

Effects of body size and sociality on the anti-predator behaviour of foraging bees

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Pollinators, like most other animals, often face a tradeoff between increasing food uptake and minimising predation. An earlier model suggests that social bees should be more likely than solitary bees to adopt riskier foraging strategies in order to increase food uptake. In this paper, we extend this model by studying the effect of body size, in addition to sociality, on the predation–intake rate tradeoff. When, following standard practice, we express the foraging strategies in terms of mortality probability and net food uptake, we find that body size should have no effect on the foraging strategies of solitary bees. Social bees, on the other hand, should change their foraging preferences according to their size. Small social bees should tend to maximise food uptake, and large social bees to minimise mortality rate. Mortality, however, is the product of two terms: the probability of suffering an attack and the probability of succumbing to it. Noting that larger bees are less susceptible to succumb to a predation attempt than smaller bees, model predictions change when foraging strategies are expressed in terms of exposure to predators. Following this second approach, exposure to predators should increase monotonically with body size in solitary bees. In social bees it should reach a minimum for medium-sized bees. We conclude that both bee body size and sociality should be considered when studying the effect of predators on resource use.

Pollinator insects are attacked by a suite of ambush predators (crab spiders, assassin bugs, ambush bugs) while collecting pollen and nectar at flowers, and several studies have shown that bees are capable of detecting the presence of these predators (Heiling and Herberstein 2004), and adjust their foraging behaviour accordingly (Dukas 2001, Dukas and Morse 2003, Gonçalves-Souza et al. 2008). Thus, ambush predator populations may affect pollinator reproductive success directly through predation, but also indirectly – inducing changes in foraging behaviour resulting in lower foraging effectiveness.

By modifying pollinator foraging behaviour, ambush predator populations may also affect plant reproductive success (Higginson et al. 2010). On the one hand, patch avoidance and/or increased flower inspection times result in decreased flower visitation rates, sometimes accompanied by reduced seed-set (Suttle 2003, Dukas 2005). On the other hand, decreasing the number of visits per individual entails higher levels of outcrossing at the expense of geitonogamy, thus lowering the risk of potential inbreeding depression (de Jong et al. 1993). Therefore, the response of pollinators to spatiotemporal heterogeneity in predation risk has the potential to affect plant community structure and composition. Where predators have been shown to affect plant fitness through a decrease in pollinator visitation, this effect has been mediated by changes in the foraging strategy of the pollinators, which tend to avoid risky patches (Suttle 2003,

Gonçalves-Souza et al. 2008), rather than by changes in pollinator density.

To predict how pollinators react to variability in predation risk, and the extent to which predators may affect plant community composition through their effects on pollinator behaviour, we must first understand how pollinators trade off intake rate for safety to maximise their expected fitness. Because of the strong link between resource acquisition and fitness in pollinating insects, pollinators have long been used as model system to test predictions of optimal foraging theory (Heinrich 1979, Pyke 1979, Dreisig 1995), and the number of experimental studies dealing with how pollinators detect and avoid predators has steadily increased over the last decade. The issue of how pollinating insects tradeoff foraging intake for predation risk, however, has received little attention despite its importance in most systems so far studied (Verdolin 2006).

A model developed by Houston et al. (1988), hereafter referred to as the HSK model, addresses the question of why social bees tend to maximise foraging efficiency, rather than intake rate. Because the model considers the effect of worker mortality on the foraging strategy of social bees, it can easily be extended to study the tradeoff between intake and safety. A later model, developed by Clark and Dukas (1994) and hereafter referred to as the CD model, illustrates how Gadagkar's (1990) 'insurance effect' can explain differences in the foraging strategies of social and solitary bees. To do so,

the model explores whether social and solitary bees differ in their response to the tradeoff between intake rate and safety. The CD model concludes that social bees should adopt riskier foraging strategies because they may have positive fitness even if they die prematurely, as other workers may continue the brood rearing process, an option not available to solitary species. Because of its original goal and simplifying assumptions, it is difficult to envisage how the CD model could be extended to answer complex ecological questions, such as the effect of ambush predators on the structure of pollination networks, or behavioural questions concerning the mechanisms involved in predator detection and avoidance.

In this paper, we build upon the CD model by removing some of the more restrictive simplifications and explicitly considering the effect of body size on predator avoidance behaviour. We address the following questions: 1) should social and solitary bees adopt different foraging strategies to solve the conflicting demands of increasing intake rate and decreasing predation risk? 2) Does body size affect the level of predation risk adopted by foragers? If so, does it affect social and solitary species similarly? Although most of our conclusions apply to other pollinator groups, we restrict our model to bees.

Social bees

Bees make foraging trips to and from their nest. Mortality risk per trip is denoted by μ_t , and the average net food uptake per trip by ϕ_t . The CD model assumes that there is an unlimited season, with constant conditions and no senescence. Although senescence can be included in the model, this refinement has a very small effect on model predictions (Appendix 1) and we deal with it no further. With the model's assumptions, the number of trips that a bee is expected to complete in her lifetime is $(1 - \mu_t)/\mu_t$ (Clark and Dukas 1994).

For social bees, the CD model assumes that fitness is maximised when individual workers maximise their total expected lifetime food recovery. With this assumption, the quantity that a social bee must maximise, $W_{CD, \text{social}}$, in order to maximise its fitness can be written as (Eq. 1 in Clark and Dukas 1994)

$$W_{CD, \text{social}} = \frac{1 - \mu_t}{\mu_t} \phi_t \quad (1)$$

For low predation rates (μ_t much lower than 1), the foraging option maximizing fitness of social bees in the CD model is the one maximizing ϕ_t/μ_t .

