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Resource partitioning among flower visitors: extensions of Possingham's model

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ABSTRACT

Question: How robust is Possingham's (1992) result that, when two nectarivore species compete for the nectar produced by two flower types, optimal foraging leads to resource partitioning?

Mathematical methods: Game theory. Each individual strives to maximize its own pay-off.

Key assumptions: Any number of nectarivore species and flower types, with like-flowers aggregated in patches. Nectar need not accumulate at a constant rate. Energy expenditure differs between flight and flower exploitation. Exploitation time increases with the amount of nectar in flowers. Pay-off can be the expected long-term net rate of energy intake, the foraging efficiency (net energy intake divided by energy expended), or the expected short-term net rate of energy intake.

Predictions: Two nectarivorous species may simultaneously exploit both flower types. This result, however, is extremely rare: the vast majority of parameter values lead to resource partitioning despite the removal of Possingham's simplifying assumptions.

Keywords: exploitation competition, floral nectar, habitat selection, ideal free distribution, optimal foraging.

INTRODUCTION

Resource partitioning through optimal foraging decisions is closely related to the problem of habitat selection studied by Rosenzweig and his collaborators (Rosenzweig, 1981, 1987; Rosenzweig and Abramsky, 1985; Abramsky *et al.*, 1991), and it has broad ecological and evolutionary implications. Resource partitioning has recently been used to explain the association between red flowers and bird pollination (Rodríguez-Gironés and Santamaría, 2004) and the evolution of structures that make nectar inaccessible to floral visitors (Rodríguez-Gironés and Santamaría, 2005). These models rely on the assumption that minor modifications in flower architecture can lead to resource partitioning, and therefore to some flower visitors exclusively exploiting some flower types and completely avoiding others. This may increase pollinator fidelity and minimize pollen loss, or it can furnish plants a means of getting rid of floral parasites. The result that slight differences in the ability of floral visitors to exploit co-occurring resources leads to resource

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partitioning was originally derived under somewhat restrictive assumptions (Possingham, 1992). The purpose of this paper is to show that the results generalize to more complex situations. If they did not, the biological relevance of the results would be questionable.

Resource partitioning is a common outcome when optimal foragers compete for available resources. Competition comes in many different colours, and it is customary to distinguish between interference and exploitation competition, although these are in fact the end points of a continuum. Under interference competition, individuals attempt to defend resources, preventing competitors from reaching them. Interference competition appears when resources are sufficiently clumped to make their defence worthwhile. Dominant individuals monopolize relatively small resource patches, and subordinate individuals forage on poorer, scattered resources. When resources are not defendable, because their density is so low that individuals would have to defend ludicrously large territories, or because the need to travel between nest and resources implies that foragers must be away from their resources most of the time, exploitation competition steps forwards. Rather than defending territories for exclusive use, the optimal foraging strategy essentially consists in ingesting food at the fastest possible pace: under exploitation competition, the only way to keep competitors away from resources is by consuming them first.

As already stated, the dichotomy between interference and exploitation competition is artificial. This general statement applies equally to the particular case of pollination networks, which, at any given time, normally consist of several flowering plant and nectarivore species. Thus, although honey bees and bumblebees are archetypal examples of exploitation competition, bees will occasionally displace competitors from attractive flowers (Brian, 1957). Nevertheless, the distinction is conceptually useful, and I will ignore intermediate situations. Interference competition, although known to occur in stingless bees [Hymenoptera, Apidae, Meliponini (Johnson and Hubbell, 1974; Nieh *et al.*, 2005)], is infrequent in nectarivore insects, and very common in hummingbirds, to the extent that hummingbird species are often classified as either territorial or trap-liners, depending on whether they defend foraging territories or not (Feinsinger, 1976). The predictions of optimality models based on interference competition agree with the foraging behaviour of territorial hummingbirds (Pimm *et al.*, 1985). Models of exploitation competition normally introduce yet another simplifying dichotomy: patch versus prey models (Stephens and Krebs, 1986). Patch models assume that the foraging strategy within a patch is fixed, and that foragers must decide what patches to visit, and for how long to stay in them. Examples of patch models are the marginal value-theorem (Charnov, 1976; Parker and Stuart, 1976) and, more relevant for the present discussion, the ideal free distribution (Fretwell and Lucas, 1970). Prey models, on the other hand, typically assume that foragers encounter several types of food items in a random sequence and must decide whether to consume or forego the items they encounter (Schoener, 1971; Emlen, 1973). When considering the feeding strategies of nectarivores, the prey model would be applicable to meadows with complex communities and no clear spatial segregation, while the patch model would apply when flowers of different types are highly clumped, be it because a single plant produces a large number of flowers (as is the case with many trees and big bushes) or because, due to habitat heterogeneity, similar plants tend to grow together.

The model developed by Possingham (1992), and the extensions presented here, fall into the patch-model category of exploitation competition. Essentially, Possingham (1992) considers two plant species, spatially segregated, and two nectarivore species exploiting their flowers. He then shows that optimal foraging will lead to resource partitioning among flower visitors, in the sense that the two nectarivore species will not simultaneously exploit both flower types. At least one nectarivore species will specialize on a single flower type, while the other may, depending on relative abundance of flowers of each type, behave as a specialist, exploiting the other flower type, or as a generalist, exploiting both flower types.

POSSINGHAM'S MODEL AND ITS ASSUMPTIONS

In this section, I review the original model, as formulated by Possingham (1992), with special emphasis on its underlying assumptions. Whenever possible, I retain the original notation to facilitate comparisons. For a full discussion and technical details, the reader is encouraged to read Possingham's (1992) lucid exposition. For reasons of continuity, I follow Possingham (1992) and assume that both nectarivore species are bees, although the model could equally apply to any other nectarivore species.

Possingham's (1992) solution admits two different interpretations: it can be viewed as the evolutionarily stable strategy of a population game, or as the unique stable equilibrium of a dynamical system, in which a fraction of foragers exploiting the less-rewarding flower type switch to the more-rewarding type in every time unit (Mesterton-Gibbons, 1992). Because the density of flower types and bee species fluctuates wildly in space and time (Herrera, 1996), it is unlikely that Possingham's (1992) solution can be reached as the end-point of an evolutionary game, and in what follows I interpret it as an ecological equilibrium. Throughout the paper, I say that a system is at ecological equilibrium if no individual has an incentive to change its foraging strategy, a sort of ideal free distribution (Fretwell and Lucas, 1970; Mesterton-Gibbons, 1992). Resource partitioning refers to a system where at least one bee species exploits a single flower type, and resource sharing denotes the case where both bee species simultaneously exploit both flower types.

