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Original Article

Possible top-down control of solitary bee populations by ambush predators

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The effect of ambush predators on bee populations has so far been neglected on the assumption that predators ambushing at flowers for the arrival of pollinators are too scarce to have significant effects on population numbers. A simple mathematical model can be used to calculate the maximum predator abundance compatible with positive growth of solitary bee populations. Using published data to estimate model parameters, the model shows that medium-sized (20–80 mg dry weight) solitary bees are very sensitive to predation and their populations can hardly grow when 1–2% of flowers are occupied by ambush predators—a predator abundance well within the range reported in most studies. Smaller and larger bees, on the other hand, can easily cope with normal predator abundances: small bees do not need to visit many flowers to provision an offspring, making it unlikely that they encounter a predator, and large bees are less vulnerable to predator attacks. According to a sensibility analysis, the parameters with the greatest impact on bee population viability are the number of flowers that bees must exploit to provision an offspring and the probability that a bee, upon landing on a predator-harboring flower, is actually captured. It follows that ambush predators cannot be excluded *a priori* from the list of factors affecting bee diversity and abundance: small changes in the abundance of ambush predators, possibly related to changes in the availability of alternative prey, could have dramatic effects on the viability of medium-sized solitary bees. *Key words:* antipredator behavior, Apoidea, pollinator decline, population regulation, predation, provisioning cost. *[Behav Ecol]*

INTRODUCTION

Understanding the factors affecting the abundance and distribution of species is one of the most relevant ecological questions. Although early assumptions about the role of top-down and bottom-up processes on the regulation of different functional groups (Hairston et al. 1960) have proven to be oversimplified (Hunter and Price 1992; Power 1992; Krebs 2011), it is today undisputed that predators can have dramatic effects on the population dynamics of their prey (e.g., Schmitz 1998). Despite this general acknowledgment, the role of predators on the regulation of bee populations has so far been ignored.

Early studies suggested that predation was too infrequent to affect even pollinator behavior. For instance, Morse (1986) estimated that, if crab spiders were the only source of mortality of bees, their lifespan would range between 33 and 108 days for honeybees, *Apis mellifera* L., and bumblebees, *Bombus terricola* Kirby, respectively. Although it is now clear that pollinators can respond adaptively to the presence of ambush predators (Dukas 2001; Schmalhofer 2001; Dukas and Morse 2003; Dukas 2005) and the number of studies on the effect of ambush predators on plant-pollinator interactions is steadily increasing, we know little about the strength of the selective pressure that ambush predators impose on pollinator behavior, and even less of the extent to which ambush predators contribute to the regulation of pollinator populations.

In order to get killed by an ambush predator, a pollinator must approach a predator-harboring flower, land on the flower, and succumb to a predator attack. These 3 steps are related to the proportion of predator-harboring flowers, the predator-avoidance ability of the pollinator, and the susceptibility to predation of the pollinator. To understand the relationship between the different parameters involved in a predation attempt and the expected reproductive success of a pollinator, in this paper, I extend previous mathematical models (Clark and Dukas 1994; Rodríguez-Gironés and Bosch 2012) to explicitly incorporate the 3 steps affecting predation risk. This exercise helps us determine what predator abundances or susceptibilities to predation can be considered to be high—in the sense of potentially affecting the dynamics of a pollinator population and imposing significant selective pressures. This work also provides information concerning the parameters that must be measured in the field if we are to know the extent to which a particular species is controlled by the effect of ambush predators. For simplicity, I focus on the case of univoltine solitary bees (Rodríguez-Gironés and Bosch 2012).

