PREDATION IN POLLINATION SYSTEMS

THE EFFECT OF FLOWER-DWELLING AMBUSH PREDATORS ON POLLINATION SYSTEMS

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Abstract

The interaction between pollinators and flowers affects the fitness of both pollinators and flowering plants, which can result in the co-evolution of pollinator and floral traits. Some pollination systems contain flower-dwelling ambush predators that attack visiting pollinators. This interaction could result in co-evolution of predator and pollinator traits as is typical in predator-prey systems. The presence of these predators could also have indirect negative fitness effects on flowering plants by killing or deterring pollinators. This raises the possibility that predator and floral traits also co-evolve. Furthermore, it is possible that this system is best described as a three-species game where predator, pollinator, and floral traits all co-evolve. The ultimate goal of my thesis is to explore this possibility. This is achieved in Chapter 5, which consists of a game theory model of the co-evolution of floral colour with predator and pollinator behavioural strategies. This model is novel, both within the pollination context described here and within a wider context. Furthermore this model is the first to propose that the evolution of floral colour might be affected by the presence of flower-dwelling ambush predators. This is particularly significant given that there has been little discussion about what floral traits might be adaptations to the presence of these predators. A secondary goal of this thesis is to explore how pollinators detect and respond to the presence of flower-dwelling ambush predators as an important subcomponent of predator-pollinator-flower co-evolutionary dynamic. Chapter 2 demonstrates that bumblebees avoid evidence of past predation events, and Chapter 3 demonstrates that the honeybee recruitment dance is affected by exposure to cues of predation risk in a way that should reduce the colony's exposure to predators. Chapter 4 is a model that suggests novel factors that might affect how a population of pollinators distributes itself between predator-free and predator-containing flowers.

Preface and Acknowledgements

This is a sandwich thesis in the sense that all of the content chapters are manuscripts that have been published, are in press, or are in preparation. This means that there is some repetition between chapters, particularly in the literature reviews. Each of the published or in press chapters begins with a reference to the published work and a clear statement as to the identity of the copyright holder. While I have received valuable assistance on all chapters (as outlined in the acknowledgement section), I have contributed significantly to each chapter which justifies their inclusion in this thesis. All work included in this thesis was conducted while I was a graduate student at McMaster University. I have included further details for each content chapter below.

Chapter 2: This chapter has been published. I am the sole author of this chapter.

Chapter 3: This chapter has been published. I am the first author of this chapter. The second author is my thesis supervisor, Reuven Dukas. Both authors contributed significantly to all aspects of this work including experimental design, data collection, data analysis, and writing.

Chapter 4: This chapter is a manuscript that is in preparation. This chapter derives from the final project of a graduate level Game Theory course taught by David Earn at McMaster University. This final project was completed in partnership with another student in the course, Olga Krylova. This partnership primarily involved developing the basic concepts of the model. I am responsible for all subsequent work that was required to make this final project into a publication-ready manuscript. This subsequent work involves significant revisions to the model, model analysis, and the writing of the manuscript. I will be the sole author of any future publication arising from this manuscript. All future copyright issues that arise from publishing this chapter, in revised form, will be dealt with as is appropriate.

Chapter 5: This chapter has been accepted for publication and is currently in press. I am the sole author of this chapter. All future copyright issues that arise from publishing this chapter will be dealt with as is appropriate.

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Chapter 1: Introduction

This thesis explores the effects of flower-dwelling ambush predators on pollination systems. This is, at minimum, a three-species system (predators, pollinators, and flowering plants) and I attempt to devote some attention to all three of these parties. As an evolutionary biologist, I have tended to focus on how the presence of flower-dwelling ambush predators affects the evolution of various traits of these three species. As a behavioural ecologist (a sub-field of evolutionary biology), I have focused on behavioural traits, or traits that influence behavioural traits of another species. As a cognitive ecologist (a sub-field of behavioural ecology), I have focused, where possible, on cognitive traits. As an unapologetic adaptationist, I have focused on how natural selection (as opposed to other evolutionary forces) has, or may have, shaped these traits.

Introduction to the predator-prey/pollinator-flower system

In pollination systems, pollinators visit flowers, collect nectar and pollen, and incidentally transfer pollen between flowers. Some pollination systems (Predator-Prey/Pollinator-Flower systems) contain flower-dwelling ambush predators such as crab spiders (Morse 2007) or ambush bugs (Balduf 1939; Mason 1986). These ambush predators cryptically wait on, or near, flowers and attempt to capture visiting pollinators. In such a predator-prey/pollinator-flower system, there are three distinct two-species interactions, and all three can have fitness consequences for the individuals involved (Figure 1). 1) In general, pollination interactions are mutualistic. Interactions between pollinators and flowers have positive fitness effects on both individuals; pollinators gain food and plants import and export pollen which is required for sexual reproduction. 2) The interaction between the pollinators and ambush predators is not mutualistic; the interaction has a positive fitness effect on the predators but a negative fitness effect on the prey. 3) While individual predators do physically interact with the individual flowers on which they hide and hunt, there is not any obvious direct fitness effect of this interaction on either the predators or the flowers. Predators do not generally acquire any resources from the flower itself, and do not generally damage the flower or plant. The interaction can, however, indirectly affect the fitness of both the predators and the flowers. Predators indirectly benefit from the interaction with a flower due to the high density of potential prey on flowers (i.e. pollinators). Flowers, however, may be indirectly negatively affected by an interaction with a predator (Knight et al. 2006; Muñoz and Arroyo 2004; Suttle 2003 but see Dukas and Morse 2005; Louda 1982; Wilkinson 1991). This indirect negative impact can result from the predator reducing the import and export of pollen by killing or deterring pollinators (Balduf 1939; Dukas 2001a; Dukas and Morse 2003, 2005; Elliott and Elliott 1994; Ings and Chittka 2009; Knight et al. 2006; Morse 1979; Muñoz and Arroyo 2004; Reader et al. 2006; Robertson and Klemash Maguire 2005; Suttle 2003 but see Dukas and Morse 2005; Elliott and Elliott 1991; Morse 1986; Reader et al. 2006; Wilkinson et al. 1991).

Co-evolution in predator-prey/pollinator-flower systems

Whenever an interaction between species has a fitness impact on one species, it can result in the evolution of traits related to the interaction. Furthermore, when the interaction has a fitness impact on both species, it can result in the co-evolution of relevant traits in the two species. This means that each of the two-species interactions described above could result in separate, but interacting, co-evolutionary dynamics.

Pollinator-flower co-evolution

Darwin (1872, pp 74-75) used a pollination example to illustrate how co-evolution could work:

> "... it may be believed that under certain circumstances individual differences in the curvature or length of the proboscis, &c., too slight to be appreciated by us, might profit a bee or other insect, so that certain individuals would be able to obtain their food more quickly than others; and thus the communities to which they belonged would flourish and throw off many swarms inheriting the same peculiarities. The tubes of the corolla of the common red and incarnate clovers (*Trifolium pratense* and *incarnatum*) do not on a hasty glance appear to differ in length; yet the hive-bee can easily suck

> the nectar out of the incarnate clover, but not out of the common red clover, which is visited by humble-bees alone; so that whole fields of the red clover offer in vain an abundant supply of precious nectar to the hive-bee. ... Thus, in a country where this kind of clover abounded, it might be a great advantage to the hive-bee to have a slightly longer or differently constructed proboscis. On the other hand, as the fertility of this clover absolutely depends on bees visiting the flowers, if humble-bees were to become rare in any country, it might be a great advantage to the plant to have a shorter or more deeply divided corolla, so that the hive-bees should be enabled to suck its flowers. Thus I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted to each other in the most perfect manner, by the continued preservation of all the individuals which presented slight deviations of structure mutually favourable to each other."

