had little influence on the effects of floral density on visitation.

Predictions When Pollinators Maximize Efficiency

Thus far, I have assumed that pollinators maximize their net rate of energy gain. However, bees sometimes seem to maximize efficiency, expressed as energy acquired per unit of energy expended (Schmid-Hempel et al. 1985; Kacelnik et al. 1986; Charlton and Houston 2010). If pollinators maximize efficiency, then predictions are identical to those for bees maximizing rate of energy gain if $k = 1$, but not if $k < 1$ ("Model Assuming That Pollinators Maximize Efficiency," available online). Most noticeably, strongly positive effects occur more frequently when pollinators maximize efficiency than when they maximize the net rate of energy gain (table 3). This is because when $k < 1$, the energy expended per flower visited decreases faster with increases in floral density than does the time expended.

Table 3: Percent of parameter combinations for which effects of floral density are predicted to be strongly positive, weak, or strongly negative

	Foraging currency	
Effect predicted	Net rate of energy gain	Efficiency
Strongly positive	38	60
Weak	56	33
Strongly negative	6	7

Note: Based on implementations of the model for the 5,375 combinations of the parameter values shown in table 2 that produce nonnegative values of net rate of energy gain and foraging efficiency, assuming that $k = 0.1$. Values are rounded to the nearest percent. A weak effect means a <10% change in visitation with a doubling in floral density. Strongly positive or negative effects mean a >10% increase or decrease, respectively, with a doubling in floral density.
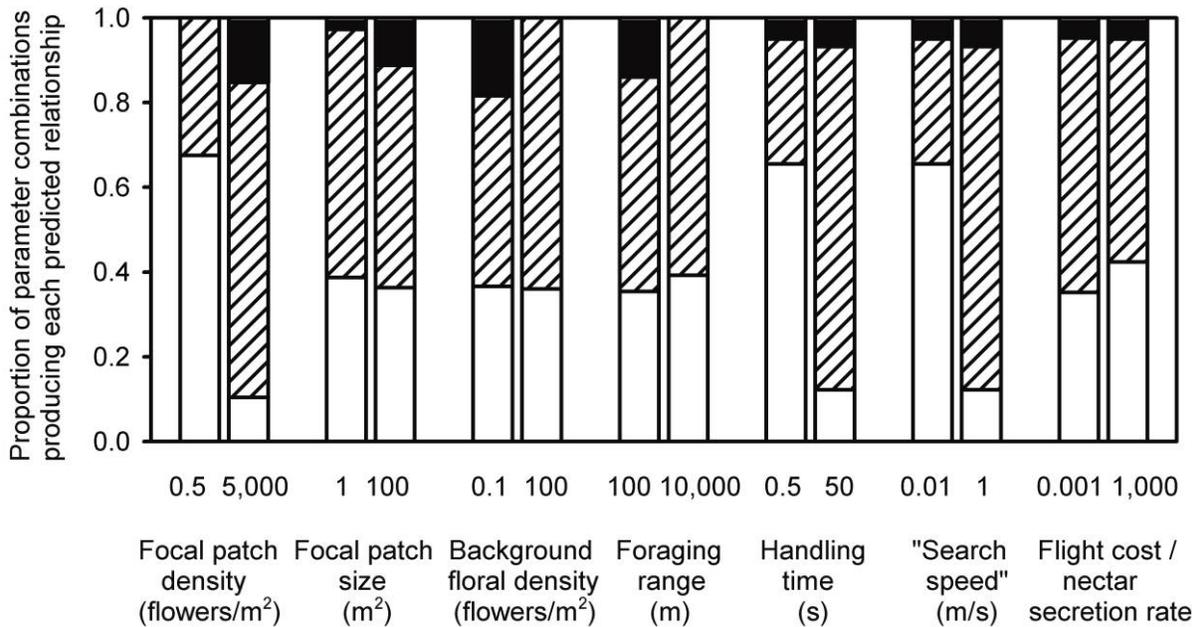
Figure 2: Effects of parameters on the relation of visitation to floral density, assuming that pollinators maximize net rate of energy gain. White = strongly positive; hatched = weak; black = strongly negative. Definitions of these categories are the same as in table 3. For each parameter value, the proportions shown are based on model results, assuming that $k = 0.1$, for all combinations of the other parameter values in table 2 for which net rate of energy gain is positive for both values of the focal parameter. The numbers of parameter combinations used for each focal parameter are 1,814 for focal-patch density, 1,824 for focal-patch size, 1,501 for background floral density, 1,798 for handling time and search speed, and 1,331 for flight cost/nectar secretion rate.