MODEL DESCRIPTION

Maintenance thresholds

The basic approach will be to determine, for different combinations of parameter values, the maximum value of predator abundance, r^*, that is compatible with population maintenance. We refer to r^* as the population maintenance threshold, and our operational definition of the maintenance threshold is the predator abundance above which expected fitness drops below 3 eggs provisioned per adult female. This seems like a rather optimistic estimate. On the one hand, female solitary bees seem to invest equally on male and female

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offspring (Bosch and Vicens 2005), so that a minimum of 2 eggs laid per female would be required for population maintenance. Furthermore, the model ignores mortality of developing offspring (about 15% in *Osmia cornuta* Latreille; Bosch and Vicens 2005), and a number of other factors, such as disease or bad weather, that will all tend to decrease expected reproductive success. Note that, by focusing only on female bees, we implicitly assume that ambush predators are more likely to affect female than male numbers.

Fitness function

Ignoring other sources or mortality and resource limitation, the number of eggs that a univoltine solitary bee can provision before dying is a good proxy for her reproductive success (Rodríguez-Gironés and Bosch 2012). We calculate the number of eggs that a bee can provision in 2 steps.

We first calculate the survival probability per egg provisioned, S_N, if the bee must harvest N flowers to provision an egg. We denote by p the probability that a flower visit results in an attack and by σ the probability that an attack results in the capture and death of the bee—her susceptibility to predation. We derive S_N by recurrence.

We first consider the case $N = 1$. If the bee is not attacked during her first flower visit, she has already survived one egg-provisioning cycle. This happens with probability $1 - p$. The bee, however, may encounter a predator during her first flower visit. If she dies, it is the end of the story. If she survives, she has escaped without collecting any nectar or pollen, and she must still harvest one flower. The probability that a bee is attacked during her first flower visit, survives the attack, and goes on to successfully provisioning one egg (i.e., harvesting one flower in this particular case) is therefore the product of 3 terms: $p \cdot (1 - \sigma) \cdot S_1$. We therefore have

$$S_1 = (1-p) + p(1-\sigma) \cdot S_1. \tag{1}$$

Rearranging,

$$S_1 = \frac{(1-p)}{1-p\cdot(1-\sigma)}. \tag{2}$$

We calculate S_2 in a similar way. A bee that is not attacked during her first flower visit will only need to harvest one more flower, so the probability that a bee is not attacked during her first visit and successfully harvests 2 flowers is simply $(1 - p) \cdot S_1$. A bee that is attacked during her first visit, on the other hand, must survive the initial attack and still harvest 2 flowers. It follows that

$$S_2 = (1-p)\cdot S_1 + p\cdot(1-\sigma)\cdot S_2 \tag{3}$$

and hence

$$S_2 = \left[\frac{(1-p)}{1-p\cdot(1-\sigma)}\right]^2. \tag{4}$$

Equations 2 and 4 suggest the general result

$$S_N = \left[\frac{(1-p)}{1-p\cdot(1-\sigma)}\right]^N. \tag{5}$$

Given that Equation 5 is correct for $N = 1$ and $N = 2$, to prove that it is always correct, it suffices to prove that if it holds for N, it is equally correct for $N + 1$. As previously, a bee that must harvest $N + 1$ flowers to provision an egg may, or may not, be attacked during the first flower visit. If she is not attacked (which happens with probability $1 - p$), she must only survive N additional harvesting events (which will happen with probability S_N). If she is attacked (probability p), however, she must survive the initial attack (probability $1 - \sigma$) and still harvest $N + 1$ flowers (probability S_{N+1}). Hence,

$$S_{N+1} = (1-p)\cdot S_N + p\cdot(1-\sigma)\cdot S_{N+1}. \tag{6}$$

Using the value of S_N from Equation 5 and rearranging, we obtain

$$S_{N+1} = \left[\frac{(1-p)}{1-p\cdot(1-\sigma)}\right]^{N+1} \tag{7}$$

This completes the proof that Equation 5 is valid for all N.

