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HABITAT SELECTION BY TWO SPECIES OF NECTARIVORE: HABITAT QUALITY ISOLINES¹

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Abstract. I present a model predicting the distribution and abundance of two species of competing nectarivore exploiting nectar in two types of flower. The model uses a sub-model of resource renewal and depletion, and the principle that individuals attempt to maximize individual fitness, to construct habitat isolines. The habitat isoline for a population of nectarivores is a line in an abundance phase-plane along which all individuals of the population, regardless of the habitat they are currently exploiting, have equal expected fitness. At equilibrium the habitat isoline determines the distribution of a population between two habitats given a fixed abundance of competitors. The habitat isolines for populations of two species exploiting two habitats can be used to predict the equilibrium distribution of both species. I illustrate the model using data about bumble bees foraging for nectar in flowers (Inouye 1978).

An asset of the model is its ability to make a priori predictions about flower exploitation patterns using information about resource dynamics and the foraging abilities of the nectarivores.

Two warnings regarding the empirical detection of exploitation competition between species emerge from the model analysis. Depending on the range over which density manipulations are carried out in exploitation competition systems, competition may or may not be detected, while interspecific competition may or may not appear to be more intense than intraspecific competition.

Although the model is directed at nectarivores competing for nectar in flowers, the results have wider implications for all systems where species compete exploitatively for resources.

Key words: *Bombus; bumble bees; exploitation competition; floral nectar; foraging; habitat selection; ideal free distribution; model; nectarivores; resource renewal.*

INTRODUCTION

Fretwell and Lucas (1970) present a theory for the distribution and abundance of mobile organisms based on the premise that individuals maximize their expected lifetime fitness. According to their "ideal free distribution" theory, individuals of a species distribute themselves between habitats so that no individual can increase its fitness by changing habitat. The theory represents a significant step towards the integration of behavioral and population ecology.

Habitat selection theory uses the premise that individuals attempt to maximize their fitness, to provide a framework for understanding the distribution and abundance of competing species. Several authors have used the idea of habitat selection to make qualitative predictions about the distribution and abundance of two competitors (Lawlor and Maynard Smith 1976, Rosenzweig 1979, 1981, Pimm and Rosenzweig 1981, Brew 1982, Rosenzweig and Abramsky 1985, Brown

and Rosenzweig 1986, Morris 1987). In some cases these predictions are used to interpret field data (e.g., Ford and Paton 1986). In particular Pimm et al. (1985) use "isoleg" theory to describe the way in which three species of hummingbird distribute their foraging activities between good and poor patches (nectar feeders, in this case). To predict the preferences of each species given the density of each species, an isoleg diagram was produced from field data. The theory is a useful way of summarizing and understanding the process of habitat selection but it does not make a priori quantitative predictions.

In this paper I present a mechanistic theory of flower choice by competing nectarivores. The theory is based on a model of resource renewal and depletion (Possingham 1988) and the assumption that individuals maximize their net rate of energy gain. A novel aspect of the theory is the construction of habitat quality isolines, which are lines in a phase-plane of species densities along which both habitats are perceived to be of equal quality to a particular species. The model is different from "isoleg" theory, but qualitatively similar in its outcome.

I begin by discussing density-dependent floral choice by a single species of nectarivore. This serves to intro-

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duce the parameters of the model, and the model of resource renewal and depletion. A two-species model is constructed and illustrated using data collected by Inouye (1978) about two species of bumble bee foraging for nectar in two species of flower.

Throughout the paper I assume that the nectarivore is a bee and the habitat that an individual bee chooses to exploit is equivalent to the flower type (species or group of similar species) on which it specializes. Despite this specific terminology the model could be applied to other situations involving nectarivores exploiting nectar sources. Indeed, the model could be applied to any ecological system involving exploitation competition for renewing resources by two species.

SINGLE-SPECIES MODEL

The number of bees foraging on different flower types will depend on the costs and rewards associated with exploiting those flower types. The reward offered by a flower type will, in turn, depend on the number of bees using that type of flower. In this section I present a model that predicts the number of bees using each type of flower given a total population of bees and the properties of the flowers they are exploiting.

Consider a population of bees exploiting nectar secreted by a single type of flower. If N is the total number of active foragers, τ is the average time spent travelling to and exploiting the nectar in a flower, P is the number of flowers, and λ is the average rate of nectar secretion by the flowers (energy per unit time), then, at equilibrium, the mean energy obtained from a flower by a bee (Pleasants and Zimmerman 1983, Possingham 1988, 1989) is

$$\mu = \lambda P \tau / N. \tag{1}$$

Assuming a bee uses energy at an average rate e , the expected long-term net rate of energy gain (E) of a bee is

$$E = \mu / \tau - e = \lambda P / N - e. \tag{2}$$

Suppose that the bees consume nectar in two types of flower, type a and type b , which have abundances P_a and P_b , respectively. Assume that the rate at which energy is expended, e , is independent of the type of flower being exploited, and that individual bees tend to specialize on particular flower types (Heinrich 1976, Inouye 1978). Ideal free distribution theory suggests that individuals of a single bee species should distribute themselves between the flower types so that the net rates of energy gain of bees specializing on different flower types are equal. Mathematically this is true if

$$\mu_a / \tau_a = \mu_b / \tau_b, \tag{3}$$

where μ_j is the mean nectar content of flowers of type j , and τ_j is the mean time spent exploiting flowers of type j . (This theory also applies to a single species of nectarivore using many flower types; Pleasants 1981.)