Therefore, efficiency increases more rapidly with floral density than does net rate of energy gain.

Comparison to Empirical Results

I carried out a field experiment to test whether the relation of visitation to floral density had the shape predicted by my model. My study system violated several model assumptions, in particular that pollinators are all identical and that floral dispersion is uncorrelated with density, making a precise correspondence between predicted and observed visitation rates unlikely. Nonetheless, the empirical results provide an opportunity to determine whether the model can make reasonably accurate predictions about the strength and direction (positive or negative) of density effects at particular density levels in a natural system.

Methods

My study plant was the yellowflower tarweed (Asteraceae: *Holocarpha virgata* ssp. *virgata*), a self-incompatible, annual composite with yellow flower heads, each bearing three to seven female ray florets and 9–25 protandrous disk florets. In the Asteraceae, flower heads, rather than individual florets, are the floral units that pollinators seek when foraging (for a review on inflorescences as units of pollination, see Harder et al. 2004). Therefore, I treated flower heads rather than individual florets as the floral units in *H. virgata* and hereafter refer to *H. virgata* flower heads as "flowers." At my field site, *H. virgata* flowers were visited by a variety of insect taxa, the most abundant of which were sweat bees (Hymenoptera: Halictidae; table 4).

I carried out the experiment in a grassland at the University of California–Davis McLaughlin Reserve, which is located in the coast range of northern California (38.86°N, 122.41°W). Species coflowering with *H. virgata* at this site included yellow starthistle (Asteraceae: *Centaurea solstitialis*), hayfield tarweed (Asteraceae: *Hemizonia congesta*), and smallflower western rosinweed (Asteraceae: *Calycadenia pauciflora*).

I collected data on five mornings a week for 4 weeks, from August 10 to September 4, 2009. On each day, I selected four 2.25 × 2.25-m plots (consisting of four 1-m² subplots divided by 25-cm-wide strips of cleared vegetation) in a large patch of *H. virgata*. Coflowering species were sparse in this patch and were never present within the plots. I randomly assigned these plots to be thinned

Table 4: Taxa observed visiting flowers of *Holocarpha virgata* in experimental plots

Taxon	Percent of total observed visits[a]
Bees (Hymenoptera: Apoidea):	
Large sweat bees (Halictidae: *Halictus ligatus, Lasioglossum titusi*)	56.0
Long-horned bees (Anthophoridae: *Melissodes lupina*)	21.7
Small sweat bees (Halictidae: *Dialictus* sp., *Halictus tripartitus*)	9.1
Other/unidentified bees	5.7
Other:	
Beeflies (Diptera: Bombyliidae) and hoverflies (Diptera: Syrphidae)	4.1
Other/unidentified	3.3

Note: I have deposited voucher specimens of these taxa at the University of California, Riverside, Entomology Research Museum.

[a] We observed a total of 3,269 visits.

to the following densities on the morning of pollinator observations: 4, 12, 32, and 72 flowers/m^2 (first and fourth weeks) or 4, 12, 36, and 104 flowers/m^2 (second and third weeks). It proved impossible to remove flowers at random with respect to their size, so to ensure consistency across different workers, we retained the largest flowers available. To minimize treatment effects on flower size that could result from this nonrandom removal, we divided each plot into 64 equal-sized squares (not including the 25-cm-wide cleared strips) and assigned each square to either be thinned to approximately four flowers or have all flowers removed. The number of squares in which flowers were retained varied with treatment, but the proportion of flowers retained in any given square varied little. To control for any remaining bias (e.g., caused by having to leave more than 4 flowers per square in the high-density treatments), I estimated the average size of the flowers that remained in each plot, using the pre- and postthinning densities in each square and data on the distribution of flower sizes in *H. virgata* (C. J. Essenberg, unpublished manuscript; "Method for Estimating *Holocarpha virgata* Flower Size in Experimental Plots," available online).