Subsequent work has suggested that proboscis and corolla length do co-evolve as Darwin envisioned (Anderson and Johnson 2008; Muchhala and Thomson 2009; Pauw et al. 2009). Further research has suggested that other floral traits may co-evolve with pollinator search strategies or preferences for those traits in at least two ways. First, consider a theoretical example from Lynn et al. (2005) where a pollinator species is simultaneously exposed to a yellowish green rewarding flower species and a bluish green unrewarding flower species. This pollinator should have an adaptive learning mechanism that produces a preference, not for the yellowish green average colour of the rewarding species, but instead for flowers that are even more yellow (i.e. less blue) in colour. This is adaptive for the pollinator species as it reduces the risk of wasting foraging time on unrewarding flowers. This pollinator adaptation can, in turn, lead to the evolution of a more yellow floral colour in the rewarding species. Secondly, in systems with multiple pollinator and flower species, adaptive niche partitioning strategies can evolve so that each pollinator species specialises on flower species that it is relatively good at detecting (Gegear and Laverty 2005; Possingham 1992; Rodríguez-Gironés and Santamaría 2004) or exploiting (Rodríguez-Gironés and Santamaría 2006). This in turn can lead to the flower species evolving to be even more easily detectable or exploitable by their specialist pollinators (Gegear and Laverty 2005; Rodríguez-Gironés and Santamaría 2004; 2006). However, even the adaptive foraging behaviour of a single pollinator species could favour the evolutionary diversification of flower species (Chittka et al. 1999). In particular, the foraging strategies of many pollinator species result in flower constancy (e.g. a pollinator that visits only blue flowers and ignores red flowers). It is possible that the benefit to plants of constant pollinators (i.e. avoiding transferring pollen between plant species) results in the evolution of distinct floral traits in different plant species (e.g. one blue flowered and one red flowered species) so as to promote flower constancy.

Predator-prey co-evolution

The co-evolution of predator and anti-predator adaptations has also been well studied (see Downes and Shine 1998 for a review as well as for a particularly complete empirical example). Two examples of co-evolution between crab spiders or ambush bugs (flower-dwelling ambush predators) and bees (pollinators/prey) are of particular relevance to this thesis. First, flower-dwelling ambush predator species have several adaptations to avoid detection by their prey. Many crab spider species have the ability to reversibly change their colour. There is evidence that the colour adopted by crab spiders matches the colour of the occupied flower as perceived by bees (Chittka 2001; Théry and Casas 2002; Théry et al. 2005). Furthermore, crab spiders and ambush predators may preferentially hunt from flowers on which they are camouflaged (Balduf 1939; Elliott and Elliott 1991; Greco and Kevan 1994), may hide among flowers (Balduf 1939; Morse 1986), remain still while waiting for prey to approach (Morse 1979; 1986), and avoid excreting on their hunting sites presumably to avoid creating a indirect cue of their presence (Morse 2008, but note that this behaviour could be a health related adaptation). These behavioural and physiological traits are likely predator adaptations as they reduce the probability of detection by prey (note that these traits are also likely anti-predator adaptations that allow flower-dwelling ambush predators to avoid detection by their own predators (Morse 2008; Théry and Casas 2002; Théry et al. 2005)). Conversely, there is evidence that the behavioural strategies of the focal prey species are counter-adapted to the problem of avoiding cryptic predators. In particular, bees avoid cryptic predators by avoiding conspicuous evidence of past predation events (Dukas 2001a; Reader et al. 2006), inspect flowers more carefully after exposure to a predator (Ings and Chittka 2008), and learn to avoid flower colours on which predators are highly cryptic (Ings and Chittka 2009).

The second example (Heiling et al. 2003; Heiling and Herberstein 2004) involves the Australian crab spider, *Thomisus spectabilis* which, unlike the crab spiders described above, does not match the colour of a non-native flower, *Chrysanthemum frutescens*, on which it hunts, but rather reflects an ultra-violet colour not found in the flower's colouration. Nonetheless, this colouration does appear to be a predator adaptation as it causes honeybees to be more likely to land on flowers that contain *T. spectabilis* individuals than on unoccupied control flowers. Apparently this colouration manipulates a standard bee preference for certain colour patterns on flowers. Furthermore, it appears that reduced susceptibility to this predator manipulation has evolved as a prey counter-adaptation in the native Australian bee, *Austroplebia australis*, as this species avoids occupied flowers (note that honeybees are not native to Australia and therefore have not co-evolved with this species of crab spider).

Predator-flower co-evolution

Pollinator/prey adaptations that emerge from a predator-prey co-evolutionary dynamic could affect the nature of the pollinator-flower co-evolutionary dynamic. Conversely, pollinator/prey adaptations that emerge from a pollinator-flower co-evolutionary dynamic could affect predator-prey co-evolution. Therefore, if both predators and flowers are co-evolving with a single pollinator/prey species, then traits of the predator and flower species could potentially co-evolve. This possibility has been proposed (Dukas 2001b) but little is known about what floral adaptations and predator counter-adaptations exist in pollination systems that contain flower-dwelling ambush predators. While there is evidence that many predator traits are adaptations that increase the predators' ability to exploit flowers (see above), there is little evidence for floral traits that evolve in response to predators and the potentially negative fitness effect that predators have on flowers. However, two examples serve to illustrate that the evolution of floral traits in response to indirect fitness effects is plausible. First, Wasserthal (1997) has proposed that the long tongues of some pollinators have evolved as an antipredator adaptation. In particular, long tongues allow these pollinators to extract nectar without landing on a flower, thereby keeping a distance from any ambush predators that might be on the flower. This in turn can favour the evolution of long floral corollas (note that more pollen is transferred, and flowers benefit, when pollinators are closer to the flower so that their bodies make contact with the flower's anthers and stigma). In this case, the presence of flower-dwelling ambush predators would indirectly select for longer corollas, but note that this interpretation is controversial (Jermy 1999; Nilsson 1998a; 1998b; Samways 1998; Svensson et al. 1998; Wasserthal 1998). Second (Heil and McKey 2003), there are cases where the presence of predators, or other aggressive species, has an indirect net positive fitness effect on plants because they reduce the density of herbivores. This can result in plant adaptations that act to attract these defender species. Two well studied examples of these adaptations are plant structures that can be used by the defender species as shelter, and structures that allow the defender species to access food resources produced by the plant. There are further plant adaptations that modify the behaviour of the defender species in a way that maximises the indirect positive fitness effect they have on the plant. For example, the spatial distribution of attractants and deterrents on the plant can act to direct the defender species towards plant structures that are more vulnerable to herbivory, and away from flowers where the defender species might act to deter pollinators.

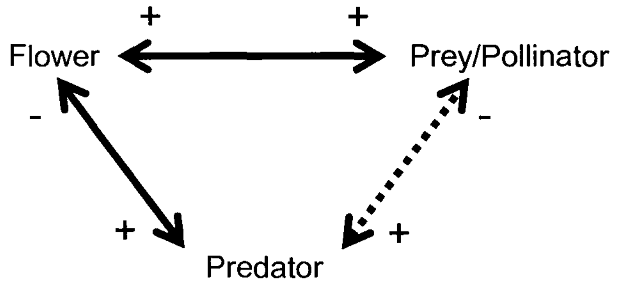
Thesis goals

The ultimate goal of my thesis is to explore how predator, prey/pollinator, and floral traits might co-evolve, with a particular emphasis on understanding what floral adaptations might arise in pollination systems that contain flower-dwelling ambush predators. This is done in Chapter 5 where I use a game theoretical model to examine how floral colour might co-evolve with predator and pollinator behavioural strategies. However, the discussion above and Figure 1 suggest that the pollinators will likely act as a linchpin in these systems. In particular, the evolution of predator and floral traits will be most directly affected by the nature of pollinator traits (i.e. traits that affect how pollinators respond to predator-free and predator-containing flowers). Furthermore, the evolution of pollinator traits will be affected by the nature of both floral and predator traits. Therefore, in Chapters 2, 3, and 4, I examine a key subcomponent of the question of how the three species co-evolve; how do pollinators detect and respond to the presence of flower-dwelling ambush predators? In Chapters 2 and 3, I explore the strategies that pollinators use to avoid flowers that contain predators, even if those predators are highly cryptic. Chapter 2 deals with avoidance of cues of past predation events as a predator avoidance strategy. Chapter 3 deals with the modulation of the honeybee waggle dance as a means of reducing the colony wide exposure to predation risk. In Chapter 4 I ignore the issue of predator crypsis and use a model to explore the conditions that should make a population of pollinators more or less willing to land on flower that harbours a predator.