It is convenient to summarize the relative produc-

tivities of each flower type by R , the ratio of total nectar production by all flowers of type a to total nectar production by all flowers of type b .

$$R = \lambda_a P_a / \lambda_b P_b. \tag{4}$$

Given a constant total number of bees, the number of bees using each flower type is obtained algebraically by combining Eqs. 1 and 3 (see the Appendix: Section I).

$$N_a = NR / (1 + R) \tag{5a}$$

$$N_b = N / (1 + R), \tag{5b}$$

where N_a is the number of bees using flower type a and N_b is the number of bees using flower type b , so $N_a + N_b = N$. In this model the number of bees using a particular flower type is determined by the relative productivity of each flower type. The time spent travelling to and extracting the nectar from the two flower types, τ_a and τ_b , does not affect the proportion of the total bee population in each habitat (Pleasants 1981).

TWO-SPECIES MODEL

Consider the more complex case of two species of bee and two types of flower. As before, I use ideal free distribution theory to predict the number of each species using each flower type.

Model

Let the species of bee be indicated by the numbers 1 and 2, so that the total number of bees of species i is N_i and the number of bees of species i using flower types a and b are N_{ia} and N_{ib} , respectively. I will use i as the generic subscript for bee species, and j as the generic subscript for flower type. The mathematical problem is to determine, at equilibrium, the number of bees of each species using each flower type.

At equilibrium the net rate of energy gain of bees using flower type a is equal to the net rate of energy gain of bees using flower type b , for both species, if

$$\mu_a / \tau_{ia} = \mu_b / \tau_{ib} \quad \text{for } i = 1, 2. \tag{6}$$

The mean energy content of flowers of type j depends on the number of bees of each species using that type (see the Appendix: Section II).

$$\mu_j = \frac{\lambda_j P_j}{N_{1j} / \tau_{1j} + N_{2j} / \tau_{2j}} \quad \text{for } j = a, b. \tag{7}$$

Substituting Eq. 7 into Eq. 6 for both i , and removing the variables N_{ib} by remembering that the total number of bees is conserved,

$$N_i = N_{ia} + N_{ib}, \tag{8}$$

yields two equations, one for each species, which express the number of one species using flower type a as a function of the number of the other species using flower type a (see the Appendix: Section III).

$$N_{1a} = \frac{R(N_2B + N_1)}{R + 1} - \frac{(BR + A)N_{2a}}{R + 1} \tag{9a}$$

$$N_{2a} = \frac{AR(N_2B + N_1)}{AB(R + 1)} - \frac{(B + AR)N_{1a}}{AB(R + 1)}, \tag{9b}$$

where $B = \tau_{1b}/\tau_{2b}$, and $A = \tau_{1a}/\tau_{2a}$ reflect the relative efficiencies with which each bee species exploits each flower type.

The habitat quality isolines

I refer to Eqs. 9a and b as habitat quality isolines because they are lines in (N_{1a}, N_{2a}) phase-space along which the quality of both flower types is equal for species 1 and 2, respectively. Eq. 9a determines the number of bees of species 1 in habitat a , N_{1a} , for a fixed number of species 2 in habitat a , N_{2a} ; Eq. 9b determines the number of bees of species 2 in habitat a for a fixed number of species 1 in habitat a .

Superficially it appears that the solution to the problem is found by solving the two linear Eqs. 9a and b for the two variables N_{1a} and N_{2a} . However, as the isolines never intersect (except in the improbable case $A = B$, see the Appendix: Section IV), this method of solution fails.

The solution to the problem relies on an understanding of the meaning of each isoline. If Eq. 9a is true, then bees of species 1 find each flower type equally profitable. (Note that N_{1a} also determines the number of bees of species 1 using flower type b , because there is a fixed total bee population size N_1 .) For a fixed number of species 2 using flower type a (fixed N_{2a}), an increase in N_{1a} above habitat quality isoline 1 will reduce the net rate of energy gain of species 1 bees using flower type a below that of species 1 bees using flower type b . At this point some bees of species 1 should shift their floral preference to type b until Eq. 9a is true. This concept is illustrated in Fig. 1. Arrows above and below the habitat quality isoline indicate the change in behavior of some bees of species 1 given a fixed floral preference of species 2. The equilibrium distribution of species 1 for a fixed number of bees of species 2 using flower type a is determined by the habitat isoline for species 1.

It is also possible to plot an isoline for species 2 as a function of N_{1a} and N_{2a} , Eq. 9b. If the current species distribution lies at a point to the right of isoline 2, then some bees of species 2 should shift their preference away from flower type a . Having constructed these isolines we can graphically determine the equilibrium flower type preference of each species in a fashion similar to the way in which phase-plane analysis is used to determine equilibrium points for two simultaneous differential equations, Fig. 2.