A team of three observers made a total of 6–12 (usually nine) 10-minute observations of each plot between 8:00 am and 12:30 pm, the period of greatest pollinator activity on *H. virgata* (C. J. Essenberg, personal observation). During each observation, a single observer recorded all flower visits made in a randomly chosen section of the plot. The size of the section observed decreased with increasing floral density, so that the difficulty of scanning all flowers was similar across treatments. I divided the number of visits observed during each observation by the number of flowers watched and averaged the results to obtain per-flower visitation rates for each plot.

To generate predicted visitation rates, I simplified the model by assuming that the focal patch's contribution to the total floral abundance is negligible (i.e., $A_f f_f = 0$, and total floral abundance $F = A_b f_b$). If $k = 1$, then

$$v_f = \frac{P/F}{h + (1/s\sqrt{\overline{f_f}})} \tag{11}$$

(from eq. [9]), where P/F is the pollinator : flower ratio. Predictions obtained from this simplified model and the full model for pollinators that maximize net rate of energy gain were nearly indistinguishable, given plausible parameter values for this system. If pollinators maximize efficiency, then a different relation is predicted if $k < 1$. Specifically,

$$v_f = \left[\frac{P/F}{hk + (1/s\sqrt{\overline{f_f}})}\right]\left[\frac{hk + (1/s\sqrt{\overline{f_b}})}{h + (1/s\sqrt{\overline{f_b}})}\right] \tag{12}$$

(from eq. [A26], available online).

Only one taxonomic group of pollinators, large sweat bees (Hymenoptera: Halictidae: *Lasioglossum titusi* and *Halictus ligatus*), visited my plots in sufficient abundance to allow a test of the model (table 4). Therefore, I parameterized each version of the model for this group. I calculated the large sweat bee : flower ratio, P/F, and background floral density, f_b, from densities that we recorded in six 1 × 30-m transects distributed across the 0.7-ha *H. virgata* patch containing the experimental plots. During the flower visitation observations described above, observers recorded durations of pollinator flights and flower visits whenever possible. To calculate the average handling time for large sweat bees, h, I averaged together mean handling times for all 381 individuals for which we recorded at least one handling time. To calculate the average search speed for large sweat bees, s, I took the inverse of the coefficient for a regression of mean between-flower flight duration per plot against (floral density)$^{-1/2}$, using all 73 plots for which we recorded at least one flight duration. The resulting parameter estimates are shown in table 5.

I determined the shape of the relations of per-flower visitation to floral density for large sweat bees and for all

Table 5: Parameter values for large sweat bees (*Halictus ligatus* and *Lasioglossum titusi*) visiting *Holocarpha virgata*

Parameter	Value
Pollinator/flower ratio (P/F; bees/flower)	3.0×10^{-4}[a]
Handling time (h; s)	3.4
Search speed (s; m/s)	.82
Background floral density (f_b; flowers/m^2)	157[a]

[a] These are averages of four weekly values, which ranged from 1.4×10^{-4} to 5.1×10^{-4} bees/flower and from 53 to 224 flowers/m^2.

visitors combined with penalized cubic regression splines in generalized additive mixed models, using the mgcv package in R (Wood 2006; R Development Core Team 2010). The other terms in the model were week (random effect) and the estimated average flower size in the plot (fixed effect). Results were similar without the flower size term, except where noted. Residuals from the sweat bee analysis were nonnormal. A square-root transformation of visitation rate resolved this problem without altering the results. I present results from the analysis without transformation.

Results

Large sweat bees made 56% of the observed visits. The remaining visits were made by a variety of insect taxa, including other bees, flies, wasps, and lepidopterans. Both versions of the model predicted a saturating relation of large sweat bee visitation to floral density. If bees maximize net rate of energy gain, little change in visitation was predicted above 10 flowers/m^2 (fig. 3A). If they maximize efficiency, visitation continued to increase strongly across the entire measured range of densities (fig. 3B). The observed relation of large sweat bee visitation to floral density was significant and nonlinear ($F_{2.8,75.2} = 4.3$, $P = .01$): visitation increased to a peak at 36 flowers/m^2 and then declined, although confidence intervals are wide at high densities (fig. 3C). When all flower visitors were included in the analysis, the relation was similar but weaker (fig. 3D; $F_{2.2,75.8} = 3.2$, $P = .04$; without the flower size term: $F_{2.3,76.8} = 0.77$, $P = .48$).

Discussion

Although many studies have found significant relations of pollinator visitation to plant or floral density, effects vary from one study to another, and the factors responsible are poorly understood. The model presented above suggests three general explanations, which are summarized in figure 4 and discussed in the next three subsections.

