

Models of optimal foraging and resource partitioning: deep corollas for long tongues

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We model the optimal foraging strategies for 2 nectarivore species, differing in the length of their proboscis, that exploit the nectar provided by 2 types of flowers, differing in the depths of their corollas. When like flowers appear in clumps, nectarivores must decide whether to forage at a patch of deep or shallow flowers. If nectarivores forage optimally, at least one flower type will be used by a single nectarivore species. Long-tongued foragers will normally visit deep flowers and short-tongued foragers shallow flowers, although extreme asymmetries in metabolic costs may lead to the opposite arrangement. When deep and shallow flowers are randomly interspersed, nectarivores must decide, on encounter with a flower, whether to collect its nectar or continue searching. At low nectarivore densities, the optimal strategy involves exploiting every encountered flower; however, as nectarivore densities increase and resources become scarce, long-tongued individuals should start concentrating on deep flowers and short-tongued individuals on shallow flowers. Therefore, regardless of the spatial distribution of flowers, corolla depth can determine which nectarivore species exploit the nectar from each flower type in a given community. It follows that corolla elongation can evolve as a means to keep nectar thieves at bay if short-tongued visitors are less efficient pollinators than long-tongued visitors. *Key words*: competition, habitat selection, nectar concealment. [*Behav Ecol* 17:905–910 (2006)]

When coexisting individuals compete for an ensemble of available resources, variability in their ability to exploit the different resources normally translates, through the operation of optimal foraging, into resource partitioning (Rosenzweig 1981, 1991). Resource partitioning has been described in natural communities of nectarivores (Heinrich 1976a; Pyke 1982; Harder 1985; Graham and Jones 1996; Irwin 2000; Stang et al. 2006), and the conditions leading to it have been modeled when nectarivores differ in the relative efficiency with which they can exploit co-occurring flower types (Possingham 1992; Rodríguez-Gironés 2006).

Possingham (1992) and Rodríguez-Gironés (2006) consider communities where all visitors can extract the same amount of nectar from flowers but differ in the time they require to do so. In many communities, nectarivores differ in the length of their tongues or proboscis and plants in the depth of their flowers' corolla tubes or spurs, so that flower visitors differ in the amount of nectar they can extract from flowers. In this paper, we consider the conditions under which optimal foraging strategies lead to an association between a nectarivore's proboscis length and the corolla depth of the flowers it visits. In practice, long-tongued visitors can extract more nectar than short-tongued visitors from deep corolla tubes and need less time to do so (Inouye 1980). Nevertheless, to study the extent to which nectar availability per se can lead to resource partitioning, we assume that there is no difference in the amount of time that the different flower visitors need to exploit flowers. (Taking this difference into account would strengthen resource partition.)

Previous models of resource partitioning in nectarivores (Possingham 1992; Rodríguez-Gironés 2006) assume that individuals choose the type of flowers they search. This makes

sense when the distribution of flowers is patchy, so that individuals essentially decide where to forage, but it is unclear to what extent the results generalize to the situation where nectarivores come across a sequence of flowers and must decide, for each flower they encounter, whether to visit it or to continue searching. For this reason, we develop 2 foraging models, a patch model and a prey model, to study the effect of the spatial distribution of resources on the expected patterns of resource partitioning.

GENERAL MODEL

Both models consider a community with 2 nectarivore species and 2 flower types. Flowers differ in the depth of the structure containing nectar (corolla tube), and nectarivores differ in the depth from which they can extract the nectar column (tongue length). Nectarivorous species will be referred to as "bees," although the results apply equally to any other taxa. Flowers are thus divided in shallow and deep flowers, and bees are divided in short- and long-tongued species. The number of i flowers ($i = 1$ for shallow or 2 for deep flowers) is F_i , and the number of j bees ($j = X$ for short- or Y for long-tongued bees) is B_j . Table 1 lists all variables used.

The corolla tube of i flowers is c_i mm deep, and the tongue of j bees is t_j mm long. We assume that $c_1 \leq t_X \leq t_Y \leq c_2$. On arrival at a flower, j bees consume any nectar within a distance t_j of the corolla tube opening.