Without loss of generality assume that $B > A$, which written in full is $\tau_{1b}/\tau_{2b} > \tau_{1a}/\tau_{2a}$. In this case isoline 1 will always lie above isoline 2. The isolines never meet and isoline 1 is steeper than isoline 2. The values of

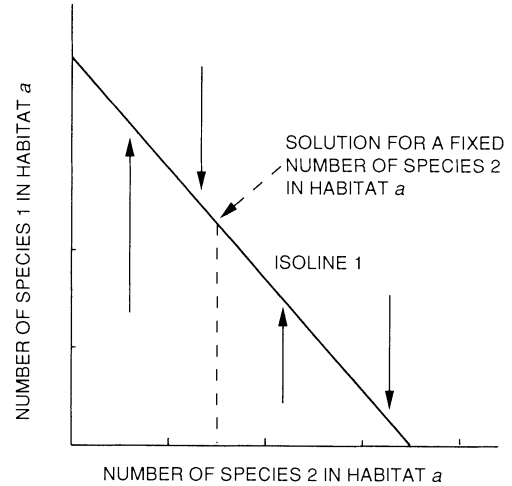


FIG. 1. Habitat quality isoline for species 1. When the number of bees of species 1 using flower type a is above the isoline, bees of species 1 using flowers of type a have a lower net rate of energy gain than their conspecifics using flower type b . Similarly, if the number of bees using flower type a has a value so that the joint abundance lies below the habitat isoline, bees of species 1 should change preference from flower type b to flower type a . The arrows above and below the isoline indicate the movement of individuals of species 1 from the poorer habitat to the better habitat. If the number of individuals of species 2 is fixed, then the intersection of the dashed line with the isoline predicts the equilibrium flower preference of species 1.

the intercepts and slopes of the respective isolines are indicated in Fig. 2 (see the Appendix: Section III). If there were no constraints on the values of N_{1a} and N_{2a} , then the solution to the problem would be found by following the arrows to the stable point: $N_{1a} = (RN_1 + RBN_2)/(R + 1)$, $N_{2a} = 0$, which forces $N_{1b} = (N_1 - RBN_2)/(R + 1)$, $N_{2b} = N_2$. However, the total number of bees of either species using either flower type cannot be more than the total number of bees of that species. Depending on the relationship between these constraints and the isolines, there are three types of solution to the problem, each of which is qualitatively distinct. Before discussing these solutions it is helpful if we first consider the case in which these constraints are ignored.

In absence of constraints bee species 2 is restricted to flower type b , while bees of species 1 are found on both flower types. The crucial inequality is, $B > A$. A measure of the efficiency with which each species uses each flower type is τ_{ij} , the time it takes a bee of species i to use a flower of type j . As stated above, B and A reflect the relative efficiencies of each species using each flower type. For example, if $B = \tau_{1b}/\tau_{2b} > 1$ then $\tau_{2b} < \tau_{1b}$ and species 2 takes less time to consume the nectar in a flower of type b than species 1; and conversely for $B < 1$. The parameter A has an equivalent interpretation with respect to flowers of type a . Now if $B > A$, then the ability of bees of species 2 to use flowers of type b relative to the ability of bees of species

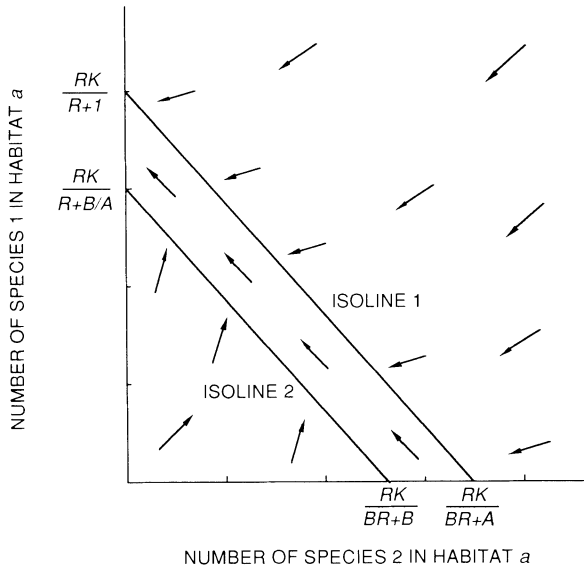


FIG. 2. Habitat quality isolines for both species 1 and 2. The isolines never intersect and isoline 1 is always steeper than isoline 2 if $B > A$ (Appendix: Section IV). The arrows are trajectories in the flower preferences of both species that qualitatively predict the way in which individuals should change their habitat preference to maximize their net rate of energy gain. In this case, without constraints on the total number of individuals of either species, the equilibrium distribution is $N_{1a} = R(N_1 + BN_2)/(R + 1)$ and $N_{2a} = 0$. In the figure $K = N_1 + BN_2$.

1 to use flowers of type b is greater than the ability of bees of species 2 to use flowers of type a relative to the ability of bees of species 1 to use flowers of type a . It is not surprising that the solution indicates species 2 bees favor flowers of type b .

Solution cases

The discussion above introduces the solution to the problem by ignoring the constraints on the total number of bees of each species. These constraints are $N_{1a} < N_1$ and $N_{2a} < N_2$. Incorporating these constraints yields three possible solution types (Table 1), each of which is shown graphically in Fig. 3. The solution types depend on the positions of the constraints relative to the positions of the isolines.

The three conditions have logical interpretations. The condition for solution type **p** means that the total population size of bee species 1 is high enough that a species 2 bee has a higher net rate of energy gain using flower type b when all bees of species 2 use flower type b and all bees of species 1 use flower type a . The condition for solution type **r** means that species 1 bees have a higher net rate of energy gain using flower type a when all bees of species 2 use flower type b and all bees of species 1 use flower type a . Because the isolines do not intersect, both species will not use both flower types simultaneously. Mesterton-Gibbons (1992) provides a

more rigorous algebraic analysis of my graphical argument.

Three examples with specific parameters illustrate the solution types, Fig. 4. It is not possible for the constraints to intersect below the lowest isoline (see the Appendix: Section IV).