Social bees – extended model in (μ, ϕ) phase space

Temperate social bees with an annual cycle typically found new colonies at the beginning of the season. Colonies first experience a phase of near exponential growth, during which only workers are produced, and then switch to the production of reproductive individuals. This type of colony cycle is found in many primitively eusocial species such as most bumblebees (*Bombus*) and some sweat bees (*Halictus*, *Lasioglossum*) (Michener 1974). While the lifespan of workers is much shorter than the season, the lifespan of

the colony is roughly as long as the season (Heinrich 1979, Kukul and May 1991, Knerer 1992). With seasons of finite duration, the reproductive success of a colony is an increasing function of its size when it switches from producing workers to reproductive individuals, and hence of its growth rate during the exponential phase (Müller and Schmid-Hempel 1992). Following the HSK model, we will therefore search for the foraging strategies that maximise colony growth rate.

It is important to point out that the principle of colony-growth maximisation probably applies to highly eusocial bees as well (Houston et al. 1988), such as honeybees (*Apis*) and stingless bees (Meliponini), in which colony growth rate determines the number of reproductive offspring that can be produced each season (Free and Williams 1975).

The first difference between our model and the original CD model for social bees is therefore the use of colony growth rate, rather than expected lifetime food harvest per bee, as fitness measure. Note that, in the absence of senescence, bees can maximise their expected lifetime food harvest following strategies associated with very low net intake rates. This happens, for instance, when the exploitation of a poor food source is virtually risk-free. When such food sources exist, our model will make very different predictions from the CD model.

How is colony growth rate maximised? The colony's capital is the sum of two terms: the food resources stored in the colony's larder (pollen and nectar), and the resources that have been invested in producing workers. Through foraging, workers increase the colony's food resources, but by exposing themselves to predation risk they decrease the colony's workforce. The lifetime net contribution of a worker to colony's growth is hence the difference between two terms, representing the amount of resources it manages to bring to the colony (referred to as Harvest in Eq. 2), and the amount of resources that were invested in producing the worker, E – as these resources leave the colony once the worker dies. The worker's contribution to colony growth rate is this amount divided by the worker's lifespan. With these considerations in mind, the fitness function for social bees, W_{social} , can be written as

$$W_{\text{social}} = \frac{\langle \text{Harvest} \rangle - E}{\langle \text{Lifespan} \rangle} \quad (2)$$

where terms in brackets represent expected values of the corresponding variables.

The amount of resources that a bee is expected to provide is the number of foraging trips she is expected to complete in her lifetime times the amount of food brought to the colony per trip, L , and $\langle \text{Lifespan} \rangle$ is the expected number of trips times the average duration of each trip, which is the number of flowers visited per trip times flower exploitation time, $t \cdot L/\phi$. Because the number of trips that a forager is expected to complete through her lifetime is $(1 - \mu_t)/\mu_t$, Eq. 2 becomes

$$W_{\text{social}} = \frac{L \times (1 - \mu_t)/\mu_t - E}{t \times (L/\phi) \times (1 - \mu_t)/\mu_t} \quad (3)$$

Because the number of flowers visited per foraging trip may change with bee size (Goulson et al. 2002), it will be

convenient to work with the probability of mortality per flower, μ , and the average net food uptake per flower, ϕ . (For notational simplicity, we omit sub-indices in the variables denoting mortality and expected net intake per flower visit.) If the amount of resources that a bee brings to her nest at the end of a foraging trip is denoted by L , then on average the bee visits L/ϕ flowers per trip, and mortality per trip is

$$\mu_t = 1 - (1 - \mu)^{L/\phi} \quad (4)$$

In terms of food uptake and mortality per flower, substituting Eq. 4 in Eq. 3 we obtain

$$W_{\text{social}} = \frac{\phi}{t} \times \left[1 - \frac{E}{L} \times \frac{1 - (1 - \mu)^{L/\phi}}{(1 - \mu)^{L/\phi}} \right] \quad (5)$$

Expected fitness of social bees depends on body size through E , investment per offspring. The explicit dependence of fitness on body size is the second difference between our model and the CD model. Note that, when the mortality rate per flower visit is low, μ is much smaller than 1, Eq. 5 can be replaced by its first-order Taylor development,

$$W_{\text{social}} = \frac{\phi - \mu \times E}{t} \quad (6)$$

which is the fitness function derived in the HSK model.

Equation 6 can be used to study the effect of body size on the optimal strategy of social bees. Let us assume that bees are using a reference strategy $S_r = (\mu_r, \phi_r)$. If given the choice, should bees switch to a comparison strategy $S_c = (\mu_c, \phi_c)$? If S_c is associated with lower mortality and higher food uptake per flower than S_r , the switch would clearly lead to an increase in fitness. Likewise, if S_c is associated with higher mortality and lower food uptake than S_r , then the bee should retain S_r . The question only becomes interesting when one strategy has higher food uptake and higher mortality than the other. Throughout this paper, we will assume that $\mu_c > \mu_r$ and $\phi_c > \phi_r$. (The fourth possible scenario is obtained reversing the roles of S_c and S_r .) Figure 1 shows the set of strategies that a large and a small bee should prefer to $S_r = (0.001, 0.45)$. Throughout this paper, we use 2.5 mg as the size of an example small bee, and 150 mg as the size of an example large bee (see Appendix 2 for the choice of model parameters). Where μ_c is small and ϕ_c large, both small and large bees prefer S_c (sector A: S_c, S_c ; in Fig. 1). Where μ_c is large and ϕ_c small, they prefer S_r (sector C: S_r, S_r). In between, there are two regions, one where small bees prefer S_c and large bees S_r (sector B: S_c, S_r), and another one where preferences are reversed (sector D: S_r, S_c). It is clear from Fig. 1 that, for small bees, increases in mortality are easily compensated by increases in food uptake. Large bees, on the other hand, will only accept an increase in mortality if it is accompanied by a very substantial increase in food uptake.