There are two flower types, segregated in space and denoted *a* and *b*. P_j is the number of flowers of type *j*, where $j = a$ or b, and λ_j is the average rate of nectar secretion by flowers of type *j*. There are two bee species, which I indicate by the numbers 1 and 2. (Throughout the paper, the index *i* refers to bee species, and the index *j* to flower type.) N_i is the total number of bees of species *i*, with $i = 1$ or 2. N_{ij} denotes the number of bees of species *i* using *j* flowers, and the average time that a bee of species *i* spends travelling to and collecting the nectar of a flower of type *j* is τ_{ij}. [It is because of this assumption that we are dealing with a patch model. Essentially, bees decide whether to search for one flower type or the other; they do not encounter flowers at random and decide whether to exploit them or not.] The rate at which bees of species *i* spend energy is e_i, independently of the flowers they exploit. With these assumptions, the expected long-term net rate of energy gain by a bee of species *i* using flowers of type *j*, E_{ij}, is (Possingham, 1992, Eqn. 2):

$$E_{ij} = \frac{\mu_j}{\tau_{ij}} - e_i \tag{1}$$

where the mean energy obtained from a flower of type *j* by a bee of any species, μ_j, is (Possingham, 1992, Eqn. 7):

$$\mu_j = \frac{\lambda_j P_j}{N_{1j}/\tau_{1j} + N_{2j}/\tau_{2j}} \tag{2}$$

The quantities $A = \tau_{1a}/\tau_{2a}$ and $B = \tau_{1b}/\tau_{2b}$ reflect the relative efficiencies with which each bee species exploits each flower type, and $R = \lambda_a P_a/(\lambda_b P_b)$ is the ratio of total nectar production by all flowers of type a to total nectar production by all flowers of type b. Assuming that bees behave optimally, Possingham (1992) demonstrated that, except for biologically irrelevant degenerate scenarios satisfying $A = B$, at least one bee species will specialize and forage on a single flower type.

In Possingham's model, nectar accumulates in flowers at a constant rate. Data from different systems provide evidence for nectar secretion rates that are constant (during finite time periods), constant to a fixed maximum, or decreasing (Cruden *et al.*, 1983). This paper studies resource partitioning when nectar accumulates in flowers according to

$$V = V_m(1 - e^{-rt}) \tag{3}$$

where V is the volume of nectar accumulated, t is the time since the flower was last visited (and depleted of nectar), V_m is the maximum level of nectar that the flower can contain, and r is a constant. Equation (3) can approximate constant accumulation of nectar during any desired length of time. It suffices to adjust the values of V_m and r properly.

Possingham (1992) assumes that the rate at which bees use up energy is independent of the flower type they exploit, and that the average time that a bee of species i spends travelling to and collecting the nectar of a flower of type j, τ_{ij}, is independent of the amount of nectar accumulated in the flower. The first assumption may constitute a good approximation if the amount of time expended at flowers is much smaller than the amount of time expended flying from flower to flower, but the validity of the approximation deteriorates as flowers become more abundant and their exploitation lengthier. As for the constancy of the duration of a foraging cycle, it will be a good approximation in systems where the time spent collecting nectar is a negligible fraction of the entire foraging cycle (as in Inouye, 1980), but not when the time spent collecting nectar constitutes a substantial fraction of the foraging time (as in Harder and Real, 1987).

Another issue is the optimization principle followed by Possingham (1992). Ideally, optimal foraging models would derive the fitness-maximizing foraging strategy of individuals. In practice, it is hardly ever possible to derive the link between foraging strategy and fitness, and most models derive the foraging strategy leading to the maximization of some other currency: a fitness surrogate (Stephens and Krebs, 1986). In most circumstances, the expected long-term net rate of energy intake is the one most directly linked to fitness changes. This was the currency chosen by Possingham (1992) in his model. There are, however, some exceptions to the rule and other currencies, such as foraging efficiency (expected long-term energy intake divided by expected long-term energy expenditure), have been proposed (Stephens and Krebs, 1986). In particular, it is notably difficult to derive the best currency for social animals, for example bees (Possingham *et al.*, 1990; Real *et al.*, 1990; Dukas and Edelstein-Keshet, 1998). Honeybees maximize efficiency (Schmid-Hempel *et al.*, 1985), bumblebees maximize neither the expected long-term net rate of energy intake nor the foraging efficiency: they seem to follow the foraging strategy that maximizes the expected *short*-term net rate of energy intake (Harder and Real, 1987).

To be as general as possible, I study resource partitioning when nectar accumulates at diminishing rates (equation 3), when the amount of energy expended at flowers is a substantial fraction of the total energy budget and when the amount of nectar encountered in flowers has a measurable effect on the duration of foraging cycles. Furthermore, I consider whether the currency to be maximized has an effect on the outcome of the model. (A precise definition and formulation of the different currencies is given below.)

The final thing to note is that Possingham's (1992) model refers to two bee species foraging at two flower types. Some of the evolutionary implications of resource partitioning require that the result can be extended to a community with at least two bee species and three flower types (Rodríguez-Gironés and Santamaría, 2005), so our last question will be whether optimal foraging leads to resource partitioning in more complex communities.

TIME–ENERGY BUDGETS AND EXPECTATIONS

The analysis of the different currencies requires detailed consideration of time and energy budgets, as well as some discussion of how expectations are calculated. (In what follows, $<X>$ denotes the expectation of the random variable X.) This section provides the background that we need to understand the analysis of currencies in the case of nectarivore animals exploiting flowers, and generalizes Possingham's (1992) model to cases where nectar accumulates in flowers at decreasing rates and where energy expenditure while at flowers differs from energy expenditure while flying from flower to flower.

A single foraging cycle comprises the following elements: searching for and flying to a flower, entering and leaving the flower, and consuming the nectar it contains. For a bee of species i using flowers of type j, the rate of energy uptake during a foraging cycle, ε_{ij}, is (Harder and Real, 1987)

$$\varepsilon_{ij} = \frac{\chi_j(1 - e^{-r_j t}) - w_i(k_i^p T_{ij}^p + k_i^f T_{ij}^f)}{T_{ij}^p + T_{ij}^f} \tag{4}$$

where χ_j is the amount of energy that a flower of type j contains when full of nectar (i.e. it is the product of the maximum volume of nectar V_m times the energy concentration of nectar for flowers of type j), t is the time since a bee (of any species) last visited the flower, w_i is the mass of bees of species i, k_i^p and k_i^f are the specific metabolic rates (i.e. rates of energy expenditure per unit mass) of bees of species i while exploiting flowers (probing) and flying respectively, T_{ij}^p is the duration of the flower visit (probing time), and T_{ij}^f is the time that a bee of species i requires to locate and reach a flower of type j. The probing time can be further decomposed in the time required to enter and leave the flower, T_{ij}^a, and the time required to consume the nectar it contains (Harder and Real, 1987),

$$T_{ij}^p = T_{ij}^a + (1 - e^{-r_j t})/I_{ij} \tag{5}$$

where I_{ij}, a measure of ingestion rate, is the inverse of the time that a bee of species i requires to consume the nectar of a flower of type j when the flower is full.