Figures

<u>Figure 1</u>

A schematic illustration of the set of fitness effects in the predator-prey/pollinator-flower system. Arrows indicate whether an interaction between individuals of two species has a positive (+) or negative (-) fitness effect on each of the two species. Solid lines indicate that the interaction directly affects the fitness of the focal individuals. Dashed lines indicate that the fitness effect is indirect (see text for further details)



Chapter 2: Bumblebees avoid flowers containing evidence of past predation events

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Abstract

Bees are at risk of predation from flower dwelling ambush predators. Since these predators tend to be cryptic, bees trying to mitigate predation risk may need to make use of indirect cues of the predator's presence. For example, they may use cues of past predation events as indirect cues of current predation risk. I conducted a series of experiments that examined how bumblebees (genus *Bombus* Latreille, 1802) respond to cues of past predation events. In two field experiments, I found that wild rose (genus *Rosa* L.) flowers containing a freshly killed bumblebee, or the scent of a freshly killed bumblebee, received fewer bumblebee visits than control flowers. To test the possibility that bumblebees in the first two experiments were avoiding cues of competition risk rather than cues of predation risk, captive reared bumblebees were given a choice between two artificial flowers, one containing a freeze-killed bumblebee (relatively more similar to a live foraging bee) and the other containing a crush-killed bumblebee (relatively more similar to a bee killed by a predator). Most bumblebees chose the flower containing the freeze-killed bee, supporting the hypothesis that the bumblebees in the first two experiments were attempting to avoid predation.

Introduction

There is a recent and growing appreciation that pollinators, such as bees, may face considerable predation risk from predators that hunt on flowers (Dukas 2001b). There is also recent evidence that these predators can reduce the pollinator visitation rates at flowers (Elliott and Elliott 1994; Dukas and Morse 2003; Suttle 2003; Muñoz and Arroyo 2004; Dukas 2005; Dukas and Morse 2005; Robertson and Klemash Maguire 2005 but see Morse 1986; Wilkinson et al. 1991; Elliott and Elliott 1991; Dukas et al. 2005). However, relatively little is currently known about what cues, if any, pollinators use to assess the predation risk associated with a flower. Similarly, little is known about how bees respond when encountering a cue of predation risk.

One simple cue that pollinators could use in assessing the predation risk associated with a flower is the observed presence of a predator. Dukas (2001a) found that honeybees (*Apis mellifera* L., 1758) avoid artificial flowers containing a conspicuous predator (a frozen spider). Ambush predators that hunt pollinators on flowers, however, are generally cryptic and difficult for pollinators to detect (Balduf 1939; Morse 1979, 1986; Elliott and Elliott 1991; Chittka 2001; Théry and Casas 2002; Heiling et al. 2005a). For example, the ambush bug *Phymata americana* Melin, 1930, remain still while waiting for prey to approach, hide between flowers (Balduf 1939) and may have a tendency to hunt on flowers on which they are camouflaged (Balduf 1939; Elliott and Elliott 1991). Similarly, some crab spiders (family *Thomisidae* Sundevall, 1833) reversibly change their colour between yellow and white to match their current background (Chittka 2001; Théry and Casas 2002; Heiling et al. 2005a), remain still while waiting for prey to approach (Morse 1979, 1986), have a tendency to choose to hunt on flowers on which they are more easily camouflaged (Greco and Kevan 1994), and may hide among flowers (Morse 1986). In some cases, crab spiders may even have an appearance that exploits pollinator sensory biases, causing them to be attracted to the flower containing the predator (Heiling et al. 2003, 2005b, but see Heiling and Herberstein 2004). A more conspicuous, and possibly more useful, cue of predation risk associated with a flower might be the presence of a dead pollinator or any other sign that another pollinator was killed on the flower recently. For example, Dukas (2001a) showed that presence of a dead conspecific reduced the likelihood that honeybees would choose to land on an artificial flower.

If pollinators can detect these cues of predation risk, then there is the possibility that they can respond in order to reduce this risk. There are a number of behavioural responses pollinators could make in the presence of a cue of predation risk (see Dukas 2001b for a full discussion). The most obvious are for individual pollinators to avoid landing on high-risk flowers (Elliott and Elliott 1994; Dukas 2001a; Suttle 2003; Muñoz and Arroyo 2004; Robertson and Klemash Maguire 2005) or to spend less time foraging on any given high-risk flower (Elliott and Elliott 1991, 1994; Suttle 2003; Muñoz and Arroyo 2004). It should be noted that if most pollinators avoid a risky flower, the competition at that flower would be reduced and the amount of available resources would be increased. Thus, it is possible that pollinators landing on a high-risk flower would actually spend more time on that flower than they would on a low-risk flower.

In order to fully understand the effects of predators on pollination systems, it is important to understand both what cues pollinators use to detect predation risk and how they respond to these cues. Therefore, I conducted a series of lab and field experiments to study whether, and how, bumblebees (genus *Bombus* Latreille, 1802) respond to evidence of past predation events. In the first experiment, I examined whether the presence of a dead bumblebee on a flower affected the number and duration of visits by wild bumblebees.

Experiment 1: Bumblebee response to the presence of a dead bee on wild rose

Methods

Data collection occurred in an old field at the Darling Marine Center, Lincoln County, Maine (described in Morse 2000) in 2004 and on the Hamilton Harbour Waterfront Trail in Hamilton, Ontario in 2005. The 2005 data was collected as the sample size and power of the 2004 data was low. As the two datasets were collected at different sites with different bee and flower populations (see below), they were analysed separately.

In both 2004 and 2005, data was collected early in the day when bumblebees were most active on wild rose (genus *Rosa* L.). Pairs of flowers were selected that were as close together as possible while still being of comparable size, colour, degree to which the petals were open and accessibility to bumblebees. One flower was randomly assigned to be the experimental flower and the other to be the control flower. A freshly killed stimulus bumblebee was pinned to the edge of a lower petal of the experimental flower. These stimulus bumblebees were killed by crushing them inside a vial (Dukas 2001a). While every effort was made to shape these crushed bees into a naturalistic form, they did tend to look abnormal. In particular, the crushed bees generally looked flatter and wetter (from leaked body fluids) than live bees and had disarrayed wings and hair. These crushed bees were pinned so their ventral side was in contact with the flower petal and their dorsal side faced away from the petal. To control for effects of the pin and petal damage, the edge of the lower petal of the control flower was pierced with a pin. Observers watched the pairs of flowers for 30 minutes and recorded the time to the nearest second that each bumblebee visitor arrived and departed (leaving the flower and immediately returning without visiting any other flowers was not considered a departure). As the data conformed to the assumptions of parametric tests, two-tailed paired t-tests were used to test whether there were any differences between experimental and control flowers in the number of bees that landed on the flower and the mean visit duration. Only trials where both flowers received at least one visitor were included in the analysis of visit duration. On trials where a flower received multiple visitors, the mean duration of these visits was used as the measure of visit duration for that flower.

In 2004, data was collected July 16-18 2004 between 09:00–14:00 on 12 pairs of pasture rose, *Rosa carolina* L., flowers (30-60 cm apart). Stimulus bumblebees were *Bombus vagans* Smith, 1854, workers captured while foraging on flowers less than one km from the study site. *B. vagans* was the only bumblebee species observed at these flowers.

In 2005, data was collected June 25-30 2005 between 07:00-11:30 on 22 pairs of wild rose flowers (10-50 cm apart). The predominant rose species that was in bloom during this time was virginia rose (*Rosa virginiana* P. Mill.). *Rosa rugosa* Thunb. and *R. carolina* bushes were also present. All three wild rose species were used but each trial involved only a single rose species. Several bumblebee species were observed foraging on these flowers (*Bombus griseocollis* (DeGeer, 1773), *Bombus impatiens* Cresson, 1863 and *Bombus rufocinctus* Cresson, 1863). Due to the fact that discriminating between similar looking bumblebee species while simultaneously recording visitation data would have been very difficult, the species of bumblebee workers visiting the experimental and control flowers was not recorded. The dead stimulus bee placed on the experimental flower was always a *B. impatiens* worker collected foraging on wild rose bushes at least three km from the Hamilton Harbour Waterfront Trail.