The effect of changing environmental conditions on the equilibrium distribution of foragers

Using the solutions for each case it is possible to explore the way in which changes in the environment alter the flower preferences of the bees. Suppose the number of bees of each species is fixed, but the productivity ratio of the two flower types, R , changes. In Fig. 5 the number of bees using each flower type is plotted as a function of R , the ratio of the productivity of flower type a to the productivity of flower type b .

As expected, no bees of either species use flower type a when its productivity is zero. As the relative productivity of flower type a increases, bees of species 1 begin to use this flower type until all bees of species 1 are exploiting flowers of type a . This is followed by a range of values of R over which neither species shows a change in floral preferences. When $R = N_1/AN_2$, bees of species 2 begin to use flower type a , after which the number of species 2 bees using flower type a increases asymptotically toward N_2 , Fig. 5.

The magnitude of the range in R over which there is no change in species preferences is proportional to the magnitude of the difference in relative efficiencies, $\tau_{1b}/\tau_{2b} - \tau_{1a}/\tau_{2a}$. For example, if bees of species 1 are a lot more efficient than bees of species 2 on flower type a , and the reverse is true for flowers of type b , the two species will usually use different flower types and we would observe complete habitat separation.

TABLE 1. The three types of solutions to the habitat selection problem, showing the conditional relationship between N_1 and N_2 and the number of bees of each species using each flower type.

p) Condition: $N_1 \geq RBN_2$.		
Solution:	Flower type a	Flower type b
Bee species 1	$\frac{RN_1 + RBN_2}{R + 1}$	$\frac{N_1 - RBN_2}{R + 1}$
Bee species 2	0	N_2
q) Condition: $RAN_2 \leq N_1 \leq RBN_2$.		
Solution:	Flower type a	Flower type b
Bee species 1	N_1	0
Bee species 2	0	N_2
r) Condition: $N_1 \leq RAN_2$.		
Solution:	Flower type a	Flower type b
Bee species 1	N_1	0
Bee species 2	$\frac{(RN_2 - N_1/A)}{R + 1}$	$\frac{(N_1/A + N_2)}{R + 1}$

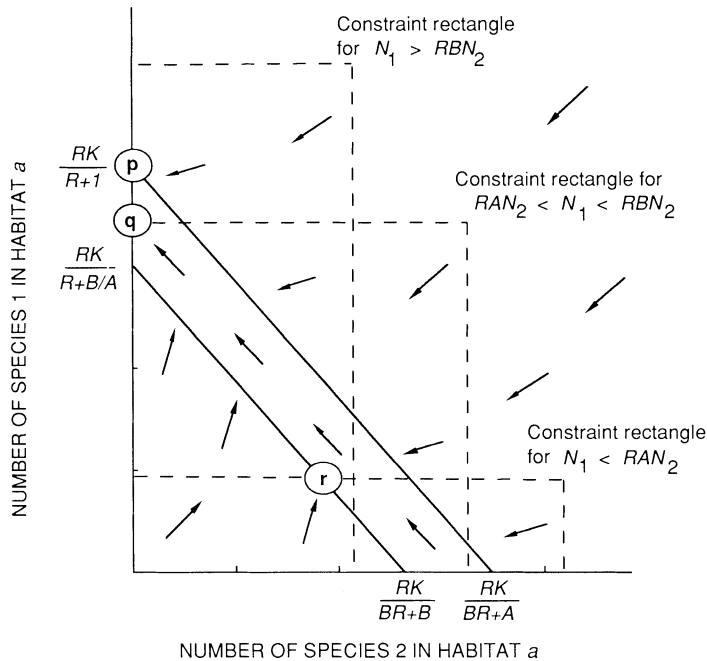


FIG. 3. Habitat quality isolines for species 1 and 2 with constraints on the population sizes of each species. When $N_1 \geq RBN_2$, the equilibrium solution is type **p**: all bees of species 2 use flower type *b*, some bees of species 1 use flower type *a*, others use flower type *b*. When $RAN_2 \leq N_1 \leq RBN_2$, the equilibrium solution is type **q**: all bees of species 1 use flower type *a* and all bees of species 2 use flower type *b*. There is complete diet separation. When $N_1 \leq RAN_2$, the equilibrium solution is type **r**: all bees of species 1 use flower type *a*, some bees of species 2 use flower type *b*, some flower type *a*. In the figure $K = N_1 + BN_2$.

The effect of changes in forager numbers on the equilibrium distribution of foragers

It is of interest to explore changes in the floral preference for each species when the abundance of the other species changes. This will give us a guide to the effect of intraspecific and interspecific exploitation competition on floral preference, and the effect of removal and addition experiments. The effect of changing abundances is determined by the three solution types.

Consider increasing the abundance of species 2 (Fig. 6). When there are very few bees of species 2, species 2 bees only use flower type *b*, and bees of species 1 using flower type *b* swap to flower type *a* as the abundance of species 2 increases. After $N_2 = N_1/RB = 44.4$, both species specialize on a single flower type. An increase in the number of species 2 within the range $N_1/RB < N_2 < N_1/RA$ has no effect on the flower preferences of species 1 bees, nor the net rate of energy gain of bees of species 1. As the number of bees of species 2 passes the second threshold, $N_2 = N_1/RA = 66.7$, bees of species 2 start using flower type *a*.

To compare the effects of increases in the number of intraspecific and interspecific competitors, I have plotted the net rate of energy gain of a bee of species 1 as a function of an increase in the number of bees of species 1 or 2, for a particular set of parameters (Fig.

