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UNIVERSITY OF CALIFORNIA  
RIVERSIDE

Understanding the Effects of Floral Density on Flower Visitation Rates  
and Species Composition of Flower Visitors

A Dissertation submitted in partial satisfaction  
of the requirements for the degree of

Doctor of Philosophy

in

Evolution, Ecology and Organismal Biology

by

Carla Jean Essenberg

June 2012

Dissertation Committee:

Dr. John T. Rotenberry, Chairperson

Dr. Kurt E. Anderson

Dr. Richard A. Redak

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The Dissertation of Carla Jean Essenberg is approved:

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## ABSTRACT OF THE DISSERTATION

Understanding the Effects of Floral Density on Visitation Rates  
and Species Composition of Flower Visitors

by

Carla Jean Essenberg

Doctor of Philosophy  
Graduate Program in Evolution, Ecology and Organismal Biology  
University of California, Riverside, June 2012  
Dr. John T. Rotenberry, Chairperson

Pollinator responses to varying floral density have important implications for plant population dynamics, conservation, and the evolution of floral traits. Floral density can influence both flower visitation rates and the species composition of flower visitors, but neither of these effects is well understood. In my dissertation, I generate and test hypotheses explaining the relations of flower visitation rate and flower visitor species composition to floral density.

In the first chapter, I present a foraging model that explores potential sources of variation in the effects of floral density on flower visitation rates. The model predicts that the relation of per-flower visitation rates to floral density will be nonlinear, with strong positive effects at low floral densities and weaker or negative effects at higher densities. Results from a field experiment using the annual composite *Holocarpha virgata* support this prediction. The model also shows that floral density in the surrounding environment and traits of both plants and their pollinators can influence the effects of floral density on visitation.

In the second chapter, I describe an observational field study, again using *H. virgata*, that shows that flower visitors respond differently to floral density at site (12.6 ha) and patch (4 m<sup>2</sup>) scales and furthermore that floral density at the site scale influences flower visitors' responses to patch-scale floral density. This study also reveals an effect of floral density on the species composition of *H. virgata*'s flower visitors.

In the final chapter, I explore effects of floral density on the species composition of flower visitors, using a variation of the model presented in the first chapter. The model identifies several flower visitor traits, including flower search speed, flower handling time, and foraging currency, that can influence whether a species uses primarily dense or sparse patches when in competition with other species.

Collectively, these studies fill a significant gap in our knowledge of pollinator responses to floral densities. By developing testable hypotheses based on biologically reasonable assumptions to explain many previously-observed phenomena, they lay the groundwork for understanding this important aspect of plant-pollinator mutualisms.

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# General Introduction

Plant-pollinator mutualisms are sensitive to variation in floral density (Kunin 1997b, Ghazoul 2005). Among other things, floral density often influences the frequency of flower visits and the species composition of flower visitors (e.g., Johnson and Hubbell 1975, Feinsinger 1976, Schaffer et al. 1979, Kunin 1993, 1997c, Feldman 2006, Bernhardt et al. 2008, Feldman 2008, Dauber et al. 2010). Many plant species suffer reduced reproductive success when pollinator visits are infrequent (Wilcock and Neiland 2002), and, because flower visitors vary greatly in their effectiveness as pollinators (e.g., Wilson and Thomson 1991; Ivey et al. 2003; Larsson 2005; Rader et al. 2012), flower visitor species composition can also influence plant reproductive success. Effects of floral density on flower visitation rates or flower visitor species composition can therefore generate relationships between plant density and fitness, which in turn have important implications for plant ecology and evolution. For instance, declines in fitness at low densities (Allee effects) can increase vulnerability to extinction, inhibit 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). On the other hand, declines in fitness at high densities strengthen competition and can stabilize population size (Murdoch 1994).

Although data from previous studies make clear that floral density often influences flower visitation rates and the species composition of flower visitors, we are far from understanding these effects well enough to predict them in novel systems. Visitation rates can increase or decrease with increasing floral density, and the factors determining

which effect will occur in any given context are not known. Likewise, in most cases we can only speculate about the traits that cause some flower visitors to use dense flower patches and others to use sparse patches when in competition with each other. My dissertation addresses these problems by developing and testing hypotheses to explain the effects of floral density on flower visitation rates and visitor species composition.

In the first chapter, I develop a foraging model to generate predictions about when floral density should have strongly positive or negative effects on per-flower visitation rates. A major aim of this model is to predict the shape of the relation of per-flower visitation rate to floral density, which was suggested by Rathcke (1983) to be hump-shaped, with positive effects occurring at low densities and negative effects at high densities. To complement this theoretical exploration, I also describe a field experiment, using the annual composite *Holocarpha virgata* ssp. *virgata*, in which I measure the shape of the relation of per-flower visitation to floral density. In the second chapter, I use a field study, again employing *H. virgata*, to investigate another potential explanation for variation in flower visitors' responses to floral density: i.e., that those responses are scale-dependent. Specifically, I compare effects of floral density on per-flower visitation rates and species composition of flower visitors at two scales, 4 m<sup>2</sup> and 12.6 ha. Finally, in the third chapter, I use a foraging model to explore how floral density can influence the species composition of flower visitors. My aim is to identify traits that determine which species will be more abundant in dense *versus* sparse flower patches.

# Chapter 1: Explaining variation in the effect of floral density on pollinator visitation

## 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 non-linear, 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 non-linear 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.

## 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, Krivan 1997, Bernstein et al. 1999, Krivan 2003). 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 1997b, Ghazoul 2005). On the other hand, decreases in pollinator visitation with increasing floral density could strengthen intra- and interspecific competition among plants (Rathcke 1983). Many studies have reported effects of plant density upon plant reproductive success, usually positive (e.g., Kunin 1997b, 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 1997b, 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, 1997c, 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 paper, 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 justification 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 paper, I model the effect of local floral density on per-flower pollinator visitation, assuming optimally-foraging, non-territorial 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 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, all pollinators are identical, and 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):

$$\text{Net rate of energy gain} = \frac{\text{Energy gain per flower} - \text{Energy used per flower}}{\text{Foraging time per flower}}. \quad (1.1)$$

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 1.1 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:

$$\text{Energy used per flower} = hkc + tc, \quad (1.2)$$

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

$$\frac{r_f - (hkc + t_f c)}{h + t_f} = \frac{r_b - (hkc + t_b c)}{h + t_b}, \quad (1.3)$$

where  $r$  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 replenishes 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 floral handling time is much smaller than the time between visits. Therefore,

$$r = \frac{n}{v}, \quad (1.4)$$

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 time per flower,  $h + t$ . Therefore,

$$v = \frac{p}{f(h+t)}, \quad (1.5)$$

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

**Table 1.1: Symbols used in the model**

Symbol*	Parameter or variable†
$A$	Area (m <sup>2</sup> )
$c$	Energetic cost per unit of traveling time (J/s)
$f$	Floral density (flowers/m <sup>2</sup> )
$h$	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 <sup>2</sup> )
$P$	Total number of actively foraging pollinators in the system (pollinators)
$r$	Average energy gained per flower visit (J/flower visit and 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 (see Appendix A.2) (m/s)
$t$	Average travel time per flower (s/flower visit/pollinator)
$v$	Visits per flower (flower visits/flower/s)

\*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.

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

$$\frac{f_f}{P_f} = \frac{f_b}{P_b} \text{ (Appendix A.1).} \quad (1.6)$$

This matching rule, whereby the ratio of resource inputs to foragers is constant across patches, is typical of ideal free distributions (Milinski 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 based on this assumption before returning to the more realistic scenario in which costs differ for handling flowers *vs.* 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

$$t = \frac{1}{s\sqrt{f}}, \quad (1.7)$$

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, Appendix A.II). 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 (Appendix A.3).

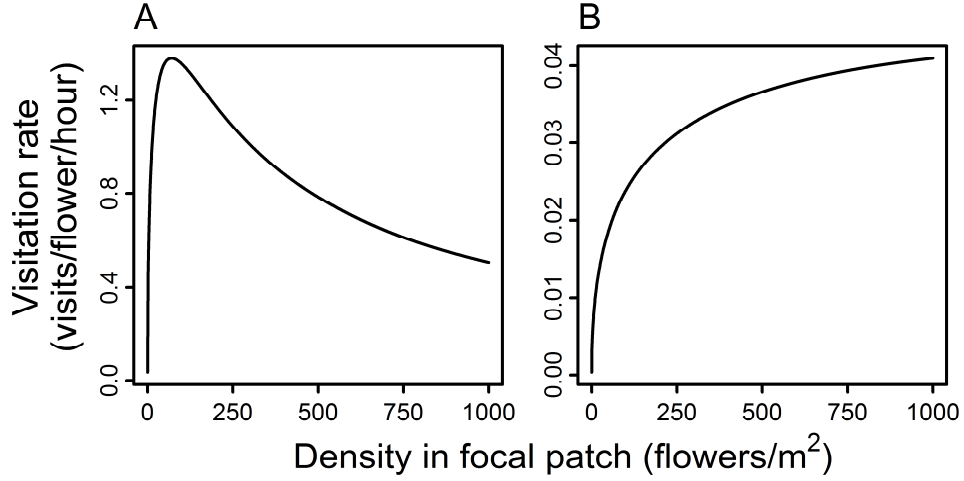
Finally, I assume that flowers in the focal patch and background area compete for a fixed number of actively foraging pollinators,  $P$ . Specifically,

$$P = p_f A_f + p_b A_b, \quad (1.8)$$

where  $A_f$  is the area of the focal patch.  $A_b$  is the area of the background, which is the area around the focal patch that is within the pollinators' foraging range. Equations 1.5 – 1.8 imply

$$v_f = \frac{P}{(A_f f_f + A_b f_b) \left( h + \frac{1}{s \sqrt{f_f}} \right)}, \quad (1.9)$$

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 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) (Figure 1.1A).



**Figure 1.1: (A) Hump-shaped and (B) saturating 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 1.2 (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<sup>2</sup> for (A) and 10 flowers/m<sup>2</sup> for (B),  $A_f = 100$  m<sup>2</sup>,  $A_b = 1.3 \times 10^5$  m<sup>2</sup>,  $P = 13$  pollinators,  $h = 0.5$  s,  $s = 0.1$  m/s,  $k = 1$ .

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 (Appendix A.1). As density approaches zero, 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

$$\frac{1}{1 + 2 h s \sqrt{f_f}} < \frac{f_f A_f}{f_b A_b} \quad (\text{Appendix A.1}), \quad (1.10)$$

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 are 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 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 1975b). Actual values of  $k$  vary, both between

bees and with ambient temperature (Heinrich 1975b, 1979a, Abrol 1992), but model predictions proved relatively insensitive to this variation, provided that  $k < 1$ .

**Table 1.2: Parameter values used to assess general patterns in the relation of pollinator visitation to floral density**

Parameter	Values*
Focal patch floral density ( $f_f$ )	0.5, 50, 5000 flowers/m <sup>2</sup>
Background floral density ( $f_b$ )	0.1, 10, 100 flowers/m <sup>2</sup>
Focal patch size ( $A_f$ )	1, 10, 100 m <sup>2</sup>
Pollinator density <sup>†</sup>	0.0001, 0.01, 1 bees/m <sup>2</sup>
Foraging range <sup>‡</sup>	100, 1000, 10000 m
Handling time ( $h$ )	0.5, 5, 50 s/flower
“Search speed” ( $s$ )	0.01, 0.1, 1 m/s
Flight cost ( $c$ ) / nectar secretion rate ( $n$ )	0.001, 1, 1000

\*These values are based on parameter estimates from published studies and my study system (see Appendix B). I use 1000 as the maximum value of flight cost / nectar secretion rate because net rate of energy gain is usually predicted to be negative at substantially higher values of this parameter.

<sup>†</sup>Pollinator density is used to calculate pollinator abundance, as follows:  $P = \text{pollinator density} \times (A_f + A_b)$ .

<sup>‡</sup>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 1.2, span the range of values reported from a variety of bee-pollinated systems (Appendix B). 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<sup>2</sup> when  $k = 0.1$  for all 1,782 combinations of the remaining parameter

values that produced non-negative net rates of energy gain for all of the 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<sup>2</sup>.

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 1.2, 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 using R (R Development Core Team 2010).

## **Results**

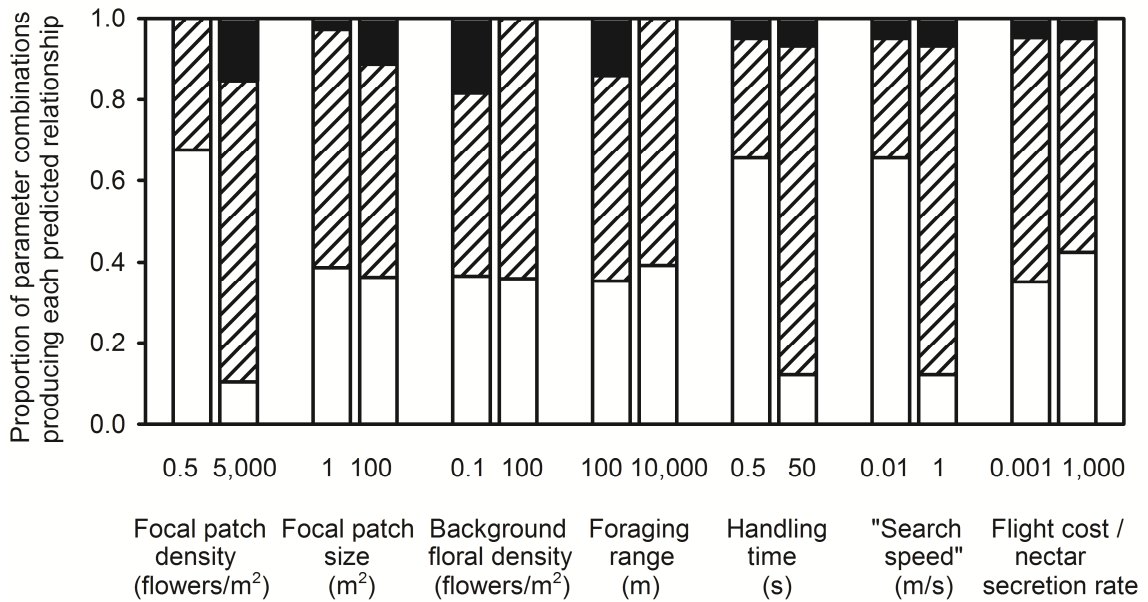
Within a realistic range of focal patch floral densities, the shape of the relation of visitation to floral density was usually predicted to be saturating rather than hump-shaped (Figure 1.1B). Indeed, visitation was still increasing with density at 1,000 flowers/m<sup>2</sup> for 81% of the parameter combinations. As predicted for the simpler model in which  $k = 1$ , positive effects were always strongest at the lowest focal patch floral densities.

**Table 1.3: Percent of parameter combinations for which effects of floral density are predicted to be strongly positive, weak, or strongly negative\***

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

\*Based on implementations of the model for the 5,375 combinations of the parameter values shown in Table 1.2 that produce non-negative values of net rate of energy gain and foraging efficiency, assuming that  $k = 0.1$ . Values are rounded to the nearest percent. Weak = <10% change in visitation with a doubling in floral density. Strongly positive or negative = >10% increase or decrease, respectively, with a doubling in floral density.

Weak and strongly positive effects of increasing floral density on visitation were both predicted for many parameter combinations, whereas strongly negative effects were seldom predicted (Table 1.3). At low focal patch floral densities, effects were usually strongly positive, whereas at high densities, effects were usually weak (Figure 1.2). A low background floral density, small pollinator foraging range, or 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.



**Figure 1.2: Effects of parameters on the relation of visitation to floral density, assuming that pollinators maximize net rate of energy gain**

White = strongly positive; Striped = weak; Black = strongly negative. Definitions of these categories are the same as in Table 1.3. 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 1.2 for which net rate of energy gain is positive for both values of the focal parameter. Numbers of parameter combinations used for each focal parameter are: focal patch density, 1,814; focal patch size, 1,824; background floral density, 1,501; handling time and search speed, 1,798; flight cost / nectar secretion rate, 1,331.

## 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, predictions are identical to those for bees maximizing rate of energy gain if  $k = 1$ , but not if  $k < 1$  (Appendix A.4). Most

noticeably, strongly positive effects occur more frequently when pollinators maximize efficiency than when they maximize the net rate of energy gain (Table 1.3). This is because, when  $k < 1$ , the energy expended per flower visited decreases faster with increases in floral density than does the time expended. 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 3-7 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*’s flowers were visited by a variety of insect taxa, the most abundant of which were sweat bees (Hymenoptera: Halictidae) (Table 1.4).

**Table 1.4: Taxa observed visiting flowers of *H. virgata* in experimental plots**

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

<sup>\*</sup>I have deposited voucher specimens of these taxa at the University of California–Riverside Entomology Research Museum.

<sup>†</sup>We observed a total of 3,269 visits.

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 co-flowering 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 four weeks, from August 10 to September 4, 2009. On each day, I selected four 2.25 x 2.25 m plots (consisting of 4 1-m<sup>2</sup> subplots divided by 25-cm-wide strips of cleared vegetation) in a large patch of *H. virgata*. Co-flowering species were sparse in this patch and were never present within the plots. I randomly assigned these plots to be thinned to the following densities on the morning of pollinator observations: 4, 12, 32, and 72 flowers/m<sup>2</sup> (first and fourth weeks) or 4, 12, 36, and 104 flowers/m<sup>2</sup> (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 be either 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 post-thinning densities in each square and data on the distribution of flower sizes in *H. virgata* (C. J. Essenberg, unpublished manuscript; Appendix A.6).

A team of three observers made a total of six to twelve (usually nine) ten-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, pers. obs.). 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 flower 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  $k = 1$ ,

$$v_f = \frac{P/F}{h + \frac{1}{s\sqrt{f_f}}} \quad (1.11)$$

(from Equation 1.9), where  $P/F$  is the pollinator to 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, a different relation is predicted if  $k < 1$ .

Specifically,

$$v_f = \left( \frac{P/F}{hk + \frac{1}{s\sqrt{f_f}}} \right) \left( \frac{hk + \frac{1}{s\sqrt{f_b}}}{h + \frac{1}{s\sqrt{f_b}}} \right) \quad (1.12)$$

(from Equation A.26).

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 1.4). Therefore, I parameterized each version of the model for this group. I calculated the large sweat bee to flower ratio,  $P/F$  and background flower density,  $f_b$ , from densities we recorded in six 1 x 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 (flower density)<sup>-1/2</sup>, using all 73 plots for which we recorded at least one flight duration. The resulting parameter estimates are shown in Table 1.5.

I determined the shape of the relations of per-flower visitation to flower density for large sweat bees and for all visitors combined with penalized cubic regression splines in generalized additive mixed models (GAMM), 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 non-normal. A square-root transformation of visitation rate resolved this problem without altering the results. I present results from the analysis without transformation.