In Fig. 1, the straight lines are lines of equal fitness for small (near horizontal line) and large (steep line) bees. The slope of the lines of equal fitness indicates the relative importance of changes in food uptake and mortality for the choice of foraging strategies. Near-horizontal lines indicate that choices between strategies are mainly determined by differences in food uptake, very steep lines that mortality is determinant.

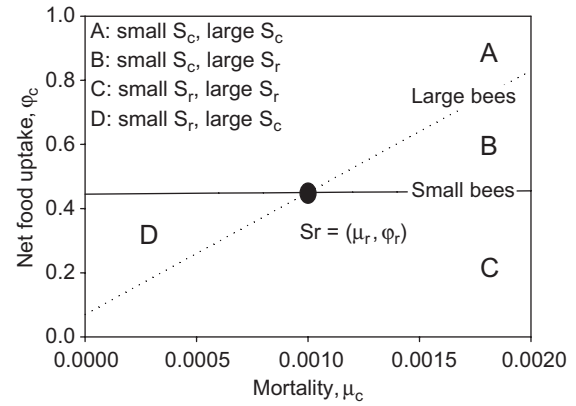


Figure 1. Optimal foraging strategies for small and large social bees in (μ, ϕ) phase space. If bees have a choice between reference strategy $S_r = (\mu_r = 0.001, \phi_r = 0.45)$, represented by the black circle, and an arbitrary comparison strategy $S_c = (\mu_c, \phi_c)$, small bees should choose S_c when it lies above the solid line, and S_r otherwise. Large bees should choose the comparison strategy when it lies above the dotted line. Each of the four sectors in which the two straight lines divide the plane corresponds to a combination of foraging choices by small and large bees, as indicated in the figure. Small social bees readily accept foraging options with higher food uptake; large social bees are less likely to accept foraging options with higher mortality. For small bees, $E = 5$ mg, $L = 2.5$ mg; for large bees, $E = 380$ mg, $L = 14$ mg; $t = 10$ s.

The example of Fig. 1 can be generalised with the use of fitness contour plots and lines of equal fitness. Figure 2a–b shows the fitness contour plots for social bees. (Because Eq. 5 and 6 yield almost identical predictions, in what follows we use Eq. 6 for model analysis.) Lines of constant fitness are nearly straight lines, evenly spaced, with slope E . Because E , the cost of producing an offspring, increases with body size, lines of equal fitness for social bees become progressively steeper as body size increases. For small bees, the lines of equal fitness are almost horizontal and fitness is maximised essentially maximising net food uptake per flower. For very large bees, the lines of equal fitness would become almost vertical: fitness maximisation would be roughly equivalent to minimisation of mortality per flower.

Figure 2c–d shows the contour plots for social bees according to the CD model (Eq. 1). Because the CD model is based on mortality and food uptake per trip, the two models are not directly comparable. Nevertheless, there is a dramatic change in the shape of the fitness functions. In the CD model, lines of constant fitness are no longer parallel: they are straight lines through the origin. According to the CD model, the relative importance of mortality and food uptake when choosing between the reference and a comparison strategy does not depend on bee size, but on the position of the reference strategy. The relative importance of minimising mortality increases as we move from reference strategies with low ϕ_r/μ_r ratios to reference strategies with high ϕ_r/μ_r ratios.

Social bees – maintenance threshold

To study the ecological conditions allowing for the maintenance of bee populations, we define the maintenance