The three currencies that I will explore are all derived from equation (4) (or a closely related form in the case of foraging efficiency, see below) by averaging in different ways. The averages will be done with respect to the random variable t, while all other variables will be taken to be fixed parameters. It will be assumed that inter-arrival times follow a gamma distribution (for justification, see Possingham, 1989; Rodríguez-Gironés and Vásquez, 2002). Appendix 1 shows how the parameters of the gamma distribution are related to the parameters of the foraging model.

FORAGING CURRENCIES

I now provide detailed formulation for the three currencies that I will consider: the expected long-term net rate of energy intake, the foraging efficiency, and the expected short-term net rate of energy intake.

The expected long-term net rate of energy intake is defined as the ratio of expected net energy intake to expected foraging time, and it is therefore calculated as:

$$L_{ij} = \frac{\left\langle \chi_j(1 - e^{-r_j t_j}) - w_i(k_i^p(T_{ij}^a + (1 - e^{-r_j t_j})/I_{ij}) + k_i^f T_{ij}^f) \right\rangle}{\left\langle T_{ij}^f + T_{ij}^a + (1 - e^{-r_j t_j})/I_{ij} \right\rangle} \tag{6}$$

The foraging efficiency is defined as the ratio of expected net energy intake to expected energy expenditure, and it is therefore calculated as:

$$R_{ij} = \frac{\left\langle \chi_j(1 - e^{-r_j t_j}) - w_i(k_i^p(T_{ij}^a + (1 - e^{-r_j t_j})/I_{ij}) + k_i^f T_{ij}^f) \right\rangle}{\left\langle w_i(k_i^p(T_{ij}^a + (1 - e^{-r_j t_j})/I_{ij}) + k_i^f T_{ij}^f) \right\rangle} \tag{7}$$

Finally, the expected short-term net rate of energy intake is defined as the expectation of the ratio of net energy intake to foraging time:

$$S_{ij} = \left\langle \frac{\chi_j(1 - e^{-r_j t_j}) - w_i(k_i^p(T_{ij}^a + (1 - e^{-r_j t_j})/I_{ij}) + k_i^f T_{ij}^f)}{T_{ij}^f + T_{ij}^a + (1 - e^{-r_j t_j})/I_{ij}} \right\rangle \tag{8}$$

Both the expected long-term net rate of energy intake and the foraging efficiency can be calculated analytically (as functions of $<t_j>$, itself calculated numerically), since the averages involved are readily reduced to equation (A4) in Appendix 1. On the other hand, I have been unable to integrate equation (8) analytically. All the results presented below have thus been obtained by numerical integration, using the Bulirsch-Stoer algorithm (Press *et al.*, 1997).

RESOURCE PARTITIONING UNDER DIFFERENT CURRENCIES

Methods

Possingham (1992) was able to solve analytically his foraging model. An analytical solution, however, cannot be found when his simplifying assumptions are removed. My approach has therefore been to study a large number of special cases (see below). When the different parameters of the model take specific values, it is possible to conduct the calculations numerically and thus check whether at the ecological equilibrium there is resource partitioning. This is done as explained by Possingham (1992), so I will only describe the method briefly.

The state of the system can be represented by a point on the (N_{1a}, N_{2a}) plane. In fact, only a region of this plane, determined by $0 \le N_{ia} \le N_i$, $i = 1, 2$, needs to be considered. I call this region the 'system's rectangle'. Within the system's rectangle ($0 < N_{ia} < N_i$, $i = 1, 2$), there is resource sharing. On its boundary, there is resource partitioning. Given an initial state for the system, if a certain number of bees of species $i = 1$ swap from *a* to *b* flowers, the point representing the system shifts leftwards along a horizontal line. If bees of species $i = 1$ swap from *b* to *a* flowers, the point shifts rightwards, and if it is bees of species $i = 2$ that move, the point moves vertically (up if they move to *a* flowers, down if they move to *b* flowers).

The $i = 1$ isoline is the set of points (N_{1a}, N_{2a}) where bees of species $i = 1$ obtain the same pay-off regardless of whether they exploit flowers of type *a* or *b*. The $i = 2$ isoline is defined in a similar manner, by swapping indexes. The isolines can be obtained as described by Possingham (1992). In all the results that follow, the equations have been solved numerically using Brent's method (Press *et al.*, 1997).

It is easy to show that the point representing a system at ecological equilibrium must be at the intersection of the two isolines or on the boundary of the system's rectangle. Suppose that the point is within the system's rectangle, and not on the intersection of the two isolines. (For concreteness, assume that it is not on the $i = 1$ isoline, regardless of whether it is on the $i = 2$ isoline.) Because we are within the system's rectangle, there are bees of species $i = 1$ foraging at both flower types. Because the point is not on the $i = 1$ isoline, bees of species $i = 1$ experience a higher pay-off at one flower type than at the other. It follows that those foraging at the less rewarding flowers will have an incentive to shift to the other flower type, so the system is not at equilibrium. This proves that within the system's rectangle, only the intersection between the two isolines can represent a system at equilibrium.

If the two isolines do not intersect within the system's rectangle, the equilibrium must be on the boundary (resource partitioning). To determine what happens when the two isolines do not cross within this region, consider the case where the isoline for $i = 1$ bees lies above the isoline for $i = 2$ bees (Fig. 1). This situation implies that bees of species 1 are relatively more efficient than bees of species 2 at exploiting *a* flowers: whenever bees of species 1 obtain the same intake rate at *a* and *b* flowers, bees of species 2 obtain a higher intake rate at *b* than at *a* flowers. On the upper-right corner of the system's rectangle (above the $i = 1$ isoline), most bees forage at *a* flowers. In this region, *b* flowers are almost unexploited and have high amounts of nectar, so bees of both species would benefit by swapping to *b* flowers. A system represented by a point in this region will tend to shift left- and downwards (see arrows). A similar reasoning shows that systems represented by points below the $i = 2$ isoline will evolve moving right- and upwards. In the region between the two isolines, the system will tend to shift right- and downwards. This is because, in this region, bees of species $i = 1$ benefit by moving from *b* to *a* flowers, while bees of species $i = 2$ benefit by