The rate at which flowers secrete nectar depends on factors such as the age of the flower and the time of day (McDade and Weeks 2004). It can decrease as time elapses (Cruden et al. 1983; Castellanos et al. 2002) or remain constant and cease abruptly (Cruden et al. 1983). In our models, we assume that the nectar column in i flowers raises at a constant rate r_i until the column is completely full. This is the most conservative assumption, in the sense that it is the least likely to induce resource partitioning.

Depending on the spatial distribution of deep and shallow flowers, bees will encounter uninterrupted bouts of same-type

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Received 20 February 2006; revised 2 June 2006; accepted 12 June 2006.

Table 1
List of symbols used

F_i	Number of i flowers ($i = 1$ for shallow, $i = 2$ for deep flowers)
B_j	Number of j bees ($j = X$ for short-tongued, $j = Y$ for long-tongued bees)
r_i	Nectar secretion rate
c_i	Corolla depth
t_j	Tongue length
ρ_i	Energy contents per unit length of nectar column
I_{ij}	Expected amount of nectar consumed by j bee at i flower
v_{ij}	Rate at which i flowers are visited by j bees
λ_{ij}	Rate at which j bees find i flowers
E_{ij}	Expected payoff of j bees at i flowers (patch model)
q_{ij}	Probability that a j bee exploits an i flower on encounter (prey model)
k_j^f	Metabolic rate while flying
k_j^p	Metabolic rate while probing flowers for nectar

flowers, random sequences of flowers of each type, or something in between. For simplicity, we consider only the 2 extremes of this continuum, and we ignore the possibility that flowers have a tendency to alternate.

In the models considered below, we will assume that bees visit flowers at random and that the duration of the intervals between consecutive visits by any 2 j bees to a randomly chosen i flower follows an exponential distribution with parameter v_{ij} , which depends on the foraging behavior of the 2 bee species. Given these assumptions, it is possible to determine (Appendix) the average nectar volume that a j bee will consume on arrival at an i flower, I_{ij} :

$$I_{1X} = I_{1Y} = \frac{r_1}{v_{1X} + v_{1Y}} [1 - e^{-(v_{1X} + v_{1Y})c_1/r_1}], \tag{1}$$

$$I_{2X} = \frac{r_2}{v_{2X} + v_{2Y}} e^{-v_{2Y}(t_Y - t_X)/r_2} [1 - e^{-(v_{2X} + v_{2Y})t_X/r_2}], \tag{2}$$

$$I_{2Y} = \frac{r_2}{v_{2Y}(v_{2X} + v_{2Y})} \{v_{2X}[1 - e^{-v_{2Y}(t_Y - t_X)/r_2}] + v_{2Y}[1 - e^{-(v_{2X}t_X + v_{2Y}t_Y)/r_2}]\}. \tag{3}$$

The corresponding energy intake is obtained by multiplying I_{ij} and the energy content per unit length of the nectar column ρ_j . We denote by k_j^f the metabolic rate of j bees while flying and by k_j^p their metabolic rate while foraging (probing) at i flowers. To simplify the algebra, it will be convenient to define the net gain between consuming the nectar of an i flower and ignoring it,

$$e_{ij} = \rho_i I_{ij} - (k_j^p - k_j^f) h_{ij}, \tag{4}$$

where h_{ij} is the time that j bees require to extract the nectar from an i flower (Stephens and Krebs 1986). We further define the profitability of an i flower to a j visitor as e_{ij}/h_{ij} .

FLOWERS WITH CLUMPED DISTRIBUTION (PATCH MODEL)

First, consider the case in which the distribution of each plant species is clumped and bees exploiting a patch encounter flowers of a single type. Bees must decide whether to forage at patches of shallow or deep flowers. Let p_{ij} be the fraction of j bees foraging at i flowers. Within patches, flowers are visited at random, and the duration of the intervals between consec-

utive visits by j bees on an individual i flower follow an exponential distribution with parameter v_{ij} ,

$$v_{ij} = \frac{B_j \lambda_{ij} p_{ij}}{F_i (1 + \lambda_{ij} h_{ij})}, \tag{5}$$

where λ_{ij} is the rate at which j bees encounter flowers while searching in a patch of i -type flowers.