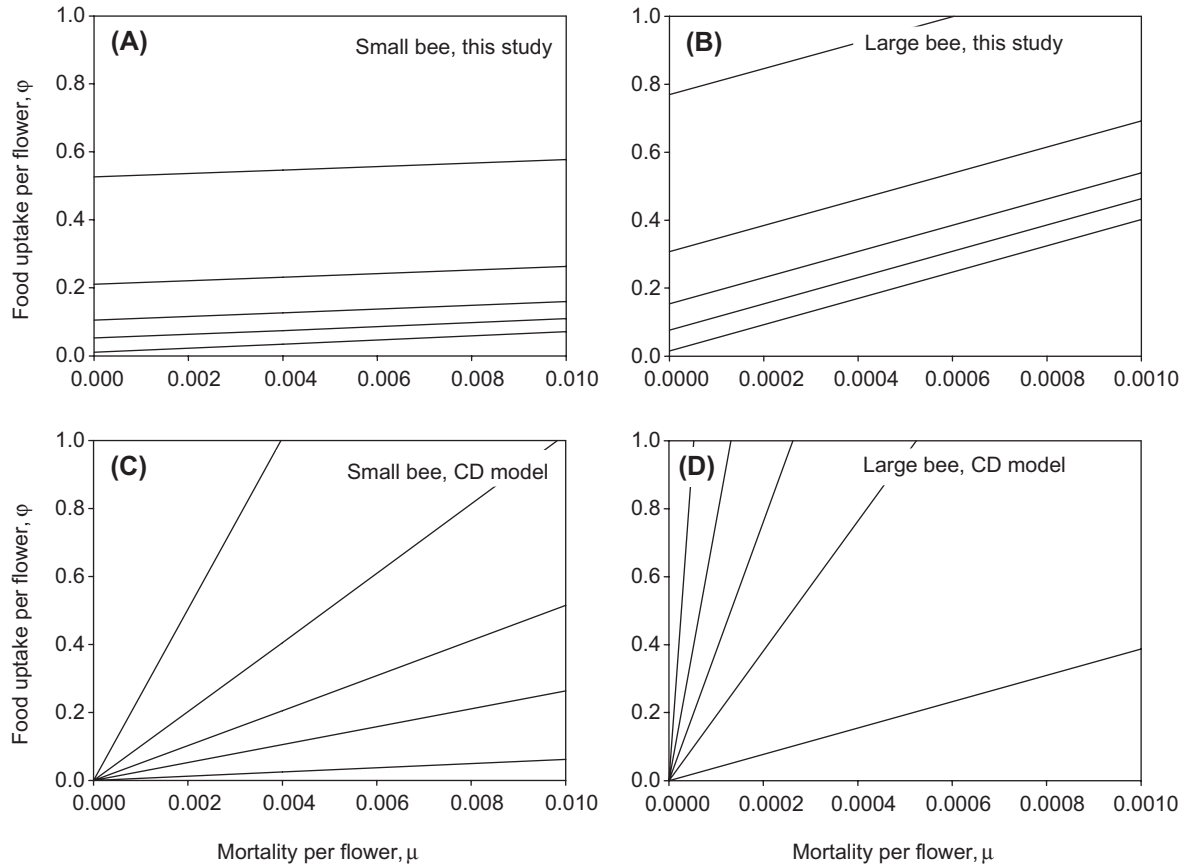


Figure 2. Contour plots for the expected fitness of social bees as a function of net food uptake, ϕ , and mortality rate, μ , per flower. Upper panels correspond to our fitness function (Eq. 5), lower panels to the CD model (Eq. 1). Panel (A) and (C) refer to small bees, (B) and (D) to large bees. Within each panel, as we move from the lower-right to the upper-left section, lines represent the set of foraging strategies leading to the production of 1, 5, 10, 20 and 50 offspring per worker. A scale change has been introduced in fitness functions to express them in the same units (offspring produced). For small bees, $E = 5$ mg, $L = 2.5$ mg, $T = 4,750$ s; for large bees, $E = 380$ mg, $L = 14$ mg, $T = 247,000$ s; $t = 10$ s.

threshold, ϕ^* , as the minimal foraging uptake per flower allowing for a positive growth rate. In the CD model, because fitness is measured in units of resource provisioning per bee, the minimum requirement for population viability is that each worker obtains, on average, at least sufficient resources to produce a replacement worker, so $\phi_{CD, social}^*$ is obtained from the equation $W_{CD, social} = E$. Equation 5 is directly given in terms of colony growth rate, so the viability condition in this case, ϕ_{social}^* , is simply derived from $W_{social} = 0$. Needless to say, these thresholds are overoptimistic, but they provide convenient benchmarks for model comparison, and will become important when we compare how social and solitary bees respond to the mortality-intake trade-off. For realistic values of mortality per flower, the maintenance thresholds are obtained by solving for ϕ in the equations above and linearising. We obtain

$$\phi_{CD, social}^* = \frac{1}{\frac{E}{L} \times \text{Log} \left[\frac{1 + E/L}{E/L} \right]} \times E \times \mu \quad (7)$$

$$\phi_{social}^* = E \times \mu \quad (8)$$

The maintenance threshold predicted by the CD model for social bees is more restrictive than the one predicted by

our extended model, but differences are much greater for small (23%) than for large bees (1%).

Social bees – extended model in (ρ, ϕ) phase space

So far, we have assumed that mortality per flower, μ , and net food uptake, ϕ , are free model parameters. We refer to this formulation as the (μ, ϕ) phase space. The main advantage of working in the (μ, ϕ) phase space is that it minimises the number of free parameters in the model. This is the formulation used in the HSK and CD models. The disadvantage of this formulation is that it obscures the relationship between body size and expected fitness: mortality and net food uptake per flower cannot be univocally assigned to a given environment or resource, because these variables are also affected by phenotypic traits of the bees. This shortcoming is avoided if we work in ' (ρ, ϕ) phase space' – at the cost of introducing extra parameters and making some restrictive assumptions in the model. The transformation between the two formulations is achieved defining ϕ as the gross food uptake per flower and ρ as the "predator exposure" per flower. We define ρ as the probability that a bee is attacked by a predator upon landing on a flower, regardless of whether the bee manages to escape. Net food uptake per flower, ϕ , equals gross uptake, ϕ , minus metabolic cost, χ . Flight metabolic cost in bees

increases with body size with an exponent of 0.7 (Darveau et al. 2005), but, as shown below, model predictions are not greatly affected by the shape of the relationship between metabolic cost and body size, and it suffices to note that metabolic cost increases with body size. Mortality, on the other hand, decreases with body size because large bees are less susceptible to predation (Dukas and Morse 2003, 2005). We will assume that mortality rate is the product of two factors: the predator exposure, ρ , which will depend on the type and abundance of predators associated with the flowers where the bee chooses to forage, and the susceptibility of the bee (probability of being captured upon attack), σ , which will depend on its body size and other phenotypic traits.

In (ϕ, ρ) phase space, fitness of social bees can be expressed as

$$W_{\text{social}} = \frac{\phi - \chi - \rho \times \sigma \times E}{t} \quad (9)$$

and the equation for the lines of constant fitness becomes

$$\phi = \chi + W_{\text{social}} \times t + \rho \times \sigma \times E \quad (10)$$

Essentially, then, the shift from (μ, ϕ) to (ρ, ϕ) phase space implies just a change in the slope of the boundary between those strategies that are better or worse than a reference strategy. In (μ, ϕ) phase space, the slope equals E and increases with bee body size. In (ρ, ϕ) the slope equals $\sigma \times E$. This product could increase or decrease as body size increases. Investment per offspring has been reported to increase with body size, m , as $m^{1.15}$ (Müller et al. 2006). Susceptibility, on the other hand, is bounded between 0 and 1. It is therefore likely to follow an inverse sigmoid function, being close to its maximum value for small bees and close to 0 for large bees. If the relationship between susceptibility and body mass is an inverse sigmoid function, then the product $\sigma \times E$ is bell shaped. Lines of equal fitness are very shallow for very small (low E) and very large (low σ) bees, and reach a maximum for intermediate body sizes. In other words, for small and large social bees (shallow lines of equal fitness) the optimal strategy lies close to the maximisation of intake rate, and predator avoidance only becomes an issue for social bees of intermediate size.