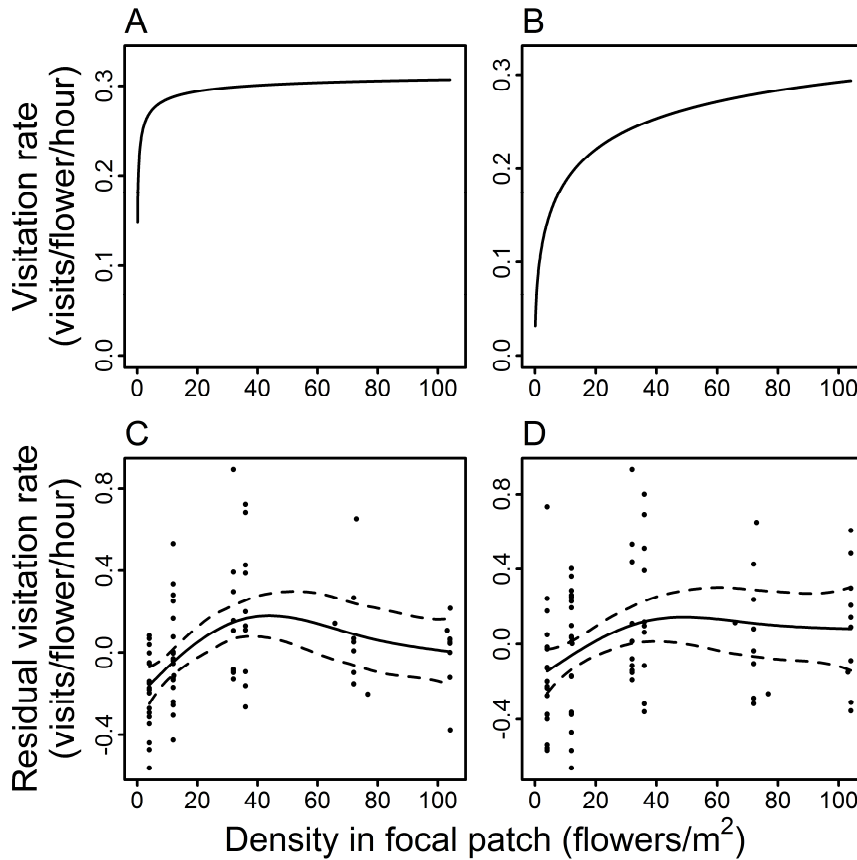
**Table 1.5: Parameter values for large sweat bees (*H. ligatus* and *L. titusi*) visiting *H. virgata***

Parameter	Value
Pollinator : flower ratio ( $P / F$ )	$3.0 \times 10^{-4}$ bees/flower*
Handling time ( $h$ )	3.4 s
“Search speed” ( $s$ )	0.82 m/s
Background flower density ( $f_b$ )	157 flowers/m <sup>2</sup> *

\* These are averages of four weekly values, which ranged from  $1.4 \times 10^{-4}$  to  $5.1 \times 10^{-4}$  bees/flower and 53 to 224 flowers/m<sup>2</sup>.

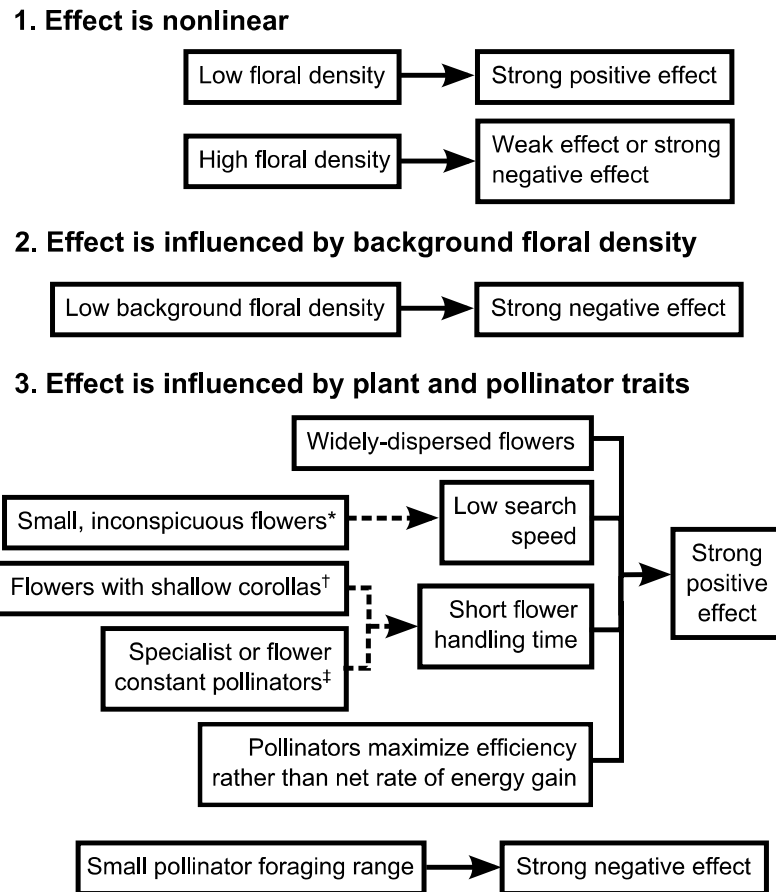
## Results

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 ten flowers/m<sup>2</sup> (Figure 1.3A). If they maximize efficiency, visitation continues to increase strongly across the entire measured range of densities (Figure 1.3B). The observed relation of large sweat bee visitation to floral density was significant and nonlinear ( $F_{2,8,75.2} = 4.3, p = 0.01$ ): visitation increased to a peak at 36 flowers/m<sup>2</sup> and then declined, although confidence intervals are wide at high densities (Figure 1.3C). When all flower visitors were included in the analysis, the relation was similar but weaker (Figure 1.3D;  $F_{2,2,75.8} = 3.2, p = 0.04$ ; without flower size term:  $F_{2,3,76.8} = 0.77, p = 0.48$ ).



**Figure 1.3: Observed and predicted effects of *H. virgata* flower density on per-flower visitation**

(A and B) Predicted relations for large sweat bees assuming that (A) pollinators maximize net rate of energy gain (Equation 1.11; parameter values shown in Table 1.5) or (B) pollinators maximize efficiency (Equation 1.12;  $k = 0.1$ ; other parameter values shown in Table 1.5). (C and D) Observed relations for (C) large sweat bees and (D) all taxa combined. The solid lines are penalized cubic regression splines generated by GAMM models of the effect of flower 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 are partial residuals.



**Figure 1.4: 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 the following empirical studies: \*Spaethe et al. 2001; <sup>†</sup>Inouye 1980, Harder 1983, although see Dohzono et al. 2011; <sup>‡</sup>Strickler 1979, Chittka and Thomson 1997.

## 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 1.4 and discussed in the next three sections.

## **1. 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 (Figure 1.1). As a result, plants are predicted to facilitate one another's pollinator attraction at low densities and, sometimes, 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 (Figures 1.1B and 1.2), whereas in others, visitation is expected to decline at high densities (Figures 1.1A and 1.2).

Facilitative and competitive interactions for pollinators can in turn have significant effects on plant ecology and evolution. When plants within a species facilitate each others' ability to attract pollinators, declines in plant density can cause average plant fitness to decrease (Kunin 1997b, 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 total floral density could strengthen competition between plant species, whereas increases in visitation with 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 Tschardt 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 (Appendix A.5). 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 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 (Figure 1.3). Both versions of the model predict curves that are too steep at the lowest densities, 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 (Figure 1.3C) and in a subsequent study, in which I included higher flower 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 intermingled 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 co-flowering 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).

## **2. 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 (Figures 1.2 and 1.4.2) and therefore, 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 only valid 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.

## **3. 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 (Figures 1.2 and 1.4.3). 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, flowers are widely dispersed rather than clumped, pollinator search speeds are low, or 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 due to 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, although 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. All else being equal, these traits could make Allee effects more likely (Figure 1.4). 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 (Orrians 1997). However, having accessible rewards should increase visitation rates, making Allee effects less likely (Orrians 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 Vasquez 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 (Figure 1.1A). 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 Figure 1.1B) 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 (Figures 1.2 and 1.4).

## **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 towards understanding an ecologically important aspect of the relationship between plants and their pollinators.

## Chapter 2: Scale-dependent shifts in the species composition of flower visitors with changing floral density

### Abstract

Responses of flower-visiting animals to floral density can alter interactions between plants, influencing a variety of biological processes, including plant population dynamics and the evolution of flowering phenology. Many studies have found effects of floral or plant density on pollinator visitation rates at patch scales, but little is known about responses of flower visitors to floral densities at larger scales. Here I present data from an observational field study in which I measured the effects of floral density on visitation to the annual composite *Holocarpha virgata* at both patch (4m<sup>2</sup>) and site (12.6 ha) spatial scales. The species composition of flower visitors changed with floral density, and did so in different ways at the two scales. At the site scale, average floral density within patches of *H. virgata* or within patches of all summer-flowering species combined had a significant positive effect on per-flowerhead visitation by the long-horned bee *Melissodes lupina* and no significant effects on visitation by any other taxa. At the patch scale, per-flowerhead visitation by honeybees significantly increased whereas visitation by *M. lupina* often decreased with increasing floral density. For both species, responses to patch-scale floral density were strongest when site-scale floral density was high. The scale-dependence of flower visitor responses to floral density and the interactions between site- and patch-scale effects of floral density observed in this study underscore

the importance of improving our understanding of pollinators' responses to floral density at population scales.

## **Introduction**

Flowers of many plant species suffer reduced reproductive success when pollinator visits are rare. As a result, pollinator responses to floral density and abundance have important implications for plant fecundity and population dynamics (Kunin 1997a, Ghazoul 2005). Increases in per-flower visitation rates with increasing floral density or abundance can be mechanisms of facilitation between plants, either within or between species (Kunin 1997a, Lundberg and Ingvarsson 1998, Feldman et al. 2004, Ghazoul 2005). Conversely, reductions in per-flower visitation at high floral density or abundance can strengthen competition (e.g., Chittka and Schurkens 2001). Flower visitors vary markedly in their quality as pollinators (e.g., Wilson and Thomson 1991, Ivey et al. 2003, Larsson 2005), and therefore, changes in visitor species composition with increasing floral density can also alter plant reproductive success and serve as mechanisms of competition or facilitation between plants.

Many studies have found effects of plant or floral densities on flower visitation rates or visitor species composition at patch scales (i.e.,  $< 1 \text{ m}^2$  to a few hundred  $\text{m}^2$ ; reviewed by Kunin 1997a, Ghazoul 2005; also see Johnson and Hubbell 1975, Kwak 1987, Grindeland et al. 2005, Cheptou and Avendano 2006, Feldman 2006, Zorn-Arnold and Howe 2007, Bernhardt et al. 2008, Dauber et al. 2010). However, pollinator responses to floral density or abundance could also be important at the scale of entire plant

populations. For instance, declines in pollinator visitation rates as flowers become fewer or more widely spaced could cause plant reproductive success to be lower in small or sparse populations than in large, dense ones, which in turn could increase plant populations' vulnerability to extinction and impede invasion of new habitats (Stephens and Sutherland 1999, Courchamp et al. 2008). In addition, pollinator responses to seasonal variation in floral density could influence the evolution of flowering phenology, particularly the length and synchrony of flowering times (Devaux and Lande 2010).

Plant populations often occupy areas of thousands of  $m^2$  or more (e.g., Dauber et al. 2010), but because of logistical challenges, relatively few studies have measured relationships between floral density and pollinator visitation rates at scales of more than a thousand  $m^2$  (although see Feinsinger et al. 1991, Kunin 1997c, Mustajarvi et al. 2001, Field et al. 2005, Feldman 2008, Aschero and Vazquez 2009, Dauber et al. 2010, Ikemoto et al. 2011). Studies of the effects of seasonal variation in resource densities on visitation rates are especially rare (although see Veddeler et al. 2006 and Jha and Vandermeer 2009, both of which were carried out in agricultural systems). Forager responses to variation in resource densities can be driven by different mechanisms at different spatial scales (e.g., Morgan et al. 1997). For instance, flower visitors might prefer to forage in dense rather than sparse flower patches because they expend less time and energy traveling between flowers in the former than in the latter (C. J. Essenberg, unpublished manuscript). However, at larger scales, the abundance of resources associated with high floral densities could lead to forager satiation, thereby reducing per-flower visitation rates. Strategies for locating resource patches could also vary with spatial scale. For

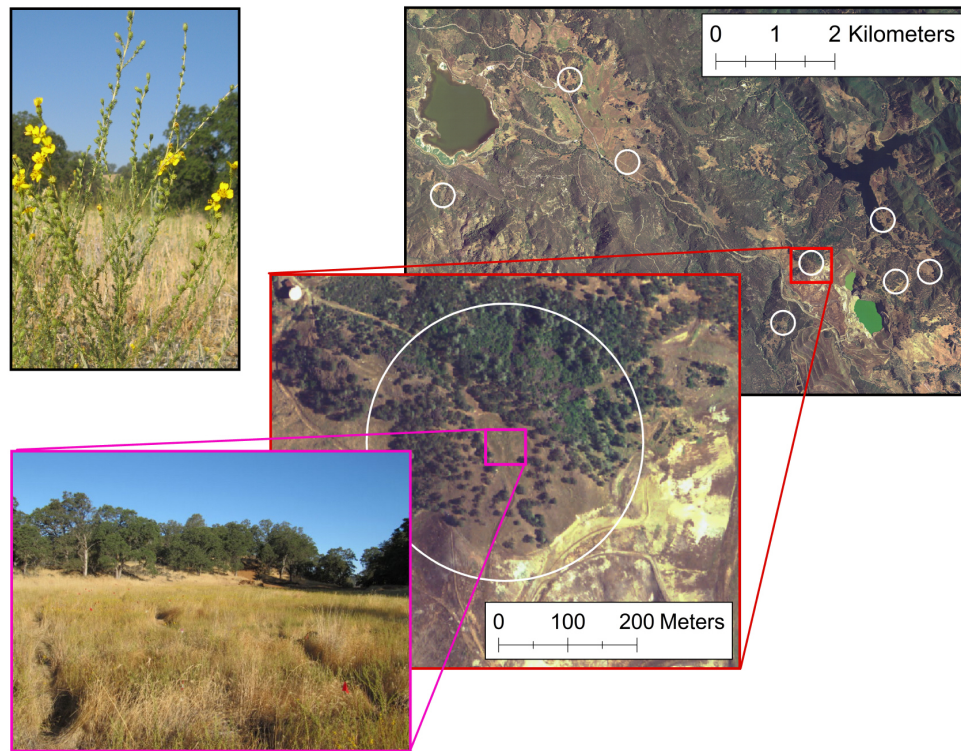
instance, honeybee workers can communicate locations of high-quality foraging sites to nest mates using the waggle dance, but the information conveyed by the dance is apparently too imprecise to guide patch choices at fine scales (such as a few m<sup>2</sup>; Dyer 2002, Tanner and Visscher 2008). For these reasons, effects of seasonal or site-to-site variation in floral densities on flower visitation rates could be quite different from the more frequently-measured effects of patch-scale variation in floral densities.

In this study, I measured the effects of floral density on per-flowerhead visitation rates to the annual composite *Holocarpha virgata* at two different scales: 4m<sup>2</sup> plots and 12.6 ha sites. A reduction in flight times at high flowerhead densities is one of the main reasons pollinators might prefer to visit flowerheads in dense patches, so I also measured the relationship between flowerhead density and between-flowerhead flight times at the patch scale.

## Methods

### Study species, sites, and sampling dates

My study species, *Holocarpha virgata* ssp. *virgata* (Asteraceae, common name: the yellowflower tarweed), is a self-incompatible, summer-flowering, annual composite with yellow flowerheads, each bearing 3-7 female ray florets and 9-25 protandrous disk florets (Figure 2.1) (Kyhos et al. 1990, Hickman 1993). The study took place at the University of California's Donald and Sylvia McLaughlin Reserve in northern California, near the intersection of Lake, Yolo, and Napa Counties. I identified eight sites within the reserve, each containing a large (0.1 to >10 ha) patch of *H. virgata* (Figure 2.1). In all but two of



**Figure 2.1: Study design**

The upper-left image shows the study species: *Holocarpha virgata*. The locations of the eight sites are shown with white circles in the upper-right image. The middle image shows the boundaries of a representative site, and the bottom-left image shows the *H. virgata* patch used for pollinator observations at that site. Source of aerial photographs: USDA Farm Service Agency - National Agriculture Imagery Program 2005. The other photographs were taken by the author.

these sites, *H. virgata* was the dominant summer-flowering species. The terrain was mountainous, and sites varied in their time of peak flowering by nearly six weeks. My sampling took place between 8-Aug and 22-Sept-2010. I collected data at each site three times, once as close as possible to *H. virgata*'s flowering peak and at least once well before the flowering peak. Because *H. virgata* flowered unusually late in 2010, logistical constraints only allowed sampling well after peak flowering at three of the eight sites.

Each of these sampling events occupied two days, usually consecutive. I always sampled two sites simultaneously, choosing sites with contrasting phenology or *H. virgata* density.

## **Effects of floral density on visitation rates**

### *Patch-scale floral density*

During each sampling event at each site, I placed five 2x2m flower visitor observation plots at the center of the site so that they spanned the range of *H. virgata* flowerhead densities available. The plots never contained flowers of other species. In each plot, an observer recorded the number of *H. virgata* flowerheads and the size (no. male-phase disk florets) of each of 7-12 randomly-chosen flowerheads. The amount of nectar and pollen produced per flowerhead was strongly correlated with flowerhead size (no. male-phase disk florets) and was not significantly related to patch-scale flowerhead density (Appendix C). Therefore, I used the estimated density of male-phase disk florets, obtained by multiplying the flowerhead density by the average flowerhead size found in each plot, as my measure of patch-scale floral density.

### *Site-scale floral density*

I mapped boundaries of all patches of *H. virgata* within 200m of the center of each site using Garmin eTrex GPS units (typically accurate within 7m or less) and ESRI® ArcMap™ 9.3 software. I calculated the area occupied by patches of *H. virgata* at each site, or site-scale extent of *H. virgata*, using ArcMap™. During each sampling event, an observer recorded the number of *H. virgata* flowerheads in a 0.25-m-radius plot at each of 60 sampling points that had been placed randomly within patches of *H. virgata* using Hawth's Tools (Beyer 2004). From these data, I calculated the average floral density

within *H. virgata* patches during each sampling event. I again used average density of male-phase disk florets, obtained by multiplying flowerhead density by the average flowerhead size observed in visitor observation plots during that sampling event at that site, as my measure of site-scale floral density for *H. virgata*.

Several other plant species also bloomed abundantly at some sites during the study and were visited by many of the same insect species as *H. virgata*. These species were: serpentine sunflower (Asteraceae: *Helianthus exilis*), yellow starthistle (Asteraceae: *Centaurea solstitialis*), and two tarweed species, hayfield tarweed (Asteraceae: *Hemizonia congesta*) and smallflower western rosinweed (Asteraceae: *Calycadenia pauciflora*). Total floral density could influence the abundance of flower visitors. Therefore, I measured the total area of all patches of summer-flowering plant species at each site, or total extent (excluding species whose patches covered <1% of the site), and the total floral density within those patches, with species weighted according to their floral reward production rates (Appendix D).

### *Site-scale floral diversity*

Floral diversity can influence pollinator visitation rates (e.g., Ghazoul 2006, Hegland and Boeke 2006, Kandori et al. 2009) and was correlated with all of my measures of floral density (Table 2.1). To enable me to control for these effects, I calculated floral diversity during each sampling event at each site using Simpson's index. Specifically, I defined floral diversity to be  $1 - \sum_{i=1}^S p_i$ , where  $p_i$  was the unweighted floral abundance of

species  $i$  divided by the sum of all species' floral abundances at the site and  $S$  was the number of species whose patches covered at least 1% of the site.

### *Flower visitor observations*

During each of the three sampling events at each site, a team of four observers carried out a total of nine seven-minute observations per 2x2m visitor observation plot to record per-flowerhead visitation rates. These observations occurred in the mornings, beginning when air temperatures reached approximately 20°C, because visitation to *H. virgata* is highest under these conditions at this site (C. J. Essenberg, *pers. obs.*). During each observation, an observer watched a randomly-selected subset of the plot whose size decreased with flowerhead density to ensure that the time needed to scan the flowerheads being observed was approximately the same for all plots. The observer identified each visitor to the narrowest taxonomic category possible and recorded the number of flowerheads it visited. From these data, I calculated the average per-flowerhead visitation rate in each plot. I have deposited voucher specimens collected from *H. virgata* at locations distributed across the study area between 14-Aug and 13-Sept-2010 at the Univ. of California-Riverside Entomology Research Museum.

### *Temperature measurements*

I used data loggers (HOBO<sup>®</sup> Pendant Temperature Data Logger) suspended under a shade placed near the plots to record the air temperature every five minutes during these observations. I averaged together the temperatures recorded during flower visitor observations at each sampling event at each site.

## *Analysis*

I analyzed the effects of patch-scale floral density, site-scale floral density, and site-scale extent of *H. virgata* on per-flowerhead visitation rates using a mixed effects model, with sampling event nested within site as random effects. Similar analyses using total floral density and extent are presented in Appendix D. The models included the two-way interactions between patch-scale floral density and each of the two site-scale density variables (floral density and extent) because of previous evidence that population-level plant abundance can influence effects of patch-scale floral density on visitation (Dauber et al. 2010). Patch-scale floral density and site-scale extent were  $\log_{10}$ -transformed and all three variables were mean-centered to eliminate correlations between interaction terms and main effects. Initially, the model also included the covariates number of days since the beginning of the study, average temperature during observations, and site-scale floral diversity, but these were retained only if they were at least marginally significant ( $p < 0.1$ ). There were significant correlations between several of the terms in the model, including significant positive correlations between the three measures of floral density, significant negative correlations between site-scale floral diversity and all three measures of floral density, and a significant positive correlation between day and site-scale floral density (Table 2.1).