7). A small increase in the abundance of species 2 has no effect on the net rate of energy gain of species 1. For larger increases in the abundance of species 2 the per-individual effect of species 2 on the net rate of energy gain of species 1 is greater than the effect of an increase in species 1 on its own per-individual net rate of energy gain! This example shows that the magnitude of intraspecific and interspecific competition can be completely reversed depending on the range over which population manipulations are carried out. For any example there is a range of population sizes for a species within which a change in abundance does not influence the net rate of energy gain of the other species, nor the relative distribution of either species.

The examples presented here raise important problems for experimentalists studying exploitation competition, and comparing the effects of intraspecific and interspecific competition, in situations where the species can use more than one habitat. The example displayed in Fig. 6 shows that we may reject or fail to reject the null hypothesis that there is no interspecific competition, depending on the range of population sizes over which density manipulations are carried out. Similarly we may reject or fail to reject the null hypothesis that interspecific competition is more intense than intraspecific competition (Fig. 7).

Floral preferences in exploitation competition systems

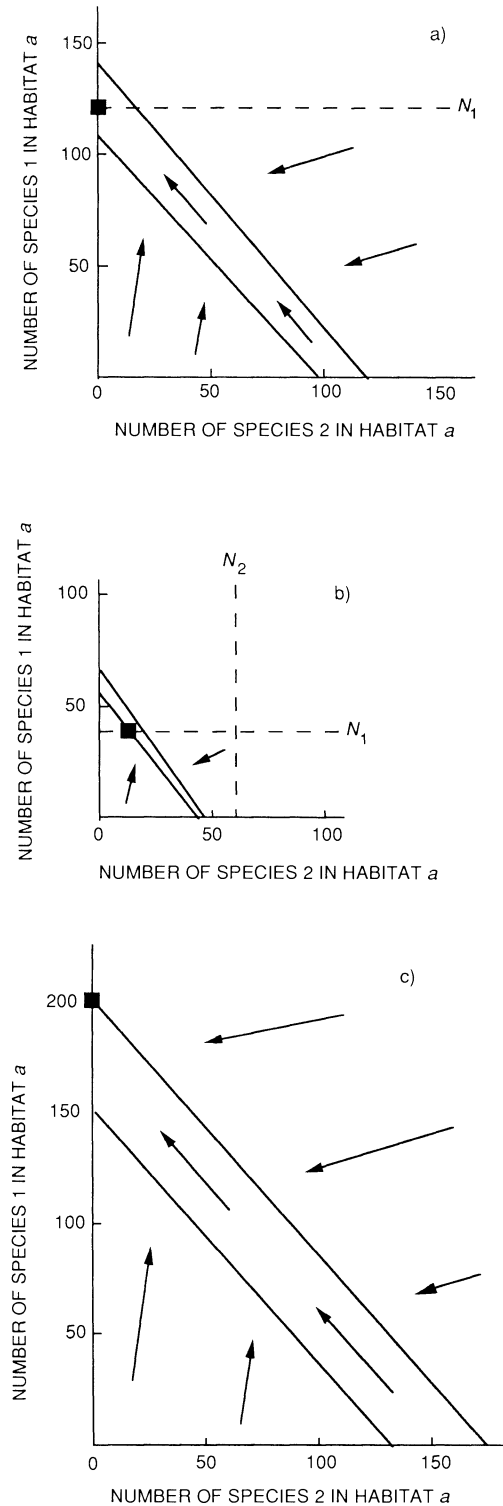


FIG. 4. Examples of the three solution types for particular parameter sets. In each case the arrows indicate the changes in behavior of both species leading to an equilibrium distribution (indicated by ■). In all cases $1 = A < B = \frac{1}{2}$. (a) A type q solution: $N_1 = 120$, $N_2 = 200$ and $R = \frac{1}{2}$. (b) A type r solution: $N_1 = 40$, $N_2 = 60$ and $R = 4$. (c) A type p solution: $N_1 = 300$, $N_2 = 200$ and $R = \frac{1}{2}$.

Before applying the model to some data, one final observation warrants discussion. In all the examples discussed so far species 1 tends to favor flowers of type *a* and species 2 favors flowers of type *b*. The important parameter in determining these preferences is the time it takes a bee of each species to use a flower of each type, τ_{ij} . Initially we might guess that the species that uses flowers of type *a* most efficiently will be the species that favors flowers of type *a*. For example if $\tau_{1a} < \tau_{2a}$, then we might expect more bees of species 1 to be using flowers of type *a* than bees of species 2. This kind of reasoning has been used by many authors to imply that the flower type most efficiently used by a species will be favored by that species in the absence of interference competition from other species (Gill and Wolf 1978, Schaffer et al. 1979, Inouye 1980, Ranta and Lundberg 1980, Ranta et al. 1981, Pyke 1982, Bowers 1985, Harder 1985, Soltz 1987). This assertion can be disproved by a counterexample.

Let the total number of bees of each species be: $N_1 = 200$, $N_2 = 200$, and let all the flowers of type *a* produce twice the quantity of nectar as all the flowers of type *b*, $R = 2$. Assume bees of species 1 are more efficient than bees of species 2 at using flowers of type *a*, $1 = \tau_{1a} < \tau_{2a} = 2$, so $A = \frac{1}{2}$. At this point our intuition would lead us to hypothesize that most of the bees using flower type *a* would be species 1. However, we can show that the number of bees of each species using flower type *a* will also depend on their relative abilities on flower type *b*, so much so that it is possible for species 2 to dominate flower type *a*.