Results

For both the 2004 and the 2005 datasets, there were significantly fewer visitations to experimental flowers than the control flowers (2004, two tailed paired t-test $t_{11}=-2.54$, $p=0.027$; Fig. 1, left set of bars; 2005, two tailed paired t-test $t_{21}=-5.64$, $p<0.0001$; Fig. 1, centre set of bars). For both the 2004 and the 2005 datasets, mean visit duration was not significantly different between experimental and control flowers (2004, two tailed paired t-test $t_6=1.41$, $p=0.21$; Fig. 2, left set of bars; 2005, two tailed paired t-test $t_{10}=1.18$, $p=0.27$; Fig. 2, centre set of bars). Note that the sample size for the tests of mean visit duration is much smaller than that for the tests of number of visitations due to the fact that a difference score for mean visit duration could not be calculated on trials where one, or both, of the flowers in a pair received no visitations. This resulted in low power for the test of mean visit duration, particularly for the 2004 dataset. To illustrate, for the 2004 dataset the overall mean visit duration, calculated for all visits to experimental and control flowers, was 10.48 seconds. However, there were visits to both the experimental and control flowers on only seven of the 12 trials. Thus, even if the mean difference in visit duration between experimental and control flowers was as high as 75% of the overall mean visit duration ($0.75\times10.48=7.86$ seconds), the probability of detecting this difference would have only been about 52%. In the 2005 dataset, only 11 of the 22 trials were useable for the mean visit duration test and the overall mean visit duration was 7.26 seconds. Using the same analysis as for the 2004 dataset, the probability of detecting a difference in mean visitation duration between experimental and control flowers that was 75% of the overall mean visit duration ($0.75\times7.26=5.44$ seconds) would have been about 74%. It should be noted that it may be unrealistic to expect such a large mean difference in visit duration between experimental and control flowers.

Experiment 2: Bumblebee response to the scent of a dead bee on wild rose

Rationale

While Experiment 1 suggests that the presence of a dead bumblebee is a potential cue of predation risk, it is unclear to which aspect of this stimulus the live bumblebees were responding. Foraging bees rely heavily on scent (e.g. Dobson et al. 1999). In particular, honeybees are repelled or attracted to feeders containing various sting gland components (Free 1987, pp. 142-143). Therefore, it is possible that the smell emitted by the dead stimuli bumblebees is what caused the avoidance response. Experiment 2 further studies the cues of predation risk to which bumblebees respond, by examining whether the scent of a dead bumblebee is sufficient to cause the avoidance response seen in Experiment 1.

Methods

Experiment 2 was similar to Experiment 1 with the following exceptions. Experiment 2 was conducted July 11-15 2005 between 06:30-10:00 at LaSalle Park in Burlington, Ontario. This experiment was conducted on two large adjacent prairie rose (*Rosa setigera* Michx.) bushes. The bumblebee species seen on these rose bushes were the same as reported for the 2005 dataset in Experiment 1, with the addition of *B. vagans*. As in Experiment 1, visitations by all bumblebee workers, but not species identity, were recorded. For 18 separate trials, stimulus bumblebees (*B. impatiens* worker individuals collected while foraging on wild rose at least 8 km from LaSalle Park) were killed as in Experiment 1 but instead of being pinned to the experimental flower, they were cut open along the medial axis and rubbed on the petals of the experimental flower. This was done to transfer the smell of these freshly killed bees to the experimental flowers. The control flowers were rubbed for a comparable length of time with a clean piece of paper towel to control for any effects of disturbance or of human odours. The distance between the experimental and control flowers varied from approximately 10-40 cm. Because the visitation rates at this site were much higher than in Experiment 1 (see Figure 1), 15 minute trials, rather than 30 minute trials, were used. In addition, the high visitation rates made recording arrival and departure times unreliable, so data on mean visit duration was ignored and only data on the number of bees landing on experimental and control flowers was analysed.

Results

Relative to control flowers, there were fewer visitations to experimental flowers (two tailed paired t-test t_{17}=-3.28, p=0.004; Fig. 1, right set of bars). On nine of the 18 trials, rubbing the stimulus bee on the experimental flower caused small dark smudges on the petals. Removing these trials from the analysis made the results marginally non-significant (two tailed paired t-test t_8=-2.06, p=0.07). The mean difference between the number of visits on control and experimental flowers (where positive numbers indicate more visits on control flowers and therefore greater apparent avoidance of experimental flowers), however, is lower for trials with smudging (3.11) than for trials with no apparent smudging (3.56) making it unlikely that the significant difference in the number of visitations was caused by this discolouration.

Experiment 3: The presence of a dead bee as a cue of predation risk or competition risk

Rationale

Experiments 1 and 2 suggested that the presence of a dead bumblebee is a cue of predation risk that affects the foraging behaviour of other live bumblebees. There is, however, a non-mutually exclusive alternative explanation. It is possible that the dead bumblebee (or the smell of a dead bumblebee) is viewed as a cue of competition, rather than predation, risk. While Dukas (2001a) and I (Experiments 1 and 2) interpreted avoidance of crushed bees as evidence of avoidance of predation risk, Somers (2004) interpreted avoidance of flowers containing freeze-killed bees as evidence of competition avoidance. It is plausible that the way in which the stimulus bees are killed affected how they were perceived by foraging bumblebees. Specifically, a bee comparing freeze and crush-killed bees will likely perceive the freeze-killed bee as relatively more like a live foraging competitor (cue of competition risk) and the crush-killed bee as relatively more like a dead bee killed by a predator (cue of predation risk). Crushing bees damages the exoskeleton, which may cause damage specific odours. In addition, it is possible that like honeybees (Balderrama et al. 1996), bumblebees emit a distinctive smell when alarmed, such as when being crushed inside a vial. Freshly crushed bumblebees do emit a strong detectable odour (pers. obs.). It is likely that at least some of these odours are emitted by bees being attacked or killed by a predator. In contrast, a freeze-killed bee will not emit damage specific odours and may not emit any alarm related odours.

Given the uncertainty of the cause of the avoidance response seen in Experiments 1 and 2, Experiment 3 tested whether at least some component of that response can be attributed to avoidance of cues of predation risk. This was done by determining whether bumblebees avoid artificial flowers containing a crush-killed bumblebee relative to ones containing a freeze-killed bumblebee.

Methods

This experiment was conducted in the lab from October 14 - November 5 2005 using workers from two captive reared *B. impatiens* colonies foraging on artificial flowers in a flight cage (54x54x17 cm LxWxH wooden box with a transparent plastic top) attached to the colony. Twelve individuals were trained to forage on a single artificial flower (a 9 cm diameter purple disk with a 1.5 ml centrifuge vial with the lid removed inserted in the centre to hold sucrose solutions). During initial training, the flower contained 50% (w/w) sucrose solution with honey added for scent. Towards the end of training, the honey was removed so that there would be no scent emitted from the flower except that from the stimulus bumblebees. Over the course of training, the single artificial flower was moved from near the entrance to the back of the flight cage. At all times, the training flower was in the centre of the flight cage (in the right-left dimension from the perspective of a bumblebee entering the cage). Training trials were run until the bumblebee reliably flew directly to, and drank from, a single artificial flower at the back of the cage containing unscented sucrose solution.