Nonlinear Relation of Pollinator Visitation to Floral Density

My model predicts that increasing floral density has a strong positive effect on per-flower visitation at low densities and a weaker or negative effect at high densities (fig. 1). As a result, plants are predicted to facilitate one another's pollinator attraction at low densities and, sometimes, to compete for pollinators at high densities. My model also shows that the shape of the relation of visitation to floral density can differ markedly across systems. For instance, in some cases, visitation is expected to increase strongly across the entire natural range of floral densities (figs. 1B, 2), whereas in others, visitation is expected to decline at high densities (figs. 1A, 2).

Facilitative and competitive interactions for pollinators can, in turn, have significant effects on plant ecology and evolution. When plants within a species facilitate each other's ability to attract pollinators, declines in plant density can cause average plant fitness to decrease (Kunin 1997a; Ghazoul 2005). These Allee effects, in turn, can increase a species' probability of extinction, delay the spread of introduced species, truncate species' ranges, and favor the evolution of compensatory traits, such as self-pollination (e.g., Orians 1997; Stephens and Sutherland 1999; Courchamp et al. 2008; Eckert et al. 2010). Because individual pollinators often visit multiple plant species during a single foraging bout (e.g., Heinrich 1979b; Waser 1986), pollinator responses to floral density can also influence interactions between plant species (e.g., Rathcke 1983; Feldman et al. 2004; Mitchell et al. 2009). In fact, empirical studies show that visitation to a focal species can be increased or decreased by another species that increases local floral density, although accompanying changes in floral diversity and relative floral density could also influence these observed effects (e.g., Campbell and Motten 1985; Roy 1994; Chittka and Schurkens 2001; Ghazoul 2006; Kandori et al. 2009; Nienhuis et al. 2009; Lázaro and Totland 2010). Decreases in visitation with increasing total floral density could strengthen competition between plant species, whereas increases in visitation with increasing density could favor species coexistence, provided that the increase in visitation was strong enough to counteract negative effects of interspecific pollen transfer (e.g., Feldman et al. 2004; Mitchell et al. 2009).

Although Allee effects and pollinator-mediated interactions between plant species are particularly interesting at the scale of the plant population or community, some care is needed when applying my model to this scale. My model assumes that the population density of the pollinators is not influenced by the floral density of the focal patch. Floral resources are, however, thought to influence pollinator population densities (Steffan-Dewenter and
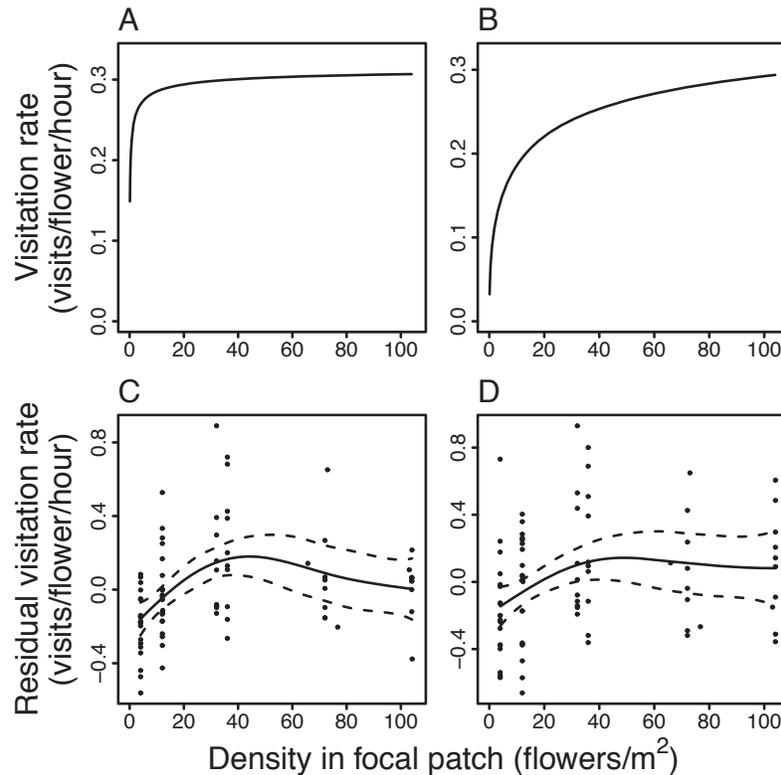
Figure 3: Observed and predicted effects of *Holocarpha virgata* floral density on per-flower visitation. *A*, *B*, Predicted relations for large sweat bees under the assumptions that pollinators maximize net rate of energy gain (eq. [11]; parameter values shown in table 5; *A*) or that pollinators maximize efficiency (eq. [12]; $k = 0.1$; other parameter values shown in table 5; *B*). *C*, *D*, Observed relations for large sweat bees (*C*) and all taxa combined (*D*). The solid lines represent penalized cubic regression splines generated by generalized additive mixed models of the effect of floral density on per-flower visitation that included estimated flower size as a covariate and week as a random effect. The dotted lines show the bounds of 95% confidence bands (Bayesian critical intervals), and the points represent partial residuals.