If $B > \frac{1}{2}$, and species 2 is the most efficient forager on flowers of type *b*, our intuition is correct and all bees of species 1 use flower type *a*. However if $B < \frac{1}{2}$ (at this point the fundamental assumption that $A < B$ is violated and to calculate the number of bees of each species using each flower type means relabelling the flower types), species 2 only forages on flowers of type *a*, and species 1 is split between flowers of type *a* and flowers of type *b* (Fig. 8). When $B < \frac{1}{2}$, species 1 is more efficient on flowers of either type than species 2, its dominance on flowers of type *b* occurs because it is "more superior" on flowers of type *b*. Note that when $B < \frac{1}{2}$, species 1 is not necessarily more efficient at using flowers of type *b* than flowers of type *a*.

Comparing foraging efficiencies for a single species on different flower types may lead to false conclusions about foraging preferences where other food sources are available, and there is interspecific competition for food. The relative, not the absolute, abilities of different species on different flower types may give a better indication of which species will prefer which flower type.

This result is similar to the observation that a competitively dominant (in an interference competition

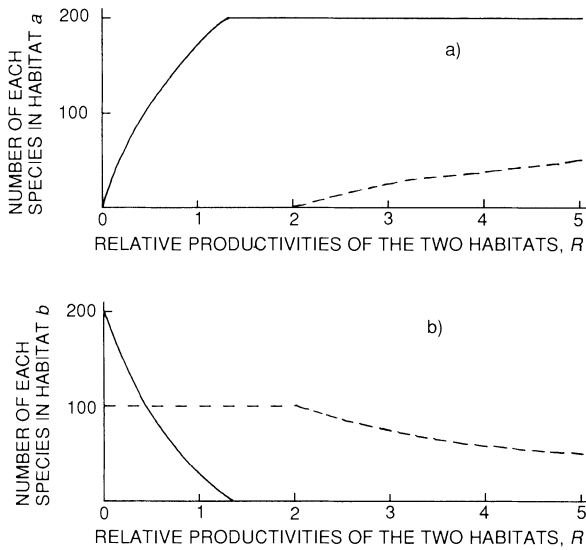


FIG. 5. The effect of changes in the relative productivities of flower type *a* relative to flower type *b*, *R*, on the flower preferences of the two species at equilibrium. The number of bees of species 2 is indicated by ---, the number of bees of species 1 is indicated by —. (a) Number of each species using flower type *a*. (b) Number of each species using flower type *b*. Parameters: $A = 1 < B = \frac{1}{2}$, $N_1 = 200$, $N_2 = 100$.

sense) species may monopolize the best food source even if the inferior competitor is more efficient (Johnson and Hubbell 1975, Morse 1977, Feinsinger and Colwell 1978). I have shown that the same result can occur even in the absence of interference competition.

Finally, note that the rate of energy usage by each bee species, *e*, has no impact on the bee distribution when a single species' rate of energy usage is independent of the flower type it is exploiting.

AN EXAMPLE UTILIZING BUMBLE BEES

Inouye (1978) set out to test the impact of interspecific competition on resource preferences in bumble bees. Inouye observed the behavior of two species of bumble bee, *Bombus flavifrons* and *Bombus appositus*, feeding on two species of flower, *Delphinium barbeyi* and *Aconitum columbianum*. Inouye's data and experimental manipulations provide information that can be used to test my model of habitat selection.

The handling times for each bee species on each flower species were significantly different

$$\begin{aligned} \tau_{1a} &= 4.1 \text{ s} & \tau_{1b} &= 2.9 \text{ s} \\ \tau_{2a} &= 6.1 \text{ s} & \tau_{2b} &= 2.0 \text{ s,} \end{aligned}$$

where henceforth flower type *a* is *Aconitum*, flower type *b* is *Delphinium*, species 1 is *B. flavifrons*, and species 2 is *B. appositus*. Bees of species 1 use flowers of type *a* more efficiently, while bees of species 2 use flowers of type *b* more efficiently. For this data $0.67 = A < B = 1.45$.

Inouye (1978) conducted two removal experiments; in each case bumble bees of one species were removed from their favored flower type. Before the removal of species 1 bees the relative numbers of each species using each flower type were (see Inouye [1978] for details):

	Flower type <i>a</i>	Flower type <i>b</i>
Bee species 1	11.4	4.2
Bee species 2	0.2	12.2.

Before the removal of species 2, an experiment conducted on a different day, the relative numbers of each species using each flower type were:

	Flower type <i>a</i>	Flower type <i>b</i>
Bee species 1	7.5	4.2
Bee species 2	0.2	9.7.

Both initial conditions correspond to a type (p) solution. Using the equations for the type (p) solution and these initial conditions it is possible to estimate the relative productivities of the flower types. Using the solution types I estimate that $R = 0.51$ for the first initial condition, while for the second initial condition $R = 0.41$. To determine the responses of the bumble