To test whether flower visitor composition was affected by floral density, I also ran this analysis using, as dependent variables, the per-flowerhead visitation rate by each of the most abundant categories of flower visitors. The visitor categories I used were: the long-horned bee *Melissodes lupina* (Anthophoridae), large-bodied sweat bees

**Table 2.1: Pearson's product-moment correlations between independent variables and interaction terms used in analyses of effects of *H. virgata* floral density on visitation rates<sup>†</sup>**

	Site Density	Site Extent	Day	Temp.	Site Diversity	Patch Density x Site Density	Patch Density x Site Extent
<b>Patch Density</b>	0.50***	0.23*	0.16	0.07	-0.24**	-0.04	0.04
<b>Site Density</b>		0.29**	0.40***	-0.002	-0.39***	0.15	0.04
<b>Site Extent</b>			0.03	-0.04	-0.23*	0.05	0.03
<b>Day</b>				-0.34***	-0.15	0.28**	0.13
<b>Temp.</b>					-0.25***	-0.01	-0.05
<b>Site Diversity</b>						0.01	0.16
<b>Patch Density x Site Density</b>							0.50***

<sup>†</sup> Patch Density = patch-scale floral density, in no. male-phase disk florets m<sup>-2</sup>; Site Density = average floral density within *H. virgata* patches at the site scale, in no. male-phase disk florets m<sup>-2</sup>; Site Extent = total area of *H. virgata* patches at the site scale, in m<sup>2</sup>; Temp. = temperature in °C; Site Diversity = site-scale floral diversity as measured by 1 – Simpson's index.

\* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001

(Halictidae: *Halictus ligatus* and *Lasioglossum titusi*), and honeybees (Apidae: *Apis mellifera*). When analyzing the per-flowerhead visitation rate of each group, I included the total per-flowerhead visitation rate by all other visitors as a covariate in the model to control for potential negative effects of other species on per-flowerhead rewards.

I carried out these analyses using the `lme` function in the `nlme` package of R (Pinheiro et al. 2009, R Development Core Team 2010). Visitation rates were square-root transformed to improve the distribution of the residuals. To compensate for heteroscedasticity in the analyses of visitation by honeybees and by *M. lupina*, I modeled the residual variance as proportional to a power of the number of days since the beginning of the study for honeybees and the number of days until the end of the study for *M. lupina*, using the `varPower` function in R (Pinheiro and Bates 2000). The d'Agostino-Pearson normality test indicated significant deviations from normality for the analyses of total visitation and visitation by honeybees and by *M. lupina* even after transformation of visitation rates. Eliminating a single outlier in the analysis of total per-flowerhead visitation solved this problem without altering the significance of any of the floral density terms, but I could not normalize residuals for the analyses of visitation by honeybees and by *M. lupina*. Therefore, I confirmed the results of these analyses using randomization tests. I generated 1,000 randomized datasets by randomly permuting visitation rates across plots, with the restrictions that each group of data points collected at the same site were always assigned, as a group, to one site and likewise that each group of data points collected during the same sampling event were always assigned, as a group, to one sampling event. To obtain a p-value for each predictor variable, I ran

likelihood ratio tests comparing the full mixed model with a model omitting that variable and calculated the p-value using the formula  $(n + 1) / (N + 1)$ , where  $N$  = the total number of randomized datasets and  $n$  = the number of randomized datasets for which the test statistic from the likelihood ratio test ( $L$ ) was as great or greater than the test statistic obtained from the same test using the observed data (Roff 2006). These p-values should be viewed as approximate; exact randomization tests are not available for multivariate analyses of the sort used in this study (Anderson and Ter Braak 2003). Analyses of a few of the randomized datasets were not possible because of singularities or convergence errors. I generated additional randomized datasets to replace these datasets.

### **Effects of patch-scale flowerhead density on flight times**

During eight of the flower visitor observations for each plot described above, the observer recorded when each flower visitor landed and took off from each flowerhead, with the following exceptions. Landing and take-off times were never recorded when multiple visitors were present in the area being observed, and occasionally observers failed to record them at other times, usually because the pace of foraging was too fast. I used these landing and taking-off times to calculate average between-flowerhead flight times for each taxonomic group in each plot. I analyzed the relationship between patch flowerhead density and average between-flowerhead flight time for each of the two groups of flower visitors for which I had sufficient data, large sweat bees (*H. ligatus* and *L. titusi*) and *M. lupina*, using simple linear regression, after  $\log_{10}$ -transforming flowerhead density to make the relationship linear. For these analyses, I used only data points that represented at least five flights.

**Table 2.2: Flower visitors observed during the observational study**

<b>Taxon</b>	<b>Number of visits</b>	<b>Percentage of total visits</b>
<b>BEES (Hymenoptera):</b>		
Large sweat bees (Halictidae: <i>Halictus ligatus</i> , <i>Lasioglossum titusi</i> )	1,640	30.6
<i>Melissodes lupina</i> (Anthophoridae)	1,401	26.1
Honeybees (Apidae: <i>Apis mellifera</i> )	804	15.0
Small sweat bees (Halictidae: <i>Dialictus</i> sp., <i>Halictus tripartitus</i> )	228	4.3
<i>Tetraloniella pomonae</i> (Anthophoridae)	95	1.8
Other/unidentified bees (including Megachilidae: <i>Ashmeadiella</i> , <i>Megachile</i> )	327	6.1
<b>FLIES (Diptera):</b>		
Large beeflies (Bombyliidae: <i>Exoprosopa</i> , <i>Paravilla</i> , <i>Villa</i> )	284	5.3
Hoverflies (Syrphidae: <i>Eristalis</i> , <i>Eupeodes</i> , <i>Toxomerus</i> )	195	3.6
Small beeflies (Bombyliidae: <i>Geron</i> , <i>Phthiria</i> )	161	3.0
<b>OTHER</b>		
Other/unidentified (including Lepidoptera: Noctuidae: <i>Heliothodes</i> ; Hymenoptera: Braconidae)	231	4.3

## Results

Altogether, we observed 5,366 flowerhead visits, of which approximately 31% were from large sweat bees, 26% from *M. lupina*, 15% from honeybees, 12% from other bees, 12% from flies, and 4% from other taxa (Table 2.2). Floral densities at the patch scale ranged from 2 to 1,460 male-phase florets m<sup>-2</sup> (mean = 227 florets m<sup>-2</sup>). At the site scale, total extent of *H. virgata* patches ranged from 0.6 to 10.7 ha (mean = 3.0 ha) and was highly correlated with site-to-site variation in *H. virgata*'s peak floral abundance ( $r = 0.98$ ). Site-scale floral densities of *H. virgata* (i.e., average densities within *H. virgata* patches) ranged from 7 to 297 male-phase florets m<sup>-2</sup> (mean = 119 florets m<sup>-2</sup>). This variation in site-scale floral density was primarily seasonal: site-scale floral densities of *H. virgata* typically varied over about an order of magnitude across the three sampling events within each site, whereas site-scale floral densities during *H. virgata*'s peak flowering time ranged from 105 male-phase florets m<sup>-2</sup> in the sparsest site to 297 male-phase florets m<sup>-2</sup> in the densest site. Total site-scale floral density and patch extent were strongly correlated with site-scale floral density and patch extent of *H. virgata* alone (floral density:  $r = 0.85$  and  $0.75$  for measures of total floral density weighted by pollen and nectar sugar production, respectively; patch area:  $r = 0.93$ ). Site-scale floral diversity ranged from  $1 - D = 0$  to  $0.69$  (mean =  $0.28$ ).

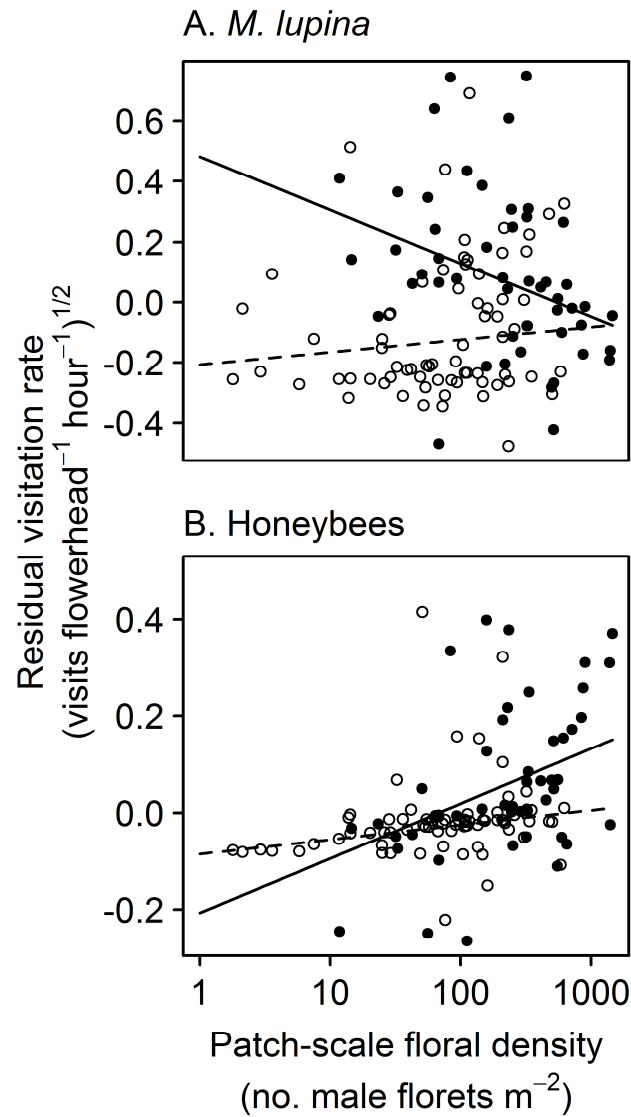
### Effects of floral density on visitation rates

The total per-flowerhead visitation rate (i.e., visitation by all taxa combined) did not respond significantly to *H. virgata*'s floral density on either the patch (4 m<sup>2</sup>) or the site (12.6 ha) scale (Table 2.3). However, flower visitor species composition was influenced

by floral density (Table 2.3; Figure 2.2). Site-scale floral density had a significant positive effect on per-flowerhead visitation by *M. lupina* (Table 2.3). Patch-scale floral density had a strong negative effect on visitation by *M. lupina* when site-scale floral density was high and a weak positive effect when site-scale floral density was low (Figure 2.2a). Site-scale extent of *H. virgata* had a negative effect on visitation by *M. lupina*, which was significant according to the randomization test but only marginally significant according to the parametric analysis. In contrast, per-flowerhead visitation by honeybees did not respond significantly to site-scale floral density or extent but increased significantly with increasing patch-scale floral density (Table 2.3; Figure 2.2b). There was also a marginally-significant interaction effect: the increase in honeybee visitation with increasing patch-scale floral density was stronger when site-scale floral density was high than when it was low (Figure 2.2b). Per-flowerhead visitation by large sweat bees did not respond to floral density at either scale.

Site-scale floral diversity had a marginally-significant negative effect on total per-flowerhead visitation (Table 2.3). Both total per-flowerhead visitation and the frequency of visits by large sweat bees decreased significantly over the course of the study. Temperature and visitation by other taxa had no significant effects on visitation by any taxa.

Analyses using total site-scale floral density and patch extent produced similar results to those just described using site-scale floral density and patch extent of *H. virgata* alone, although the negative effect of total site extent on visitation by *M. lupina* was not significant (Appendix D).



**Figure 2.2: Effects of floral density of *H. virgata* at patch (4 m<sup>2</sup>) and site (12.6 ha) scales on per-flowerhead visitation by (A) *Melissodes lupina* and (B) honeybees (*Apis mellifera*)**

Lines represent relationships predicted when site-scale floral density is one standard deviation above (solid) or below (dashed) the mean. Points are partial residuals of visitation rates observed when site-scale floral density was above (filled) or below (open) the mean. The partial residuals are (observed visitation rates) – (all terms from the models described in Table 2.3 other than those containing patch- and site-scale floral density).

**Table 2.3: Effects of patch- (4m<sup>2</sup>) and site-scale (12.6 ha) floral density of *H. virgata* on per-flowerhead visitation rates of the most abundant categories of flower visitors\***

	<i>b</i>	<i>se</i>	<i>df</i>	<i>t</i>	<i>P</i> <sup>†</sup>
<b>All visitors combined:</b>					
Patch Density	-0.033	0.042	92	-0.77	0.44
Site Density	0.00013	0.00044	13	0.30	0.77
Site Extent	-0.26	0.27	6	-0.94	0.39
<b>Site Diversity</b>	<b>-0.66</b>	<b>0.30</b>	<b>13</b>	<b>-2.20</b>	<b>0.047</b>
<b>Day</b>	<b>-0.020</b>	<b>0.0023</b>	<b>13</b>	<b>-8.74</b>	<b>&lt;0.001</b>
Patch Density x Site Density	-0.00046	0.00044	92	-1.03	0.30
Patch Density x Site Extent	-0.040	0.12	92	-0.33	0.74
<b>Long-horned bees (<i>M. lupina</i>):</b>					
Patch Density	-0.067	0.040	93	-1.69	0.09, 0.13
<b>Site Density</b>	<b>0.0013</b>	<b>0.00041</b>	<b>15</b>	<b>3.14</b>	<b>0.007, 0.008</b>
<b>Site Extent</b>	<b>-0.20</b>	<b>0.10</b>	<b>6</b>	<b>-1.91</b>	<b>0.10, 0.018</b>
<b>Patch Density x Site Density</b>	<b>-0.0011</b>	<b>0.00043</b>	<b>93</b>	<b>-2.63</b>	<b>0.010, 0.014</b>
Patch Density x Site Extent	-0.076	0.12	93	-0.66	0.51, 0.53

\* Results are from mixed effects models, with sampling event nested within site as random effects. Abbreviations are the same as in Table 2.1. Visitation rates are in visits flowerhead<sup>-1</sup> hour<sup>-1</sup> and are square-root transformed. Patch Density and Site Extent are log<sub>10</sub>-transformed. Bold indicates  $P < 0.05$ .

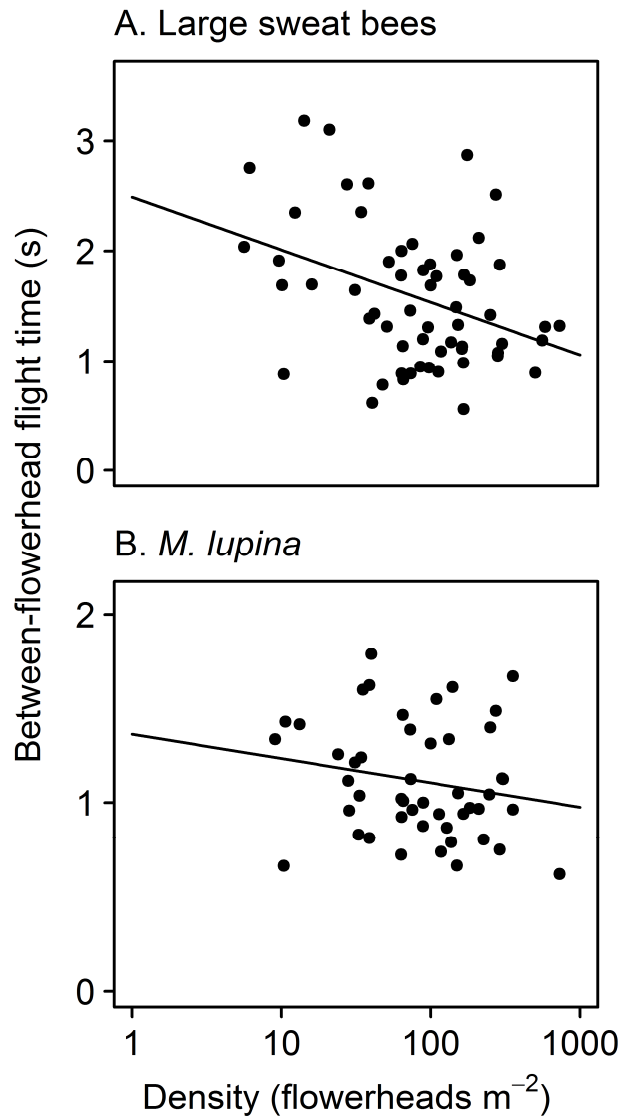
<sup>†</sup> Where two p-values are shown, the second was estimated using randomization tests.

**Table 2.3 cont'd**

	<i>b</i>	<i>se</i>	<i>df</i>	<i>t</i>	<i>P</i> <sup>†</sup>
<b>Honeybees (<i>A. mellifera</i>):</b>					
<b>Patch Density</b>	<b>0.072</b>	<b>0.021</b>	<b>93</b>	<b>3.44</b>	<b>&lt;0.001, 0.003</b>
Site Density	0.00024	0.00030	15	0.83	0.42, 0.44
Site Extent	0.061	0.11	6	0.57	0.59, 0.63
Patch Density x Site Density	0.00043	0.00022	93	1.97	0.052, 0.067
Patch Density x Site Extent	0.069	0.068	93	1.01	0.31, 0.34
<b>Large sweat bees (<i>H. ligatus</i> and <i>L. titusi</i>):</b>					
Patch Density	0.015	0.042	93	0.36	0.72
Site Density	0.00018	0.00041	14	0.44	0.67
Site Extent	-0.17	0.17	6	-1.04	0.34
<b>Day</b>	<b>-0.017</b>	<b>0.0028</b>	<b>14</b>	<b>-6.08</b>	<b>&lt;0.001</b>
Patch Density x Site Density	-0.00048	0.00045	93	-1.07	0.29
Patch Density x Site Extent	0.14	0.12	93	1.11	0.27

### **Effects of patch-scale flowerhead density on flight times**

Average between-flowerhead flight times for sweat bees decreased significantly with increasing flowerhead density (Figure 2.3a;  $b = -0.21$ ,  $se = 0.07$ ,  $n = 60$ ,  $t = -3.07$ , one-tailed test:  $P = 0.002$ ). However, *M. lupina*'s flight times responded only weakly to flowerhead density (Figure 2.3b;  $b = -0.056$ ,  $se = 0.043$ ,  $n = 48$ ,  $t = -1.31$ , one-tailed test:  $P = 0.10$ ). I lacked sufficient data to carry out a similar analysis on honeybees.



**Figure 2.3:** Effect of flowerhead density on between-flowerhead flight times by (A) large sweat bees (*Halictus ligatus* and *Lasioglossum titusi*) and (B) *M. lupina*

## Discussion

My results show that floral density influences the species composition of *H. virgata*'s flower visitors, and, furthermore, does so in different ways at different scales. At the site scale (12.6 ha), per-flowerhead visitation by the long-horned bee *M. lupina* increased with increasing floral density. In contrast, at the patch scale (4 m<sup>2</sup>), visitation by *M. lupina* often declined and visitation by honeybees increased with increasing floral density. Furthermore, site-scale floral density influenced the bees' responses to patch-scale floral density: the opposing responses of honeybees and *M. lupina* to patch-scale floral density were strongest when average floral density at the site scale was high. Floral diversity and patch extent at the site scale also appeared to influence pollinator visitation rates: there was a marginally-significant decline in total per-flowerhead visitation rates within increasing floral diversity, as measured using Simpson's index, and a marginally-significant decline in visitation by *M. lupina* with increasing total area of *H. virgata* patches.

Several previous studies have found contrasting responses of different flower visitor taxa to floral density (Johnson and Hubbell 1975, Kwak 1987, Zorn-Arnold and Howe 2007), nectar production rates (Schaffer et al. 1979), patch size (Ginsberg 1983, Sih and Baltus 1987, Sowig 1989), or population size (Conner and Neumeier 1995), suggesting that shifts in flower visitor species composition with floral resource density could be common. The amount of conspecific pollen deposited per flower visit can differ by tenfold or more across the insect species visiting a plants' flowers (e.g., Wilson and Thomson 1991, Ivey et al. 2003, Larsson 2005, Rader et al. 2012), leading to substantial

differences in the species' effects on plant reproductive success. Therefore, effects of floral density on pollinator species composition could play an important role in shaping the relationships between plant density and plant fitness.