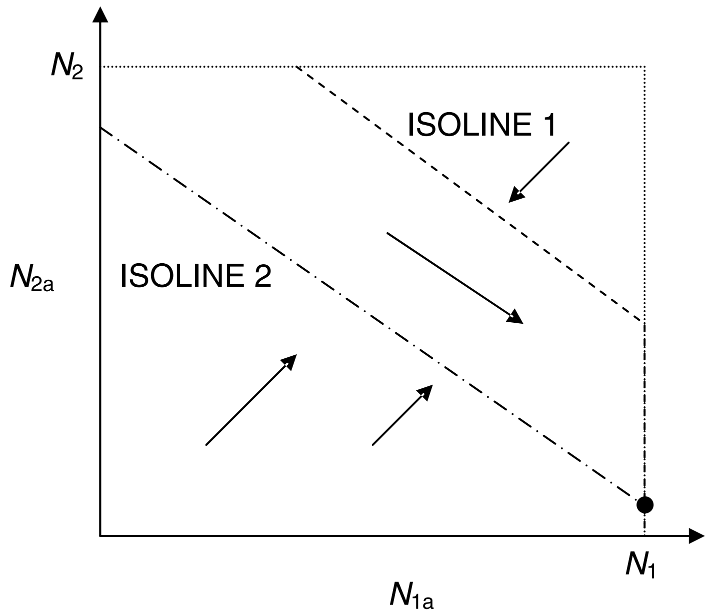

Fig. 1. System without crossing isolines. Arrows show the direction in which the system evolves. The stable point of the dynamics is indicated by a solid circle.

moving from *a* to *b* flowers. As a result, the equilibrium will be represented by the point within the two isolines that can move neither downwards nor rightwards (Fig. 1). This makes sense: because bees of species 1 are more efficient than bees of species 2 at exploiting *a* flowers, at equilibrium either all bees of species 1 will use *a* flowers, or all bees of species 2 will use *b* flowers. There are three different equilibrium types, depending on whether the bottom-right corner of the system's rectangle lies below the $i = 2$ isoline, above the $i = 1$ isoline, or between the two isolines (Possingham, 1992).

Stability criteria

As we have seen, a necessary condition for stable resource sharing is that the two isolines intersect within the system's rectangle. But this is not a sufficient condition. Depending on the relative shape of the two isolines, their intersection can represent a stable or an unstable equilibrium.

If the $i = 1$ isoline is steeper than the $i = 2$ isoline, the equilibrium is stable (Fig. 2). The arrows in the figure show the direction in which the system will tend to evolve for different starting points. In all cases, the value of N_{ia} will tend to increase if bees of species *i* obtain a higher pay-off at *a* than at *b* flowers, and it will tend to decrease if they can obtain a higher pay-off at *b* flowers. Towards the bottom-left corner of the graph (low values of N_{1a} and N_{2a}: most bees forage at *b* flowers), both bee species obtain a higher pay-off at *a* than at *b* flowers, so both N_{1a} and N_{2a} will increase. At the top-right corner of the graph, both N_{1a} and N_{2a} will decrease. In both cases, the point representing the system will move towards the isolines. Consider now starting points on one of the isolines. If the point is on the $i = 1$ isoline, bees of species $i = 1$ will experience no benefit shifting to the other flower type and N_{1a} will remain constant: the system will evolve on a vertical direction towards the $i = 2$ isoline. Left of the intersection point, the system moves downwards; right of the intersection point, the system moves upwards. In either case, the system evolves towards the area comprised

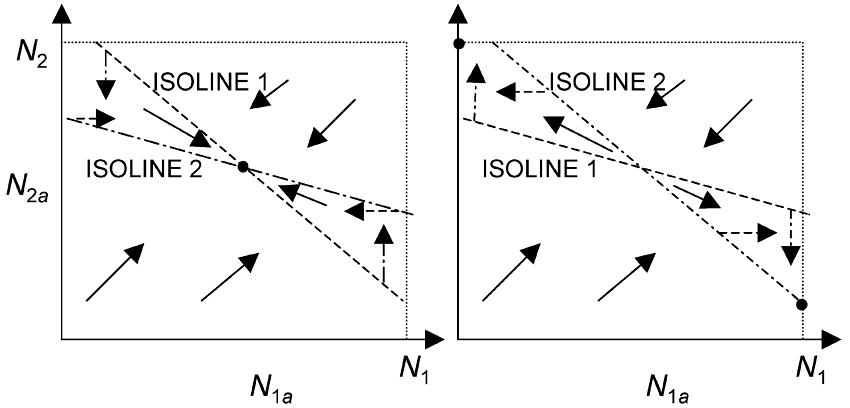

Fig. 2. Stability of the different equilibrium types. Solid arrows show the direction in which the system as a whole evolves. Dashed horizontal arrows point in the direction of the $i = 1$ isoline and dotted-dashed vertical arrows in the direction of the $i = 2$ isoline. When the $i = 1$ isoline is steeper than the $i = 2$ isoline (left), their intersection is a stable equilibrium point, but when the $i = 2$ isoline is steeper than the $i = 1$ isoline (right), the equilibrium is unstable. Stable points of the dynamics are indicated by solid circles.

between the two isolines. The same is true if the starting point is on the $i = 2$ isoline. Within the two isolines, in the triangle left of the intersection point the system moves right and downwards, whereas in the triangle right of the intersection point the system moves left and upwards – that is, the system moves towards the intersection point, which is therefore a stable equilibrium point. If, on the other hand, the $i = 2$ isoline is steeper than the $i = 1$ isoline, the equilibrium is unstable (Fig. 2), as can be shown with an argument similar to the one just presented. The critical difference is that, now, in the area between the two isolines, the system moves away from the intersection.

Parameter values

By considering a large number of possible scenarios, it is possible to study the robustness of Possingham's (1992) results. I have therefore chosen, for each of the three currencies under consideration, one million random sets of parameter values and calculated the proportion of sets leading to resource partitioning. The distributions of parameter values that I have used are given in Appendix 2.

Results

The proportion of runs with crossing isolines was slightly above 1.0×10^{-3}, but most of these cases corresponded to unstable equilibria, and the proportion of runs with stable resource sharing was around, or below, 3.0×10^{-4}. The foraging currency that most consistently led to resource partitioning was efficiency (the proportion of runs with stable resource sharing was 2.2×10^{-5}). The expected long- and short-term net rates of energy intake led to very similar results (proportions of runs with stable resource sharing: 3.5×10^{-4} and 3.1×10^{-4} respectively; Fig. 3).