In the second step, knowing the probability that a bee survives an egg-provisioning event, we proceed to calculate the number of eggs that, on average, she can be expected to provision. The probability that a bee survives at least n egg-provisioning cycles is $S_N^{\,n}$. If the maximum number of eggs that a bee can possibly provision if she avoids predation is M, where the value of M is limited by senescence, a finite season, or any other constraint, then the average number of eggs that a bee will lay, W, can be derived as follows. For $M = 1$, W is the probability of surviving an egg-provisioning event,

$$W(M=1) = S_N. \tag{8}$$

For $M = 2$, bees will provision an egg if they survive the first provisioning event and die during the second one, and 2 eggs if they survive the 2 provisioning events, so that

$$W(M=2) = S_N\cdot(1-S_N) + 2\cdot S_N^2. \tag{9}$$

For larger values of M, we note that the probability that the bee provisions n eggs equals the probability that she survives n consecutive provisioning events and she dies during the nth + 1 event. This probability is nothing but $S_N^{\,n}\cdot(1-S_N)$. The probability that the bee provisions M eggs, however, is just $S_N^{\,M}$, as the bee (by definition of M) cannot provision more eggs even if she survives predation. Hence,

$$W = \sum_{n=1}^{M-1} n\cdot S_N^n\cdot(1-S_N) + M\cdot S_N^M. \tag{10}$$

After some manipulation, we finally obtain

$$W = \frac{S_N}{1-S_N}\cdot\left(1-S_N^M\right). \tag{11}$$

Approach to predator-harboring inflorescences

We will assume that the initial approach of a bee to an inflorescence is unaffected by the presence of predators, as predators are normally not detectable at a distance. Thus, the probability of approaching a predator-harboring flower is probably very similar to the frequency of flowers harboring predators in the population, r. Note that this assumes a homogeneous distribution of ambush predators on flowers.

The proportion of predator-harboring inflorescences can be <1% (Morse 1986), but the range of values reported in different systems is quite broad: 1.4% (Llandres et al. 2011), between 6.8% and 12.5% (Suttle 2003), and between 2% and 30% (Robertson and Maguire 2005). When we compare the maintenance thresholds, r^*, with observed predator abundances, however, we must keep in mind that many studies have focused on systems where ambush predators are "common," and the values reported need not represent typical values in wild flowers.

Choice of parameter values

Although all the parameters involved in the model can, in principle, be measured, there is actually relatively little information on many of them, and virtually no information on how they scale with body size or life-history traits. We will therefore explore how model predictions change with different parameter values. The following paragraphs explain how we decided the range of parameter values to explore. Whenever possible, we have used data from solitary bees to estimate parameter values. In some cases (predator avoidance and susceptibility to predation), however, we have used data from social bees (honeybees and bumblebees). In these cases, the range of parameter values we have explored is much broader than the range actually published.

Flower visits per offspring, N

Strickler (1979) found that the average number of virgin *Echium vulgare* L. flowers that small solitary bees needed to exploit to provision an egg ranged between 34 (for *Ceratina calcarata* Robertson; adult dry weight 3.6 mg) to 240 (for *Megachile relative* Cresson; adult dry weight 16.8 mg). Müller et al. (2006) estimated that, if solitary bees could extract all the pollen produced by an inflorescence, the minimal number of inflorescences that females would have to exploit to provision an egg would range, depending on the size of the bee and pollen productivity of their main food source, between 7 (for *Chelostoma campanularum* Kirby exploiting *Campanula rotundifolia* L.) and 1140 (for *Megachile parietina* Geoffroy exploiting *Onobrychis viciifolia* Scop.). However, because typical females can extract at best 40% of the pollen produced, the range of flowers that bees must exploit seems to be closer to 17–2850 (Müller et al. 2006), and it will be much greater for very large bees such as *Xylocopa* spp. We will restrict our analysis to the range $N = 25$–2000 flowers.

Maximum number of offspring, M

M represents the maximum number of offspring that a female bee could produce avoiding predation until old age. It has been suggested that the lifespan of honeybees can be limited by the amount of energy they can spend in foraging activities (Neukirch 1982) or by the number of wing beats that their flight apparatus can support (Higginson and Gilbert 2004). We will assume that the flight apparatus of a bee limits the number of flowers she can visit, and that if a bee never encounters a predator and exploits all the flowers she visits she can provision M^* cells. If a proportion r of flowers harbor predators, however, on average the flight cost invested in visiting these $N{\cdot}M^*$ flowers leads to the production of $M = (1 - r)\cdot M^*$ cells—as a fraction r of visits are not rewarded. We will consider model predictions for $M^* = 20$, 30, and 40 (Bosch and Vicens 2005).