Tscharntke 2001; Eltz et al. 2002; Potts et al. 2003; Moeller 2004; Kremen et al. 2007), so the model is best applied either when pollinator populations have insufficient time to respond to changing resource densities or when the focal patch represents a small proportion of the total resources available to pollinators. Because of the large foraging ranges of many pollinators (i.e., up to multiple kilometers: Greenleaf et al. 2007), the latter condition may often be met even when the "focal patch" is an entire plant population. Bees are central-place foragers (Orians and Pearson 1979), and therefore a correlation between proximity of nesting sites and plant density could also alter the relation of visitation to floral density from that predicted by my model. For instance, if sparse plant populations are closer, on average, to pollinator nesting sites than are dense populations, per-flower visitation might be as high or higher in sparse populations as in dense ones.

Caution is also needed when applying my model to systems in which multiple plant species share pollinators,

because of the model's assumption that all flowers are identical. If competing species occupy separate patches, then the predicted density effects within a patch are similar to those in a single-species system ("Two-Plant-Species Model," available online). However, if species are intermingled, then density-dependent shifts between generalization and specialization by individual pollinators (i.e., flower constancy) will add complexity to the relation beyond the scope of my model (Kunin and Iwasa 1996; Chittka et al. 1999).

My field experiment supports the model's general prediction that density effects are positive at low densities and weaker or negative at higher densities. This pattern is seen for large sweat bees alone and for all flower visitors combined, and therefore it is unlikely to be a result of resource partitioning between pollinator taxa. On the other hand, the observed relation of visitation to density differs from specific model predictions (fig. 3). Both versions of the model predict curves that are too steep at the lowest den-
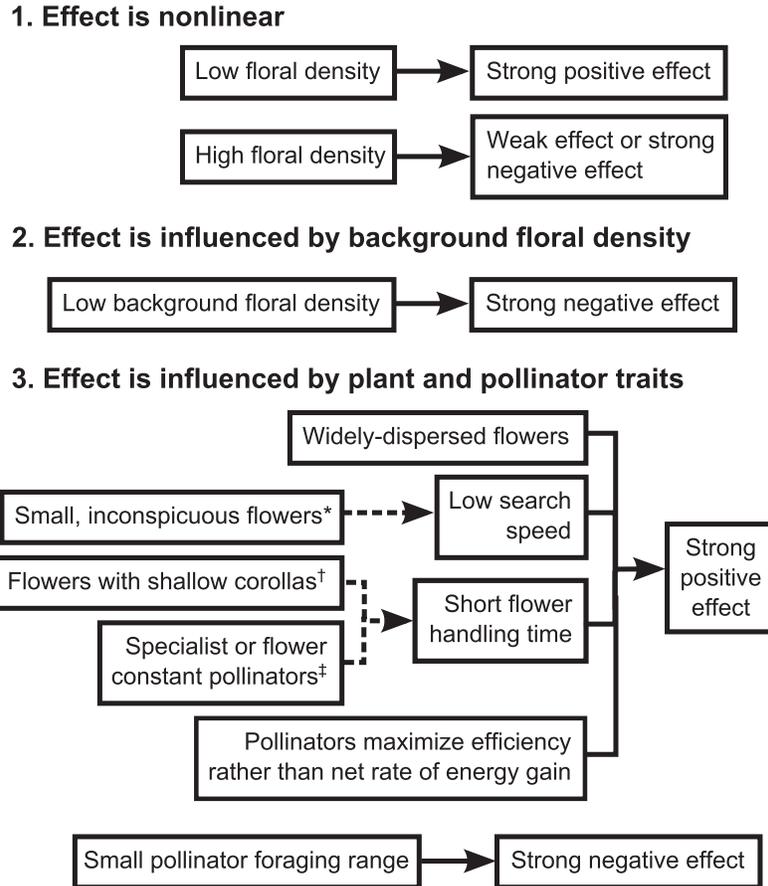
1. Effect is nonlinear