Most instances of stable resource sharing occurred when the isolines for bees of species $i = 1$ and $i = 2$ were almost identical. Consider a point (N_{1a}, N_{2a}) on the $i = 1$ isoline. By definition of isoline, bees of species 1 obtain the same intake rate on a and b flowers at (N_{1a}, N_{2a}). The vertical distance between the two isolines at this point is the number of bees of species 2 that must swap flowers before bees of species 2 obtain the same intake rate on both flower types. A small vertical difference means that only a few bees must swap flowers. Because the movement of a few bees has a small effect on expected intake rates, this in turn implies that bees of species 2 must obtain almost the same intake rate at both flower types on the $i = 1$ isoline, at the point (N_{1a}, N_{2a}). If the vertical difference between the two isolines is nowhere large, the two bee species are (virtually) ecologically equivalent or, in the terminology of Adler *et al.* (2001), there is 'resource convergence'. In fact, most cases of stable resource sharing correspond to systems where the two bee species are almost ecologically equivalent: the proportion of runs leading to stable resource sharing with isolines differing by at least 1% of the total number of bees at the point of maximum vertical distance was in all cases lower than 2.0×10^{-5} (Fig. 3).

RESOURCE PARTITIONING IN COMPLEX COMMUNITIES

In this section, I revert to the approximations of the original model. The only difference is that I consider a community with arbitrary numbers of bee species and flower types, denoted by I and J respectively, with $I, J \geq 2$.

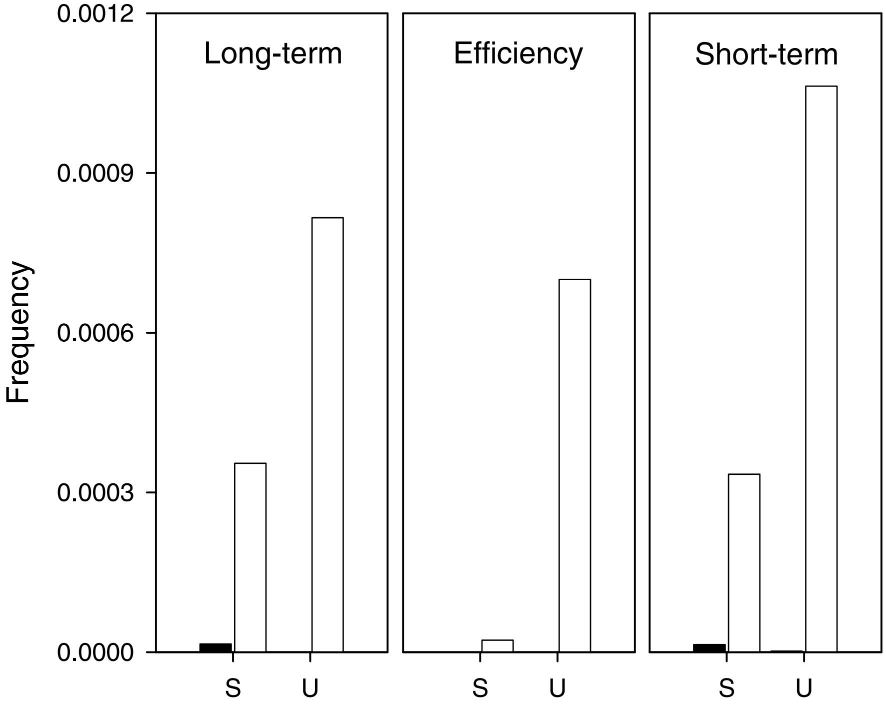

Fig. 3. Empty columns represent the proportion of runs with stable (S) and unstable (U) equilibrium points for the different foraging currencies: long-term rate (left panel), efficiency (middle panel), and short-term rate (right panel). Solid columns to the left of empty columns (not always visible) represent the proportion of runs with stable and unstable equilibrium points and with isolines differing by at least 1% of the total number of bees at the point of maximum vertical distance.

The expected long-term net rate of energy intake experienced by a bee of species *i* using flowers of type *j*, E_{ij}, is still given by equation (1), except that the mean energy that bees obtain from *j* flowers, μ_j, is now

$$\mu_j = \frac{\lambda_j P_j}{\sum_{i=1}^{I} (N_{ij}/\tau_{ij})} \tag{9}$$

This result is obtained as equation (2): each bee species constitutes an independent Poisson stream and contributes an additive term to the average rate at which bees arrive at flowers [the denominator (for details, see Possingham, 1992, Appendix: Section II)].

It is easy to demonstrate that, in general, if bees forage optimally, two bee species will not co-occur at two flower types. Suppose that bees of species *i* exploit flower types *j* and *k*, with $j \neq k$. From the assumption of optimal foraging, it follows that the individuals using *j* and *k* flowers achieve the same energy intake rate, $E_{ij} = E_{ik}$, and hence

$$\mu_j/\mu_k = \tau_{ij}/\tau_{ik} \tag{10a}$$

If another bee species, say $h \neq i$, simultaneously exploits flower types j and k, exactly the same reasoning leads to

$$\mu_j / \mu_k = \tau_{hj} / \tau_{hk} \tag{10b}$$

It is important to note that equations (10a) and (10b) must hold regardless of how many other bee species use flowers of type j and k, and regardless of how many other flower types bees of species h and i are using. Now, from equations (10a) and (10b), it is straightforward to conclude that, for bees of species h and i to simultaneously use flower types j and k, the condition

$$\tau_{hj} / \tau_{ij} = \tau_{hk} / \tau_{ik} \tag{11}$$

must be satisfied. This is an immediate generalization of Possingham's (1992) condition, $\tau_{1a}/\tau_{2a} = \tau_{1b}/\tau_{2b}$, and it is just as biologically irrelevant in the sense that the probability of obtaining this precise equality in a natural system is negligible.

DISTRIBUTION OF BEES AMONG FLOWER TYPES

With Possingham's (1992) simplifying assumptions, it is possible to prove two general results concerning the distribution of bee species among flower types, regardless of the complexity of the community.

Lemma 1: At equilibrium, no flower type remains unused.

Proof: If j flowers remain unused, nectar accumulates indefinitely (equation 9) and a hypothetical bee exploiting j flowers would obtain an infinite intake rate, which will always exceed its expected intake rate at other flower types.

Lemma 2: Consider a community with at least three flower types and two bee species. Given any pair of bees species i and j, and given any three flower types, we can assign labels a, b, and c to the different flower types in such a way that the quantities A, B, and C, defined as $A = \tau_{ia}/\tau_{ja}$, $B = \tau_{ib}/\tau_{jb}$, and $C = \tau_{ic}/\tau_{jc}$, satisfy $A < B < C$. With these definitions, at equilibrium, if bees of species i use c flowers, they also use b flowers.