Predator avoidance

Once the bee has approached a predator-harboring flower, it can either land on the flower or skip it, and search for a new one. Predator avoidance is at least in part under the control of pollinators, as certain behaviors, such as inspecting flowers prior to landing, can enhance the probability of detecting predators. The probability of landing on a predator-harboring flower, P_{LH}, can be estimated as the ratio between the rates at which randomly chosen predator-harboring and predator-free inflorescences receive pollinator visits. Predator avoidance varies between and within species. Brechbühl et al. (2010) found that, in bees confronting flowers harboring *Misumena vatia* Clerck females, P_{LH} ranged between 0.57 for some solitary bees (*Lasioglossum* sp. and *Colletes* sp.—we have estimated P_{LH} from Figure 1 of their paper) and 0.82 (*A. mellifera*) or 0.92 (*Bombus* spp.) for social bees. Reader et al. (2006) found similar values for *A. mellifera* ($P_{LH} = 0.80$) and *Eucera notata* Lepeletier ($P_{LH} = 0.82$) bees foraging at *Cistus ladanifer* L. flowers harboring *Synaema globosum* Fabricius females, but Llandres et al. (2011) found that honeybees could show a much better predator-avoidance response, as they obtained $P_{LH} = 0.34$ when honeybees foraged at *Chrysanthemum segetum* L. inflorescences harboring adult or subadult *Thomisus onustus* Walckenaer females. Thus, typical values for P_{LH} seem to be between 0.5 and 0.9, although lower values ($P_{LH} = 0.34$) have also been obtained. We will therefore evaluate model predictions in 3 scenarios, $P_{LH} = 0.1$, 0.5, and 0.9, corresponding to very strong, moderate, and weak predator-avoidance behavior. Remember that P_{LH} is the probability of landing on a predator-harboring flower. A low value of P_{LH} therefore implies high predator avoidance, while $P_{LH} = 1$ would imply that pollinators are equally likely to land on predator-harboring and predator-free flowers.

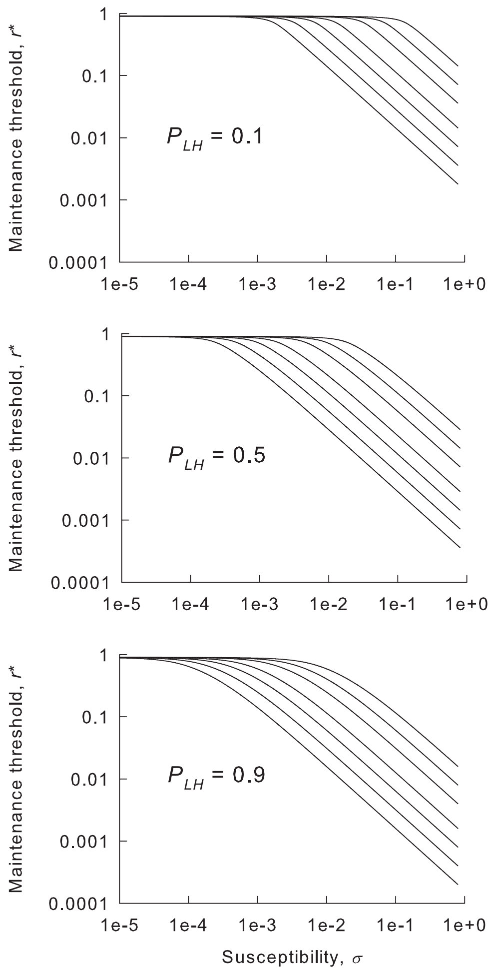

Figure 1
Relationship between maintenance threshold, r^*, and susceptibility to predation, σ. The maintenance threshold is the predator abundance above which the expected number of eggs laid per female drops below 3. Each panel corresponds to a different predator-avoidance capability (from top to bottom, $P_{LH} = 0.1$, 0.5, and 0.9). Within panels, each line corresponds to a different value of the number of flowers that bees must exploit to provision an egg (from top to bottom, $N = 25$, 50, 100, 250, 500, 1000, and 2000).