Except for the difference in expected intake rate (Equations 1–3 of this article vs. Equations 2 and 7 in Possingham [1992]), this model is equivalent to that proposed by Possingham (1992). Following the logic of the ideal free distribution (Fretwell and Lucas 1970), individual bees forage at the flower type on which they maximize their expected payoff (Dreisig 1995; Robertson and Macnair 1995; Ohashi and Yahara 2002). If j bees exploit both shallow and deep flowers, their expected payoff must be the same at both flower types:

$$E_{1j} = E_{2j}, \tag{6}$$

where E_{ij} is the expected payoff of j nectarivores exploiting i flowers,

$$E_{ij} = \frac{\lambda_{ij} e_{ij}}{1 + \lambda_{ij} h_{ij}} - k_j^f. \tag{7}$$

One can rewrite Equation 6 as a function of the p_{ij} . (All other variables describe the ecological scenario and are independent of the foraging behavior of bees.) Consider first the case of the short-tongued bees ($j = X$). If we consider p_{1Y} as given (and hence p_{2Y} too because $p_{1Y} + p_{2Y} = 1$), we can solve for p_{1X} combining Equations 6 and 7. This cannot be done analytically (because of the exponentials in Equations 1–3), but Equation 6 and the constraint $p_{1j} + p_{2j} = 1$ define an implicit function of the form $p_{1X}(p_{1Y})$. This function is the X isoline: it defines the set of points, on the (p_{1X}, p_{1Y}) plane, for which X bees obtain the same intake rate at shallow and deep flowers. In a like manner, by swapping indexes, we can define the Y isoline as the set of points where Y bees obtain the same intake rate at shallow and deep flowers. When j bees forage optimally, a community at ecological equilibrium must be on the j isoline or have $p_{ij} \in \{0, 1\}$ (Possingham 1992).

Solution types

In Possingham’s model, both flower types are always visited by some nectarivores because flowers accumulate an infinite amount of nectar if they remain unvisited (Possingham 1992). When, as in the present model, flowers can only hold a finite volume of nectar, it is possible that a flower type is never visited. Let \hat{e}_{ij} be the maximum (modified) gain that a j bee can obtain when foraging at i flowers. This is obtained by substituting, in Equation 4, I_{ij} for the amount of nectar that a j bee would be able to collect from an i flower full with nectar. Type i flowers will remain unvisited if, when all bees concentrate on the other flower type, i' , a hypothetical individual exploiting i flowers obtained a lower payoff than its conspecific. That is, if

$$\frac{\lambda_{ij} \hat{e}_{ij}}{1 + \lambda_{ij} h_{ij}} < \frac{\lambda_{i'j} e_{i'j}}{1 + \lambda_{i'j} h_{i'j}}, \tag{8}$$

where $e_{i'j}$ is evaluated at $p_{i'X} = p_{i'Y} = 1$. Any factor that decreases the left-hand side of Equation 8 will favor the existence of an unused flower type, including low abundance or detectability (low λ_{ij}), large handling time (h_{ij}), low capacity for holding nectar ($\rho_i c_i$), or high extraction cost (k_{ij}^p). Reduced competition (fewer nectarivores) will tend to increase the right-hand side of Equation 8 (through its effect on $e_{i'j}$),

leaving its left-hand side unaltered (because \hat{e}_{ij} is independent of the number of nectarivores), and will also favor the existence of unused flowers.

When both flower types are used, there is resource partitioning: at least one flower type is exploited only by one bee species (Possingham 1992).

Correlation between tongue length and corolla depth

Short- and long-tongued bees harvest the same nectar volumes at shallow flowers, whereas long-tongued bees obtain more nectar than short-tongued bees from deep flowers. In general, therefore, long-tongued bees will be relatively more efficient than short-tongued bees at exploiting deep flowers, and when both flower types are exploited, short-tongued bees should exploit shallow flowers and long-tongued bees should exploit deep flowers. However, the correlation between tongue length and corolla depth need not be perfect, depending on the relative abundance of the 2 flower types and the 2 bee species; short-tongued bees may also exploit deep flowers, or long-tongued bees may also exploit shallow flowers. In addition, the profitability of a flower type depends on a number of parameters that might alter the relative efficiency of the 2 bee species.