Proof: The proof is by contradiction. Suppose that bees of species i use c flowers but do not use b flowers. Then lemma 1 implies that bees of species j use b flowers. From equation (10), we have

$$\frac{\mu_b}{\tau_{ib}} < \frac{\mu_c}{\tau_{ic}} \tag{12a}$$

$$\frac{\mu_b}{\tau_{jb}} \geq \frac{\mu_c}{\tau_{jc}} \tag{12b}$$

where the equal sign in equation (12b) is obtained if bees of species j exploit both b and c flowers, and the greater than sign if they do not use c flowers. From equations (12a) and (12b),

$$\frac{\tau_{jb}}{\tau_{jc}} \leq \frac{\mu_b}{\mu_c} < \frac{\tau_{ib}}{\tau_{ic}} \tag{13}$$

and hence $B > C$, contrary to the starting assumption.

In exactly the same way, we can prove that, at equilibrium: if bees of species *i* use *b* flowers, they also use *a* flowers; if bees of species *j* use *a* flowers, they also use *b* flowers; and if bees of species *j* use *b* flowers, they also use *c* flowers.

For concreteness, Fig. 4 gives as a particular example the five types of possible configurations, Σ1, Σ2, . . . Σ5, when there are two bee species and three flower types. Appendix 3 lists the number of bees of each species using each flower type for the different solution types, and the conditions under which each type of solution applies.

DISCUSSION

Resource partitioning can be considered a form of habitat segregation, with which it shares many logical and formal aspects. Possingham (1992) developed a simple and elegant model showing that, under some conditions, optimal foraging leads to resource partitioning among nectarivore species. So long as like-flowers are aggregated in patches, this result is very robust and generalizes readily to more complex situations. Although some sets of parameter values can be obtained for which two bee species simultaneously exploit two flower types, the proportion of parameter sets for which resource sharing was obtained was well below 5.0×10^{-4} when nectar accumulates in flowers at diminishing rates, when flower exploitation takes a substantial fraction of the foraging cycle, and when probing and flying have clearly different metabolic costs. This result was consistent regardless of whether the currency that foraging bees maximize was the expected long-term net rate of energy intake, the foraging efficiency, or the expected short-term net rate of energy intake (Fig. 3).

Within the framework of Possingham's (1992) approximations, resource partitioning ensues regardless of the number of bee species and flower types present in the community. The precise distribution of bees can now be calculated analytically, although the number of possible solutions increases rapidly with the complexity of the community and calculations become somewhat cumbersome. As an example of how the calculations are conducted, I

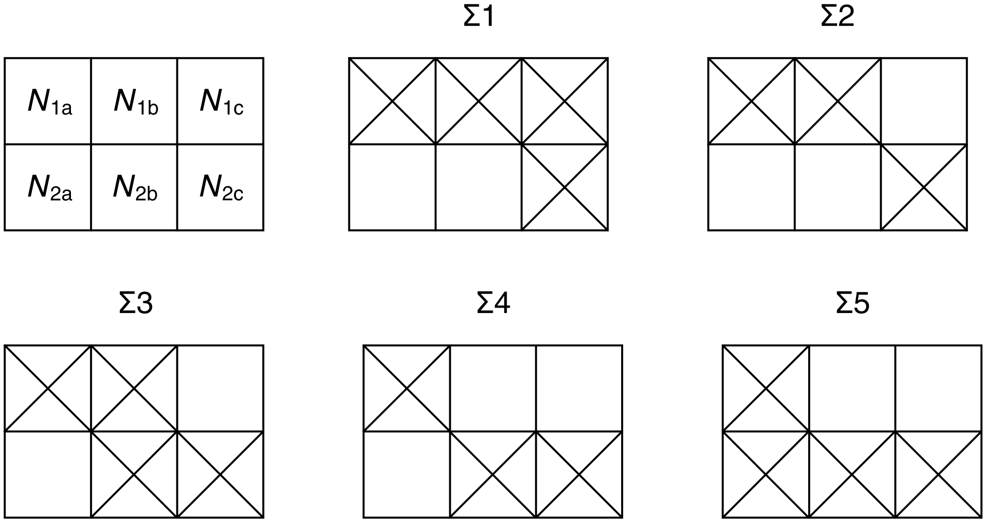

Fig. 4. Solution types (Σ1 through Σ5) for a system with two bee species and three flower types. A crossed square indicates that $N_{ij} > 0$ (with *i*, *j* as in the top-left drawing).

provide the complete solution for the case when two bee species forage in a community with three flower types.

Flowers of the same type will occur in patches if every plant has a large number of flowers (as will normally be the case with trees) or if there is a tendency for plants of the same species to be spatially aggregated. In other circumstances, however, nectarivores will encounter essentially random sequences of flowers belonging to the different types. This may be the typical case for bees foraging in meadows. In the absence of spatial aggregation, we must use 'prey models' to derive the optimal foraging strategy of nectarivores (Stephens and Krebs, 1986). Instead of asking on what flower type a nectarivore should forage, we must consider which flower types a nectarivore must exploit upon encounter. The application of prey models to the current problem is not straightforward, however, because the expected value of each encountered flower will depend on the foraging strategy of every individual in the population: the expected standing crop at a certain flower type will change with the number of individuals including that flower type in their diet. When nectarivores differ in the amount of nectar they can extract from flowers, and not in the time they need to exploit them, the prey model leads to resource partitioning when competition for resources is intense, but in the absence of competition all nectarivores exploit the nectar of every flower they encounter (M.A. Rodríguez-Gironés and L. Santamaría, unpublished). It seems likely that these results generalize to the current scenario. If this were the case, the degree of flower fidelity should increase with the density of nectarivores (relative to resource abundance), a prediction that should be easy to check in the field.

Adler *et al.* (2001) have developed some models that share many points with Possingham's (1992) model and the generalizations presented here. The key difference is that Adler *et al.* (2001) consider predators (such as filter feeders) that continuously consume resources, instead of having to search for individual prey items. Despite this difference, their models typically lead to resource partitioning, although in some of the scenarios they consider the proportion of parameter values leading to resource sharing ('resource convergence' in their terminology) is larger than within the present framework.

At the ecological level, resource partitioning among flower visitors is important because the reproductive success of entomophilous and ornitophilous plant species is, to a large extent, determined by the foraging decisions of individual birds and insects. Resource partitioning implies that some pollinator species are constant in their foraging choice, completely excluding the nectar of some flowers from their diet. At the very least, then, resource partitioning is associated with a higher probability of within-species pollen transfer.

The evolutionary consequences of resource partitioning stem from its importance at the ecological time scale: subtle changes in floral characters can make a pollinator specialize on a certain flower type, or they can discourage other species from visiting them. Rodríguez-Gironés and Santamaría (2004) used Possingham's (1992) results to suggest an explanation for the evolutionary relationship between red flowers and bird pollination. Even if bees can see red flowers, the fact that they require more time to detect red flowers than flowers of other colours (Spaethe *et al.*, 2001) suffices to predict resource partitioning along the colour dimension, with birds tending to specialize on red flowers. A more abstract model (Rodríguez-Gironés and Santamaría, 2005) used the logic of resource partitioning to show that avoidance of floral parasites (individuals that remove nectar without effecting pollination, particularly if they damage reproductive structures in the process) has very different outcomes depending on the community within which it takes place. If a pollinator and a parasite obtain their nectar from a single plant species, parasite avoidance can lead to a runaway process, whereby the plant conceals its nectar behind barriers of increasing complexity or strength, but the presence of a second source of nectar immediately breaks down this arms race.