Susceptibility to predation

A pollinator that lands on a predator-harboring flower may succumb to a predator attack or survive it. We refer to the probability of being captured as the susceptibility, σ, of the pollinator. In fact, the susceptibility depends on the combination of pollinator, predator, and inflorescence.

Susceptibility can be as low as 0.4%, 0.8% and 1.4% for *B. terricola*, *B. vagans* Smith, and *A. mellifera*, respectively, foraging on *Asclepias syriaca* L. inflorescences harboring *M. vatia* females, but this low susceptibility mainly results from the fact that, on these large inflorescences, most pollinators never get close enough for the spider to strike an attack (Morse 1986). Susceptibility to predation tends to increase as inflorescence size decreases. In *Rosa Carolina* L., where female *M. vatia* crab spiders attacked more than 60% of landing visitors, susceptibility ranged between 1.1% for large bumblebees and 21.4% for small syrphid flies (Morse 1979), and in *C. segetum*, where female *T. onustus* attacked 59% of landing visitors, susceptibility increased to 14.3% for the relatively large syrphid fly *Eristalis tenax* L. and 27% for honeybees (Llandres et al. 2011). Relative size is another important determinant of susceptibility to predation. The hunting success of *T. spectabilis* Doleschall females hunting at *Bidens alba* L. inflorescences for *A. mellifera* increased sharply with spider body size (Llandres and Rodriguez-Girones 2011). In one particular experiment, susceptibility was greater than 80% for the largest spider size group (carapace width 4.66 ± 0.07 mm, mean ± standard error). Due to the wide range of susceptibility values that have been measured in the field, we explore the effect of susceptibility on model predictions within the range [0, 0.8].

RESULTS

Maintenance thresholds

The maximum number of eggs that a bee can possibly lay in the absence of predation, M^*, has little or no effect on the population maintenance threshold, r^* (data not shown). By definition, at the population maintenance threshold, the average female lays 3 eggs, so very few females manage to lay M^* eggs, even for the lowest value that we have explored ($M^* = 20$). All other parameter values, however, have strong effects on population maintenance thresholds. When keeping N, M^*, and P_{LH} constant, log-log plots of maintenance threshold versus susceptibility show that maintenance threshold is close to 1 and unaffected by susceptibility for very low susceptibility values, and declines almost linearly (in the log-log scale) for susceptibility values higher than a certain threshold (Figure 1). As the number of flowers that bees must visit to provision an offspring, N, increases, the susceptibility value beyond which r^* starts to decrease becomes smaller. As a result, for any given susceptibility value, the maintenance threshold decreases as the number of flowers that bees must exploit to provision an egg increases (Figure 1). Bees that must exploit many flowers per offspring, however, can increase their susceptibility threshold increasing their predator-avoidance response—that is, decreasing the value of P_{LH} (Figure 1).