Solitary bees

We now turn to the foraging strategies of solitary bees. The CD model assumes that solitary bees collect food throughout the day, take it to the nests, and at the end of the day lay a number of eggs on the food provision and close the nest. If a bee makes N trips per day, the fitness contribution of a full day's foraging is supposed to be equal to the amount of food harvested during the day, $N \phi_t$. If, on the other hand, the bee dies during the day before laying any egg, the food collected through the day is wasted and does not increase the bee's fitness. With these assumptions, the expected fitness of a solitary bee, $W_{\text{CD,solitary}}$ is (Eq. 4 in Clark and Dukas 1994)

$$W_{\text{CD,solitary}} = \frac{(1 - \mu_t)^N}{1 - (1 - \mu_t)^N} N \times \phi_t \quad (11)$$

The assumption that there is a linear relationship between food gathered and fitness ignores that offspring come in discrete quanta and a minimum amount of resources is required to produce one offspring.

Solitary bees – extended model in (μ, ϕ) phase space

In order to extend the CD model for solitary bees, we make two modifications. First, we assume that there is a fixed cost of producing an offspring, E . Second, we assume that bees lay eggs whenever they have harvested enough resources to feed a larva through its development, E . This is in fact the strategy typically followed by solitary bees (Stephen et al. 1969). For univoltine species, a bee's expected fitness is proportional to the number of eggs she manages to lay. On average, a bee must visit E/ϕ flowers before she can lay an egg. The probability that the bee dies while provisioning a cell is $1 - (1 - \mu)^{E/\phi}$, and the number of eggs she is expected to lay is therefore

$$W_{\text{solitary}} = \frac{(1 - \mu)^{E/\phi}}{1 - (1 - \mu)^{E/\phi}} \quad (12)$$

With this formulation, the fitness function of solitary bees is very similar to the fitness function of social bees in the CD model (Fig. 2c–d). In both cases (data for solitary bees not shown), lines of equal fitness are straight lines through the origin, so the results of the CD model for social bees apply directly to solitary bees in the extended model, replacing mortality and food uptake per flower for mortality and food uptake per trip. In particular, solitary bees should select the foraging options maximising ϕ/μ , and preference between foraging options should be independent of bee size.

Solitary bees – maintenance threshold

The maintenance threshold for solitary bees in the extended model is obtained assuming that each bee produces a single offspring, $W_{\text{solitary}} = 1$. Assuming that mortality per flower is sufficiently small to keep only the linear term in μ , we obtain

$$\phi_{\text{solitary}}^* = \frac{1}{\log(2)} \times E \times \mu = 1.44 \times E \times \mu \quad (13)$$

Solitary bees – extended model in (ρ, ϕ) phase space

As we have seen, solitary bees should select the foraging strategy with the highest value of ϕ/μ . Consider a solitary bee that must choose between foraging strategies associated to parameters $(\mu_1 = \rho_1 \times \sigma, \phi_1 = \phi_1 - \chi)$ and $(\mu_2 = \rho_2 \times \sigma, \phi_2 = \phi_2 - \chi)$, where χ is the metabolic cost. The bee will choose the former strategy if $(\phi_1 - \chi)/(\rho_1 \times \sigma) > (\phi_2 - \chi)/(\rho_2 \times \sigma)$ and the latter otherwise. Susceptibility cancels out from the equation and the choice of foraging strategy therefore depends on the comparison between $(\phi_1 - \chi)/\rho_1$ and $(\phi_2 - \chi)/\rho_2$. Solitary bees should strive to maximise $\phi/\rho = (\phi - \chi)/\rho$.

Body size affects χ , and hence foraging choices. Figure 3 represent the set of comparison strategies, $S_c = (\rho_c, \phi_c)$ that

a large and a small solitary bee should prefer to the reference strategy S_r ($\rho_r = 0.01$, $\phi_r = 1$). If S_c has a higher predator exposure than S_r , $\rho_c > \rho_r$, it will only be selected if it also leads to a higher gross intake per flower, $\phi_c > \phi_r$. The increase in intake per flower required to accept the comparison strategy, S_c , however, is higher for small than for large solitary bees. Increasing gross food uptake, ϕ , will weight disproportionately in the foraging strategies of large solitary bees, and minimising predator exposure, ρ , in the foraging strategies of small solitary bees. Also, for bees of any size, increasing gross food uptake becomes more and more important as the metabolic cost of exploiting a flower, χ , approaches the value of its reward, ϕ . This is because the lines of equal fitness for solitary bees in (ρ, ϕ) phase space are straight lines with intercept χ (Fig. 3). As a result, if $\phi - \chi \approx 0$, the line of equal fitness is almost horizontal, corresponding to a situation where any increase in reward value, $\Delta\phi > 0$, leads to an increase in fitness – regardless of the change in predator exposure, $\Delta\rho$.