For test trials, the single artificial flower at the centre of the back of the cage was replaced with two identical artificial flowers located 7 cm to the left and right of centre at the back of the cage. Each of these artificial flowers contained unscented sucrose solution. In every test trial, one randomly selected flower contained a crush-killed bee and the other contained a freeze-killed bee. These dead stimulus bees (also captive reared *B. impatiens* workers) were placed on the edge of the flower closest to the entrance of the cage. Crush-killed bees were killed as in Experiments 1-3. As it was important that live bumblebees did not perceive the freeze killed bumblebees as predator-killed bumblebees (at least relative to crush-killed bumblebees), the freeze-killed bumblebees were handled in such a way as to minimise the release of potential alarm related odours. Rather than being captured in a vial like the crush-killed bees, freeze-killed bees were collected in a 473 ml clear plastic container attached to their colony. In order to minimise visual disturbance to the freeze-killed bees, this container was then enclosed in a cardboard box and placed in a freezer overnight. The following day, the container, with the now dead bumblebees, was removed from the cardboard box and left uncovered in the freezer for at least another day to allow any scents (e.g. alarm related odours) to dissipate. Freeze-killed bees were removed from the freezer 15 minutes before the start of test trials as preliminary work indicated that this length of time allowed the internal temperature of the bee to thaw to ambient temperature (24°C).

Foraging bees were allowed to choose between the two flowers. The identity of the flower that they chose to land on and drink nectar solution from was recorded. No bees drank from both flowers in any given trial. Flowers were cleaned with rubbing alcohol between trials to remove odours.

Results

A significant majority of bees chose the flower containing the freeze-killed bee rather than the one containing the crush-killed bee (Chi square test $X^2=5.33$, $p=0.021$; Fig. 3). One trained bumblebee refused to accept the unscented solution so the test trial was run with the scented solution. The results were statistically significant even when this bee was removed from the analysis.

Discussion

My results demonstrate that, in at least two different locations with different wild rose and bumblebee species, the presence of a dead bumblebee reduced the number of visitors that a flower received (Experiment 1). I was, however, unable to detect an effect of the presence of a dead bumblebee on visit duration but the power of this test was small (especially in the 2004 dataset) (Experiment 1). More work on this problem is warranted because the possibility that cues of predation risk, especially in the absence of an actual predator, may actually increase the amount of time individual visitors spend on a flower has interesting implications for how predators of pollinators affect plant fitness (Somers 2004). Note that previous studies have found that the presence of an ambush predator has either no (Morse 1986) or negative (Elliott and Elliott 1991, 1994; Suttle 2003; Muñoz and Arroyo 2004) effects on mean visit duration. The high-risk flowers or plants in those studies contained an actual predator. Aggressive movements by those predators may have startled the pollinators and reduced the length of the average pollinator visitation. Additionally, these results suggest that a component of the cue that elicited this avoidance response was olfactory (Experiment 2). There were numerous cues, olfactory and otherwise, that the bumblebees could have been responding to. For example, they could have been responding to the smell of a dead bee (Visscher 1983), the smell of an alarmed bee (Balderrama et al. 1996), the smell of a damaged bee (Grostal and Dicke 1999) or the sight of a non-moving bee. While Experiments 2 and 3 suggested that olfactory cues, particularly cues related to damage or alarm, were important, future studies should be done to determine what exactly elicits the avoidance response.

Furthermore Experiment 3 supports the hypothesis that at least some component of the avoidance response observed in Experiments 1 and 2 was related to avoidance of predation risk rather than just avoidance of competition risk. There are, however, other potential explanations for the avoidance response seen in all three experiments. The two most obvious alternate hypotheses have to do with 1) neophobia and 2) repellent scent marks. These are discussed below.

It is possible that the bumblebees were simply avoiding a novel object in Experiment 1, a novel smell in Experiment 2 and the most novel of two objects in Experiment 3. Even though previous work on honeybees (Dukas 2001a) and bumblebees (Somers 2004) have failed to find any avoidance of novel, but neutral, objects, it is difficult to conclusively rule out neophobia as an explanation for avoidance of cues of past predation events. In particular, it is possible that the neutral novel object used in Dukas (2001a) and Somers (2004) were less salient than the cues of past predation event used in the current study. A sophisticated psychophysical experiment would likely be required to conclusively discount neophobia as an explanation for the results presented here. It should be noted that the neophobia and predation avoidance hypotheses are not mutually exclusive. Given that bees are at risk of predation from a wide variety of predators (Dukas 2001b), neophobia could be a proximate mechanism that promotes the generalized avoidance of situations with elevated predation risk. There are, however, other reasons why neophobia could have evolved. For example, neophobia could help bees avoid damaged flowers that may contain less nectar or pollen (Krupnick et al. 1999).

Bumblebees are known to avoid flowers that have been recently visited by other bumblebees (Goulson 2003, pp. 115-121 and references therein). In bumblebees, the primary source of the repellent scent marks that cause this avoidance is thought to be the tarsal glands (Goulson 2003). It is not clear to what extent crushing bumblebees would release chemicals from the tarsal glands. It does seem, however, that more chemicals would have been released from glands in the thorax and abdomen where most of the crushing induced damage occurred. Additionally, cutting the bumblebees along the medial axis, as in Experiment 2, would not have affected the release of tarsal gland chemicals. Nonetheless, extracts from the cuticle of bumblebees have been found with a chemical composition similar to that of extracts from the tarsal glands (Goulson 2003). It therefore remains a possibility that the behaviour of the bumblebees in the current study was affected by residual scent marks on the stimulus bees. It is also possible that avoidance of cues of past predation events and avoidance of recently visited flowers are mediated by the same chemical cues. Note that avoiding recently visited flowers would reduce competition for resources but it differs from the type of competition that was dealt with in Experiment 3. The competition risk considered in Experiment 3 had to do with a competitor that was currently on the flower of interest and could potentially interfere with the focal bee as well as reducing the amount of resources available.

It should be noted that the stimuli (dead bees) used were not naturalistic. Freeze-killed bees do not perfectly resemble live competitors and crush-killed bees do not perfectly resemble a bee that has been killed by a predator. In particular, the amount of damage caused by crushing a bee probably far exceeds that caused by an invertebrate predator. The crush-killed bees used here may be a supernormal stimulus and it is possible that the response to a predator-killed bee is less extreme. Similarly, the olfactory cue used in Experiment 2 was likely stronger that what would be present after a predation event. The stimulus bees in Experiment 2 were cut along the medial axis before being rubbed on the flower. This likely released a variety of body fluids including hemolymph and chemicals from the glands that exist in the head, thorax and abdomen of bumblebees. As far as I know, no research has considered what body fluids are released during a predation event so it is not, as of yet, clear how closely the olfactory stimuli used in Experiment 2 corresponds to what would be present on a flower after a natural predation event. It does seem, however, that even predators that cause minimal damage to the exoskeleton of their prey (e.g. crab spiders, ambush bugs) should cause the release of body fluids (particularly hemolymph) and related odours that could be used as an olfactory cue of predation risk.

These results are consistent with studies showing that a dead bee is perceived as a cue of predation risk (Dukas 2001a) and that the presence of a predator (and therefore the potential presence of cues of past predation events) affects visitation rates of pollinators at flowers (Elliott and Elliott 1994; Dukas and Morse 2003; Suttle 2003; Muñoz and Arroyo 2004; Robertson and Klemash Maguire 2005). These results may also explain why other studies (Morse 1986; Wilkinson et al. 1991; Elliott and Elliott 1991; Dukas et al. 2005) have found little or no effect of predators on visitation rates. It is possible that in these situations, foraging pollinators were unable to detect cues that indicated past predation events. This could be because the predation rate was so low that few of these past predation events had occurred or because some feature of the predator, or the flower, allowed evidence of past predation events to quickly decay (see below).

My results are also consistent with studies in other systems that show that individuals respond to evidence of the predation of conspecifics as a cue of predation risk. For example, it has been found that the spider mite *Tetranychus urticae* Koch, 1836 avoids patches containing artificially damaged conspecific eggs or adults (Grostal and Dicke 1999). Similarly slimy sculpins (*Cottus cognatus* Richardson, 1836) respond to chemicals released by damaged conspecifics as if they were cues of predation risk (Bryer et al. 2001). Additionally, brook trout (*Salvelinus fontinalis* (Mitchill, 1814)) appear to use chemicals released by damaged conspecifics to learn about the odours of novel predators (Mirza and Chivers 2000).
If avoidance of flowers displaying evidence of past predation events is an adaptation for reducing predation risk, evidence of past predation events must accurately predict current predation risk. However, there are a number of situations where this may not be the case.