The absolute values of the maintenance thresholds deserve consideration. For a bee that must exploit 2000 flowers to provision an offspring, with a predator-avoidance response of $P_{LH} = 0.9$, the maintenance threshold drops <0.001 if her susceptibility to predation is >0.15 (honeybee susceptibility to predation by *T. onustus* ambushed at *C. segetum* flowers was 0.27, Llandres et al. 2011). The maintenance threshold for bees that must only exploit 1000 flowers per offspring increases to 0.002—a value that is still much lower than the typical predator flower occupancy (Schmalhofer 2001; Dukas and Morse 2003; Suttle 2003; Llandres et al. 2011). Susceptibility to predation must drop to 0.015 ($N = 2000$) or 0.03 ($N = 1000$) before the average bee can lay 3 eggs in an environment where 1% of flowers are occupied by predators. While predator avoidance allows bees to survive on resources with higher predator abundance, even when bees are able to detect and avoid 90% of the predators they encounter ($P_{LH} = 0.1$; an extremely good predator-avoidance response compared with the values reported in the literature), when 1% of flowers harbor predators bees that must exploit 1000 or 2000 flowers cannot attain the average of 3 eggs per female unless their susceptibility to predation is lower than 0.29 and 0.13, respectively. Bees that can provision an offspring with the resources gathered at a few flowers, on the other hand, can deal with much higher predator abundances even if their susceptibility to predation is as high as 0.8 (Figure 1).

Effect of size on population maintenance thresholds

To investigate the relationship between bee body size and population maintenance threshold we must first determine how model parameters scale with body size. Because maintenance threshold was essentially independent of lifespan, we will assume that $M^* = 30$ for all bees. Predator avoidance is to a large extent a behavioral trait, and in principle both large and small bees should be able to avoid predator-harboring flowers. Hence, we will once again explore model predictions for $P_{LH} = 0.1$, 0.5, and 0.9.

Investment per offspring increases with $m^{1.15}$ (Müller et al. 2006), where m is dry body mass (in mg). We will therefore assume that

$$N = k \cdot m^{1.15}. \tag{12}$$

Because the relationship between the number of flowers exploited and the amount of resources harvested depends on flower profitability, itself a function of flower species and the strength of competition for resources, we will consider model predictions for $k = 6.667$, 10, and 15, leading to $N = 1032$, 1548, and 2322, respectively, for an 80 mg bee such as *M. parietina*. (Given that Müller et al. 2006 estimate that this species must visit 2850 flowers per egg, our estimates seem rather conservative.) For the relationship between body size and susceptibility, we assume

$$\sigma = \frac{1}{2} \cdot [1 + \tanh(a - b \cdot m)], \tag{13}$$

where a and b are parameters that determine the slope and inflexion point of the curve. We considered 2 possible scenarios, characterized by $a = 0$ or 0.4 and $b = 0.02$ in both cases. According to the first scenario, the susceptibility of a bee decreases from 0.47 to 0.06 as dry body weight increases from 2.5 to 70 mg, and reaches the value of 0.004 reported by Morse (1986) for *B. terricola* foraging on *A. syriaca*, when $m = 138$ mg. In the second scenario, susceptibilities for the same body sizes become 0.67, 0.12, and 0.009, respectively. As we can see, then, the difference predicted by the 2 scenarios is greatest for small bees and progressively decreases as bee body size increases.

The relationship between bee body size and population maintenance threshold is U shaped, with a flat section when dry body mass lies between 20 and 80 mg (Figure 2). For smaller or larger bees, population maintenance thresholds increase sharply. Maintenance thresholds increase for small bees because they need to only exploit a few flowers to provision each egg—thus increasing their chance of provisioning 3 eggs without ever encountering a predator. For large bees, the reason why maintenance thresholds increase is that their susceptibility to