From Equations 4 and 7 (in particular, because E_{ij} is an increasing function of I_{ij} and λ_{ij} and a decreasing function of h_{ij} and k_{ij}^p), it is easy to see that for the 2 isolines to intersect, at least one of the following 3 conditions must be satisfied: (1) $\lambda_{1Y} - \lambda_{2Y} > \lambda_{1X} - \lambda_{2X}$, (2) $h_{1Y} - h_{2Y} < h_{1X} - h_{2X}$, or (3) $k_{1Y}^p - k_{2Y}^p < k_{1X}^p - k_{2X}^p$. These conditions imply that, relative to short-tongued bees, long-tongued bees are more efficient at detecting and exploiting shallow than deep flowers. Equations 4 and 7 also imply that the vertical intercept of the Y isoline increases when $\lambda_{1Y} - \lambda_{2Y}$ increases, when $h_{1Y} - h_{2Y}$ decreases, and when $k_{1Y}^p - k_{2Y}^p$ decreases. From these two results, it follows that, if $\lambda_{1Y} - \lambda_{2Y} \leq \lambda_{1X} - \lambda_{2X}$, $h_{1Y} - h_{2Y} \geq h_{1X} - h_{2X}$, and $k_{1Y}^p - k_{2Y}^p \geq k_{1X}^p - k_{2X}^p$, the Y isoline is completely under the X isoline. (This is a sufficient, not a necessary condition.) When the Y isoline is below the X isoline, long-tongued bees are preferentially associated with deep flowers: all long-tongued bees forage at deep flowers and/or all short-tongued bees forage at shallow flowers.

Figure 1 shows how asymmetries in the handling time and/or the metabolic costs associated with nectar extraction might swap the sign of the correlation between tongue length and corolla depth. As the metabolic cost of long-tongued bees foraging at deep flowers increases (all other parameters remain fixed), the system shifts from an equilibrium where short-tongued bees forage at shallow flowers and long-tongued bees at deep flowers to a region where there is resource partitioning, but where 2 equilibria are possible, to a region where all short-tongued bees forage at deep flowers and long-tongued bees use both flower types, eventually reaching a point with total (and reversed) habitat segregation, with long-tongued bees foraging at shallow flowers and short-tongued bees foraging at deep flowers.

FLOWERS WITH RANDOM DISTRIBUTION (PREY MODEL)

In this situation, nectarivores search their environment for individual plants rather than clumps of a favored species. Encounters with shallow and deep flowers follow 2 independent Poisson processes, and λ_{ij} is the rate at which a j visitor encounters i flowers. (Notice that λ_{ij} has slightly different meaning in the 2 models.) On encounter with an i flower, bees must decide whether to exploit it or to continue searching for another flower. If the probability that a j bee exploits an i flower

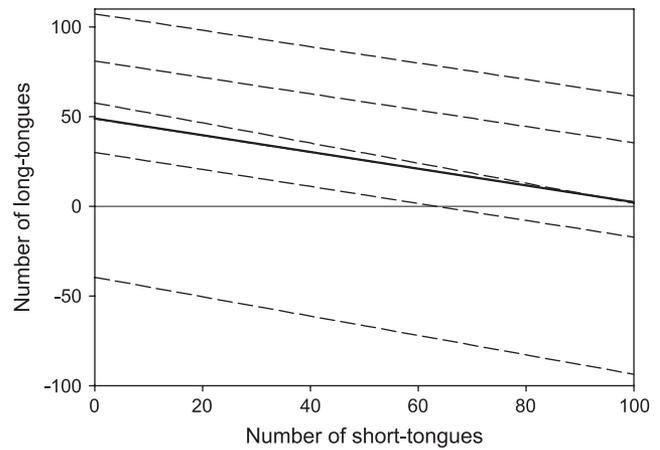


Figure 1 Isoline for short-tongued visitors (solid line) and isolines for long-tongued visitors (dashed lines) for a system with 100,000 flowers of each type and 100 bees of each species. Parameter values are as follows: $c_1 = 5$ mm, $c_2 = 20$ mm, $t_X = 10$ mm, $t_Y = 15$ mm, $r_i = 0.01$ mm s⁻¹, $\lambda_{ij} = 0.1$ s⁻¹, and $h_{ij} = 0.1$ s. Metabolic costs satisfy the condition $k_{ij}^p - k_j^f = 0.01$ energy equivalents of a millimeter of nectar column per second, for all flower types and bee species except for the long-tongued bees foraging at deep flowers. For this combination, $k_{2Y}^p - k_Y^f = \kappa_{2Y}$. Each dashed line corresponds to a different value of κ_{2Y} . From bottom to top, $\kappa_{2Y} = 0.01, 30, 40, 60,$ and 80 .