Firstly, if predators are very mobile, any cue of predation risk based on past events may be useless. While avian and wasp predators may capture bees on flowers, they search for them while flying over large areas (Dukas 2001b; Dukas 2005). This means that a flower where a predation event involving an avian or wasp predator has occurred in the past may not be more risky than any other flower. It is likely that any avoidance based on cues of past predation events evolved in response to the risk imposed by ambush predators such as crab spiders or ambush bugs that attempt to catch many prey items on the same flower, umbel or plant.

Secondly, the presence of cues of past predation events may actually signal the presence of a feeding or satiated predator and could possibly be a cue of reduced predation risk. This concern does not apply if predators have large appetites, in which case cues of recent predation events may not mean that the predator is no longer actively hunting. As well, if the cue of past predation events is persistent, then it might predict the presence of a predator that is no longer satiated. For example, if the corpses of past prey items remain on, or near, the area in which the predator is hunting, then bees may be able to respond to current predation risk. Similarly, if as suggested in Experiment 2, a major component of the cue of past predation events is olfactory, then it is possible that bees could respond long after the corpses have been removed. Additionally, if predators are aggregated then the presence of one feeding or satiated predator may predict the presence of other actively hunting predators. However, while many ambush bugs are found in pairs, with one male mate-guarding one female, they appear to share captured prey so that one member of this pair will not be hunting while the other is feeding (Balduf 1939; Greco and Kevan 1995).

Lastly, if predators remove corpses from their hunting sites, if the architecture of the plant causes discarded corpses to fall off the plant or if scavengers remove corpses from flowers (Elliott and Elliott 1991; Morse 2001) then evidence of past predation events may be a cue that is not available to potential prey individuals and would therefore be uninformative. As noted above, if the smells associated with a corpse are persistent, the actual presence of the corpse may not be necessary.
It is also possible that cues of past predation events predict current predation, harassment or competition risk due to the fact that these cues attract other animals. For example, if an animal that is both a predator and a scavenger is attracted to the scent of dead insects, then bees might avoid flowers with dead insects to avoid encounters with this animal rather than avoiding encounters with the predator that killed the insect. Visscher (1983) found that the wasp, *Vespula germanica* Fabricius, 1793, foraged on honeybee corpses. While these wasps may be too small to threaten bumblebees, it is plausible that other larger predator/scavengers will also seek out dead insects. Bees may also avoid flowers that attract small predator/scavengers to minimise the risk of harassment or competition, even if the risk of mortality is small.

Figures

Figure 1

The mean number of bumblebee (genus *Bombus* Latreille, 1802) visitations (+ S.E.M) at experimental and control flowers per trial for Experiments 1 (2004 dataset, leftmost pair of bars; 2005 dataset, centre pair of bars) and 2 (rightmost pair of bars). In Experiment 1, the experimental flower contained a freshly killed bumblebee. In Experiment 2, the experimental flower was rubbed with a freshly killed bumblebee in order to transfer the scent to the flower. Trials for experiment 1 were 30 minutes long whereas trials for experiment 2 were only 15 minutes long. For all three experiments, there were significantly fewer visitations at experimental than control flowers (p's<0.05, see text for details).

Chapter 2: Figure 1

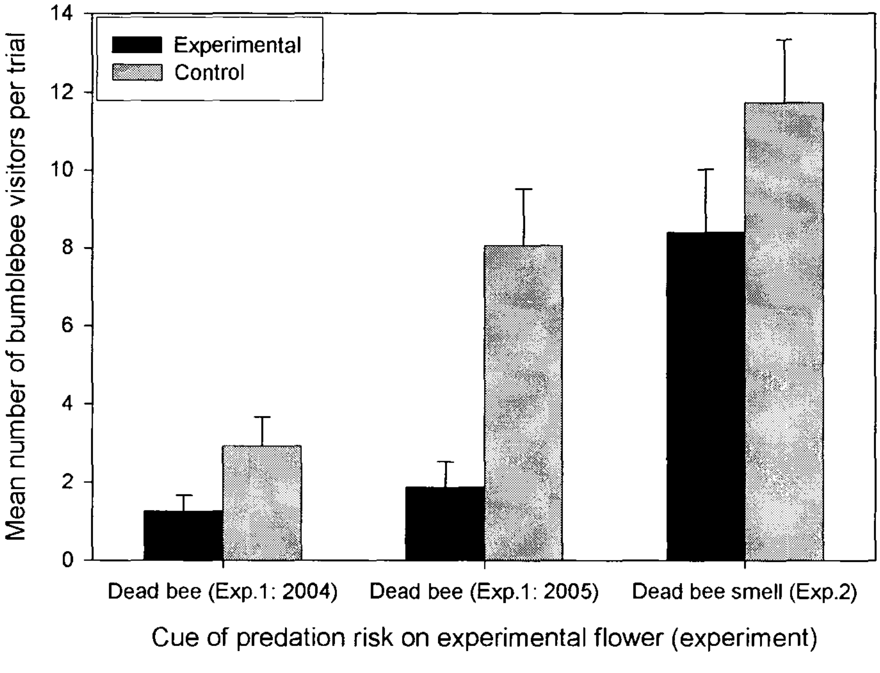


Figure 2

The mean duration of bumblebee visitations (+ S.E.M) at experimental and control flowers for Experiment 1 (2004 dataset, leftmost pair of bars; 2005 dataset, rightmost pair of bars). In this experiment, the experimental flower contained a freshly killed bumblebee. The differences in visit duration between experimental and control flowers was not significant for either dataset (p's>0.2, see text for details).

Chapter 2: Figure 2

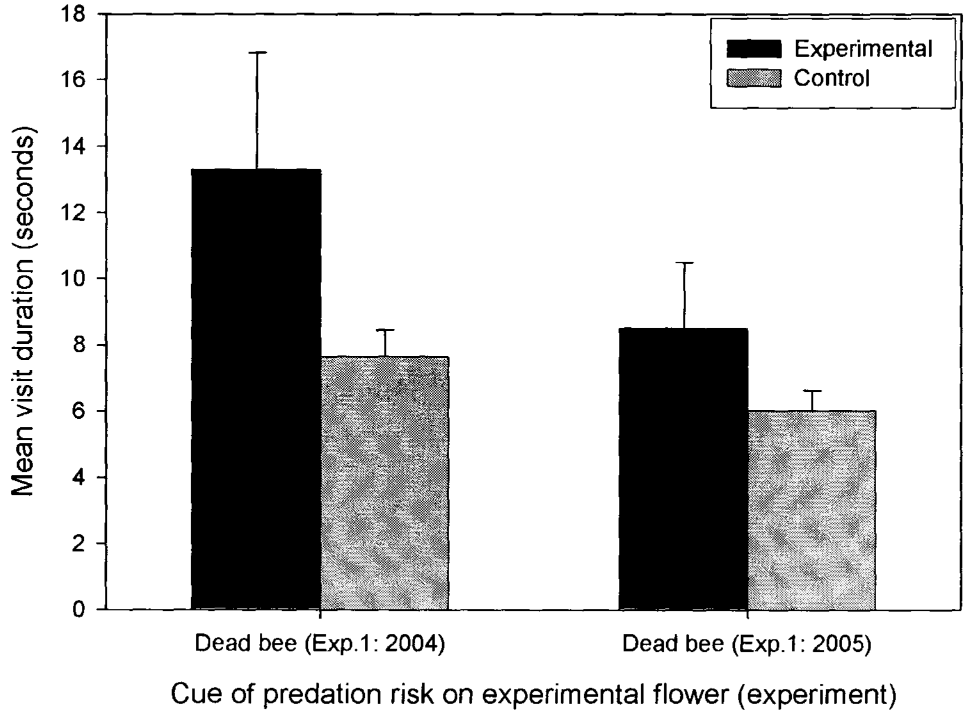
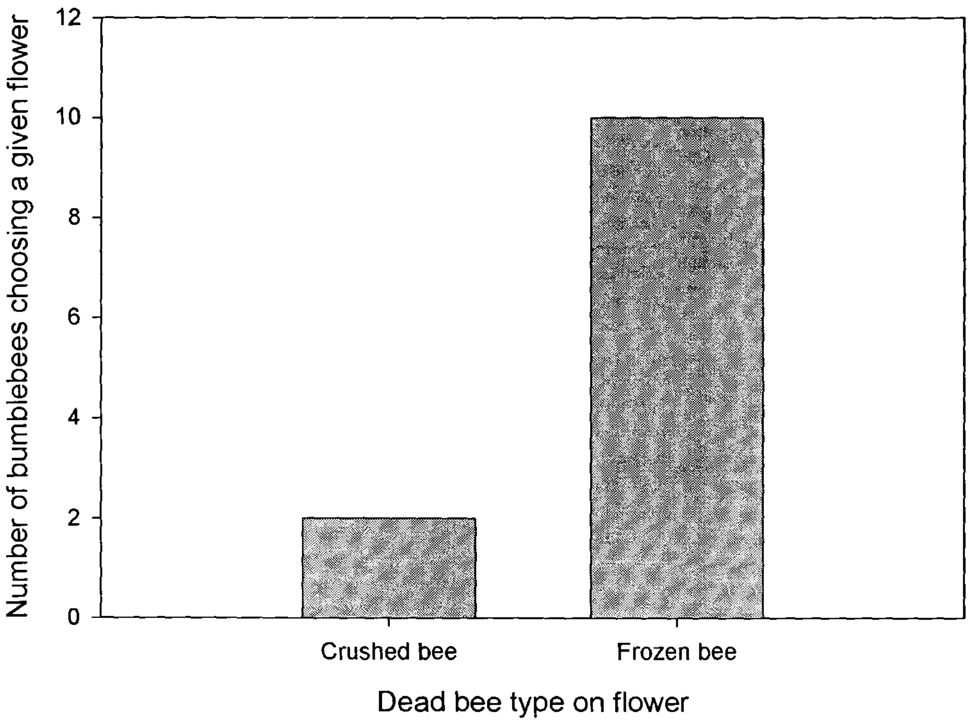