Although some efforts have been made to explain why flower visitors differ in their responses to floral density (Johnson and Hubbell 1975, Schaffer et al. 1979), no general framework is yet available to predict which taxa will dominate dense *versus* sparse resources. However, empirical studies to date do support one general pattern: honeybees often become more dominant when floral resources are denser, at both patch (Ginsberg 1983, Kwak 1987, Sih and Baltus 1987) and plant population scales (Schaffer et al. 1979, Conner and Neumeier 1995), whereas solitary or primitively social bees tend to be more common at relatively sparse resources (Schaffer et al. 1979, Sih and Baltus 1987). My findings are consistent with this pattern at the patch scale but not at the site scale: at the site scale, honeybees did not respond significantly to floral density and visitation by the solitary bee *M. lupina* increased with increasing floral density.

Although I can only speculate about the mechanisms driving the shifts in species composition with floral density observed in this study, my data contain some interesting hints regarding those mechanisms. First, between-flowerhead flight times declined significantly with increasing flowerhead density for sweat bees but not for *M. lupina*, suggesting that floral density may have relatively little influence on foraging efficiency in *M. lupina*. The absence of a strong advantage to foraging in dense patches could help to explain why *M. lupina*'s visitation declined with patch-scale floral density whereas visitation by sweat bees did not. Second, the opposing responses of honeybees and *M.*

*lupina* to patch-scale floral density suggest that their distributions may have been shaped at least in part by competition with each other. Although we did not notice aggressive interactions between honeybees and *M. lupina*, these species could have influenced each other's distributions through exploitative competition (e.g., Schaffer et al. 1979).

My study measured effects of two different aspects of floral density at the site scale: the total area of *H. virgata* patches and the average floral density within those patches. Total patch area was highly correlated with floral abundances at the height of the flowering season at each site and therefore was a measure of site-to-site variation in floral abundance. Pollinator responses to between-population variation in floral abundance are of particular importance for predicting how vulnerable small populations will be to extinction, but thus far consistent patterns in these responses have not emerged. In my study, total patch area had a marginally-significant negative effect on visitation by *M. lupina* but no significant effects on visitation rates by other taxa. Because of low sample size (only eight sites), effects would need to have been strong to be detected. Some previous studies have found significant effects, both positive and negative, of plant population size or site-to-site variation in floral abundance on per-plant or per-flower visitation rates (Conner and Neumeier 1995, Mustajarvi et al. 2001, Ehlers et al. 2002, Field et al. 2005, Brys et al. 2008, Sober et al. 2009), although others have, like mine, failed to find such effects (e.g., Kunin 1997c, Bernhardt et al. 2008, Aschero and Vazquez 2009, Dauber et al. 2010, Wagenius and Lyon 2010, Ikemoto et al. 2011). Variation in within-patch floral densities in my study was primarily seasonal. Pollinator responses to seasonal variation in floral densities could influence the evolution of

flowering phenologies (e.g., Devaux and Lande 2010) but have rarely been measured. At the site scale, my study found a significant, positive effect of the average floral density within patches on per-flowerhead visitation by one species, *M. lupina*, but not on visitation by any other taxa. Two previous studies measuring effects of seasonal variation in floral density, both in coffee plantations, also found significant effects, although their results differed from each other and from mine. Veddeler et al. (2006) found that the number of bees per coffee shrub declined with the proportion of shrubs in bloom whereas Jha and Vandermeer (2009) found that honeybee visits but not native bee visits per inflorescence increased with the proportion of shrubs in bloom in low-shade coffee.

Although we are still far from understanding pollinator responses to floral density well enough to predict those responses with confidence at any scale, this study, along with previous work, does make clear that these responses are scale-dependent, in both natural and agricultural systems (Veddeler et al. 2006, Bernhardt et al. 2008, Jha and Vandermeer 2009, Dauber et al. 2010, Ikemoto et al. 2011). For instance, a study of 10 insect-pollinated plant species by Dauber et al. (2010) found significant effects of floral density on pollinator visitation rates at patch but not population scales. Similarly, Ikemoto et al. (2011) found a significant increase in syrphid abundance with increasing floral density in 25m<sup>2</sup> plots but not in 2,500m<sup>2</sup> plots. Jha and Vandermeer (2009) found negative effects of floral density on native bee visitation to coffee flowers at local scales (79-310 m<sup>2</sup>) but not large scales (3.1 ha) and, conversely, positive effects of floral density on honeybee visitation at large but not local scales.

Site- or population-scale floral density and abundance can also influence pollinator responses to patch-scale floral densities. In this study, patch-scale floral density had little influence on visitation rates by either honeybees or *M. lupina* when site-scale floral densities were low (dashed lines in Figure 2.2). However, when site-scale floral densities were high, visitation by honeybees strongly increased and visitation by *M. lupina* strongly decreased with increasing patch-scale floral density (solid lines in Figure 2.2). A different effect of large-scale floral abundance on effects of patch-scale floral density was observed by Dauber et al. (2010). They found that patch-scale floral density had a positive effect on per-flower visitation in small plant populations but a negative effect in large populations. The causes of these interaction effects are still unclear. In this study, changes in the intensity of competition may have played a role, because visitation rates by *M. lupina* were higher when site-scale floral densities were high than when they were low.

I found a marginally-significant decrease in total per-flowerhead visitation rates to *H. virgata* with increasing site-scale floral diversity, as measured by Simpson's index. Effects of diversity on visitation rates have been measured at patch scales by several previous studies, and can be either positive or negative (e.g., Ghazoul 2006, Hegland and Boeke 2006, Kandori et al. 2009). Negative effects of floral diversity on visitation to particular plant species, such as that observed in this study, may be caused by competition between plant species for flower visitors.

## **Conclusions**

This study shows that flower visitors can respond differently to floral densities at different spatial scales and furthermore that site-scale floral density can influence pollinators' responses to patch-scale floral density. Data on the effects of plant population-scale floral density on pollinator behavior are therefore needed to inform our understanding of both population-level phenomena such as plant population dynamics or the evolution of flowering phenology and patch-scale effects of floral density on plant fitness. This study also adds to a growing body of evidence that floral density can influence the species composition of flower visitors. Flower visitor species composition can have strong effects on pollination success and therefore density-related shifts in visitor species composition could have important implications for the relationship between plant density and plant fitness. Greater efforts are needed to explain why flower visitor species composition changes with floral density and to characterize pollinator responses to population-scale floral densities.

## Chapter 3: Explaining the effects of floral density on flower visitor species composition

### 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 demonstrates that variation in flower search speeds, flower handling times, energy consumption rates, or foraging currencies can cause shifts in the species composition of non-territorial flower visitors with increasing floral density. In particular, species with slow search speeds compared to competitors and those maximizing energetic efficiency rather than net rate of energy intake are usually predicted to dominate dense flower patches. The model is able to predict some aspects of a previously-observed effect of floral density on species composition of flower visitors to the yellowflower tarweed (*Holocarpha 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.

## 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 1997a, 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, C. J. Essenberg, unpublished manuscript). 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, 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, Hugie 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 compare model predictions to observed shifts in flower visitor species composition with floral density in an annual composite, the yellowflower tarweed (Asteraceae: *Holocarpha 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, 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 average energy cost per flower visit for species  $i$  in patch  $j$  (see Table 3.1 for a list of symbols used in the model).

**Table 3.1: Symbols used in the models in Chapter 3**

Symbol <sup>*</sup>	Parameter or variable <sup>†</sup>
$c_i$	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

<sup>\*</sup>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.

<sup>†</sup>Possible units are listed in parentheses.

**Table 3.1 cont'd**

<b>Symbol</b>	<b>Parameter or variable</b>
$h_i$	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)

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,

$$I_j = \frac{r}{V_j}. \quad (3.1)$$

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

$$V_j = V_{a,j} + V_{b,j}. \quad (3.2)$$

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,

$$V_{i,j} = \frac{n_i p_{i,j}}{f_j T_{i,j}}, \quad (3.3)$$

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

$$T_{i,j} = h_i + \frac{d_j}{s_i}, \quad (3.4)$$

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:

$$E_{i,j} = c_i k_i h_i + c_i \frac{d_j}{s_i}. \quad (3.5)$$

For insects that land on flowers while feeding,  $k_i$  will typically be much less than 1 (Heinrich 1975b, 1979a), 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

$$\frac{I_D}{E_{i,D}} = \frac{I_S}{E_{i,S}}. \quad (3.6)$$

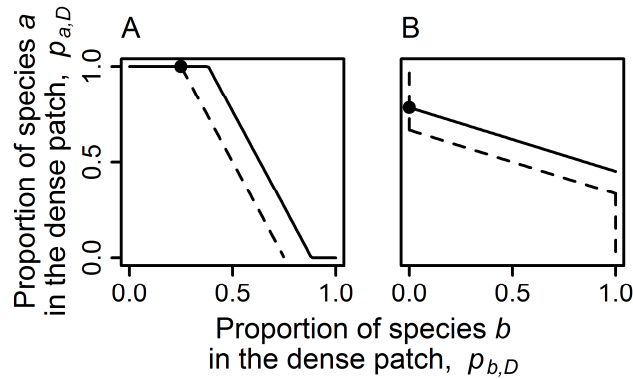
If equation 3.6 is not satisfied, species  $i$  will forage exclusively in the patch offering the highest foraging efficiency. Equations 3.1-3.6 specify a unique, optimal distribution of forager species  $a$  for any possible distribution of species  $b$ ,

$$\hat{P}_{a,D} = \frac{E_{a,S} f_D T_{a,D} (n_a T_{b,S} + n_b T_{a,S})}{n_a T_{b,S} (E_{a,S} f_D T_{a,D} + E_{a,D} f_S T_{a,S})} - \frac{n_b T_{a,D} T_{a,S} (E_{a,S} f_D T_{b,D} + E_{a,D} f_S T_{b,S})}{n_a T_{b,D} T_{b,S} (E_{a,S} f_D T_{a,D} + E_{a,D} f_S T_{a,S})} P_{b,D}, \quad (3.7)$$

and *vice versa*,

$$\hat{p}_{b,D} = \frac{E_{b,S}f_D T_{b,D}(n_a T_{b,S} + n_b T_{a,S})}{n_b T_{a,S}(E_{b,S}f_D T_{b,D} + E_{b,D}f_S T_{b,S})} - \frac{n_a T_{b,D} T_{b,S}(E_{b,S}f_D T_{a,D} + E_{b,D}f_S T_{a,S})}{n_b T_{a,D} T_{a,S}(E_{b,S}f_D T_{b,D} + E_{b,D}f_S T_{b,S})} p_{a,D} \quad (3.8)$$

(Online Appendix E.1). Equations 3.7 and 3.8 represent the “best response curves” for species *a* and *b*, respectively (Grand and Dill 1999). Points on the best response curve for species *i* represent distributions of the two species for which members of species *i* obtain equal foraging success in both patches. Of course, only values of  $\hat{p}_{i,D}$  between 0 and 1 are possible. Therefore, if  $\hat{p}_{i,D} < 0$ , then species *i* will be confined to the sparse patch, and if  $\hat{p}_{i,D} > 1$ , then species *i* will forage only in the dense patch (Figure 3.1).



**Figure 3.1: 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.

Equilibrium distributions can be determined graphically from these best response curves (Grand and Dill 1999). Suppose both best response curves are plotted against  $p_{a,D}$  and  $p_{b,D}$ , as in Figure 3.1. 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:

$$\frac{E_{a,D}}{E_{a,S}} = \frac{E_{b,D}}{E_{b,S}} \text{ (Online Appendix E.2).} \quad (3.9)$$

However, if the ratio of energy expended per flower in the dense vs. the sparse patch is less for species *a* than it is for species *b*,

$$\frac{E_{a,D}}{E_{a,S}} < \frac{E_{b,D}}{E_{b,S}}, \quad (3.10)$$

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* (Online Appendix E.2, Figure 3.1). 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 3.1A), 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 3.1B). Therefore, a species will tend to dominate dense patches if it obtains a greater advantage from choosing dense rather than sparse patches, in terms of energy required per flower visit, than do the species with which it competes. 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 (Parker and Sutherland 1986, Milinski and Parker 1991).

Inequality 3.11 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

$$k_a h_a s_a < k_b h_b s_b \text{ (Online Appendix E.2, Figure 3.2A).} \quad (3.11)$$

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. Therefore, increasing floral density will have the strongest influence on energy expenditures of flower visitors that have high metabolic rates during flight compared to their metabolic rates while handling flowers ( $k_i$ ) and flower visitors that spend a high proportion of their foraging time traveling between flowers, either because of short flower handling times ( $h_i$ ) or low search speeds ( $s_i$ ).

## **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 3.1-3.5). The mathematics is too complex in this case for an analytical solution to be informative (Online Appendix E.3). 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.

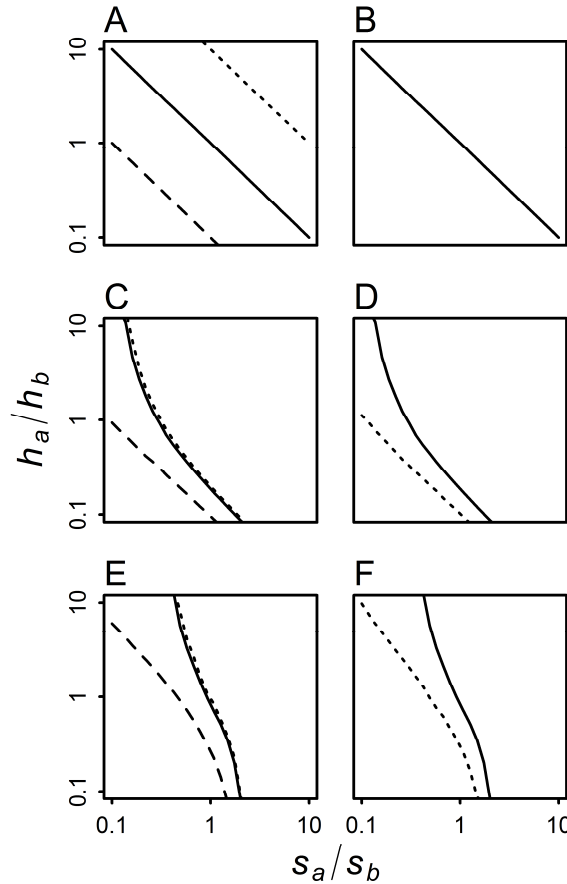
## Methods

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 Online Appendix E.3. 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 3.2; C. J. Essenberg, unpublished manuscripts). 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 3.2, Online Appendix E.4). 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, especially when forager : flower ratios are high (Figure 3.2C-F, Online Appendix E.4: Figure E.1). The differing importance of handling time *versus* search speed is a result of their opposite effects on energy and time costs per flower. Flowers in dense patches should, at equilibrium, experience more frequent visits and therefore offer lower rewards per visit than flowers in sparse patches. This difference in rewards per flower 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 3.2C-D, Online Appendix E.4: Figure E.2). This is because, for foragers whose metabolic rate is higher when traveling between flowers than when handling them ( $k_i < 1$ ), energy expended per flower visited decreases faster with increases in floral density than does time expended.



**Figure 3.2: 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 3.2). Predictions for other forager : flower

ratios are given in Online Appendix E.4.

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,  $c_i$ , or a low energetic cost of handling flowers compared to the cost of flight,  $k_i$ , makes a species more likely to exploit dense flower patches (Figure 3.2C-F, Online Appendix E.4). However, the influence of both traits is weak in comparison to the strong influence of  $k_i$  when both species maximize efficiency (Figure 3.2A). 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  $k_i < 1$ ).

## Comparison to empirical results

I compared model predictions to changes in the species composition of flower visitors to the yellowflower tarweed recorded in a previous study. Although these field data were collected for another purpose and are not ideal for testing my model, they can nonetheless provide insight into the degree to which the model's predictions correspond with the behavior of real pollinator communities. The visitation observations are described elsewhere (C. J. Essenberg, unpublished manuscript), so I present only the most salient points here.

## Methods

I recorded per-flower visitation to the yellowflower tarweed in five 2 x 2m 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 used an individual-based simulation to extend my model’s predictions to a situation with three pollinator taxa: long-horned bees, large sweat bees, and honeybees. 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 3.1-3.5). I assumed that total visitation by species other than the three focal taxa was independent of floral density,

**Table 3.2: Parameter values for simulation of bees visiting yellowflower tarweed (*Holocarpa virgata*)**

A.

Parameter	Value(s)
Patch floral densities	5, 20, 45, 95, and 205 flowers/m <sup>2</sup> *
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 consumption rate while handling flowers : energy consumption rate while traveling ( $k_i$ )	0.1 <sup>†</sup>

\*Measured in the bee-yellowflower tarweed system as described in Online Appendix E.5.

<sup>†</sup>Based on a bumblebee at 30° C (Heinrich 1975b).

**Table 3.2 cont'd****B.**

<b>Pollinator taxon</b>	<b>Number of foragers</b> ( $n_i$ ) <sup>*</sup>	<b>Flower handling time</b> ( $h_i$ ), in s <sup>*</sup>	<b>Search speed (<math>s_i</math>),</b> <b>in m/s<sup>*</sup></b>	<b>Flight metabolic rate</b> ( $c_i$ ), in J/s <sup>§</sup>
Sweat bees ( <i>Halictus ligatus</i> and <i>Lasioglossum titusi</i> )	560	4.9 (297) <sup>‡</sup>	0.12 (30) <sup>‡</sup>	0.01
Long-horned bee ( <i>Melissodes lupina</i> )	330	2.1 (200)	0.21 (8)	0.02
Honeybee ( <i>Apis mellifera</i> )	130	3.7 (93)	0.09 (23)	0.04

<sup>\*</sup>Measured in the bee-yellowflower tarweed system as described in Online Appendix E.5.

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

<sup>§</sup>Estimated from body size as described in Online Appendix E.5 (Cane 1987, Niven and Scharlemann 2005).

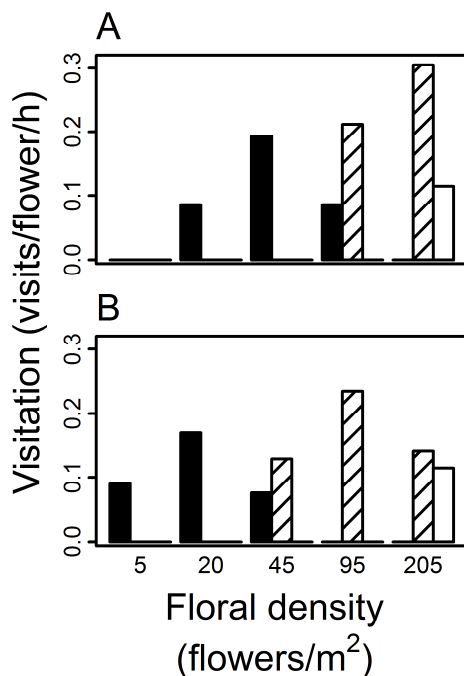
which is what I observed in my field study. I repeated this procedure, each time randomizing the order of foragers, until no forager could improve its foraging success. I carried out this simulation in R (R Development Core Team 2010).

With the exception of forager energy consumption rates, parameter values came from measurements made in the bee-tarweed system (Table 3.2, Online Appendix E.5). 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* (Online Appendix E.5). 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,  $c_i$ , from body sizes (Online Appendix E.5) and set  $k_i$ , the ratio of energy consumption rate while handling flowers to energy consumption 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

Species composition of flower visitors was predicted to differ across patches of differing floral densities, with sweat bees confined to low-density patches, long-horned bees found in intermediate-to-high-density patches, and honeybees confined to high-density patches (Figure 3.3). Observed visitation rates were only partially consistent with these predictions. As expected, per-flower visitation by honeybees peaked at high floral densities ( $F_{2,3,56.7} = 12.6$ ,  $p < 0.001$ ; Figure 3.4). 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 3.4). Finally, per-flower visitation by sweat bees did not respond significantly to floral density ( $F_{1,113} = 0.6$ ,  $p = 0.4$ ). Overlap between the distributions of the three taxa was greater than expected: although the model predicted a truncated distribution in which at most two species overlapped in the same patch (Figure 3.3), all three species often overlapped across a broad range of floral densities (Online Appendix E.6).