on encounter is q_{ij} (the condition $q_{1j} + q_{2j} = 1$ need not, and generally will not, apply), then the problem involves finding the values of q_{ij} that maximize the expected net energy intake rate (or similar currency) of X and Y visitors.

The expected net energy intake rate of a j individual accepting i flowers with probability q_{ij} is (Stephens and Krebs 1986)

$$E_j = \frac{\sum_i q_{ij} \lambda_{ij} e_{ij}}{1 + \sum_i q_{ij} \lambda_{ij} h_{ij}} - k_j^f, \tag{9}$$

and the rate at which i flowers are visited by j nectarivores is

$$v_{ij} = \frac{B_j \lambda_{ij} q_{ij}}{F_i (1 + \lambda_{1j} q_{1j} h_{1j} + \lambda_{2j} q_{2j} h_{2j})}. \tag{10}$$

A standard result of the basic prey model is that a given prey type should be always accepted or always rejected on encounter. That is, at the optimal strategy, $q_{ij} \in \{0, 1\}$ for all i and j , the so-called “zero-one rule” (Stephens and Krebs 1986). Essentially, a prey should be accepted if its profitability exceeds the payoff that the forager can expect to obtain by excluding this prey type from its diet and rejected otherwise. What happens when the profitability of a prey type is exactly the same as the payoff that the forager can expect to obtain by excluding it from the diet? In this case, the forager obtains the same payoff regardless of the proportion of prey of this type it consumes on encounter. The optimal strategy is therefore undetermined and the zero-one rule breaks down. When the profitability of prey is independent of the foraging strategy of predators, only a coincidence can make the profitability of a prey type exactly equal the expected payoff obtained by excluding this prey type from the diet. The probability that this happens when parameter values are chosen at random is zero, and this possibility is therefore regarded as a mathematical curiosity (a so-called “degenerate” scenario), with no biological relevance.

This is not the case when the foraging strategy of predators determines the profitability of prey: what in the standard prey model was a mere “pathology” may now become an equilibrium

condition. The model may have an internal solution, if there is at least one q_{ij} with $0 < q_{ij} < 1$, or an external solution if the zero-one rule is satisfied. To find the optimal foraging strategy, we first check whether the model has an external solution. An external solution is a set $\Theta = \{q_{1X}, q_{1Y}, q_{2X}, q_{2Y}\}$, with $q_{ij} \in \{0, 1\}$ for all i and j , such that: (1) if $q_{ij} = 0$, then the profitability of i flowers to j bees is lower than the expected payoff of j bees, both of them calculated at Θ ; and (2) if $q_{ij} = 1$, then the expected payoff of j bees exceeds the payoff that a hypothetical j bee would obtain if it did not visit j flowers (which is calculated setting $q_{ij} = 0$ in Equation 9, leaving the e_{ij} unaltered). There are 16 possible external solutions, but most of them can be automatically discarded because the most profitable flower type must always be included in the diet (Stephens and Krebs 1986).

If the model has no external solution, then the zero-one rule is broken. This can happen because the profitability of a flower type decreases with the frequency with which that flower type is visited. Visiting a flower type may be unprofitable when it is heavily exploited, but if the same flower type is systematically avoided, nectar may accumulate in its corolla until its exploitation becomes worthwhile.