Figure 3

Number of bumblebees choosing to land and drink from either an artificial flower containing a freshly crush-killed bumblebee or one containing a thawed freeze-killed bumblebee. Significantly more bees chose the flower with the freeze-killed bee (p=0.021, see text for details).

Chapter 2: Figure 3



Chapter 3: Honeybees consider flower danger in their waggle dance

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Abstract

Like most animals, honeybees, *Apis mellifera*, possess a suite of antipredatory adaptations used to defend their colony against intruders and to avoid flowers associated with predation risk. Honeybees also possess a remarkable ability to communicate the direction, distance and relative profitability of flower patches to hivemates using the well-studied waggle dance. Here we show that honeybees returning from foraging on dangerous flowers are less likely to perform the waggle dance and engage in fewer waggle runs than foragers returning from equally rewarding, safe flowers. Our results indicate that experienced foragers effectively steer naïve recruits away from dangerous flowers and raise interesting questions as to how information about the reward and risk properties of patches are integrated into the waggle dance.

Introduction

The honeybee waggle dance is a well-studied and surprisingly sophisticated example of animal communication. The waggle dance was first deciphered by von Frisch (1967), who determined that honeybee foragers communicate the location of profitable flower patches to hivemates using the waggle-run portion of the dance, where the direction and distance to a patch are indicated by the angle and duration of the waggle run, respectively. Subsequent work has demonstrated the flexibility of this mode of communication. For example, honeybees are more likely to dance and perform more waggle runs when returning from food sources that contain more concentrated sucrose solutions (von Frisch 1967; Seeley 1994; Seeley et al. 2000). It thus appears that foragers integrate a number of relevant foraging parameters into a measure of profitability, and that the probability of dancing, and the number of waggle runs performed are positively correlated with this measure of profitability (von Frisch 1967; Waddington 1982; Seeley 1994). While honeybees tune the waggle dance in a way that, under natural settings, would lead to greater recruitment of foragers to patches with better reward properties, it is unknown whether honeybees can also tune the waggle dance in response to predation risk at flowers, which may render a patch less valuable to their colony (Clark & Dukas 1994).

Several recent studies have documented that honeybees avoid flowers containing cues of elevated predation risk. For example, honeybees avoided flowers where they had previously experienced a simulated predator attack, flowers that harboured ambushing spiders and flowers that contained dead conspecifics (Dukas 2001a; Suttle 2003; Reader et al. 2006). Furthermore, in a large-scale field experiment with crab spiders (*Misumena vatia*), which are common flower-dwelling ambush predators (Morse 2007), milkweed (*Asclepias syriaca*) patches that contained crab spiders received significantly fewer honeybee visits than did control patches with no crab spiders (Dukas & Morse 2005). Since individual honeybees avoid locations with elevated risk of predation, it seems plausible that experienced foragers might modify the waggle dance in response to the perceived risk at flowers in order to facilitate the avoidance of predation risk by naïve recruits.

To determine whether perceived danger affects the waggle dance, we trained honeybees to visit two equally profitable artificial flowers. One flower was safe whereas the other contained a cue of predation risk. We predicted that bees returning from foraging trips on the dangerous flower would perform fewer waggle runs than foragers arriving from the safe flower.

Methods

The experiment was conducted in the summer of 2008 at the Wildlife Research Station in Algonquin Park, Ontario, Canada (see Dukas 2008 for description of field site and basic set-up). We trained honeybees from a two-frame observation hive, with approximately 2000 workers, to forage on two artificial flowers that were approximately 250 m from the colony and 60 m apart. Flowers consisted of jars of scented sucrose solution inverted over grooved Plexiglas plates (von Frisch 1967). To aid in recruitment, and to facilitate the faithfulness of foragers to a single flower, one flower was consistently scented with anise extract, and the other was consistently scented with mint extract. Whenever additional foragers were required, we habituated established foragers to a 1.25 M sucrose solution for at least 1 h before increasing the concentration to 2.5 M . This increase in sucrose concentration is known to promote dancing by established foragers and, thus, the recruitment of new foragers (von Frisch 1967; Seeley 1996; Higo et al. 1995). The dance response of foragers to increased nectar concentration (i.e. probability of dancing and number of waggle runs performed) was relatively weak throughout the experiment, probably because of an abundance of natural sources of nectar. All the bees used in this experiment were faithful to a single flower, and preliminary analyses indicated that the number of waggle runs performed was similar for the anise and mint flowers (two-tailed Mann–Whitney U test: $U = 108$, $N_{mint} = 15$, $N_{anise} = 17$, $P = 0.4$).

Trials were run on warm (>20 °C), sunny afternoons (1400–1800 hours) with one to four individually marked focal bees that had been feeding on a 1.25 M sucrose solution for at least 1 h. To equalize the number of foragers on the two feeders as closely as possible, we removed excess bees from the more active feeder before the start of the trial. At the beginning of each trial, the concentration of the sucrose solution at each flower was increased to 2.5 M to encourage dancing. Two recently killed stimulus bees (Dukas 2001a) were placed on the experimental flower so that they were conspicuous but did not interfere with foraging. For the duration of the 30 min trials, observers at the flowers recorded the number of bee visits and notified hive observers by radio when focal bees that had completed a full flower visit lasting at least 1 min departed for the hive. Two hive observers, blind to flower treatment, recorded the number of waggle runs performed by the focal bees. The dance behaviour of a single focal bee was observed up to three times per trial. A focal bee was only tested in one trial and only bees that had not previously visited a flower containing a dead bee were tested. We could not quantify recruitment because many recruits approached the dangerous flower but did not land, and such bees could often not be identified.

We ran eight matched trials, with anise and mint flowers serving on half the trials as the safe flower and on half the trials as the dangerous flower in random order. Technical difficulties in three trials interfered with counting the number of visitors, which reduced the sample size in the rate-of-visits analysis by two (see below; in one of these trials, the rate could still be calculated based on a 23 min observation period, rather than a 30 min observation period). Owing to small sample sizes and non-normal data, we used nonparametric statistical tests.