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APPENDIX 1: RELATIONSHIP BETWEEN THE PARAMETERS OF THE GAMMA DISTRIBUTION AND THE FORAGING MODEL

A random variable T has a gamma distribution with parameters α and β ($\alpha > 0$, $\beta > 0$) if T has a continuous distribution for which the probability density function is $f(t|\alpha, \beta) = \beta^{\alpha} t^{\alpha-1} e^{-\beta \cdot t} / \Gamma(\alpha)$ when $t > 0$, and $f(t|\alpha, \beta) = 0$ otherwise. The mean and variance of the gamma distribution are

$$\langle t \rangle = \frac{\alpha}{\beta} \tag{A1}$$

$$\sigma^2 = \frac{\alpha}{\beta^2}$$

The coefficient of variation (the standard deviation divided by the mean), v, of the gamma distribution is therefore $v = 1/\sqrt{\alpha}$. Since β is essentially a scale parameter, the shape of the distribution is solely determined by α. When $v = \alpha = 1$, we have an exponential distribution and flowers are visited at random (Poisson process). For $v < 1$, foraging is systematic: inter-arrival times tend to have roughly the same duration (in the limit $v = 0$, inter-arrival times are perfectly constant). For $v > 1$, the dispersion of inter-arrival times is greater than with random foraging (Fig. A1).

If we assume that the coefficient of variation of inter-arrival times is fixed for a given community, then the average value of the inter-arrival times, $<t>$, can be calculated from the number of bees exploiting each flower type. It is therefore possible to relate the

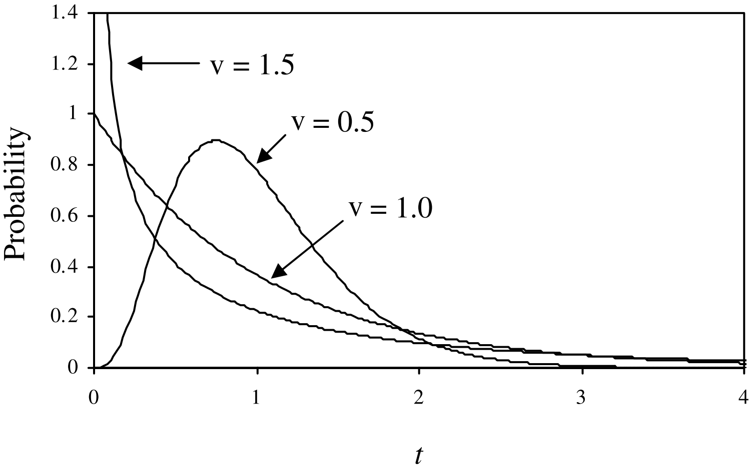

Fig. A1. Gamma distribution with three different values of the coefficient of variation, *v*, and expected value $<t> = 1$.

parameters of the gamma distribution to the parameters of the foraging model. To calculate $<t>$, we first note (Possingham, 1992, Appendix: Section II) that

$$\langle t_j \rangle = \frac{P_j}{N_{1j}/\langle \tau_{1j} \rangle + N_{2j}/\langle \tau_{2j} \rangle} \tag{A2}$$

The only problem lies in the fact that the $<\tau_{ij}>$ are themselves functions of $<t>$, since

$$\langle \tau_{ij} \rangle = T^f_{ij} + T^a_{ij} + \langle 1 - e^{-r_j t_j} \rangle / I_{ij} \tag{A3}$$

The expectation in the right-hand side of equation (A3) can be integrated (Possingham, 1989), giving

$$\left\langle 1 - e^{-r_j t_j} \right\rangle = 1 - \left(\frac{1}{1 + r_j \langle t_j \rangle v_j^2} \right)^{1/v_j^2} \tag{A4}$$

Substituting equations (A3) and (A4) in equation (A2) we obtain a (non-linear) equation for $<t_j>$ that must be solved numerically. Provided that all the parameters in equations (A2) to (A4) are non-negative and that $P_j\,(N_{1j} + N_{2j}) > 0$, equation (A4) has a unique solution for $<t_j> > 0$. In all the results presented in the main paper, $<t_j>$ has been calculated using the bisection method (Press *et al.*, 1997). Knowing $<t_j>$ and v_j, we can calculate α_j and β_j from equation (A1).

APPENDIX 2: DISTRIBUTION OF PARAMETER VALUES USED IN THE SIMULATIONS

- Number of *a* flowers: P_a uniformly distributed in (1000, 9000).
- Number of *b* flowers: $P_b = 10{,}000 - P_a$. The total number of flowers is thus 10,000, and the proportion of *a* flowers varies between 0.1 and 0.9. The total number of flowers can be kept fixed without loss of generality, since all that matters for the model is the ratio of bees to flowers.