Low floral density →	Strong positive effect
High floral density →	Weak effect or strong negative effect

2. Effect is influenced by background floral density

Low background floral density →	Strong negative effect

3. Effect is influenced by plant and pollinator traits

Widely-dispersed flowers

Small, inconspicuous flowers* ⇢ Low search speed

Flowers with shallow corollas†

Specialist or flower constant pollinators‡ ⇢ Short flower handling time

→ Strong positive effect

Pollinators maximize efficiency rather than net rate of energy gain

Small pollinator foraging range →	Strong negative effect

Figure 4: Explanations for variation in effects of local floral density on per-flower visitation suggested by my model. Solid arrows represent predicted influences of parameters on the probability of particular effects. Where I do not specify otherwise, the opposite values of these parameters make weak effects more likely. Dashed arrows represent relations supported by empirical studies: asterisk: Spaethe et al. (2001); dagger: Inouye (1980) and Harder (1983), but see Dohzono et al. (2011); double dagger: Strickler (1979) and Chittka and Thomson (1997).

sities, and neither version predicts the observed decline in sweat bee visitation at high densities. In fact, the efficiency model predicts a marked increase in visitation at high densities. However, my empirical evidence for the decline at high densities is weak: confidence intervals at high floral densities are large (fig. 3*C*), and in a subsequent study, in which I included higher floral densities (C. J. Essenberg, unpublished manuscript), I failed to find a decline in sweat bee visitation with floral density. Nonetheless, the discrepancies between the experimental data presented here and model predictions could indicate that sweat bee distributions are influenced by constraints not considered in this model, such as competition with other pollinator taxa or limited information about resource availability in alternative patches (Abrahams 1986; Bernstein et al. 1988; Milinski and Parker 1991). The poor performance of the efficiency model also suggests that efficiency is less important to these sweat bees than is net rate of energy gain.

Few other data are yet available regarding the shape of the relation of visitation to floral density. Although some empirical studies have found relations that appear nonlinear, as predicted here (Kunin 1993; Feldman 2008), the only previous study to test whether nonlinear effects were present, to my knowledge, is Feldman's (2006) experimental study of pollinator visitation to *Brassica rapa*. Feldman found that per-plant visitation to *Brassica* declined across the entire range of plant densities he used, with the strongest decline occurring at low densities. If background floral densities were sufficiently low and pollinator foraging ranges sufficiently small, Feldman's results could be consistent with my model, but data on these parameters are not available for his study system.

Finally, two studies have found density-related changes in interspecific interactions for pollinators that are consistent with my model's predictions. Ghazoul (2006) found that inflorescence density of *Cirsium arvense* growing in-

termingled with *Raphanus raphanistrum* had a positive effect on visitation to *R. raphanistrum* at low densities and a negative effect at high densities. Likewise, for two native species, *Hypochaeris thrincioides* and *Perezia carthamoides*, Muñoz and Cavieres (2008) found a negative effect of a coflowering invasive plant, *Taraxacum officinale*, on flower visitation and seed set only at high densities. However, in both the Ghazoul (2006) and Muñoz and Cavieres (2008) studies, increases in total floral density were accompanied by declines in the relative floral density of the focal species. Their results could therefore also be explained by effects of relative floral density on the pollinators' floral preferences (Kunin and Iwasa 1996; Ghazoul 2006).

Background Floral Density Influences the Relation of Visitation to Floral Density

My model predicts that the background floral density will influence the relation of pollinator visitation to floral density (figs. 2, 4.2) and therefore that floral-density effects could differ between sites and across seasons. Specifically, plants flowering together may be more likely to hinder one another's pollination when surrounding floral densities are low. As discussed above, this prediction is valid only if floral density in the focal area does not influence the pollinators' population density. If a higher floral density in the focal area allows the pollinator population to grow, then plants may facilitate each other's pollination rather than compete for pollinators (e.g., Moeller 2004). Because only a few studies of floral-density effects on pollinator visitation have recorded the floral context (e.g., Grindeland et al. 2005; Dauber et al. 2010; Lázaro and Totland 2010), more data are needed to assess these competing predictions.