Comparison between social and solitary bees

Comparing the foraging strategies of social and solitary bees is easiest in (μ, ϕ) phase space. For solitary bees, the optimal foraging strategy is the one that maximises ϕ/μ . For social bees, on the other hand, optimal foraging choices are size-dependent. In particular, very small social bees should tend to maximise net food uptake per flower, and very large social bees to minimise mortality per flower. We now compare the optimal foraging strategies of social and solitary bees of the same size. Let E be the cost of rearing a bee. Bees cannot subsist on resources for which $\phi/\mu < E$ (Eq. 8, 13), so we restrict our comparison to strategies that lie above the $\phi = \mu E$ line. For any reference

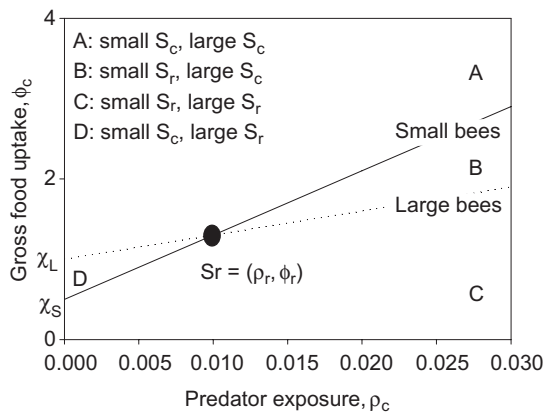


Figure 3. Optimal foraging strategies for small and large solitary bees in (ρ, ϕ) phase space. If bees have a choice between reference strategy $S_r = (\rho_r = 0.01, \phi_r = 1.3)$, represented by the black circle, and an arbitrary comparison strategy $S_c = (\rho_c, \phi_c)$, small bees should choose S_c when it lies above the solid line, and S_r otherwise. Large bees should choose the comparison strategy when it lies above the dotted line. Each of the four sectors in which the two straight lines divide the plane corresponds to a combination of foraging choices by small and large bees. Large solitary bees are more likely to adopt strategies with high predator exposure than small solitary bees. Metabolic cost per flower, χ , equals 0.5 and 1 mg for small and large bees, respectively.

strategy S_r above the $\phi = \mu E$ line, the increase in net food uptake $\Delta\phi_{\text{social}}$ that a social bee requires to accept an increase in mortality $\Delta\mu$, is smaller than the increase in net food uptake $\Delta\phi_{\text{solitary}}$ that the solitary bee requires to accept the same increase in mortality (Fig. 4). We therefore recover the result obtained by Clark and Dukas (1994) with a qualification: social bees will expose themselves to higher mortality rates than solitary bees of the same size.

It is helpful to visualise these general results with a specific example, similar to the one proposed by Jones (2010). Let us assume that bees can choose between a set of foraging strategies, such that the predator exposure of a strategy increases with the square of its gross food uptake:

$$\rho = 0.005 \times \phi^2 \quad (14)$$

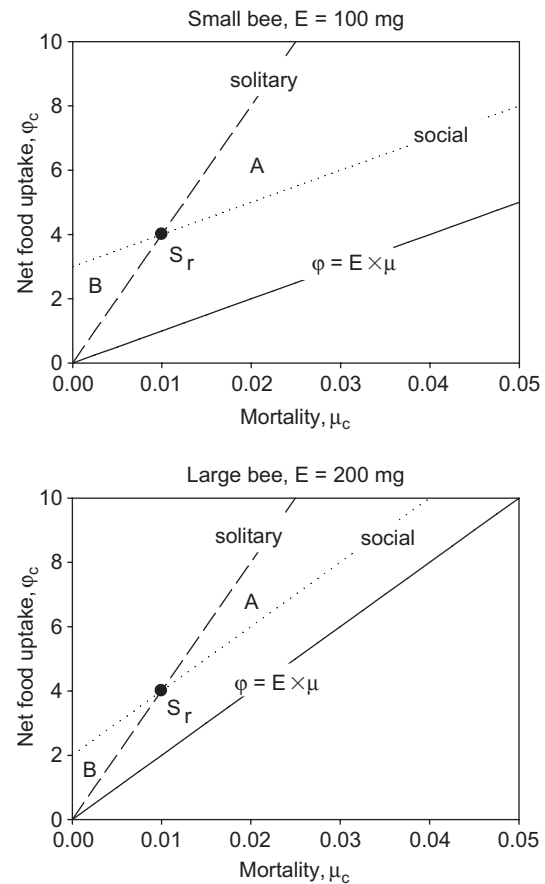


Figure 4. Comparison of the optimal strategy of social and solitary bees as a function of net food uptake, ϕ , and mortality rate, μ per flower. Bee populations can only subsist on resources represented by points above the solid line. If social bees have to choose between strategy $S_r = (\mu_r = 0.01, \phi_r = 4)$, (denoted by a black circle) and a comparison strategy, $S_c = (\mu_c, \phi_c)$, they will favour S_c only if it lies above the line through S_r with slope E (dotted line). Solitary bees, on the other hand, will prefer the alternative resource if it lies above the line joining S_r to the origin (dashed line). The strategies favoured by social bees but not by solitary bees are therefore those in sector A between the dotted and dashed lines, and the strategies favoured by solitary bees but not by social bees are those in sector B. For a given body size, social bees are expected to take higher risks than solitary bees. The two panels differ in the value of E : $E = 100$ mg in the top panel and $E = 200$ mg in the bottom panel. The discrepancy between the strategies favoured by social and solitary bees (total area of A and B sectors) decreases as body size (and therefore E) increases.

where ρ must be bounded in the interval $[0, 1]$. For this particular example, we will make specific assumptions concerning the allometric relationships between body size and the model parameters. Susceptibility should decrease with body size, being close to σ_{\max} for very small bees and to 0 for very large bees. We therefore set

$$\sigma = \frac{1}{2} \times \left[1 + \tanh(2 - 0.025 \times m) \right] \quad (15)$$