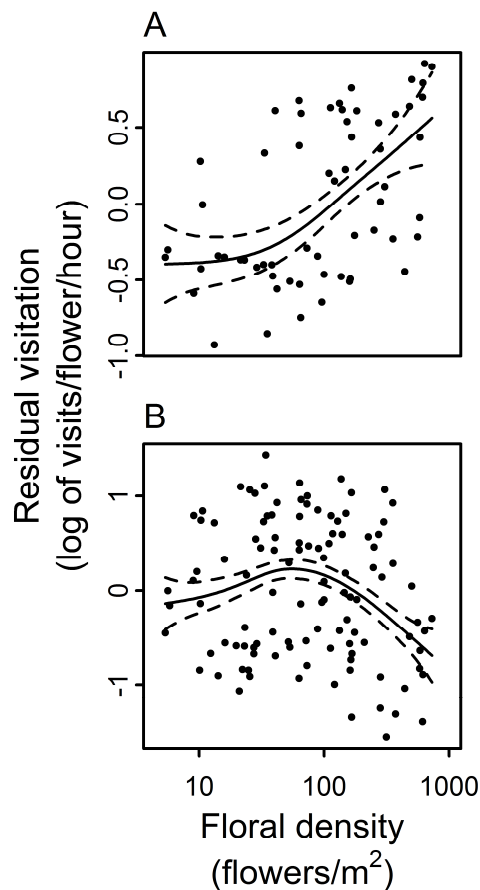


**Figure 3.3: Predicted effects of floral density on species composition of flower visitors to the yellowflower tarweed if (A) all species maximize energetic efficiency or (B) honeybees maximize efficiency and the other taxa maximize NREI**  
 Black = large sweat bees, striped = long-horned bees, white = honeybees. Parameter values are listed in Table 3.2.

## Discussion

Flowers in dense patches are often visited by different 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 demonstrates that variation in flower visitor search speeds, flower handling times, foraging currencies, or energy consumption rates can cause changes in flower visitor species composition with changing floral density (Figure 3.2). Observations of bees

visiting the yellowflower tarweed are partly in agreement with these predictions, although discrepancies indicate that some constraints ignored by this model are probably important. The effects of floral density on flower visitor species composition explored by this model have important implications for the relation of plant fitness to plant density.



**Figure 3.4: 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.

## **Explanations for density effects on flower visitor species composition**

### *Search speed*

My model predicts that forager 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 (Figure 3.2). Specifically, having a slow search speed makes a species more likely to favor dense flower patches. Data on pollinator search speeds are limited, but variation in this trait (e.g., Table 3.2) is probably attributable to differences in both flight and sensory capabilities. Maximum speeds in a wide range of taxa, including flies, bees, lepidopterans, and birds increase with body size (Lighthill 1978, Calder 1984, Full 1997). However, a pollinator foraging in a flower patch will need to change direction and velocity frequently, and its speed may therefore be limited by its agility, which is predicted to decrease with increasing body size (Dudley 2002). Large wings are predicted to reduce both agility and optimal flight speed in animals of a given body mass and therefore should reduce flower visitor search speeds (Lighthill 1978, Dudley 2002). Spaethe et al. (2001) found that flower search time in bumblebees was strongly influenced by floral size and color contrast with the background. Because both of these factors influence the conspicuousness of the flowers, this result suggests that visual abilities could limit search speeds in insect pollinators. In general, larger eyes are capable of higher resolution and sensitivity than smaller eyes (Land and Nilsson 2002), and as a result, large animals should have better visual capacities than small ones. Spaethe and Chittka (2003) demonstrate that visual abilities do, indeed, increase with

increasing body size in worker bumblebees. Different eye designs can also lead to differences in visual capabilities amongst animals of similar sizes. For instance, the superposition eyes of many moths and skippers can be orders of magnitude more sensitive for their size and resolution than the typical apposition eyes of most diurnal insects, giving moths and skippers better eyesight in low light conditions than taxa 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*

Flower handling time can also strongly influence which species exploit dense *versus* sparse flower patches, particularly when flower visitors maximize energetic efficiency (Figure 3.2). Species with relatively short flower handling times should be found primarily in dense flower patches whereas species with long handling times should be more abundant in sparse patches. 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 some species maximize efficiency and others maximize NREI, the species maximizing efficiency should usually dominate in dense flower patches, whereas those maximizing NREI should be more abundant in sparse patches (Figure 3.2C 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). Rasheed and Harder (1997) show that bumblebees foraging for pollen behave as though maximizing the amount of pollen collected per unit of energy expended, which is analogous to energetic efficiency. Data collected thus far on nectar-foraging behavior in bumblebees appear equally consistent with maximization of either NREI or energetic efficiency (Charlton and Houston 2010).

In hummingbirds, behavior consistent with both currencies has been found in different individuals (Tamm 1989).

One hypothesis to explain why some animals appear to maximize energetic efficiency rather than NREI is that a forager's lifetime foraging performance is limited by the amount of energy it can expend over its lifespan rather than by the total time available for foraging. Oxidative metabolism produces reactive oxygen species that damage cellular structures and are associated with ageing (Tolkamp et al. 2002). Behaviors associated with energy consumption during foraging, such as flight, could also contribute to senescence, causing foragers to behave as though maximizing efficiency (Schmid-Hempel et al. 1985). For instance, in bees, wing wear increases mortality and can reduce foraging performance (Cartar 1992, Dukas and Dukas 2011). Another hypothesis to explain maximization of energetic efficiency rather than NREI is that foragers are 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).

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 consumption 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 (Wcislo 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 bees from colonies with abundant nectar reserves.

### *Energy consumption rates*

If flower visitors maximize NREI, 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 consumption rates while handling flowers in relation to their metabolic rates while traveling (that is, high values of  $k_i$ ) will be more likely to dominate sparse flower patches whereas species with low values of  $k_i$  will be more likely to dominate dense patches, especially if both species maximize efficiency. Values of  $k_i$  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  $k_i \geq 1$  in species that hover at flowers. For species that land on flowers,  $k_i$  will usually be much less than 1 (Heinrich 1975b, 1979a). Amongst the latter species, values of  $k_i$  will depend on air temperatures and thermoregulatory efficiency. Flight is possible only if flight muscles are sufficiently warm. Therefore, when air temperatures are low, many flower visitors, including insects such as bees, may expend substantial energy maintaining high muscle temperatures between flights (Heinrich 1975b, 1979a). Adaptations for efficient thermoregulation, such as dark coloration and insulating structures, should therefore reduce the value of  $k_i$  during cool weather.

### **Are the model's predictions realistic?**

Observed shifts in the species composition of bee visitors to the yellowflower tarweed are only partly consistent with the model's predictions. The model correctly predicted that visitation by honeybees would be highest in the densest flower patches and that long-horned bees would, 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 sharp peak at low floral densities as predicted, long-horned bees appeared to use low-density patches more than expected, and overlap in the distributions of the three species was much greater than predicted. These discrepancies suggest that constraints ignored by the model may have significant effects on pollinator distributions across floral density gradients. In particular, the assumption that foragers are omniscient regarding patch qualities is a great oversimplification. Individual foragers will in fact

have only incomplete information about qualities of alternative floral patches and therefore may often choose to forage in sub-optimal patches. These sub-optimal choices should have the effect of broadening each species' distribution across a floral density gradient. Previous models in other systems also suggest that perceptual constraints can shift distributions towards patches with low resource input rates (i.e., low floral densities in a pollinator-flower system) (Gray and Kennedy 1994, Spencer et al. 1996). In addition, differing availability of information across forager taxa could affect their distributions: 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. Social flower visitors may have access to better information about resources than solitary taxa. For instance, honeybee foragers can assess the rate of nectar influx into their colony and thereby obtain information about the current availability of resources in the habitat (Seeley 1995), which might improve the accuracy of their patch assessments compared to those of solitary taxa such as the long-horned bees studied here. Honeybees and some other social taxa, such as many stingless bees, also recruit nestmates to rewarding patches (Dyer 2002, Nieh 2004), making high-density patches, which can be shared with many nestmates, especially profitable to them. Finally, 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, without data on responses to temperature in *H. virgata*'s visitors, the effects of changing temperatures on their distributions are difficult to predict.

### **Implications for plant fitness**

Flower visitor species can vary greatly in their quality as pollinators. For instance, fivefold or greater variation in the amount of conspecific pollen deposited per visit (i.e., pollen deposition effectiveness in Ne'eman et al. 2010) across a plant's flower visitor fauna is not uncommon, even when only bee species are considered (e.g., Wilson and Thomson 1991, Cane and Schiffhauer 2003, Ivey et al. 2003, Larsson 2005, Adler and Irwin 2006, Rader et al. 2012). Effects of pollinator visits on seed and fruit production likewise can vary considerably across pollinator taxa (e.g., Olsen 1997, Kandori 2002, Klein et al. 2003). Furthermore, when better pollinators are available, visits by low-quality pollinators can actually reduce pollination success of flowers by stripping them of nectar and pollen, thereby reducing their attractiveness and leaving little pollen to be transferred by subsequent visitors (Wilson and Thomson 1991).

The effects of floral density on flower visitor composition explored by my model therefore could influence the relationship between density and plant reproductive success. Pollination success often declines at low densities (Kunin 1997a, Ghazoul 2005) and resulting decreases in fitness can heighten vulnerability to local extinction, truncate species' ranges, hinder invasion of new habitats, and favor the evolution of compensatory adaptations such as self-pollination (e.g., Orians 1997, Stephens and Sutherland 1999, Courchamp et al. 2008, Eckert et al. 2010). Declines in seed production with reductions

in conspecific density can be caused by a variety of mechanisms, including reduced pollinator visitation rates, increased rates of interspecific pollen transfer, and increased levels of inbreeding (e.g., Kunin 1993, Karron et al. 1995, Morales and Traveset 2008). The changes in flower visitor species composition investigated by my model could exacerbate, reduce, or even reverse the declines in fitness produced by these processes, depending on the relative effectiveness of the species exploiting dense *versus* sparse patches.

## **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.

## General conclusion

Prior to the studies described here, it was clear that floral density can influence flower visitation rates and the species composition of flower visitors, but there was little theory to explain why it should have the observed effects. Different studies had found markedly different effects of plant or floral density on per-flower or per-plant visitation rates. Rathcke (1983) suggested one potential explanation for this variation. She hypothesized that at low densities, floral density has a positive effect on per-flower visitation rates because it increases the attractiveness of flower patches, but that at high densities, the available pool of pollinators becomes saturated and increasing floral density has a negative effect on visitation rates. However, little had been done since to explore this idea or to develop additional hypotheses to explain variation in effects of floral density on visitation rates. Similarly, studies from a wide variety of systems had reported changes in the species composition of flower visitors with increasing floral density, but only a few theoretical studies had attempted to explain those effects. Those few models were applicable to only a fraction of the systems in which density-related changes in flower visitor species composition had been observed. In particular, effects of patch-scale floral density on the species composition of non-territorial flower visitor species remained unexplained.

The studies described in the preceding chapters represent a substantial step towards understanding how flower visitors respond to floral densities. In the first chapter, I used a foraging model to generate predictions about when per-flower visitation should be expected to increase or decrease with increasing floral density. My model predicts a

nonlinear relation of per-flower visitation to floral density that is similar to the relationship hypothesized by Rathcke (1983) except that visitation is usually predicted to level off rather than decline at high floral densities. My model also identifies a variety of plant and pollinator traits that could influence the relation of visitation rate to floral density, particularly traits that influence flower visitors' flower handling times and speed in searching for flowers.

A key simplifying assumption of the model presented in the first chapter was that all flower visitors were identical. In fact, flowers of most plants are visited by multiple animal species, which can have widely differing traits. In the third chapter, I explored how variation in flower visitor traits could give rise to differences in visitor species composition between patches of differing floral densities. I showed that variation in flower search speeds, flower handling times, foraging currencies, or energy consumption rates can cause density-related shifts in flower visitor species composition, with species that obtain greater advantages from foraging in dense patches, for instance because of slow search speeds, being most abundant in those patches, while other species are more abundant in sparse patches.

Models can produce plausible hypotheses that serve as valuable guides to research but, of course, they cannot tell us what the world is actually like. Therefore, I accompanied my theoretical work with field studies. In both the first and third chapters, I presented field data relevant to evaluating model predictions. In both cases, the data provided partial support for the models while suggesting that further variables or constraints on behavior may be important and should be explored in the future. In the

second chapter, I presented a study designed to explore an additional hypothesis to explain variation in flower visitor responses to floral density: i.e., that those responses are scale-dependent. I show that effects of floral density on flower visitor species composition at widely different scales (4 m<sup>2</sup> and 12.6 ha) can differ from each other and furthermore, that floral densities at the larger scale can influence flower visitor responses to floral densities at the smaller scale.

Altogether, the studies described here constitute an important step towards understanding the effects of floral density on flower visitation rates and flower visitor species composition. Those effects, in turn, play an important role in determining how plant density influences plant fitness and therefore have implications for a variety of biological processes, including plant population dynamics, invasion of new habitats, and floral evolution.

## Appendix A: Chapter 1 models and methods

### Appendix A.1: Model assuming that flight and handling flowers are equally costly

Most of the early steps in this model are presented in the main text. Equations 1.3, 1.4, and 1.5 imply:

$$\frac{f_f}{p_f} - \frac{c(hk + t_f)}{n(h + t_f)} = \frac{f_b}{p_b} - \frac{c(hk + t_b)}{n(h + t_b)}. \quad (\text{A.1})$$

When  $k = 1$ , this simplifies to

$$\frac{f_f}{p_f} = \frac{f_b}{p_b}, \quad (\text{A.2})$$

which is equation 1.6.

As I show in the main text (equation 1.9), when  $k = 1$ , the per-flower visitation rate is

$$v_f = \frac{P}{(A_f f_f + A_b f_b) \left( h + \frac{1}{s \sqrt{f_f}} \right)}. \quad (\text{A.3})$$

The derivative of equation A.3 with respect to floral density is:

$$\frac{\partial v_f}{\partial f_f} = \frac{P \left( \frac{f_b A_b}{2s} - f_f A_f \left( h \sqrt{f_f} + \frac{1}{2s} \right) \right)}{\sqrt{f_f} (f_f A_f + f_b A_b)^2 \left( h \sqrt{f_f} + \frac{1}{s} \right)^2}. \quad (\text{A.4})$$

As the focal patch density,  $f_f$ , approaches zero, the numerator of equation A.4 approaches

$$\frac{P f_b A_b}{2 s},$$

and the denominator approaches zero. Because all the variables are positive, the formula as a whole approaches positive infinity. Therefore, the relation of pollinator visitation to floral density is strongly positive at low densities.

As the focal patch density increases, the value of the denominator increases and the value of the numerator decreases. Therefore, the positive effect of floral density on pollinator visitation becomes weaker as floral density increases. The effect becomes negative when the numerator of equation A.4 becomes negative, which occurs when

$$\frac{f_b A_b}{2 s} < f_f A_f \left( h \sqrt{f_f} + \frac{1}{2 s} \right), \quad (\text{A.5})$$

which simplifies to

$$\frac{1}{1 + 2 h s \sqrt{f_f}} < \frac{f_f A_f}{f_b A_b}. \quad (\text{A.6})$$

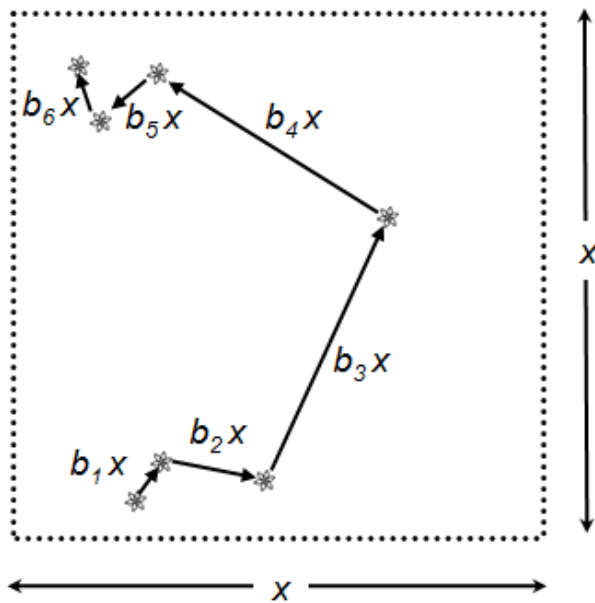
## Appendix A.2: Derivation of the equation for travel time per flower

If items are uniformly distributed in space, the distance between nearest neighbors is  $\frac{1}{\sqrt{\text{density}}}$ . Pielou (1977) shows that, when items are randomly distributed in space, the

average distance between nearest neighbors is  $\frac{1}{2\sqrt{\text{density}}}$ . Here I discuss an example

that suggests that if pollinators travel directly between neighboring flowers and floral

dispersion is not a function of density (i.e., flowers are not more or less clumped when dense than when sparse), the average between-flower travel distance should always be proportional to  $\frac{1}{\sqrt{\text{density}}}$ .



**Figure A.1: A hypothetical pollinator itinerary in a flower patch**  
The arrows represent pollinator flights between flowers and the symbols indicate distances.

Suppose that a pollinator travels between neighboring flowers in a patch as shown in Figure A.1. The boundaries of the patch have length  $x$ , and the density of flowers in the patch,  $f$ , is therefore

$$f = \frac{n}{x^2}, \tag{A.7}$$

where  $n$  is the number of flowers in the patch. If we express the distances that the pollinator travels between flowers as proportions of  $x$ :  $b_1x, b_2x, b_3x, \dots, b_Nx$ , where  $N$  is the number of flights the pollinator makes, the average flight distance,  $D$ , is

$$D = \frac{\sum_{i=1}^N b_i x}{N} = \frac{x}{N} \sum_{i=1}^N b_i \quad (\text{A.8})$$

Equations A.7 and A.8 imply:

$$D = \frac{1}{C\sqrt{f}}, \text{ where } C = \frac{1}{\frac{\sqrt{n}}{N} \sum_{i=1}^N b_i}. \quad (\text{A.9})$$

$C$  is influenced only by floral dispersion and therefore can be treated as a constant, provided that dispersion is independent of density.

If pollinators travel at a constant velocity,  $v$ , then the between-flower flight time,  $t$ , is:

$$t = \frac{D}{v} = \frac{1}{vC\sqrt{f}}. \quad (\text{A.10})$$

Combining the two constants,  $v$  and  $C$ , into a single variable,  $s$ , produces the equation shown in the text:

$$t = \frac{1}{s\sqrt{f}}. \quad (\text{A.11})$$

### Appendix A.3: Model assuming that pollinators use scent marks to reject flowers that have recently been visited

Suppose that whenever a pollinator harvests nectar from a flower, it leaves a scent mark that persists for a certain length of time,  $T$ , and then disappears. While the scent mark is present, any pollinator that flies to the flower detects the mark when it arrives and departs without visiting the flower. The rate of change in the proportion of flowers that are marked is  $\nu - \frac{M}{T}$ , where  $\nu$  is the per-flower visitation rate,  $M$  is the proportion of flowers that are marked, and individual marked flowers lose their marks at a rate of  $\frac{1}{T}$ .

At equilibrium, the proportion of flowers that are marked is constant. Therefore,

$$\nu = \frac{M}{T} \text{ and } M = \nu T. \quad (\text{A.12})$$

The average number of flowers that a pollinator must travel to in order to find one that is not marked is  $\frac{1}{1-M}$ . Therefore,

$$\text{Average travel time per flower visited} = \frac{t}{1-M}, \quad (\text{A.13})$$

where  $t$  is the time required to travel from one flower to another. Just as in the other versions of the model,

$$t = \frac{1}{s\sqrt{f}} \quad (\text{A.14})$$

where  $f$  is the floral density and  $s$  is the “search speed” (Appendix A.2).