Plant and Pollinator Traits Influence the Relation of Visitation to Floral Density

My model suggests several plant and pollinator traits that could influence the effects of floral density on pollinator visitation (figs. 2, 4.3). Strong declines in visitation at high floral density are more likely when pollinator foraging ranges are small. On the other hand, strong increases in visitation with increasing floral density are more likely when pollinators maximize efficiency rather than net rate of energy gain, when flowers are widely dispersed rather than clumped, when pollinator search speeds are low, or when flower-handling times are short. Pollinator search speeds and flower-handling times are, in turn, influenced by both plant and pollinator traits. Spaethe et al. (2001) showed that bumblebee search speeds increase with increasing floral size or increasing color contrast with the background. Search speeds also vary across pollinator taxa

(C. J. Essenberg, unpublished data), probably because of multiple traits, such as flight ability and visual capacity. Flower-handling times are often longer in flowers with deep corollas, particularly when the pollinator has a short proboscis (Inouye 1980; Harder 1983; but see Dohzono et al. 2011). Limited data also suggest that specialist and flower-constant pollinators can handle flowers more quickly than can generalists (Strickler 1979; Chittka and Thomson 1997).

Having small, inconspicuous, widely dispersed flowers with readily accessible rewards should therefore make a plant species more likely to experience strong increases in pollinator visitation with increasing floral density (fig. 4.3). All else being equal, these traits could make Allee effects more likely. Indeed, having small, inconspicuous flowers should also reduce visitation rates to all flowers, increasing the probability that flowers at low densities will receive too few visits to be fully pollinated (Orians 1997). However, having accessible rewards should increase visitation rates, making Allee effects less likely (Orians 1997).

Comparison to Previous Models

A number of theoretical studies have explored the relation of foraging intensity to resource density, but for the most part their assumptions are not a good fit for a pollinator-flower system. Most of these previous models assume that foragers search for prey, each of which provides the same amount of food, in patches that vary in prey density (Sutherland 1983; Lessells 1985; Bernstein et al. 1988, 1991; Sutherland and Anderson 1993; Dolman and Sutherland 1997; Rodríguez-Gironés and Vásquez 1997; Olsson and Holmgren 2000; Ward et al. 2000). Other models assume that food resources continuously enter patches at rates that vary from one patch to another (e.g., Lessells 1995; Hakoyama 2003). In contrast, flowers can vary in both density and quality, because each accumulates food resources that can be depleted by other foragers.

Several models have explored how relative frequencies of different floral types will influence pollinator visitation or pollination success (Levin and Anderson 1970; Straw 1972; Bobisud and Neuhaus 1975; Waser 1978; Campbell 1986; Goulson 1994; Kunin and Iwasa 1996; Ferdy et al. 1998). However, previous theoretical exploration of the effects of absolute floral density on pollinator visitation appears to be limited to Rathcke's (1983) conceptual model. Whereas Rathcke's model produced only general, qualitative predictions, my model uses optimal-foraging theory to generate system-specific, quantitative predictions. These predictions partially support Rathcke's (1983) hypothesis that plants will facilitate each other's ability to attract pollinators at low densities and compete for pollinators at high densities (fig. 1*A*). However, my model

suggests that competition at high densities will occur in only a minority of systems and therefore that the shape of the relation will more often be saturating (as in fig. 1*B*) rather than hump shaped. My model also generates novel predictions about the influence of floral context and traits of the plants and pollinators on density effects, which are discussed above (figs. 2, 4).

Conclusion

The model presented here provides a theoretical framework that could explain much of the bewildering diversity of effects of floral density on pollinator visitation rates uncovered by past empirical studies. It provides theoretical support for the long-standing hypothesis that the relation of pollinator visitation to floral density is density dependent, with positive effects strongest at low floral densities (Rathcke 1983). It also identifies several variables, including pollinator search speeds, flower-handling times, background floral density, and foraging currency, that could explain the existence of different effects in different systems. Although further theoretical and empirical work is needed to confirm and extend these predictions, my model represents an important early step toward understanding an ecologically important aspect of the relationship between plants and their pollinators.

Acknowledgments

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