With this choice, the susceptibility of a bee decreases to 0.5 for $m = 80$ mg and to 0.25 for $m = 100$ mg. Investment per offspring increases as $m^{1.15}$ (Müller et al. 2006). To fit this power relationship to our choice of parameter values for small and large bees, we set

$$E = 1.2 \times m^{1.15} \quad (16)$$

Metabolic cost increases with $m^{0.7}$ (Darveau et al. 2005). Note that χ represents metabolic cost per flower exploited, not per unit time. In this example, we let

$$\chi = 0.01 \times m^{0.7} \quad (17)$$

We have been unable to find the relationship between body size and the last model parameter, average amount of resources brought to the nest per trip, L . To fit the values used throughout the paper, we let

$$L = 1.7 \times m^{0.4} \quad (18)$$

With Eq. 14–18, it is possible to calculate the expected fitness of social and solitary bees of any size, as a function of the foraging strategy they select. Bees can select a level of predator exposure, ρ , or gross food uptake, ϕ . A single choice determines the value of the other parameter of the foraging strategy (through Eq. 14), and the values of net food uptake, mortality and eventually fitness. Figure 5 shows the relationship between bee body size, m , and the optimal foraging strategy, in terms of predator exposure, mortality, gross and net food uptake. The first point to notice is that, for any given size, solitary bees select foraging strategies with lower predator exposure and lower gross food uptake than social bees. In solitary bees, the level of predator exposure accepted increases monotonically with body size. However, the level of mortality experienced by the bees, the product of predator exposure and susceptibility to predation, follows a different pattern. In small solitary bees, susceptibility is high and mortality increases with body size, paralleling the increase in predator exposure. Beyond a certain size, however, susceptibility quickly decreases and mortality starts to decrease with body size despite the continuous increase in predator exposure. The pattern is different for social bees. For social bees the relationship between predator exposure and body size is concave-up: for small social bees, predator exposure is a decreasing function of body size, but after a certain value predator exposure starts increasing, until it reaches the maximum possible value of 1. Mortality follows a similar pattern for small and medium-sized social bees, but once the bees reach the maximum level of exposure mortality starts to decrease due to the continuous decrease in susceptibility. Because of the assumed link between predator

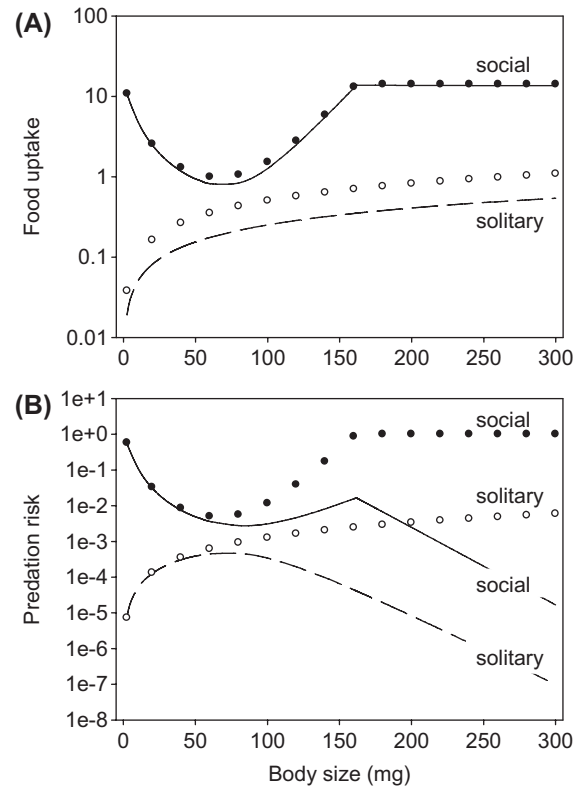


Figure 5. Effect of body size on the optimal foraging strategy of bees when predator exposure increases with the square of gross food uptake. (A) Gross (circles) and net (lines) food uptake per flower for social (solid line, black circle) and solitary (dashed line, empty circle) bees. (B) Predator exposure (circles) and mortality (lines) per flower for social (solid line, black circle) and solitary (dashed line, empty circle) bees.

exposure and food uptake, food uptake follows a similar pattern to predator exposure.

Discussion

Our models expand those developed by Clark and Dukas (1994) by explicitly introducing body size in the fitness functions and by changing some assumptions to more precisely match life history traits of social and solitary bees. For social bees, while we still assume that conditions remain constant throughout the season, we remove the assumption of an infinite season, and associate fitness with the growth rate of the colony. For solitary bees, we acknowledge that larvae require a minimum amount of resources to survive and relax the assumption that females lay eggs at the end of each day. Despite these differences, we recover the main result of the CD model: solitary bees should use safer foraging modes than social bees of the same size.

Fitness is tightly linked to survival of individual bees in solitary, but not in social species. As a result, there is a range of environmental conditions under which populations of social bees are sustainable but those of solitary bees are not. Incorporating the effect of bee size is not so straightforward. Equation 8 and 13 tell us that bee populations are only sustainable when $\phi > k \times E \times \mu$, where $k = 1$ for social

bees and $k = 1.44$ for solitary bees. This suggests that large bees require richer or safer environments for their maintenance – a result that is not necessarily true. In (ρ, ϕ) phase space the condition for sustainability becomes $\phi > \chi + k \times E \times \sigma \times \rho$. Large bees require habitats with more resources to fulfil their energetic requirements, but the abundance of predators in the environment will play a minor role for large (low σ) bees, as well as small (low E) bees. As a result, predators have the potential to make habitats unsuitable for medium-sized bees, but they are unlikely to play a major role on the spatial distribution of small and large bees.

Moving beyond the overall comparison between social and solitary bees, our model also shows that there is a complex interplay between sociality, body size and the predation-intake trade-off. Thus, while solitary bees should adopt increasing levels of predator exposure as their size increases, medium-sized social bees should show lower levels of predator exposure than small and large social bees (Fig. 5). It follows that we cannot fully understand how bees distribute themselves among available resources (Jones 2010) unless we take into account the difference between social and solitary bees, and the size of the bees involved. A full understanding of how large and small bees face the tradeoff between maximising food uptake and minimising predation, however, requires detailed knowledge about the relationship between the different parameter values and body size.