Average reward per flower visit is equal to the nectar secretion rate,  $n$ , multiplied by the average time between visits, which is approximately  $\frac{1}{v}$ , or, employing equation A.12,

$\frac{T}{M}$ . Therefore, average reward received per flower,  $r$ , is:

$$r = \frac{nT}{M}. \quad (\text{A.15})$$

As in the other versions of the model, the total number of pollinators is a constant,  $P$ .

$$P = p_f A_f + p_b A_b \text{ and therefore, } p_b = \frac{P - p_f A_f}{A_b}, \quad (\text{A.16})$$

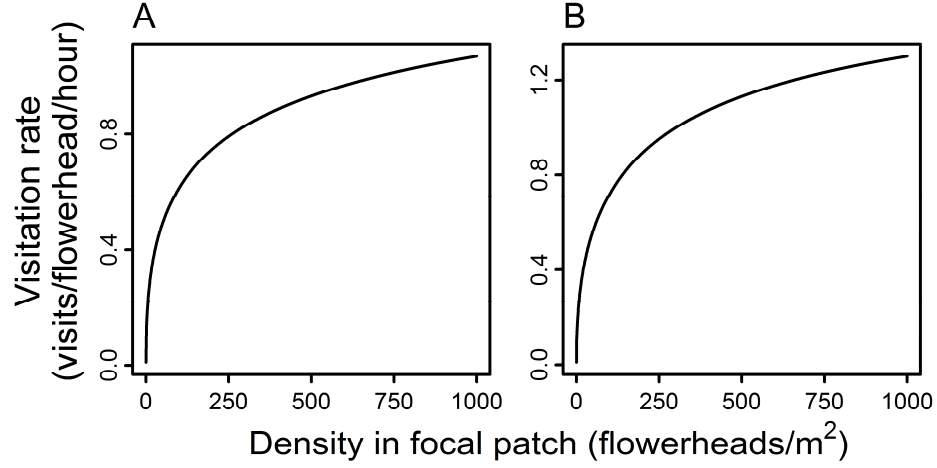
where  $p_f$  and  $p_b$  are pollinator densities in the focal patch and the background area and  $A_f$  and  $A_b$  are the areas of the focal patch and background.

Pollinators distribute themselves so that their net rate of energy gain is equal in the focal patch and the area with which it competes (Equation 1.1). Therefore,

$$\frac{\frac{nT}{M_f} - \left( h k c + \frac{t_f}{1 - M_f} c \right)}{h + \frac{t_f}{1 - M_f}} = \frac{\frac{nT}{M_b} - \left( h k c + \frac{t_b}{1 - M_b} c \right)}{h + \frac{t_b}{1 - M_b}}, \quad (\text{A.17})$$

where  $h$  is the handling time per flower,  $c$  is the energetic cost per unit of travel time,  $k c$  is the energetic cost per unit of flower handling time, and the subscripts  $f$  and  $b$  refer to the focal patch and the area with which it competes, respectively.

Just as in the other versions of the model, the visitation rate in a patch is equal to the ratio of pollinators to flowers in the patch divided by the average time each pollinator spends traveling to and handling each flower it visits. Therefore:



**Figure A.2: Examples of predicted effects of floral density on per-flower visitation rates for models (A) with and (B) without scent marks, assuming that pollinators maximize net rate of energy gain**

The parameter values used to produce these curves were:  $f_b = 10$  flowers/m<sup>2</sup>,  $A_f = 100$  m<sup>2</sup>,  $A_b = 1.3 \times 10^5$  m<sup>2</sup>,  $P = 13$  pollinators,  $h = 0.5$  s,  $s = 0.1$  m/s,  $c/n = 0.1$ ,  $k = 0.1$ ,  $T = 20$  min.

$$v = \frac{p}{f \left( h + \frac{t}{1-M} \right)}, \quad (\text{A.18})$$

where  $p$  is the density of pollinators. Setting  $v = \frac{M}{T}$  and rearranging the equation, one

obtains:

$$hM^2 - \left( h + t + \frac{TP}{f} \right) M + \frac{TP}{f} = 0 \quad (\text{A.19})$$

Using the quadratic formula, along with equation A.16, I obtain the following formulae for the proportion of marked flowers in the focal patch and in the area with which it competes:

$$M_f = \frac{\left( h + t_f + \frac{T p_f}{f_f} \right) - \sqrt{\left( h + t_f + \frac{T p_f}{f_f} \right)^2 - 4h \frac{T p_f}{f_f}}}{2h} \quad (\text{A.20})$$

$$M_b = \frac{\left( h + t_b + \frac{T(P - p_f A_f)}{f_b A_b} \right) - \sqrt{\left( h + t_b + \frac{T(P - p_f A_f)}{f_b A_b} \right)^2 - 4h \frac{T(P - p_f A_f)}{f_b A_b}}}{2h} \quad (\text{A.21})$$

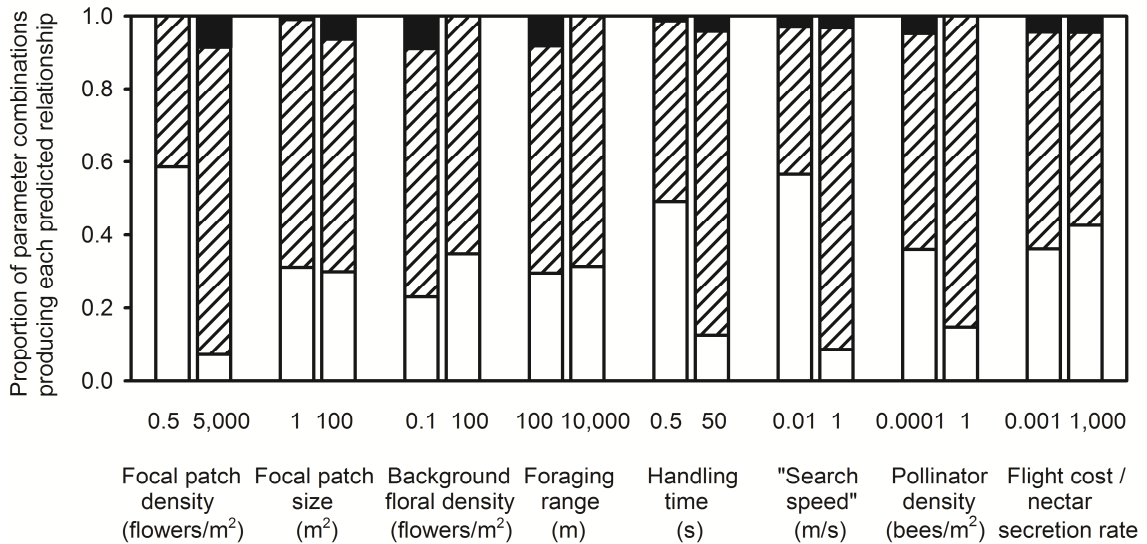
These represent only one of the two roots produced by the quadratic equation; the other root can be ignored because it produces values for  $M$ , the proportion of marked flowers, that are greater than 1 for all combinations of the parameter values in Table 1.2.

I calculated the relation of visitation to density using equations A.17, A.20, A.21, and A.14. The resulting predictions are usually similar to those obtained without including

**Table A.1: Percent of parameter combinations for which effects of floral density are predicted to be strongly positive, weak, or strongly negative for models with and without scent marks, assuming that pollinators maximize net rate of energy gain\***

Effect predicted	Without scent marks	With scent marks		
		$T = 5 \text{ min}$	$T = 20 \text{ min}$	$T = 2 \text{ hours}$
Strongly positive	38	35	31	24
Weak	56	61	66	74
Strongly negative	6	4	3	3

\*Based on implementations of the model for the 5,362 combinations of the parameter values shown in Table 1.2 that produce non-negative net rates of energy gain for both versions of the model, assuming that  $k = 0.1$ . Values are rounded to the nearest percent. Definitions of weak, strongly positive, and strongly negative are the same as in Table 1.3.



**Figure A.3: Effects of parameters on the relation of visitation to density, assuming that pollinators use scent marks and maximize net rate of energy gain**

White = strongly positive; Striped = weak; Black = strongly negative. Definitions of these categories are the same as in Table 1.3. For each parameter value, the proportions shown are based on model results, assuming that  $k = 0.1$  and  $T = 20$  min, for all combinations of the other parameter values in Table 1.2 for which net rate of energy gain is positive for both values of the focal parameter. Numbers of parameter combinations used for each focal parameter are: focal patch density and size, 1,782; background floral density, 1,473; handling time, 1,785; search speed, 1,787; pollinator density, 1,225; flight cost / nectar secretion rate, 1,222.

scent marks in the model, although sometimes, particularly when pollinator densities are high, the model with scent marks predicts weaker relations of visitation to density than does the model without scent marks (Table A.1, Figures A.2 and A.3). The discrepancies between the predictions of models with and without scent marks that are shown in Table A.1 occur only when a high proportion of flowers are scent-marked (i.e., 60-100%), which is probably not realistic. In nature, the duration of scent marks' repellent effects,  $T$ , appears to be inversely related to nectar secretion rates (Stout and Goulson 2002). Long-lasting repellent effects should therefore be seen on flowers that have low nectar

secretion rates, which in turn should receive low visitation rates, limiting the proportion of flowers that will be scent-marked at any given time.

## Appendix A.4: Model assuming that pollinators maximize efficiency

Here I develop a version of the model in which pollinators maximize efficiency, where

$$\text{Efficiency} = \frac{\text{Energy gain per flower} - \text{Energy used per flower}}{\text{Energy used per flower}}. \quad (\text{A.22})$$

(Efficiency is sometimes defined as gross energy gain per unit of energy used, rather than net energy gain per unit of energy used. Both produce identical results in this model.) Pollinators distribute themselves so that

$$\frac{r_f - (hkc + t_f c)}{hkc + t_f c} = \frac{r_b - (hkc + t_b c)}{hkc + t_b c}, \quad (\text{A.23})$$

where the terms are defined as in the main text. Equation A.23 along with equations 1.4 and 1.5 in the main text imply:

$$\frac{f_f (h + t_f)}{p_f (h k + t_f)} = \frac{f_b (h + t_b)}{p_b (h k + t_b)}. \quad (\text{A.24})$$

When  $k = 1$ , this equation simplifies to

$$\frac{f_f}{p_f} = \frac{f_b}{p_b}, \quad (\text{A.25})$$

which is identical to the prediction when pollinators maximize net rate of energy gain and  $k = 1$  (equation 1.6). If  $k \neq 1$ , then equation A.24 along with equations 1.5, 1.7, and 1.8 in the main text imply:

$$v_f = \frac{P \left( hk + \frac{1}{s\sqrt{f_b}} \right)}{f_b A_b \left( h + \frac{1}{s\sqrt{f_b}} \right) \left( hk + \frac{1}{s\sqrt{f_f}} \right) + f_f A_f \left( h + \frac{1}{s\sqrt{f_f}} \right) \left( hk + \frac{1}{s\sqrt{f_b}} \right)}, \quad (\text{A.26})$$

where  $v_f$  is the visitation rate in the focal patch. To make the algebra simpler in what follows, I define the following variables:

$$T_b = h + \frac{1}{s\sqrt{f_b}} \quad \text{and} \quad (\text{A.27})$$

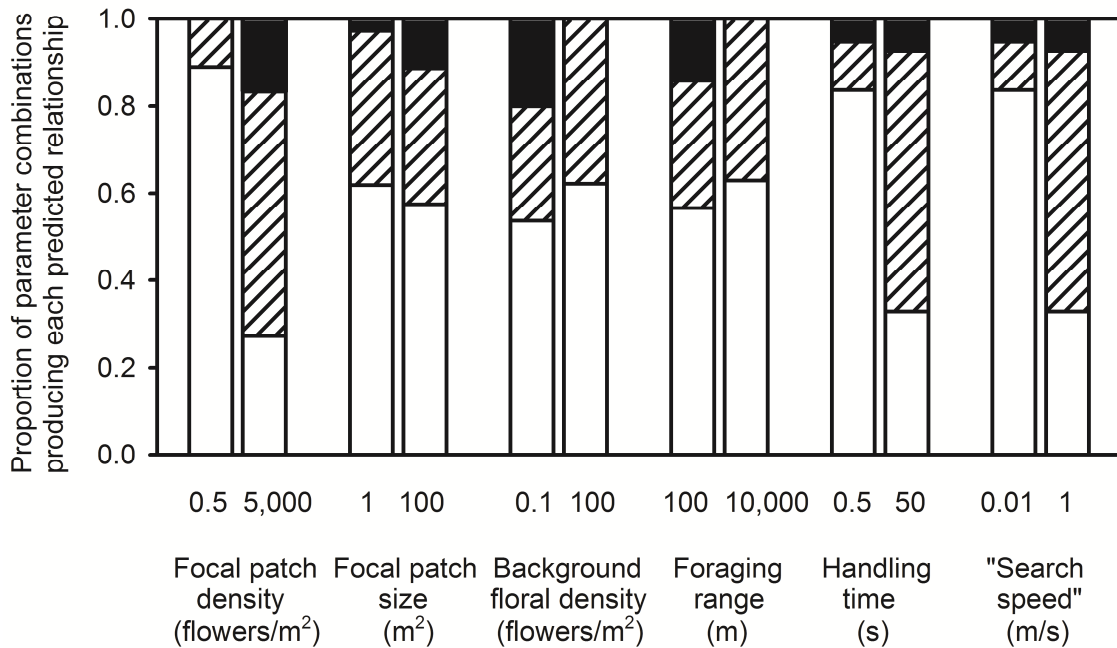
$$E_b = hk + \frac{1}{s\sqrt{f_b}}. \quad (\text{A.28})$$

The derivative of the per-flower visitation rate,  $v_f$ , with respect to focal patch floral density,  $f_f$ , is:

$$\frac{\partial v_f}{\partial f_f} = \frac{(PE_b) \left( \frac{f_b A_b T_b}{2s} - f_f A_f E_b \left( h\sqrt{f_f} + \frac{1}{2s} \right) \right)}{\sqrt{f_f} \left( f_b A_b T_b \left( hk\sqrt{f_f} + \frac{1}{s} \right) + A_f f_f E_b \left( h\sqrt{f_f} + \frac{1}{s} \right) \right)^2}. \quad (\text{A.29})$$

As  $f_f$  approaches zero, the numerator approaches

$$\frac{PE_b f_b A_b T_b}{2s},$$



**Figure A.4: Effects of parameters on the relation of per-flower visitation to floral density, assuming that pollinators maximize efficiency**

White = strongly positive; Striped = weak; Black = strongly negative. Definitions of these categories are the same as in Table 1.3. 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 1.2 for which foraging efficiency is positive for both values of the focal parameter. Numbers of parameter combinations used for each focal parameter are: focal patch density, 1,782; focal patch size, 1,783; background floral density, 1,486; handling time and search speed, 1,789.

and the denominator approaches zero. Because all variables are positive, the formula as a whole approaches positive infinity. Therefore, as before, the relation of pollinator visitation to floral density is strong and positive at low densities.

As the focal patch density,  $f_f$ , increases, on the other hand, the value of the denominator increases and the value of the numerator decreases. Therefore, the positive effect of floral density on pollinator visitation becomes weaker as floral density increases.

The effect becomes negative when the numerator of equation A.29 becomes negative, which occurs when

$$\frac{f_b A_b T_b}{2s} < f_f A_f E_b \left( h\sqrt{f_f} + \frac{1}{2s} \right). \quad (\text{A.30})$$

This inequality can also be expressed as:

$$\left( \frac{h + \frac{1}{s\sqrt{f_b}}}{hk + \frac{1}{s\sqrt{f_b}}} \right) \left( \frac{1}{1 + 2hs\sqrt{f_f}} \right) < \frac{f_f A_f}{f_b A_b} \quad (\text{A.31})$$

which is similar to the corresponding inequality for the case when  $k = 1$  (inequality A.6).

Effects of each variable, given biologically plausible parameter values, are shown in Figure A.4.

## Appendix A.5: Two plant species model

Suppose that the flowers in the focal patch belong to a different species from those outside the focal patch and therefore have different nectar secretion rates ( $n$ ) and flower handling times ( $h$ ) from their competitors. Also suppose that the costs of travel and handling flowers are the same (i.e.,  $k = 1$ ). In this case, equation 1.9 becomes

$$v_f = \frac{n_f P}{\left( n_f A_f f_f + n_b A_b f_b \right) \left( h_f + \frac{1}{s\sqrt{f_f}} \right)}. \quad (\text{A.32})$$

The derivative of equation A.32 with respect to focal patch floral density is:

$$\frac{\partial v_f}{\partial f_f} = \frac{n_f P \left( \frac{n_b f_b A_b}{2s} - n_f f_f A_f \left( h_f \sqrt{f_f} + \frac{1}{2s} \right) \right)}{\sqrt{f_f} (n_f f_f A_f + n_b f_b A_b)^2 \left( h_f \sqrt{f_f} + \frac{1}{s} \right)^2} \quad (\text{A.33})$$

As the focal patch density,  $f_f$ , approaches zero, the numerator of equation A.33 approaches

$$\frac{n_f n_b P f_b A_b}{2s},$$

and the denominator approaches zero. Because all variables are positive, the formula as a whole approaches positive infinity. Therefore, as before, the relation of pollinator visitation to floral density is strong and positive at low densities.

As the focal patch density,  $f_f$ , increases, on the other hand, the value of the denominator increases and the value of the numerator decreases. Therefore, the positive effect of floral density on pollinator visitation becomes weaker as floral density increases. The effect becomes negative when the numerator of equation A.33 becomes negative, which occurs when

$$\frac{n_b f_b A_b}{2s} < n_f f_f A_f \left( h_f \sqrt{f_f} + \frac{1}{2s} \right), \quad (\text{A.34})$$

which simplifies to

$$\frac{1}{1 + 2h_f s \sqrt{f_f}} < \frac{n_f f_f A_f}{n_b f_b A_b} \quad (\text{A.35})$$

This inequality closely resembles that in the one-species model (inequality A.6), except that the ratio on the right side of the inequality includes the nectar production rates of the

two species. A negative effect is more likely if the focal plant species has a high nectar secretion rate compared to its competitors. The other variables have similar effects on the relation as in the one-species model.

## **Appendix A.6: Method for estimating *H. virgata* flower size in experimental plots**

I collected data on the number of open disk florets on each of 685 *H. virgata* flowers (i.e., flower heads) selected randomly from plots spanning a similar range of flower densities to the plots used in the current study (C. J. Essenberg, unpublished manuscript). These data provided the size distribution of flowers.

Suppose a  $1/16\text{th-m}^2$  subplot contained  $N$  flowers prior to thinning and  $n$  flowers after thinning. To estimate the average flower size in the subplot after thinning, I randomly drew  $N$  values from the flower size distribution, then selected the  $n$  largest flowers in the sample and calculated their average size. I repeated this calculation 1,000 times for each subplot and averaged the results. For plots thinned after August 18, we left only flowers that had at least one open disk floret. For these plots, therefore, I threw out and replaced any of the 1,000 random samples that did not contain at least  $n$  flowers with one or more open disk florets.

## Appendix B: Sources of Chapter 1 parameter estimates

**Table B.1: Sources of the parameter estimates listed in Table 1.2**

Parameter	Values observed*	Species and context	Source
Focal patch floral density ( $f_f$ )	37-219 flowers/m <sup>2</sup> 11.5-83.6 flowers/m <sup>2</sup> 2-55 flowers/m <sup>2</sup> 0-4518 flowers/m <sup>2</sup> 0-815 flowers/m <sup>2</sup>	Bindweed ( <i>Convolvulus arvensis</i> ), in a large, dense population Red catchfly ( <i>Viscaria vulgaris</i> ), in a natural population Dandelion ( <i>Taraxacum officinale</i> ), in natural populations Alfalfa ( <i>Medicago sativa</i> ), planted for hay Yellowflower tarweed ( <i>Holocarpha virgata</i> ), in natural populations	Waddington 1976 (Table I): Densities in 1-m <sup>2</sup> plots Dreisig 1995 (p. 162): Densities in 12-m <sup>2</sup> plots Lázaro and Totland 2010 (p. 761): Densities in 0.49-m <sup>2</sup> plots Pitts-Singer and Bosch 2010 (Table 1): Densities in 37.21-m <sup>2</sup> enclosures This study: Densities in 1-m <sup>2</sup> transect segments

\*Some values were obtained by examination of figures and are therefore only approximate.