Solution types

Given that $q_{1j} + q_{2j} = 1$ need not hold, we must work with 4 independent variables. This makes it impractical to use the isoline method described above. Instead, one can find the solution as the equilibrium of a system of differential equations. This is tantamount to assuming that the probabilities of visiting flowers on encounter change through time (t) in the direction that increases intake rate (Mesterton-Gibbons 1992). An ecological equilibrium is a set Θ where no individual bee can increase its intake rate by modifying the values of q_{ij} . Given that a system is in state $\Theta = \{q_{1X}, q_{1Y}, q_{2X}, q_{2Y}\}$, we can define Δ_{ij} as

$$\Delta_{ij} = \frac{e_{ij}}{h_{ij}} - \frac{\sum_{i' \neq i} q_{i'j} \lambda_{i'j} e_{i'j}}{1 + \sum_{i' \neq i} q_{i'j} \lambda_{i'j} h_{i'j}}. \quad (11)$$

The optimal foraging equilibrium is the equilibrium point of the system of differential equations:

$$\frac{dq_{ij}}{dt} = \alpha \Delta_{ij} (q_{1X}, q_{1Y}, q_{2X}, q_{2Y}), \quad (12)$$

with $\alpha > 0$ and subject to $0 \leq q_{ij} \leq 1$. This set of differential equations can be solved numerically.

There is no simple relationship between the parameters of the model and the equilibrium values of the q_{ij} , and many combinations can be obtained by introducing asymmetries in metabolic costs (as in Figure 1). Typically, when competition is scarce, all bees exploit every flower they encounter. As competition increases, either the long-tongued bees start avoiding shallow flowers or the short-tongued bees start avoiding deep flowers (possibly both). There is a set of conditions for which bees exploit the nonpreferred flowers with finite probability ($0 < q_{1Y} < 1$ or $0 < q_{2X} < 1$), but when competition for resources is sufficiently high, the nonpreferred flowers are totally avoided ($q_{1Y} = 0$ or $q_{2X} = 0$). Figure 2 shows 2 examples of the relationship between the ecological equilibrium and the density of bees. Increased metabolic cost of flying shifts curves C and D to the right.

DISCUSSION

Differences in the ability of 2 nectarivore species to exploit the nectar of 2 co-occurring flower types will lead to resource