- Total number of bees: $N_1 + N_2$ uniformly distributed in (10, 1000). There are thus between 10 and 1000 flowers per bee, which is a rather broad range.
- Proportion of bees belonging to species $i = 1$: uniformly distributed in (0.1, 0.9).
- Coefficient of variation of the inter-arrival time distribution, v_j: normally distributed, with mean of 1 and standard deviation of 0.3. The distribution was truncated to the left at $v_j = 0.5$. Lower values would imply inter-arrival times unrealistically constant.
- Rate of nectar production, r_j: uniformly distributed in (0.0001 s^{-1}, 0.001 s^{-1}). With these rates of nectar accumulation, it takes between 10 min and 2 h before the amount of nectar accumulated reaches half of the maximum volume. I have not explored lower values of r_j because they can be well approximated by constant rates of nectar production, which lead to resource partitioning (Possingham, 1992). Higher values are utterly unrealistic.
- Body mass of bees, w_i: uniformly distributed in (0.05 g, 0.5 g). In principle, the model applies equally to hummingbirds or lizards consuming nectar, which can have substantially higher body masses, but specific metabolic rates are very different for each type of animal and I have therefore restricted this part of the analysis to bees.
- Specific metabolic rate of probing, k_i^p: uniformly distributed in (0.02 $J \cdot g^{-1} \cdot s^{-1}$, 0.04 $J \cdot g^{-1} \cdot s^{-1}$). Heinrich (1975) gives the value $k_i^p = 0.034\ J \cdot g^{-1} \cdot s^{-1}$.
- Specific metabolic rate of flying, k_i^f: uniformly distributed in (0.3 $J \cdot g^{-1} \cdot s^{-1}$, 0.5 $J \cdot g^{-1} \cdot s^{-1}$). Heinrich (1975) gives the value $k_i^f = 0.435\ J \cdot g^{-1} \cdot s^{-1}$.
- Ingestion rate, I_{ij}: uniformly distributed in (0.1 s^{-1}, 2.0 s^{-1}). Bees would require between 0.5 s and 10 s to consume the nectar of a completely full flower. This range most likely over-represents the long values of ingestion time, but when ingestion time can be neglected we revert to Possingham's (1992) approximation.
- Time to enter and leave the flower, T_{ij}^a: uniformly distributed in (0.01 s, 2.0 s).
- Time to locate and reach a flower, T_{ij}^f: uniformly distributed in (0.1 s, 10.0 s). This range excludes some tropical solitary bees and moths that fly hundreds of metres from flower to flower, but these systems are probably rather exceptional and might not fit into the framework of the model for other reasons. [Essentially: as developed by Possingham (1992) and extended here, this is a patch-choice model, while solitary bees and moths searching isolated flowers would fit better in a prey-choice model. See Stephens and Krebs (1986) for further discussion of foraging models.]
- Maximum amount of energy that a flower can contain, χ_j: uniformly distributed in (127.4 J, 190.5 J). The choice of χ_j was made as follows. When parameters are chosen at random, it is possible that the amount of nectar produced by all flowers is insufficient to sustain the bee population, in which case it is useless to consider whether at ecological equilibrium there is resource partitioning or not. (At ecological equilibrium most bees would be dead.) I therefore assumed that χ_j was uniformly distributed in the range (x, 1.5 x) and ran several series of 10,000 iterations to determine the value of x for which the probability that the flower community produced enough nectar to maintain the bee community was 0.5. The value turned out to be $x = 127.4$ J, and it was this value that was used for the longer run of simulations from which I calculated the proportion of parameter sets leading to resource partitioning. This longer run continued until one million sets of parameter values producing sustainable communities were obtained. The unsustainable communities obtained in the process were ignored in the analysis of resource partitioning. All 'random' numbers were generated with the functions 'ran1' and 'gasdev' (for uniform and normal distributions, respectively) of Press *et al.* (1997).

APPENDIX 3: SOLUTION OF THE SPECIAL CASE: TWO BEE SPECIES, THREE FLOWER TYPES

The numbers of bees using each type of flower are obtained as the result of a set of linear equations having the N_{ij} as unknown. There are two equations (one for each bee species) of the form $N_{ia} + N_{ib} + N_{ic} = N_i$, plus equation (10) which should appear as many times as required. (If bees of species i use m types of flowers, equation (10) should appear $m - 1$ times for these bees.) Below, $R_{ab} = \lambda_a P_a / (\lambda_b P_b)$, $R_{bc} = \lambda_b P_b / (\lambda_c P_c)$, and $R_{ac} = \lambda_a P_a / (\lambda_c P_c)$. The conditions under which each solution type applies are obtained by demanding that all the $N_{ij} \geq 0$ and that if a bee species does not use a certain flower type, the intake rate that it would achieve at that flower type would be smaller than the intake rate it achieves at the flowers it uses.

Solution type Σ1:

$$\left.\begin{array}{ll} N_{1a} = \dfrac{R_{ac}(N_1 + CN_2)}{1 + R_{ac} + R_{bc}} & N_{2a} = 0 \\[2ex] N_{1b} = \dfrac{R_{bc}(N_1 + CN_2)}{1 + R_{ac} + R_{bc}} & N_{2b} = 0 \\[2ex] N_{1c} = \dfrac{N_1 - (R_{ac} + R_{bc})CN_2}{1 + R_{ac} + R_{bc}} & N_{2c} = N_2 \end{array}\right\}$$

Condition:

$$N_1 \geq (R_{ac} + R_{bc})CN_2$$

Solution type Σ2:

$$\left.\begin{array}{ll} N_{1a} = \dfrac{R_{ab}N_1}{1 + R_{ab}} & N_{2a} = 0 \\[2ex] N_{1b} = \dfrac{N_1}{1 + R_{ab}} & N_{2b} = 0 \\[2ex] N_{1c} = 0 & N_{2c} = N_2 \end{array}\right\}$$

Condition:

$$(R_{ac} + R_{bc})BN_2 \leq N_1 \leq (R_{ac} + R_{bc})CN_2$$

Solution type Σ3:

$$\left.\begin{aligned}
&N_{1a} = \frac{R_{ac}}{1 + R_{ac} + R_{bc}} (N_1 + BN_2) && N_{2a} = 0 \\
&N_{1b} = \frac{1}{1 + R_{ac} + R_{bc}} [(1 + R_{bc}) N_1 - BR_{ac} N_2] && N_{2b} = \frac{1}{1 + R_{ac} + R_{bc}} \left[(R_{ac} + R_{bc}) N_2 - \frac{1}{B} N_1 \right] \\
&N_{1c} = 0 && N_{2c} = \frac{1}{1 + R_{ac} + R_{bc}} \left(\frac{1}{B} N_1 + N_2 \right)
\end{aligned}\right\}$$

Condition:

$$\frac{R_{ac}}{1 + R_{bc}} BN_2 \leq N_1 \leq (R_{ac} + R_{bc}) BN_2$$

Solution type Σ4:

$$\left.\begin{aligned}
&N_{1a} = N_1 && N_{2a} = 0 \\
&N_{1b} = 0 && N_{2b} = \frac{R_{bc}}{1 + R_{bc}} N_2 \\
&N_{1c} = 0 && N_{2c} = \frac{1}{1 + R_{bc}} N_2
\end{aligned}\right\}$$

Condition:

$$\frac{R_{ac}}{1 + R_{bc}} AN_2 \leq N_1 \leq \frac{R_{ac}}{1 + R_{bc}} BN_2$$

Solution type Σ5:

$$\left.\begin{aligned}
&N_{1a} = N_1 && N_{2a} = \frac{R_{ac} N_2 - (1 + R_{bc}) \dfrac{1}{A} N_1}{1 + R_{ac} + R_{bc}} \\
&N_{1b} = 0 && N_{2b} = \frac{R_{bc} \left(\dfrac{1}{A} N_1 + N_2 \right)}{1 + R_{ac} + R_{bc}} \\
&N_{1c} = 0 && N_{2c} = \frac{\dfrac{1}{A} N_1 + N_2}{1 + R_{ac} + R_{bc}}
\end{aligned}\right\}$$

Condition:

$$N_1 \leq \frac{R_{ac}}{1 + R_{bc}} AN_2$$