**Table B.1 cont'd**

<b>Parameter</b>	<b>Values observed*</b>	<b>Species and context</b>	<b>Source</b>
Background floral density ( $f_b$ )	0.06-0.8 flowers or inflorescences/m <sup>2</sup>	All species that were visited by bumblebees ( <i>Bombus</i> spp.), in logged and unlogged boreal forest	Cartar 2005 and R. Cartar, <i>personal communication</i> : Average densities recorded for each logging treatment and part of the season; each density estimate comes from transects distributed across 6-20 8-10-ha sections of forest
	7-37 flowers or inflorescences/m <sup>2</sup>	All species that were visited by bumblebees ( <i>Bombus</i> spp.), in montane meadows	Elliott 2009 (Figure 2A): Average densities recorded for subplots distributed across each of 6 widely-spaced 0.5-ha plots
	29.6 to 85.6 inflorescences/m <sup>2</sup>	Canola ( <i>Brassica</i> oilseed), in agricultural plantings	Arthur et al. 2010 (Table 1): Average densities from plots distributed across each of 6 20-86-ha fields

**Table B.1 cont'd**

<b>Parameter</b>	<b>Values observed*</b>	<b>Species and context</b>	<b>Source</b>
	0.10 to 35 flowers/m <sup>2</sup>	Summer-flowering species (primarily yellowflower tarweed ( <i>H. virgata</i> )) visited by sweat bees and other insects in habitats containing a mixture of grassland, chaparral, and oak woodland	C. J. Essenberg, unpublished manuscript: Total flower densities, with flowers of different species weighted according to amount of nectar produced so as to be equivalent to <i>H. virgata</i> flowers, for three different time periods at each of 8 different sites; each estimate is obtained by multiplying area occupied by flowering species within a 12.5-ha area by the average densities recorded in plots randomly distributed across those patches
Pollinator density	1.0 bee/m <sup>2</sup>	Sweat bees ( <i>Agapostemon texanus</i> , <i>Augochlorella striata</i> , and <i>Dialictus</i> sp.) in a large patch of bindweed ( <i>Convolvulus arvensis</i> )	Waddington 1976 (Table 1): Average density observed across all plots in a single site

**Table B.1 cont'd**

<b>Parameter</b>	<b>Values observed*</b>	<b>Species and context</b>	<b>Source</b>
	0.00030-0.0016 bees/m <sup>2</sup>	Bumblebees ( <i>Bombus</i> spp.) in a boreal forest, including logged and unlogged sections	Cartar 2005 and R. Cartar, <i>personal communication</i> : Average densities recorded for each part of the season; each density estimate comes from transects distributed across 50 8-10-ha sections of forest
	0.067 and 0.16 bees/m <sup>2</sup>	Various native bees and honeybees ( <i>Apis mellifera</i> ) in canola ( <i>Brassica</i> oilseed) fields	Arthur et al. 2010 (Table 2): Average densities, observed in transects distributed across all fields, for the two different bee categories
	0.0004-0.05 bees/m <sup>2</sup>	Small sweat bees ( <i>Halictus tripartitus</i> , <i>Dialictus</i> sp.), large sweat bees ( <i>L. titusi</i> , <i>H. ligatus</i> ), long-horned bees ( <i>Melissodes lupina</i> ), and honeybees ( <i>A. mellifera</i> ) sampled across multiple weeks in a large patch of the yellowflower tarweed ( <i>H. virgata</i> )	This study: Average densities in transects, for each group in each of the four weeks

**Table B.1 cont'd**

<b>Parameter</b>	<b>Values observed*</b>	<b>Species and context</b>	<b>Source</b>
Foraging range	20-24000 m	Wide range of bee species in a wide range of locations	Greenleaf et al. 2007 (Tables S1-S3): Estimates drawn from a large number of studies, using a variety of methods
Handling time ( <i>h</i> )	5.7-31.7 s	Various bees ( <i>Hoplitis anthocopoides</i> , <i>Hoplitis producta</i> , <i>Megachile relativa</i> , <i>Osmia caerulescens</i> , <i>Ceratina calcarata</i> ) visiting common viper's bugloss ( <i>Echium vulgare</i> )	Strickler 1979 (Table 5): Averages for the different bee species
	1.3-3.8 s	Bumblebees ( <i>B. flavifrons</i> , <i>B. kirbyellis</i> , and <i>B. sylvicola</i> ) visiting various meadow wildflower species ( <i>Aconitum columbianum</i> , <i>Mertensia ciliata</i> , <i>Pedicularis groenlandica</i> , <i>Delphinium barbeyi</i> , and <i>Oxytropis splendens</i> )	Laverty 1980 (Table 2): Averages for the different species combinations

**Table B.1 cont'd**

<b>Parameter</b>	<b>Values observed*</b>	<b>Species and context</b>	<b>Source</b>
	0.5-3 s	Bumblebees ( <i>B. flavifrons</i> ) visiting various wildflower species ( <i>Chrysopsis villosa</i> , <i>Senecio bigelovii</i> , <i>Helianthella quinquenervis</i> , <i>Cirsium</i> sp., <i>Mertensia ciliata</i> , <i>Vicia americana</i> , and <i>Delphinium barbeyi</i> )	Inouye 1980 (Figure 1): Averages for different plant species
	1-3 s	Bumblebees ( <i>B. flavifrons</i> , <i>B. kirbyellus</i> , <i>B. californicus</i> , <i>B. appositus</i> ) visiting subalpine larkspur ( <i>Delphinium barbeyi</i> )	Inouye 1980 (Figure 2): Averages for different bee species
	1.8-7.0 s	Small sweat bees ( <i>H. tripartitus</i> , <i>Dialictus</i> sp.), large sweat bees ( <i>L. titusi</i> , <i>H. ligatus</i> ), and long-horned bees ( <i>M. lupina</i> ) visiting the yellowflower tarweed ( <i>H. virgata</i> )	This study: Average handling times recorded for 23-143 individuals per taxonomic group; the estimate for each individual bee is based on a minimum of 4 flower visits

**Table B.1 cont'd**

<b>Parameter</b>	<b>Values observed*</b>	<b>Species and context</b>	<b>Source</b>
“Search speed” ( <i>s</i> )	0.0065-0.15 m/s	Bumblebees ( <i>B. terrestris</i> ) visiting artificial flowers spaced 30 cm apart	Spaethe et al. 2001 (Table 2): Distance between flowers divided by average time required to travel between them (including time spent searching) for different flower sizes and colors
	0.5 m/s	Bumblebees ( <i>B. terrestris</i> ) repeatedly visiting two artificial flowers, spaced 60 cm apart	J. Spaethe, <i>personal communication</i> : Distance between flowers divided by average time required to travel directly between them (indirect flights were not counted)
	0.09-0.2 m/s	Small sweat bees ( <i>H. tripartitus</i> , <i>Dialictus</i> sp.), large sweat bees ( <i>L. titusi</i> , <i>H. ligatus</i> ), long-horned bees ( <i>M. lupina</i> ), and honeybees ( <i>A. mellifera</i> ) visiting a large, dense patch of the yellowflower tarweed ( <i>H. virgata</i> )	C. J. Essenberg, <i>unpublished data</i> : Calculated from recorded flight times and estimated distances between flowers; estimates are average search speeds for 6-25 individuals per taxonomic group; the estimate for each individual bee is based on a minimum of 4 flights

**Table B.1 cont'd**

<b>Parameter</b>	<b>Values observed*</b>	<b>Species and context</b>	<b>Source</b>
	0.53-0.72 m/s	Large sweat bees ( <i>L. titusi</i> , <i>H. ligatus</i> ) and long-horned bees ( <i>M. lupina</i> ) in patches of yellowflower tarweed ( <i>H. virgata</i> )	This study: Inverse of the slope of the regression line for the relation of between-flower flight time to (flower density) <sup>-1/2</sup> for each taxonomic group
Flight cost (c) <sup>†</sup>	2-300 J/hr	Various bees ( <i>Apis florea</i> , <i>A. dorsata</i> , <i>A. mellifera</i> , <i>Xylocopa fenestrata</i> , <i>X. pubescens</i> , <i>Pithitis smaragdula</i> , <i>Megachile lanata</i> , <i>M. cephalotes</i> ), ranging in size from 0.01-0.6 g, flying at temperatures from 15-40°C	Abrol 1992 (Figure 1, Table 1): Values are estimated from regression lines for each species predicting mass-specific metabolic rate from temperature
	110-900 J/hr	18 species of male orchid bees (Apidae: Euglossini), ranging in size from 0.05-1 g, hovering at temperatures of 25-30°C	Darveau et al. 2005 (p. 3585): Averages for different species

<sup>†</sup>To calculate these estimates, I am using Heinrich's (1975) estimate of 5 calories per mL of O<sub>2</sub> used or mL of CO<sub>2</sub> produced.

**Table B.1 cont'd**

<b>Parameter</b>	<b>Values observed*</b>	<b>Species and context</b>	<b>Source</b>
Nectar secretion rate ( $n$ ) <sup>‡</sup>	0-10 J/hr	Shin-dagger ( <i>Agave schottii</i> ) flowers, sampled every 3-6 hours	Schaffer et al. 1979 (Tables 5 and 6): Averages for different sites and times of day
	0.008 J/hr	Mountain laurel ( <i>Kalmia latifolia</i> ) flowers, sampled every 24 hours	Real and Rathcke 1991 (Table 1 and p. 150)
	0.04-70 J/hr	Flowers of 17 bee-visited trees and shrubs native to Israel, allowed to accumulate nectar for a 24-hour period (species that produced too little nectar for the authors to measure nectar concentration are omitted)	Keasar and Schmida 2009 (Appendix Table 4): Averages for different species
	0-200 J/hr	Male flowers of the field pumpkin ( <i>Cucurbita pepo</i> ), sampled every hour	Nepi et al. 2011 (Figure 2): Averages for different times of day

<sup>‡</sup>To calculate these estimates, I am using Heinrich's (1979) estimate of 4 calories per mg of sugar. Where necessary, I converted nectar concentration from the Brix scale (weight of sugar/weight of solution) to weight of sugar/volume of solution using the table of conversions in Kearns and Inouye (1993).

# **Appendix C: Relationship between patch-scale flowerhead density, floret number, and pollen and nectar production in the study described in Chapter 2**

## **Methods**

My estimates of floral resource density in Chapter 2 assume that the number of male florets is a reliable proxy for the quantity of rewards produced by a flowerhead and that rewards produced per floret are not correlated with flowerhead density. To determine whether this was the case, I measured nectar and pollen production in four 1x1m “floral quality” plots per sampling event: two at the lowest density available, one at an intermediate density, and one at the highest density available. (During one sampling event, I omitted the intermediate density level and during two sampling events, I did not collect pollen data.) At each of these three density levels, I sampled nectar production of 5 randomly-chosen flowerheads and pollen production of 3 to 5 randomly-chosen flowerheads, as described below. An observer also counted the male-phase disk florets on each flowerhead prior to nectar or pollen measurements. For the pollen measurements, I used only flowerheads that had male-phase florets.

I measured nectar production as follows. Before flower visitors became active in the morning, each flower was enclosed in a bag made of bridal veil to exclude flower visitors. After the completion of flower visitor observations, an assistant removed each bag and collected the nectar using Drummond 0.2- $\mu$ L microcapillary tubes, pooling

together nectar from all open florets on the flowerhead. I measured the length of the nectar column in the tube to obtain the nectar volume and measured sugar concentration using a Bellingham & Stanley Eclipse range refractometer designed for low nectar volumes and calibrated for concentrations from 45-80 Brix. When volumes were too small to measure nectar concentration I assumed that the concentration was equal to the average concentration I recorded. For about 9% of flowerheads, concentrations were lower than the refractometer was calibrated to measure and I recorded the concentration as 40 Brix. I converted concentration from the Brix scale to mass of sugar per volume of solution using the conversion table listed in Kearns and Inouye (1993), and then used these nectar volume and concentration data to calculate the total amount of sugar produced per flowerhead.

I measured pollen production as follows. Each flowerhead was harvested before flower visitors became active in the morning and stored in ethanol. I later diluted each sample with water to approximately 4 mL and sonicated it for 30 seconds (using a Branson Sonifier Cell Disruptor 185 set to level 5) to release the pollen grains. I then used a hemacytometer to count the number of pollen grains in each of eight 0.9- $\mu$ L subsamples and measured the volume of the sample. I used these data to estimate the total number of pollen grains produced per flowerhead.

I analyzed the relationship between flowerhead density and floral reward production (no. pollen grains and amount of nectar sugar produced per flowerhead) using mixed effects models, with plot nested within sampling event as random effects, and the continuous variables plot flowerhead density and flowerhead size (no. male-phase florets)

as fixed effects. The residuals for the pollen analysis were significantly non-normal according to a d'Agostino-Pearson test, so I confirmed the results using a randomization test. To generate the randomized datasets, I randomly permuted pollen production values across flowerheads. In other respects, the methods were the same as described in the main text for randomization tests analyzing effects of floral density on visitation.

## Results

Both the number of pollen grains and the amount of nectar sugar produced by a flowerhead were strongly and positively correlated with flowerhead size (no. male-phase disk florets) (Table C.1). After variation in flowerhead size was taken into account, pollen and nectar production were not significantly related to flowerhead density.

**Table C.1: Effects of flowerhead density and number of male-phase disk florets on pollen and nectar production\***

	<i>b</i>	<i>se</i>	<i>df</i>	<i>t</i>	<i>P</i> <sup>†</sup>
<b>Nectar sugar produced per flowerhead</b>					
Plot flowerhead density	-0.00020	0.00062	70	-0.32	0.75
Flowerhead size	0.73	0.069	259	10.53	<0.001
<b>Pollen produced per flowerhead</b>					
Plot flowerhead density	0.00048	0.00032	62	1.51	0.14, 0.12
Flowerhead size	0.55	0.037	172	14.83	<0.001, 0.001

\* Results are from mixed effects models with plot nested within sampling event as random effects. The response variables were square-root transformed. Units are as follows: plot flowerhead density (flowerheads m<sup>-2</sup>), flowerhead size (no. male-phase disk florets), nectar sugar produced per flowerhead (μg), pollen produced per flowerhead (thousands of pollen grains).

<sup>†</sup> Where two p-values are shown, the second was estimated using a randomization test.

# Appendix D: Effects of total floral density on pollinator visitation in the study described in Chapter 2

## Methods

At each site, I mapped patch boundaries of each summer-flowering species that covered at least 1% of the site. The species I sampled at one or more sites were serpentine sunflower (Asteraceae: *Helianthus exilis*), yellow starthistle (Asteraceae: *Centaurea solstitialis*), and two tarweed species, hayfield tarweed (Asteraceae: *Hemizonia congesta*) and smallflower western rosinweed (Asteraceae: *Calycadenia pauciflora*), all of which appear to be visited at least occasionally by all of the most common visitors to *H. virgata* (except possibly honeybees on *C. pauciflora*; personal observation). Floral densities of each species were recorded at the 60 sampling points in *H. virgata* patches described in the main text and 10-20 additional random sampling points in patches that did not contain *H. virgata*. From these data, I estimated the total floral abundance of each plant species across the entire site. I measured pollen and nectar sugar production per flowerhead by each species in relation to that of *H. virgata* as described below. I then added together the floral abundances of all species, weighted according to their pollen or nectar sugar production rates in relation to *H. virgata*, to obtain the total floral abundance at the site. The floral abundance of *H. virgata* used in these calculations was the estimated number of flowerheads in the site multiplied by the average flowerhead size during that sampling event divided by the overall average

flowerhead size across all sampling events. From these data, I obtained the average floral density within patches of summer-flowering plant species during each sampling event.

I measured nectar production of 8-12 flowerheads per species simultaneously with measurements of nectar production in *H. virgata*. I selected flowerheads for these and the pollen measurements by haphazardly putting down a stick in a flower patch, selecting the flowerhead that was closest to it, and then walking at least 1m before selecting another flowerhead. I bagged flowerheads before flower visitors became active in the morning and then returned in the late morning or early afternoon to measure nectar volume and concentration. The tarweed species (*H. virgata*, *H. congesta*, and *C. pauciflora*) partially close their flowers in the late morning and typically receive few visits thereafter, so I assumed that nectar production in the afternoon for these species was minimal. For *H. exilis* and *C. solstitialis* (and the *H. virgata* flowerheads to which I was comparing them), I took another measurement in the late afternoon and summed values across the entire day. Methods for measuring nectar volume and concentration were the same as those described in Appendix C, except that I estimated total flowerhead nectar production for *C. solstitialis* and *H. exilis* from subsamples of the florets. In addition, nectar volumes in *C. pauciflora* were too small for nectar concentration measurements to be possible, so I assumed that *C. pauciflora*'s nectar concentration was the same as the average nectar concentration of *H. virgata*, to which it is related.

I measured pollen produced by 7-12 flowerheads per species, using methods similar to those describe in Appendix C (except that I used only a randomly-chosen fraction of

the florets in each *H. exilis* flowerhead for these measurements). My estimate of the average number of pollen grains produced per *C. solstitialis* flowerhead was simply the average observed across the 12 flowerheads I sampled, and my estimate of the average number of pollen grains produced per *H. virgata* flowerhead was the average observed across all flowerheads sampled for the analyses described in Appendix C. For the remaining three species, I multiplied the average number of pollen grains produced per male floret by the average number of male florets counted in 20-44 flowerheads per species to obtain my estimate of pollen produced per flowerhead. I calculated the average volume of a pollen grain in each species, assuming that the grains were spherical, from the diameters of 1-3 pollen grains from each of 7-12 flowerheads per species. From these data I calculated the total volume of pollen produced per flowerhead in each species.

## Results

The two measures of total site-scale floral density, based on nectar sugar and pollen production, were highly correlated with each other ( $r = 0.92$ ) and both produced similar results to site-scale floral density of *H. virgata*. I present results using the measure based on nectar sugar production in Table D.1.

**Table D.1: Effects of patch- (4m<sup>2</sup>) and site-scale (12.6 ha) total floral density on per-flowerhead visitation rates of the most abundant categories of flower visitors\***

	<i>b</i>	<i>se</i>	<i>df</i>	<i>t</i>	<i>P</i> <sup>†</sup>
<b>All visitors combined:</b>					
Patch Density	-0.035	0.041	92	-0.84	0.41
Site Density	0.00059	0.00082	13	0.72	0.48
Site Extent	-0.15	0.32	6	-0.48	0.65
Site Diversity	-0.56	0.26	13	-2.16	0.050
<b>Day</b>	<b>-0.021</b>	<b>0.0025</b>	<b>13</b>	<b>-8.44</b>	<b>&lt;0.001</b>
Patch Density x Site Density	-0.00057	0.00080	92	-0.71	0.48
Patch Density x Site Extent	0.0046	0.14	92	0.03	0.97
<b>Long-horned bees (<i>M. lupina</i>):</b>					
Patch Density	-0.023	0.039	93	-0.60	0.55, 0.26
<b>Site Density</b>	<b>0.0020</b>	<b>0.00080</b>	<b>15</b>	<b>2.51</b>	<b>0.024, 0.014</b>
Site Extent	-0.14	0.14	6	-0.97	0.37, 0.20
<b>Patch Density x Site Density</b>	<b>-0.0021</b>	<b>0.00079</b>	<b>93</b>	<b>-2.60</b>	<b>0.011, 0.005</b>
Patch Density x Site Extent	-0.11	0.13	93	-0.82	0.42, 0.74

\* Results are from mixed effects models, with sampling event nested within site as random effects. Site Density = average total floral density, weighted according to average nectar sugar production, within patches of summer-flowering plant species at the site scale, in *H. virgata* flowerhead equivalents m<sup>-2</sup>; Site Extent = total area of patches of summer-flowering plant species at the site scale, in m<sup>2</sup>; other variables are as defined in Table 2.1 in the main text. Visitation rates are in visits flowerhead<sup>-1</sup> hour<sup>-1</sup> and are square-root transformed. Patch Density and Site Extent are log<sub>10</sub>-transformed. Bold indicates *P* < 0.05.

<sup>†</sup> Where two p-values are shown, the second was estimated using randomization tests.