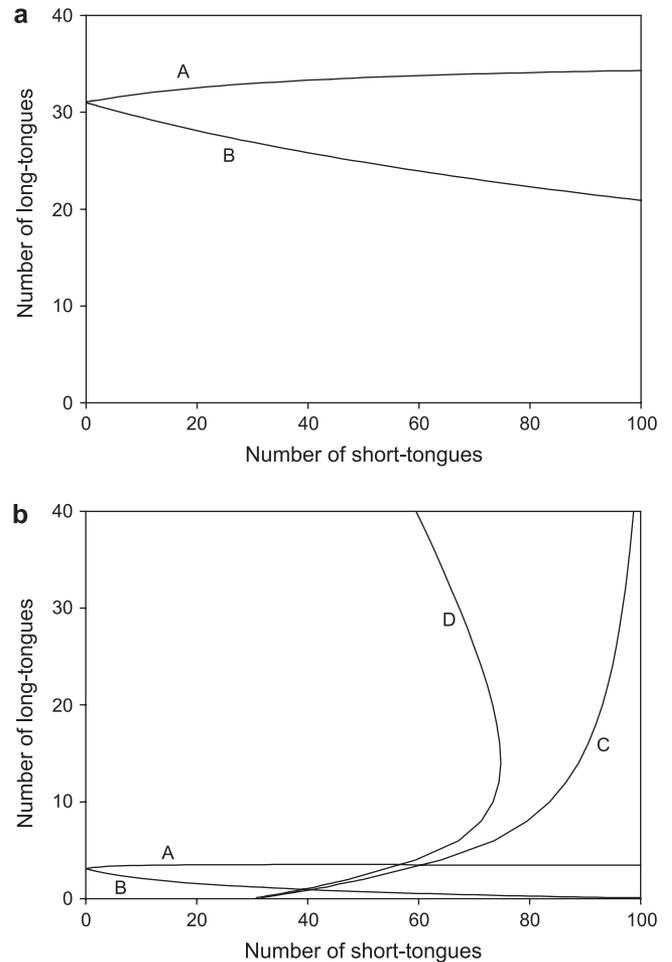


Figure 2

Relationship between the abundance of nectarivores and the ecological equilibrium type. Both panels represent communities with 2,500 deep and shallow flowers, with $c_1 = 5$ mm, $c_2 = 20$ mm, $t_X = 10$ mm, $t_Y = 15$ mm, $\lambda_{ij} = 0.05$ s⁻¹, and $h_{ij} = 0.5$ s. Metabolic costs (in energy equivalents of a millimeter of nectar column per second) are $k_{ij}^d = 0$ and $k_{ij}^s = 0.1$ for all flower types and nectarivore species. The 2 scenarios differ in the rate at which nectar is secreted by flowers, with (a) $r_i = 0.001$ mm s⁻¹ and (b) $r_i = 0.0001$ mm s⁻¹. Short-tongued bees visit all flowers below line B, and completely avoid deep flowers above line A. In between, they exploit some, but not all the deep flowers they encounter ($0 < q_{2X} < 1$). Long-tongued bees exploit all flowers to the left of line D, only deep flowers to the right of line C, and in between these lines they exploit some, but not all, of the shallow flowers they encounter ($0 < q_{1Y} < 1$).

partitioning, in the sense that at least one nectarivore will refrain from exploiting one flower type. This result was originally derived by Possingham (1992) and generalized by Rodríguez-Gironés (2006) when nectarivores differ in the duration of flower visits. The models that we have developed here extend these findings in 2 directions: flower visitors differ in the amount of nectar they can collect from flowers, not in the time they require to exploit them, and foragers may have to decide whether to exploit flowers on encounter.

When foragers choose a patch type to search for food and encounter a single type of flower within that patch, the predictions of the model are essentially the same as those of Possingham (1992): at least one nectarivore will specialize on a single flower type, whereas the other nectarivore may act as a specialist or a generalist, depending on the conditions of the

model. Under most conditions, long-tongued bees exploit deep flowers and short-tongued bees shallow flowers (regardless of which bee species, if any, exploits both flower types), but this correlation need not always hold, and it can be reversed by introducing asymmetries in the exploitation costs (Figure 1).

When flowers are encountered at random, there need not be resource partitioning. In particular, if competition for nectar is scarce, long- and short-tongued bees forage indiscriminately at shallow and deep flowers. As competition increases, short-tongued bees start avoiding deep flowers and long-tongued bees shallow flowers, avoidance being complete when competition is sufficiently high. As in the previous case, it is in principle possible to swap the correlation between tongue length and the corolla depth of the preferred flowers by introducing asymmetries in metabolic costs, but for most realistic parameter values, long-tongued bees will prefer deep flowers and short-tongued bees shallow flowers.

Because our results are based on conservative assumptions concerning the pattern of nectar secretion and the relationship between tongue length and handling time at deep flowers, resource partitioning should be more prevalent than the model predicts. In some colonial species, such as honeybees, *Apis mellifera*, and bumblebees, *Bombus* spp., individual foragers tend to specialize on a single flower type (Heinrich 1976b). Although the reasons for this specialization lie beyond the scope of this paper (but see Darwin 1876; Lavery 1980; Lewis 1986), specialization implies that individuals are searching for particular flower types. When this is the case, the patch model should apply regardless of the spatial distribution of flowers. Once again, this factor should increase the prevalence of resource partitioning.

Short-tongued bees will stop visiting deep flowers as soon as long-tongued bees keep the nectar column of most flowers beyond their reach. On the other hand, long-tongued bees will always encounter some nectar in shallow flowers, no matter how many short-tongued bees are there, and therefore, competition must be intense before long-tongued bees specialize on deep flowers. In general, although a long tongue can be seen as an evolutionary specialization, at the ecological level, long-tongued bees will normally behave as generalists, whereas the short-tongued bees behave as specialist foragers (Harder 1985; Graham and Jones 1996; Borrell 2005; Stang et al. 2006). In flowers, however, evolutionary and ecological specialization go hand in hand because deep flowers are visited by fewer pollinator species.

It is normally assumed that deep corolla tubes evolved because plants that “compelled the moths to insert their probosces up to the very base, would be best fertilised” (Darwin 1862, p. 202). Although this hypothesis has received considerable empirical support (Nilsson 1988; Johnson and Steiner 1997; Alexandersson and Johnson 2002), there are reasons to doubt the universality of this mechanism: flowers with longer corolla tubes are not always better at exporting or receiving pollen than flowers with shorter corolla tubes (Herrera 1993; Lindberg and Olesen 2001; Lasso and Naranjo 2003). Our results suggest an alternative explanation that corolla elongation may be favored because it deters floral parasites from visiting flowers (Rodríguez-Gironés and Santamaría 2005).