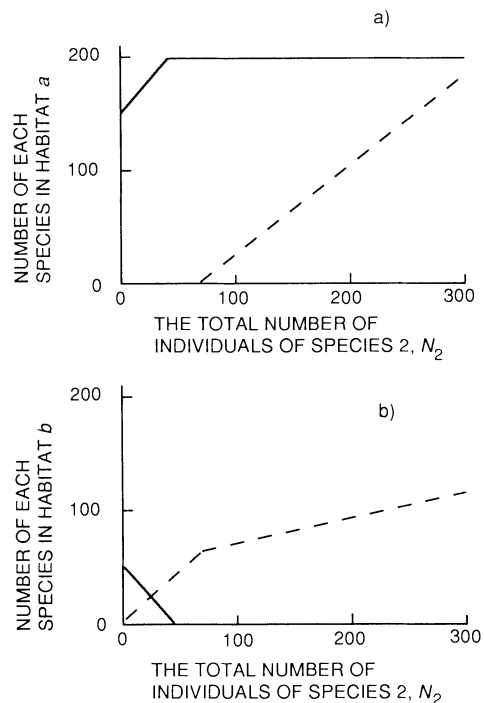


FIG. 6. The effect of an increase in the abundance of species 2 on the distribution of both species in both habitats. The number of individuals of species 2 is indicated by ---, the number of individuals of species 1 is indicated by —. (a) Number using flower type *a*. (b) Number using flower type *b*. Parameters: $A = 1 < B = \frac{1}{2}$, $R = 3$, $N_1 = 200$.

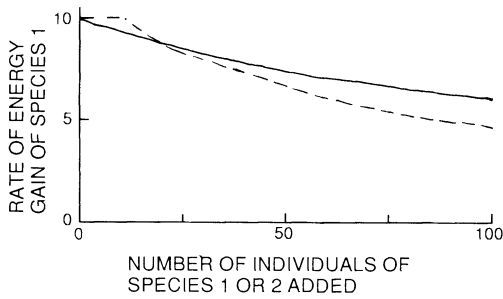


FIG. 7. The net rate of energy gain of species 1 as a function of an increase in the number of individuals of species 1 (—) or species 2 (---). For small increases in the number of bees, intraspecific competition is more intense than interspecific competition; however if the number of bees added is large, the per capita effect of species 2 on the rate of energy gain of species 1 is greater than the per capita effect of species 1 on itself. Parameters: $N_1 = 100$, $N_2 = 12.5$, $R = 2$, $\tau_{1a} = 2$, $\tau_{2a} = 1$, $\tau_{1b} = 4$, $\tau_{2b} = 1$, so $A = 2 < B = 4$, $\lambda_1 P_1 = 1000$.

bees to the experimental manipulations, I use the average of the two values, $R = 0.46$. Clearly it would be better if I could directly calculate productivity for each flower type; however, in this case the data were not available.

The net productivity of flowers of type *b* is greater than that of flowers of type *a*. This explains the total preference of species 2 for its preferred flower type, while species 1 only partially prefers the flower type that it exploits most efficiently, flower type *a*.

After reducing the population size of species 1 by removing bees of this species from type *a* flowers, the distribution of bees became:

	Flower type <i>a</i>	Flower type <i>b</i>
Species 1	4.4 ± 2.3 (6.3)	1.9 ± 1.1 (0.0)
Species 2	1.5 ± 1.3 (0.0)	12.3 ± 3.0 (12.0)

The prediction of my model is indicated in parentheses and the mean values are shown with standard deviations.

The model predicts that bees of species 1 previously using flower type *b* should use flower type *a*. This occurs, but not all species 1 bees change their preference. In the experiment very few bees of species 2 responded to the removal of species 1 bees from flower type *a* by moving to flower type *a*, a result consistent with the model. The separation of species preferences is not as strong as predicted by the model.

After reducing the population size of species 2 by removing bees of this species from type *b* flowers, the relative abundance of species using each flower type was:

	Flower type <i>a</i>	Flower type <i>b</i>
Species 1	6.8 ± 2.3 (6.1)	6.5 ± 2.4 (7.2)
Species 2	0.2 ± 0.4 (0.0)	3.8 ± 2.7 (4.0)

The response of species 1 to the removal of species 2

from flower type *b* is much stronger than the response of species 2 to the removal of species 1. This response is predicted qualitatively by the model.

I believe that Inouye's data provide some support for the model, at least qualitatively.

DISCUSSION AND CONCLUSION

Despite a large number of simplifying assumptions the model appears to provide a reasonable representation of flower type selection by competing bumble bees. Incorporating complexities such as volume-dependent secretion rates by flowers, or net rates of energy use by foragers that depend on flower type, may improve the model quantitatively but detract from its simplicity.

The model presented here is an equilibrium model. Like other models of habitat selection I assume that the choice of flowers by bees reaches an equilibrium distribution. Mesterton-Gibbons (1992) shows that the equilibrium distributions derived in this paper may be interpreted in two ways: first, as the outcome of a com-