Our models provide a tool to explore the effect of ambush predators on plant–pollinator relationships. In the present model, bee foraging strategies are defined by their average predator exposure and food uptake per flower visit. These quantities, however, are partially under the control of foraging bees. Suppose that a plant species harbours crab spiders in 50% of its flowers. A bee visiting every flower it encounters will be exposed to a spider attack on 50% of the visits, and this is the underlying assumption of some models (Jones 2010), but this proportion can be reduced substantially if the bee spends some time inspecting flowers prior to landing (Ings and Chittka 2008) or if she avoids patches on which she has been attacked (Ings and Chittka 2009). Indeed, bees can avoid spider-harboured flowers (Dukas 2001, Dukas and Morse 2003, Gonçalves-Souza et al. 2008). A bee's foraging strategy determines her average predator exposure and food uptake per flower, and our models can then be used to determine the optimal strategy in particular scenarios.

Our models can also be used to explore the effect of predators on plant–pollinator interactions. The resources a bee encounters on a flower depend on the flower type, but also on the behaviour of other pollinators. In this paper, we have ignored the effect of bee choices on resource availability, but at the community level it is clear that there is a strong feedback between the foraging strategies used by the bees and the profitability of these strategies (Dreisig 1995). Coupling these models with game theoretical arguments will allow us to understand how and if predators affect the topology of plant–pollinator networks.

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Appendix 1

Senescence

Neukirch (1982) proposed that foraging honeybees have a set amount of energy that can be spent in foraging activities, and more recently it has been suggested that the flight apparatus of bees is only capable of a finite number of wing beats (Higginson and Gilbert 2004). We can introduce senescence by assuming that bees possess a fixed foraging budget, T , which is depleted as bees forage.

Social bees

For social bees, the constraint of a finite maximum foraging time is most easily introduced in Eq. 4. If mortality per trip, μ_t , is independent of age but a bee cannot perform more than N_{\max} trips in her lifetime, then the number of trips that the bee is expected to accomplish in her lifetime is

$$\langle \text{Number of trips} \rangle = \frac{1 - \mu_t}{\mu_t} \left[1 - (1 - \mu_t)^{N_{\max}} \right] \quad (\text{A1})$$

If maximum foraging time is T and average trip duration $t \times L/\phi$, then $N_{\max} = T \times \phi / (t \times L)$ in Eq. A1. Using Eq. A1, rather than $(1 - \mu_t)/\mu_t$, in the calculation of $\langle \text{Harvest} \rangle$ and $\langle \text{Lifespan} \rangle$ and substituting in Eq. 4, we obtain:

$$W_{\text{social,s}} = \frac{\phi}{t} \times \left\{ 1 - \frac{E}{L} \times \frac{1 - (1 - \mu)^{L/\phi}}{(1 - \mu)^{L/\phi} \times \left[1 - (1 - \mu)^{T/t} \right]} \right\} \quad (\text{A2})$$

Numerical analysis shows that the foraging choices predicted for social bees with (Eq. A2) and without (Eq. 4) senescence are virtually identical, for both small and large bees, even when the foraging budget is just sufficient to rear two offspring (unpubl.).

Solitary bees

When the maximum number of trips that a bee can possibly accomplish is restricted by her foraging budget, T (Eq. A1),

the number of eggs that a solitary bee is expected to lay in her lifetime becomes

$$W_{\text{solitary,s}} = \frac{(1 - \mu)^{E/\phi}}{1 - (1 - \mu)^{E/\phi}} \left[1 - (1 - \mu)^{T/t} \right] \quad (\text{A3})$$

For large solitary bees, fitness functions with and without senescence are almost identical. For small solitary bees the fitness function changes somewhat if the foraging budget is very small, but the differences disappear when the foraging budget is sufficient for a bee to provision 10 cells. Ten cells per nesting female is a good average for *O. cornuta* females (range: 8.5–17.5; Bosch and Vicens 2005, 2006), and appears to be a good estimate for *C. persimilis* females, which provision 1 to 6 cells per day (Danforth 1990).

Appendix 2

Model parameterization

Other than the variables that characterize the foraging options, ϕ , μ and t , the models involve three parameters that depend on the size of the bees: the amount of resources required to rear an offspring, E ; the amount of resources that bees collect per foraging trip, L , and susceptibility to predation, σ . Ideally, we would want to express these parameters as functions of body size. Unfortunately, however, we lack the data to do so. The amount of resources required to rear an offspring (Bosch and Vicens 2002, Müller et al. 2006) and, at least in some species, the amount of resources collected per trip (Tomkins et al. 2001, Goulson et al. 2002) increase with body size, while susceptibility to predation decreases with body size (Dukas and Morse 2003, 2005) – but the shape of these relationships is unknown. Rather than assuming arbitrary functions for these parameters, we will study the optimal foraging strategy of bees with different life histories in two scenarios: ‘small’ and ‘large’ bees, adjusting the parameter values to two well-studied species.

As an example of small bee we use male *Calliopsis persimilis*. In this species, females provision their male eggs with $E = 5$ mg (dry weight) of pollen and nectar, leading to an adult body mass of $m = 2.5$ mg, gathered in two foraging trips (Danforth 1990). The average load per foraging trip is therefore $L = 2.5$ mg. As an example of large bee we select female *Osmia cornuta* (in reality, this species would be considered medium-sized, but we do not have enough data to parameterise the model for very large bees, such as

Xylocopa). In *O. cornuta*, the cost of rearing a female offspring, with $m = 150$ mg, is $E = 380$ mg (dry weight) of pollen and nectar, and the load carried to the nest per foraging trip is $L = 14$ mg (Bosch 1994, Bosch and Vicens 2002). The reason for choosing male offspring in *C. persimilis* and female offspring in *O. cornuta* is that, in these species, males are smaller than females. Thus, male *C. persimilis* and female *O. cornuta* provide a wider size range.