APPENDIX

Calculating the expected amount of nectar encountered by a *j* individual at *i* flowers, I_{ij}

Arrival times of *X* and *Y* visitors are independent and exponentially distributed, so if we select an *i* flower at random, the

probability that the time since the departure of the last *X* visitor is between τ_X and $\tau_X + d\tau_X$, and the time since the departure of the last *Y* visitor is between τ_Y and $\tau_Y + d\tau_Y$ is

$$P(\tau_X, \tau_Y) = v_{FX}v_{FY} e^{-v_{FX}\tau_X} e^{-v_{FY}\tau_Y} d\tau_X d\tau_Y. \tag{A1}$$

Let $n_{ij}(\tau_X, \tau_Y)$ be the amount of nectar within reach of a *j* visitor at an *i* flower, given that the time since the departure of the last *X* visitor was τ_X and the time since the departure of the last *Y* visitor was τ_Y . The amount of nectar that a *j* individual can expect to encounter at *i* flowers, I_{ij} , is:

$$I_{ij} = \iint_{0 \leq \tau_X, \tau_Y < \infty} n_{ij}(\tau_X, \tau_Y)P(\tau_X, \tau_Y) d\tau_X d\tau_Y. \tag{A2}$$

The $n_{ij}(\tau_X, \tau_Y)$ (measured as the depth of the nectar column consumed) are calculated as follows.

Shallow (i = 1) flowers

Both short- and long-tongued bees can reach the bottom of the corolla tube; hence, every visitor depletes the nectar of the flower, and the amount of nectar a visitor encounters is the amount that has been produced since the last visit, or the amount that the flower can hold if the time that the flower has remained unvisited exceeds the time that the flower requires to refill its corolla tube with nectar. Hence,

$$i_{1Z}(\tau_X, \tau_Y) = \begin{cases} \tau_X r_1, & \tau_X \leq \tau_Y; \tau_X < c_1/r_1, \\ \tau_Y r_1, & \tau_Y < \tau_X; \tau_Y < c_1/r_1, \\ c_1, & \text{otherwise.} \end{cases} \tag{A3}$$

Deep (i = 2) flowers, short-tongued (X) visitors

For this calculation, we must take into account the fact that short-tongued bees can only consume nectar if the time since the last long-tongued bee visited the flower exceeds $(t_Y - t_X)/r_B$ (this is the time required for the nectar column to rise from t_Y , where it is left by long-tongued visitors, to t_X , where short-tongued bees first reach the nectar).

$$n_{2X}(\tau_X, \tau_Y) = \begin{cases} 0, & \tau_Y \leq (t_Y - t_X)/r_2, \\ \tau_Y r_2 - (t_Y - t_X), & 0 < \tau_Y - (t_Y - t_X)/r_2 \leq \tau_X; \\ & \tau_Y \leq t_Y/r_2, \\ \tau_X r_2, & \tau_X < \tau_Y - (t_Y - t_X)/r_2; \\ & \tau_X \leq t_X/r_2, \\ t_X, & \text{otherwise.} \end{cases} \tag{A4}$$

Deep (i = 2) flowers, long-tongued (Y) visitors

The calculation is done as before, leading to

$$n_{2Y}(\tau_X, \tau_Y) = \begin{cases} \tau_Y r_2, & \tau_Y - (t_Y - t_X)/r_2 \leq \tau_X; \\ & \tau_Y \leq t_Y/r_2, \\ (t_Y - t_X) + \tau_X r_2, & \tau_X < \tau_Y - (t_Y - t_X)/r_2; \\ & \tau_X \leq t_X/r_2, \\ t_Y, & \text{otherwise.} \end{cases} \tag{A5}$$

Substituting Equations A3–A5 into A2 and integrating leads to Equations 1–3.

This research was funded by the Spanish Ministry of Science and Technology (project INVASRED, REN2003-06962). We thank Göran Arnqvist and 2 anonymous reviewers for comments on a previous version of the manuscript.

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