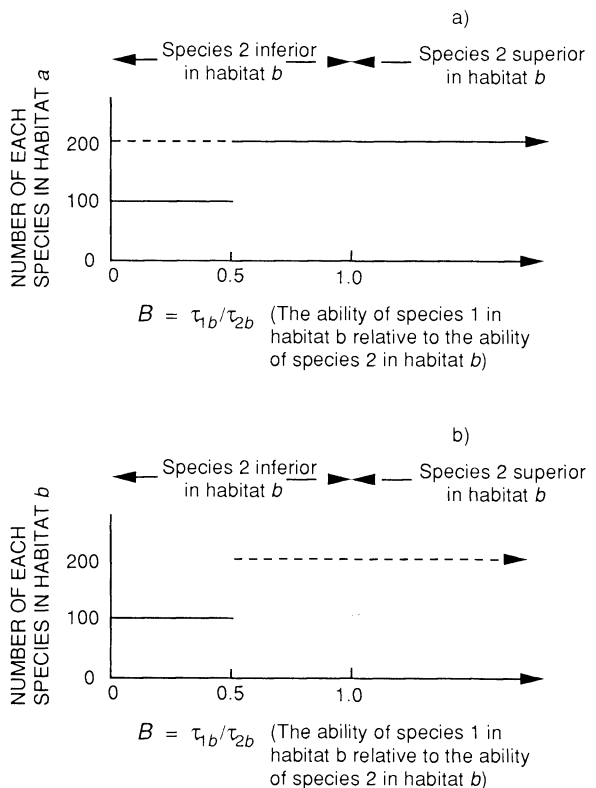


FIG. 8. The number of bees of species 1 (—) and species 2 (---) using: (a) flower type *a*, and (b) flower type *b*, as a function of their relative abilities using flowers of type *b*, B . When $B > 1/2$ the solution types described in the text hold, and species 1 dominates flower type *a*. When $B < 1/2$ the assumption $A < B$ fails and the new solutions (found by reversing the indices) show that species 2 now dominates flower type *a*. Parameters: $N_1 = 200$, $N_2 = 200$, $R = 2$, $\tau_{1a} = 1$, $\tau_{2a} = 2$, so $A = 1/2$.

petitive two-species game, and second, as the stable equilibrium point of two simultaneous differential equations where the variables are the number of each species in one habitat. In reality, however, nectar secretion rates and forager numbers will vary diurnally and seasonally. Consequently I believe that a profitable area of future research would be a study of the dynamics of habitat selection incorporating appropriate rules for habitat choice and learning.

In the single-species and two-species models both flower types will always be visited by some bees. This conclusion relies on the assumption that the rate of nectar secretion is independent of the volume of the nectar in the flower so that flowers can theoretically acquire an infinite nectar volume. If a flower type has a finite nectar volume (or lifetime), then it is possible that no foragers will use that flower type (Possingham 1987).

Two messages of general empirical value emerge from the analysis of this model. First, the results of removal and addition experiments need to be interpreted with caution when inferring the presence or absence of interspecific competition. Using this model of habitat selection I have shown that it is possible for potentially strong competition to go undetected by manipulations of species abundances (Rosenzweig 1979), while it is virtually impossible to evaluate the relative importance of intraspecific and interspecific competition. Where the relative efficiencies of the two species on each flower type are very different, the range of population abundances over which the no-effect manipulations can occur is large. Second, where there is competition by a number of species for a number of resources, the relative efficiencies with which a particular species uses different resources do not necessarily give a good indication of its realized habitat use. When exploitation competition is important, the foraging efficiencies of other species influence the habitat selection of their competitors. The species which is most efficient at utilizing a particular habitat or food source is not necessarily the species that will monopolize that habitat.

Although the model was targeted at a specific data set, modifications to include a much wider variety of situations are possible. The key to the model is the sub-model of renewal and depletion that enables the construction of habitat quality isolines, which are used to predict the distribution and abundance of two species in two habitats. The model can be modified and tested using data on the distribution and abundance of two competitors in two habitats where there is a model of resource dynamics.

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APPENDIX

I) To derive Eq. 5a use Eq. 1 and Eq. 3 to show that

$$N_a = N_b \lambda_a P_a / \lambda_b P_b = N_b R;$$

therefore

$$N = N_a + N_b = N_b(1 + R),$$

which implies Eq. 5a.

II) To derive Eq. 8 remember that the mean nectar content of a flower of type j is λ_j , multiplied by the mean time between visits to that type of flower. If the probability a bee of either species visits a particular flower is independent of previous visits, then the arrival of the bees of each species can be regarded as two independent Poisson streams. The average rate at which bees arrive at the flowers is equal to the sum of the average arrival rates for bees of each species. The mean time between visits to a particular flower is the reciprocal of the average rate at which flowers are visited. Hence the mean energy content of a flower of type j is

$$\mu_j = \lambda_j P_j / (N_{1j} / \tau_{1j} + N_{2j} / \tau_{2j}). \quad (7)$$

III) To derive the habitat isolines we invoke ideal free distribution theory. For species 1, bees using both types of flower have the same net rate of energy gain if

$$\mu_a / \tau_{1a} = \mu_b / \tau_{1b}.$$

Using this equation with Eq. 7 for both flower types gives

$$R(N_{1b} + BN_{2b}) = N_{1a} + AN_{2a},$$

where $A = \tau_{1a} / \tau_{2a}$ and $B = \tau_{1b} / \tau_{2b}$. Using the identities $N_1 = N_{1a} + N_{1b}$ and $N_2 = N_{2a} + N_{2b}$ yields the isoline for species 1,

$$N_{1a} = \frac{R(N_{2a}B + N_{1a})}{R + 1} - \frac{(BR + A)N_{2a}}{R + 1} \quad (9a)$$

and similarly for isoline 2.

IV) To prove that the two isolines do not intersect unless $A = B$, we rewrite Eq. 9 as:

$$(R + 1)N_{1a} + (A + BR)N_{2a} = R(N_1 + BN_2) \\ = (R + B/A)N_{1a} + B(R + 1)N_{2a},$$

implying

$$(B - A)(N_{1a} + AN_{2a}) = 0,$$

which has no solution unless $A = B$.

If the constraint on the number of species 1 is below the intercept of isoline 2 with the y axis, then

$$N_1 < AR(N_1 + BN_2) / (RA + B)$$

so

$$N_1 < ARN_2.$$

The intersection of this constraint with isoline 2 occurs when

$$N_{2a} = \frac{(ARN_2 - N_1)}{A(R + 1)},$$

which is less than N_2 , so the constraints cannot meet below isoline 2.