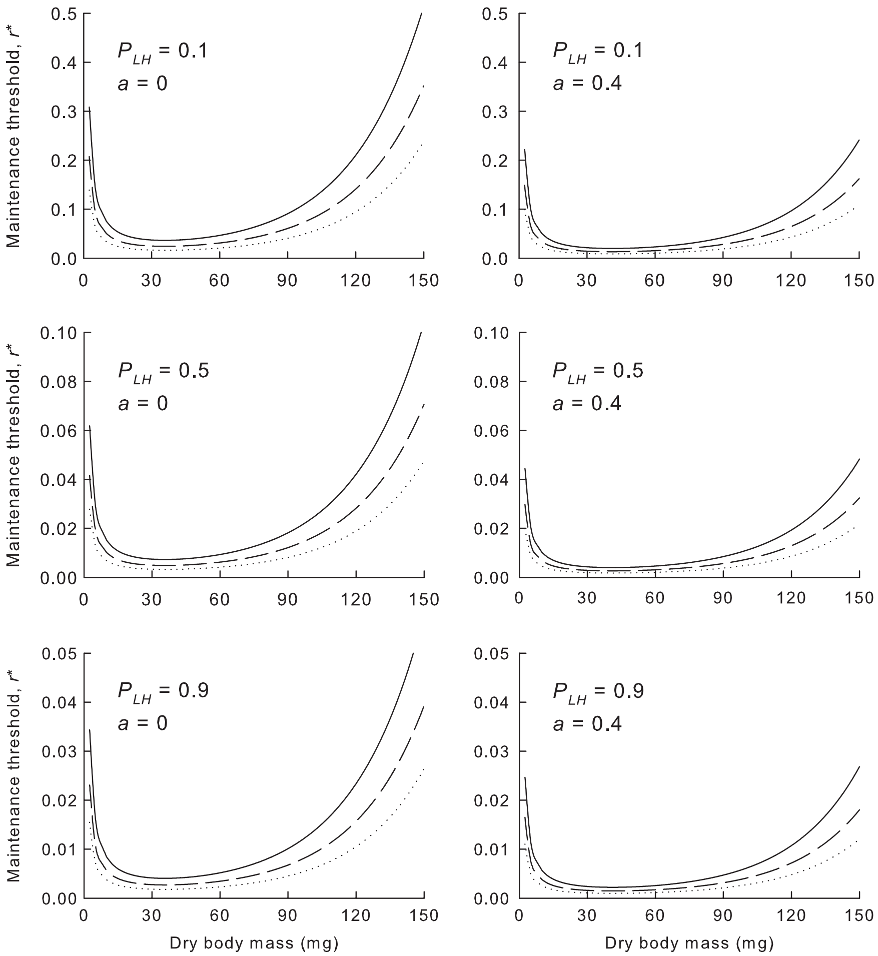

Figure 2
Relationship between maintenance threshold, r^*, and bee body size, m. The maintenance threshold is the predator abundance above which the expected number of eggs laid per female drops below 3. Panels correspond to different combinations of predator-avoidance capability (from top to bottom, P_{LH} = 0.1, 0.5, and 0.9) and susceptibility to predation (a = 0 and 0.4 in the left and right panels, respectively). Within panels, each line corresponds to a possible relationship between body size and the number of flowers required to provision an egg (k = 6.667, 10 and 15 for the solid, dashed, and dotted lines, respectively).

predation is very low, so that landing on predator-harboring flowers has little effect on their reproductive success.

In agreement with the results presented in the previous section, population maintenance thresholds decrease when the number of flowers that bees must exploit to provision an egg increases (increasing k) and their predator avoidance response deteriorates (increasing P_{LH}). Not surprisingly, maintenance thresholds also decrease when susceptibility to predation increases (increasing a). Predator avoidance has the strongest effect on maintenance thresholds. It is noteworthy that medium-sized bees (20–80 mg dry weight) have low population maintenance thresholds (below 1% of flowers harboring predators) for realistic parameter values ($P_{LH} \geq 0.5$).

DISCUSSION

The model presented here provides a tool to determine how the different steps leading to a predation event affect the expected reproductive success of univoltine solitary bees. Although it shares many of the simplifying assumptions of previous models (Clark and Dukas 1994; Rodríguez-Gironés and Bosch 2012), the explicit consideration of the processes involved in a predation event allows us to predict the conditions under which predators can impose strong selective pressures and affect population dynamics of solitary bees.