**Table D.1 cont'd**

	<i>b</i>	<i>se</i>	<i>df</i>	<i>t</i>	<i>P</i> <sup>†</sup>
<b>Honeybees (<i>A. mellifera</i>):</b>					
<b>Patch Density</b>	<b>0.061</b>	<b>0.018</b>	<b>93</b>	<b>3.37</b>	<b>0.001, 0.005</b>
Site Density	0.00078	0.00057	15	1.38	0.19, 0.25
Site Extent	-0.0019	0.12	6	-0.02	0.99, 0.98
Patch Density x Site Density	0.0012	0.00040	93	2.92	0.004, 0.040
Patch Density x Site Extent	0.023	0.071	93	0.32	0.75, 0.12
<b>Large sweat bees (<i>H. ligatus</i> and <i>L. titusi</i>):</b>					
Patch Density	0.020	0.041	93	0.48	0.63
Site Density	0.00048	0.00078	14	0.62	0.55
Site Extent	-0.21	0.21	6	-0.98	0.37
<b>Day</b>	<b>-0.017</b>	<b>0.0026</b>	<b>14</b>	<b>-6.63</b>	<b>&lt;0.001</b>
Patch Density x Site Density	-0.00035	0.00080	93	-0.44	0.66
Patch Density x Site Extent	0.11	0.14	93	0.77	0.44

## Appendix E: Appendices to Chapter 3

### Appendix E.1: Best response curve for a flower visitor that maximizes efficiency

If flower visitor species  $i$  maximizes efficiency and forages in both patches, then species  $i$  foragers must obtain equal efficiency in both patches:

$$\frac{I_D}{E_{i,D}} = \frac{I_S}{E_{i,S}} \text{ (Equation 3.6).}$$

From equations 3.1, 3.2, and 3.3,

$$I_j = \frac{rf_j T_{a,j} T_{b,j}}{n_a T_{b,j} p_{a,j} + n_b T_{a,j} p_{b,j}}. \quad (\text{E.1})$$

Therefore, when flower visitor species  $i$  obtains equal efficiency in both patches,

$$\frac{rf_D T_{a,D} T_{b,D}}{E_{i,D} (n_a T_{b,D} p_{a,D} + n_b T_{a,D} p_{b,D})} = \frac{rf_S T_{a,S} T_{b,S}}{E_{i,S} (n_a T_{b,S} p_{a,S} + n_b T_{a,S} p_{b,S})}. \quad (\text{E.2})$$

Setting  $p_{i,S} = 1 - p_{i,D}$  and rearranging to solve for the proportion of each species in the dense patch produces

$$p_{a,D} = \frac{E_{i,S} f_D T_{a,D} (n_a T_{b,S} + n_b T_{a,S})}{n_a T_{b,S} (E_{i,S} f_D T_{a,D} + E_{i,D} f_S T_{a,S})} - \frac{n_b T_{a,D} T_{a,S} (E_{i,S} f_D T_{b,D} + E_{i,D} f_S T_{b,S})}{n_a T_{b,D} T_{b,S} (E_{i,S} f_D T_{a,D} + E_{i,D} f_S T_{a,S})} p_{b,D} \quad (\text{E.3})$$

and

$$p_{b,D} = \frac{E_{i,S} f_D T_{b,D} (n_a T_{b,S} + n_b T_{a,S})}{n_b T_{a,S} (E_{i,S} f_D T_{b,D} + E_{i,D} f_S T_{b,S})} - \frac{n_a T_{b,D} T_{b,S} (E_{i,S} f_D T_{a,D} + E_{i,D} f_S T_{a,S})}{n_b T_{a,D} T_{a,S} (E_{i,S} f_D T_{b,D} + E_{i,D} f_S T_{b,S})} p_{a,D} \quad (\text{E.4})$$

Equations 3.7 and 3.8 in the main text are easily obtained from equations E.3 and E.4.

## Appendix E.2: Influence of species traits on equilibrium distribution when both species maximize efficiency

A single, stable equilibrium in which species  $a$  has a higher relative abundance in the dense patch than species  $b$  is predicted if, when plotted as in Figure 3.1, species  $a$ 's best response curve is higher than species  $b$ 's best response curve for all possible distributions of species  $b$ . This will be the case if species  $a$ 's best response curve has higher intercepts on both axes than does species  $b$ 's best response curve. Species  $i$ 's best response curve has its  $p_{b,D}$  intercept at

$$p_{b,D} = \frac{E_{i,S} f_D T_{b,D} (n_a T_{b,S} + n_b T_{a,S})}{n_b T_{a,S} (E_{i,S} f_D T_{b,D} + E_{i,D} f_S T_{b,S})} \quad (\text{from Equation E.3}), \quad (\text{E.5})$$

and its  $p_{a,D}$  intercept at

$$p_{a,D} = \frac{E_{i,S} f_D T_{a,D} (n_a T_{b,S} + n_b T_{a,S})}{n_a T_{b,S} (E_{i,S} f_D T_{a,D} + E_{i,D} f_S T_{a,S})} \quad (\text{from Equation E.4}). \quad (\text{E.6})$$

Therefore, species  $a$ 's best response curve has a higher intercept on the  $p_{b,D}$  axis than species  $b$ 's best response curve when

$$\frac{E_{a,S} f_D T_{a,D} (n_a T_{b,S} + n_b T_{a,S})}{n_a T_{b,S} (E_{a,S} f_D T_{a,D} + E_{a,D} f_S T_{a,S})} > \frac{E_{b,S} f_D T_{a,D} (n_a T_{b,S} + n_b T_{a,S})}{n_a T_{b,S} (E_{b,S} f_D T_{a,D} + E_{b,D} f_S T_{a,S})} \quad (\text{E.7})$$

and a higher intercept on the  $p_{a,D}$  axis when

$$\frac{E_{a,S} f_D T_{b,D} (n_a T_{b,S} + n_b T_{a,S})}{n_b T_{a,S} (E_{a,S} f_D T_{b,D} + E_{a,D} f_S T_{b,S})} > \frac{E_{b,S} f_D T_{b,D} (n_a T_{b,S} + n_b T_{a,S})}{n_b T_{a,S} (E_{b,S} f_D T_{b,D} + E_{b,D} f_S T_{b,S})}. \quad (\text{E.8})$$

Both inequalities simplify to

$$\frac{E_{a,D}}{E_{a,S}} < \frac{E_{b,D}}{E_{b,S}}, \quad (\text{E.9})$$

which is inequality 3.10. Therefore, the best response curves of species  $a$  and  $b$  cannot cross. Similar steps to those above show that the two best response curves will have the same intercepts and therefore overlap at every point when

$$\frac{E_{a,D}}{E_{a,S}} = \frac{E_{b,D}}{E_{b,S}}, \quad (\text{E.10})$$

which is equation 3.9 in the main text.

Combining inequality E.9 with equation 3.5, species  $a$  will have a higher relative abundance in the dense patch when

$$\frac{c_a k_a h_a + c_a \frac{d_D}{s_a}}{c_a k_a h_a + c_a \frac{d_S}{s_a}} < \frac{c_b k_b h_b + c_b \frac{d_D}{s_b}}{c_b k_b h_b + c_b \frac{d_S}{s_b}}. \quad (\text{E.11})$$

Flowers will be farther apart in the sparse patch than in the dense patch, so  $d_S > d_D$ .

Therefore,

$$d_S = d_D + u, \quad (\text{E.12})$$

where  $u > 0$ . Substituting equation E.12 into inequality E.11 and simplifying produces

$$k_a h_a s_a < k_b h_b s_b, \quad (\text{E.13})$$

which is inequality 3.11.

### Appendix E.3: Best response curve for a flower visitor that maximizes NREI

If flower visitor species  $i$  maximizes NREI and forages in both patches, then species  $i$  foragers must obtain equal NREI in both patches:

$$\frac{I_D - E_{i,D}}{T_{i,D}} = \frac{I_S - E_{i,S}}{T_{i,S}} \quad (\text{E.14})$$

Combining this equation with equation E.1 for  $I_j$  produces

$$\frac{\frac{rf_D T_{a,D} T_{b,D}}{n_a T_{b,D} p_{a,D} + n_b T_{a,D} p_{b,D}} - E_{i,D}}{T_{i,D}} = \frac{\frac{rf_S T_{a,S} T_{b,S}}{n_a T_{b,S} p_{a,S} + n_b T_{a,S} p_{b,S}} - E_{i,S}}{T_{i,S}}. \quad (\text{E.15})$$

Setting  $p_{i,S} = 1 - p_{i,D}$  and rearranging produces

$$0 = A_a p_{a,D}^2 + B_a p_{a,D} + C_a, \quad (\text{E.16})$$

where

$$\begin{aligned} A_a &= -E_{rat,i} T_{b,D} T_{b,S} n_a^2 \\ B_a &= n_a (T_{b,D} T_{b,S} (f_D T_{a,D} T_{i,S} + f_S T_{i,D} T_{a,S}) + E_{rat,i} N_{sum} T_{b,D} - E_{rat,i} (T_{b,D} T_{a,S} + T_{a,D} T_{b,S}) n_b p_{b,D}) \\ C_a &= T_{a,D} (-f_D N_{sum} T_{b,D} T_{i,S} + (T_{a,S} (f_D T_{b,D} T_{i,S} + f_S T_{i,D} T_{b,S}) + E_{rat,i} N_{sum}) n_b p_{b,D} - E_{rat,i} T_{a,S} n_b^2 p_{b,D}^2), \end{aligned}$$

and

$$E_{rat,i} = \frac{E_{i,D} T_{i,S} - E_{i,S} T_{i,D}}{r}$$

$$N_{sum} = n_a T_{b,S} + n_b T_{a,S}.$$

Equation E.16 can be solved for  $p_{a,D}$  using the quadratic formula.

Similarly, equation E.16 can be rearranged to produce

$$0 = A_b p_{b,D}^2 + B_b p_{b,D} + C_b, \quad (\text{E.17})$$

where

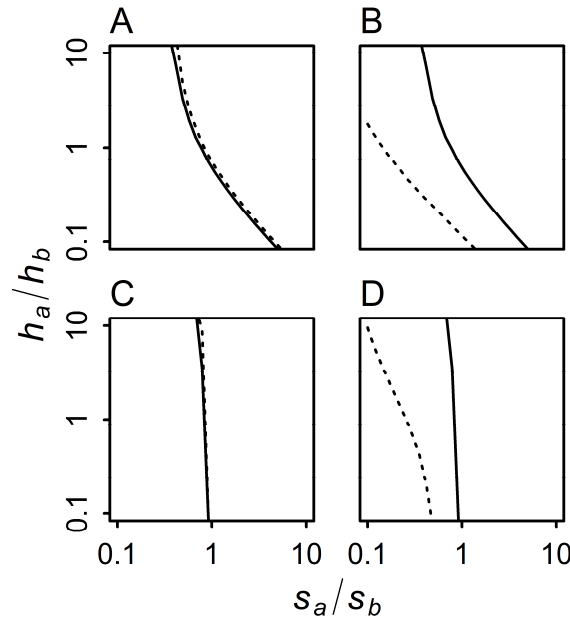
$$A_b = -E_{rat,i} T_{a,D} T_{a,S} n_b^2$$

$$B_b = n_b (T_{a,D} T_{a,S} (f_D T_{b,D} T_{i,S} + f_S T_{i,D} T_{b,S}) + E_{rat,i} N_{sum} T_{a,D} - E_{rat,i} (T_{b,D} T_{a,S} + T_{a,D} T_{b,S}) n_a p_{a,D})$$

$$C_b = T_{b,D} (-f_D N_{sum} T_{a,D} T_{i,S} + (T_{b,S} (f_D T_{a,D} T_{i,S} + f_S T_{i,D} T_{a,S}) + E_{rat,i} N_{sum}) n_a p_{a,D} - E_{rat,i} T_{b,S} n_a^2 p_{a,D}^2),$$

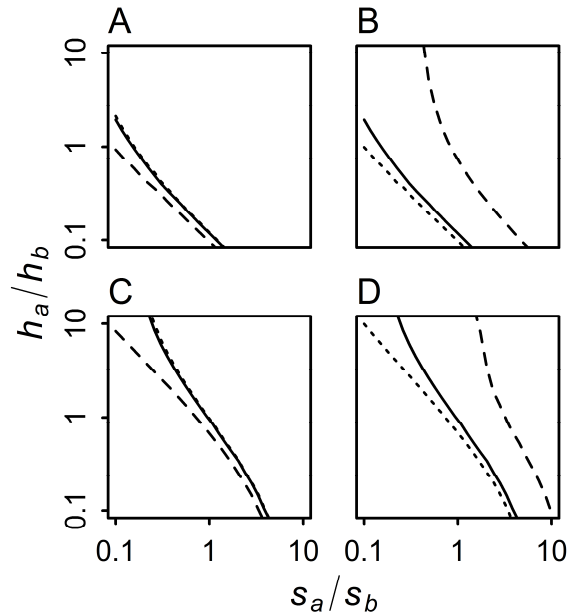
which can be solved for  $p_{b,D}$ .

## Appendix E.4: Effects of forager to flower ratio on model predictions



**Figure E.1: Effects of flower visitor traits on equilibrium distributions when forager : flower ratios are high, if (A-B) species *a* maximizes NREI and species *b* maximizes efficiency, or (C-D) both species maximize NREI**

Curves indicate trait combinations for which the flower visiting 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. The three lines in each plot give predictions for different relative values of (A and C)  $k_i$  or (B and D)  $c_i$ . Solid line:  $k_a = k_b$  and  $c_a = c_b$ ; Dotted line:  $k_a/k_b$  or  $c_a/c_b = 0.1$ . (Predictions for  $c_a/c_b = 10$  and  $k_a/k_b = 10$  are not shown because in these cases one or both flower visiting species is unable to achieve positive foraging success for every combination of the remaining parameter values.) Parameter values are the same as in Figure 3.2 except for the following:  $n_a = n_b = 2,250$  insects.



**Figure E.2: Effects of flower visitor traits on equilibrium distributions when forager : flower ratios are low, if (A-B) species *a* maximizes NREI and species *b* maximizes efficiency, or (C-D) both species maximize NREI**

Curves indicate trait combinations for which the flower visiting 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. The three lines in each plot give predictions for different relative values of (A and C)  $k_i$  or (B and D)  $c_i$ . 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:  $k_a/k_b$  or  $c_a/c_b = 10$ . (Dotted and solid lines largely overlap in A and C.) Parameter values are the same as in Figure 3.2 except for the following:  $n_a = n_b = 250$  insects.

## Appendix E.5: Measurements of parameter values in the bee-tarweed system

Floral densities were measured in 60 0.25m-radius plots placed randomly in patches of the yellowflower tarweed within 200m of the center of each site during each sampling event. I calculated the 10<sup>th</sup>, 30<sup>th</sup>, 50<sup>th</sup>, 70<sup>th</sup>, and 90<sup>th</sup> percentiles of the floral densities

recorded during each sampling event, not including zeroes, and set the patch floral densities in the simulation to the median values of these percentiles, rounded to the nearest 5 flowers/m<sup>2</sup>. To convert floral densities to between-flower spacing,  $d_j$ , I used the formula for average nearest-neighbor distance assuming that flowers were randomly dispersed:

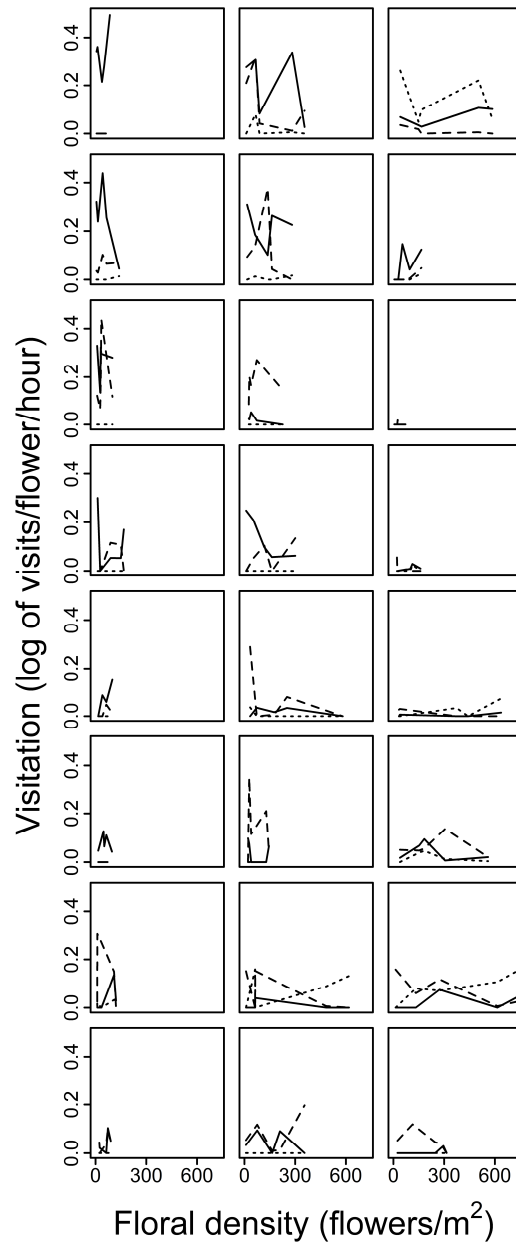
$$\frac{1}{2\sqrt{\text{density}}} \text{ (Pielou 1977).}$$

The nectar secretion rate estimate,  $r$ , is the average nectar secretion rate of eleven yellowflower tarweed flowers measured between approximately 7:00 and 11:00 am by emptying each floret of nectar at the start of the period and then measuring volume and concentration of accumulated nectar approximately every two hours. This period is when flower visitation to the yellowflower tarweed is greatest and was approximately the period used for visitation observations. Flower visitor densities were recorded using 14 instantaneous counts in each plot used for visitation observations, carried out during the same time periods as the visitation observations. The number of foragers in each flower visiting group,  $n_i$ , is set so that forager : flower ratios would be equal to the average forager : flower ratios observed during these counts. Per-flower visitation by groups other than the focal taxa is set to the mean value observed across all plots in all sampling events. Flower handling times were recorded whenever possible during flower visitation observations. (Handling times were recorded for 75-80% of flower visits by the focal taxa.) I calculated an average flower handling time,  $h_i$ , for each flower visiting taxon by averaging together the mean flower handling times of each bee observed. The two sweat

bee species, *L. titusi* and *H. ligatus*, are lumped together because we were able to distinguish them only 42% of the time. Mean flower handling times of the few *H. ligatus* individuals we were able to identify during visitation observations were higher on average than mean handling times for *L. titusi*, although variance across individuals was high (*H. ligatus*:  $\bar{x} = 7.5$  s,  $sd = 6.1$  s,  $n = 14$ ; *L. titusi*:  $\bar{x} = 4.1$  s,  $sd = 2.8$  s,  $n = 59$ ). I obtained my search speed estimates from flight durations and estimated distances between flowers recorded for bees foraging in a large patch of yellowflower tarweed between Aug. 5 and Sept. 5, 2009. I calculated the average search speed by averaging together the mean search speeds of each bee that could be followed for at least three flights. We were not able to distinguish *H. ligatus* and *L. titusi* for any of these observations, but *H. ligatus* accounted for nearly 40% of the 145 large-bodied sweat bees collected near the search speed observation site between Aug. 8 and Sept. 8, 2009. Therefore, the average search speed estimated from these data is probably intermediate between the true values of the two species. Finally, I estimated flight energy consumption rates from body size using the scaling equation given in Niven and Scharlemann (2005). My measure of body size was intertegular span, which is a robust estimator of body size across bee taxa (Cane 1987). I measured intertegular spans of 10 *H. ligatus* individuals and 16 individuals each of *L. titusi* and *M. lupina*, randomly selected from the specimens collected at the McLaughlin Reserve during 2010, and five honeybees collected at the McLaughlin Reserve in 2009. I converted intertegular span to dry weight using the equation given in Cane (1987) and assumed that dry weight was 30% of wet weight. The resulting estimated flight metabolic rate for honeybees, 0.04 J/s,

was consistent with values of 0.039 to 0.046 J/s previously reported for honeybee foragers (Schippers et al. 2010). The two sweat bee species had similar estimated flight metabolic rates.

## Appendix E.6: Observed overlap between pollinator species distributions across floral density gradients



**Figure E.3: Average per-flower visitation rates to the yellowflower tarweed by large sweat bees (solid line), long-horned bees (dashed line), and honeybees (dotted line) in plots of varying floral densities**

Each row of panels represents a separate site and each panel in a row represents a different sampling date.

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