The model can be used to predict the average reproductive success of solitary bees for which all relevant parameters have been measured under field or laboratory conditions. In these cases, it can also be used to predict how changes in predator abundance or bee avoidance behavior will influence population dynamics. Nevertheless, and given the uncertainty surrounding the values of model parameters, the main contributions of the model are 1) highlighting the parameters that we must measure the better to understand the extent to which ambush predators affect bee population dynamics, and 2) demonstrating that even low densities of ambush predators can affect the dynamics of bee populations. In this respect, it should be noted that the analytical model assumes an infinite population. In populations near the maintenance threshold, the distribution of female reproductive success is highly skewed, with most females producing at most one offspring and a few females producing many more offspring. Due to sampling error, a different modeling approach, taking into account the finiteness of real populations (i.e., individual based models) would show an even greater effect of predation. The maintenance thresholds presented here are, in this sense, conservative.

The parameters with the strongest effect on population maintenance thresholds were predator avoidance, P_{LH}, and the number of flowers that must be exploited to provision an egg, N. A number of studies have looked at nest provisioning by solitary bees and the relationship between bee body size and provisioning (Danforth 1990; Bosch and Vicens 2002; Müller et al. 2006; Bosch 2008). Nevertheless, to determine the number of flowers that bees must exploit to harvest these resources, we must also know the amount of resources (particularly pollen) that bees collect in an average flower visit. Measuring this parameter will not be easy, as it depends both on the amount of resources produced per flower per day (itself a function of several factors, including flower species), and the strength of inter- and intraspecific competition. Predator avoidance would seem like an easier parameter to measure in the field. Nevertheless, the seemingly inconsistent results obtained in different studies, with the same bee species sometimes avoiding predators and other times ignoring them (Morse 1986; Brechbühl et al. 2010; Llandres et al. 2012), demonstrate that we have much to learn on this respect as well.

In view of laboratory results (Ings and Chittka 2008), understanding the effect of learning on predator avoidance under field conditions would seem particularly important. As it stands, the model assumes that ambush predators are randomly distributed throughout the habitat. If the distribution of predators were strongly clumped, bees could substantially increase their expected fitness avoiding areas with high predator concentrations. Although some experiments show that social bees can avoid patches where ambush predators are abundant (Dukas and Morse 2003; Llandres et al. 2012), the effect of predators on the foraging range of solitary bees has not been investigated, and ambush predators are also known to choose flowers with high visit rates (Morse 2007), so the extent to which learning will modify model predictions is as yet unclear. At any rate, it should be noted that bumblebees needed an average of 7 failed attacks to learn to avoid robotic crab spiders (Ings and Chittka 2008). If this value is representative for bees as a whole, it means that learning can only play a significant role in species with low susceptibility to predation.

The most striking prediction of our model is that low densities of ambush predators, with flower occupancies well below the range of reported values (Schmalhofer 2001; Dukas and Morse 2003; Suttle 2003; Llandres et al. 2012), can have significant effects on the population densities of medium-sized solitary bees. When predator abundance is greater than the population maintenance threshold of a solitary bee in a given ecological context, population growth will be negative and bee abundance will decline. The species, however, need not be driven to local extinction. A reduction in bee abundance will reduce intraspecific competition for resources, thus increasing net profitability per flower visit, with a concomitant reduction in the number of flowers that must be exploited to provision an egg and an increase in the population maintenance threshold. If the population maintenance threshold in the absence of resource competition is greater than the abundance of ambush predators, predators will simply down-regulate bee population density. Only when the maintenance threshold in the absence of resource competition is lower than predator abundance will bees be driven to local extinction.

Another complication that we have so far ignored is that a decline in bee population densities could have a negative effect on predator populations, possibly leading to predator–prey cycles as those predicted by Lotka–Volterra (Volterra 1926; Lotka 1932) and related models. This possibility, however, seems unlikely given that most ambush predators are generalist predators, which can survive on alternative resources. Indeed, an increase in the abundance of alternative prey, particularly of small prey that can increase the survival rate of juvenile predators, could endanger the viability of solitary bee populations. In the face of the global pollinator crisis, with a generalized reduction in pollinator abundance and diversity (Cane and Tepedino 2001; Biesmeijer et al. 2006; Pauw and Hawkins 2011), our results suggest that the relationship between ambush predators and solitary bees cannot be ignored.

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