Results

On average, bees returning from safe flowers performed about 20 times more waggle runs than bees returning from dangerous flowers (two-tailed Mann–Whitney U test: $U = 46.5$, $N_{safe} = 18$, $N_{dangerous} = 14$, $P = 0.001$; Fig. 1). We also conducted a matched comparison using trials as the independent experimental units. This analysis indicated that approximately 30 times more waggle runs were performed by bees visiting the safe flower than the dangerous flower (two-tailed Wilcoxon signed-ranks test: $T = 0$, $N = 8$, $P = 0.012$; Fig. 1).

The above analyses included many cases where the focal bee did not dance on one or more observations. This allowed us to examine whether the experimental manipulation also affected the probability of dancing. An analysis including only the dance data from the first foraging bout for each bee in a trial revealed that bees that had visited the safe flower were eight times more likely to perform at least one waggle run than bees that had visited the dangerous flower (10 of 18 safe-flower bees danced and 1 of 14 dangerous-flower bees danced; two-tailed Fisher's exact test: $P = 0.008$).

Consistent with previous findings indicating that honeybees avoid flowers associated with danger (Dukas 2001a; Suttle 2003; Reader et al. 2006), the safe flower received significantly higher rates of bee visits than did the dangerous flower (mean ± SE = 0.68 ± 0.11 versus 0.41 ± 0.07 visits/min; two-tailed Wilcoxon signed-ranks test: $T = 0$, $N = 5$, $P = 0.043$)

even though the number of bees visiting each flower was equalized before the start of each trial.

Discussion

Our results demonstrate that the presence of a cue of predation risk depresses the dance behaviour of honeybees. Previous studies have shown that the waggle dance is modulated by the reward properties of flowers (von Frisch 1967; Waddington 1982; Seeley 1994; Seeley et al. 2000; Afik et al. 2008; Seefeldt & De Marco 2008). Our study indicates that predation risk, a property unrelated to the quality, quantity, accessibility, or distribution of reward, also affects honeybees' dance behaviour.

The simplest interpretation of our results is that honeybees, which are well known to show antipredatory behaviour at flowers (Dukas 2001a; Suttle 2003; Dukas & Morse 2005; Reader et al. 2006), also extend their individual response to cues of predation to their waggle dance. That is, the mechanism that allows individual honeybees to evaluate danger and to prefer safe over dangerous flowers also increases their tendency to perform the waggle dance when returning from safe, rather than dangerous, flowers. An unlikely alternative is that the fewer waggle runs for dangerous flowers than for safe flowers merely indicate bees' perception of lower profitability owing to increased vigilance. This alternative is not consistent with either the data indicating antipredatory behaviour of honeybees cited above, or the very large, 20–30-fold decrease in waggle runs for the dangerous flower than for the safe flower (Fig. 1). Nevertheless, it is possible that bees in the two conditions perceived different levels of profitability. The interacting effects of cues of predation risk and perceived profitability on dance behaviour would be a suitable target for future research. Regardless of the exact mechanism involved, however, any reduction in recruitment to dangerous patches should reduce the predation costs incurred by recruits and thus increase colony fitness (Clark & Dukas 1994).

We have assumed that the foragers perceived the dead bees as a cue of predation risk and acted accordingly. There are two other ways in which the dead bees could have been perceived that might affect our interpretation. The first is as a novel object, and our results could be the result of neophobia. Dukas (2001a) showed, however, that honeybees that avoided a recently killed conspecific did not avoid a comparable novel object. Alternatively, foragers may have perceived the dead bees as competitors (i.e. they may not have perceived them as dead) and our results could be the result of an aversion to cues of competition risk. However, the artificial flowers used in our experiment were designed for the simultaneous use by numerous honeybees (von Frisch 1967; Seeley 1996), so the presence of two live bees at the feeder should not reduce the perceived quality of that feeder. Furthermore, crush-killed honeybees emit alarm pheromone that is highly conspicuous to humans as well as conspecifics, which show characteristic alarm behaviour (Dukas 2001a). Indeed, Abbott (2006) found that when bumblebees (*Bombus* spp.) were given a choice between an artificial flower containing a freshly crush-killed conspecific (killed as in this experiment and emitting alarm pheromones) and one containing a freeze-killed conspecific (not emitting alarm pheromones), the foragers preferred the flower with the freeze-killed bee.

Our study suggests that honeybees integrate two distinct types of information, patch profitability and predation risk, into a single signal, the number of waggle runs. This suggests a promising line of research investigating the mechanisms underlying such integration at the neural and behavioural levels. For example, using the proboscis extension reflex paradigm, Hammer (1993) identified a honeybee interneuron that produces more action potentials when either sucrose or an odour previously paired with sucrose is presented. A neuroeconomic study (Hammer 1997; Sanfey et al. 2006) that combines this approach with cues of predation risk could lead to the identification of either individual neurons or neural networks that are involved in the integration of information about food quality and predation risk and its translation into a communication output.

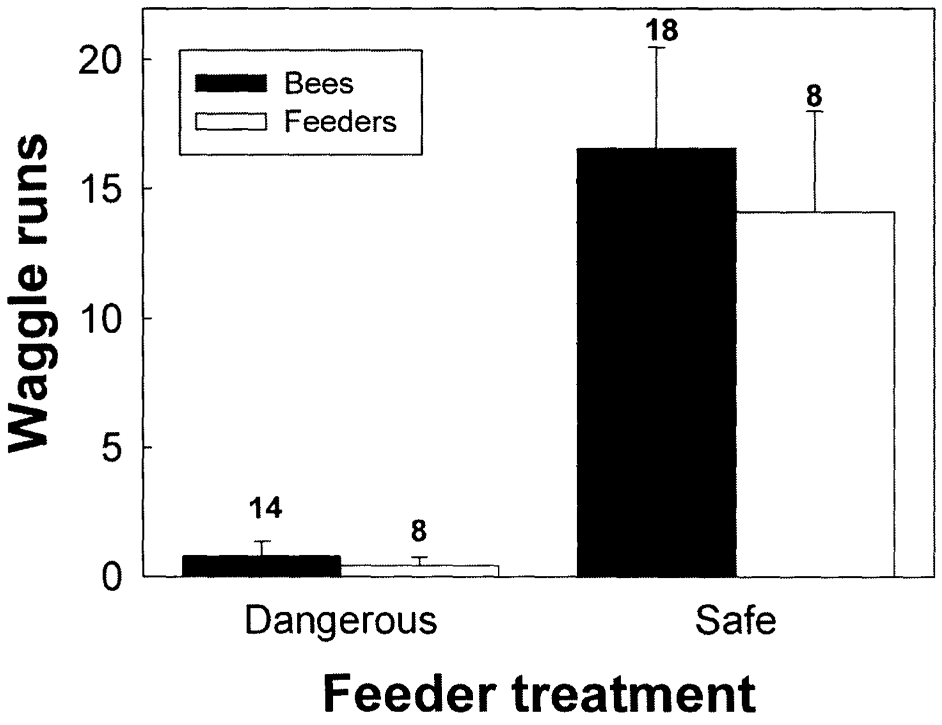
The waggle dance is a remarkable example of social learning about food as well as other resources, such as water and nest sites (von Frisch 1967; Seeley 1996; Dyer 2002; Visscher 2007). A variety of animals also show social learning about predators (Griffin 2004). Although our results do not address explicit social learning about predation risk, they do illustrate that implicit social learning about danger can be achieved merely by modulating the social transmission of information about food, which results in a disproportionate recruitment of naïve individuals to safe sites. Similar forms of implicit social learning of danger may allow ants to avoid foraging sites associated with predation risk (Nonacs 1990) or nesting sites associated with intraspecific aggression (Franks et al. 2007), and allow rats to avoid poisonous food (Galef 1985). Such indirect communication about predation risk may have had an important yet underappreciated effect on the dynamics and spatial distribution of predators and prey (Sih 1998), and on insect–plant interactions (Dukas 2001b).

Figures

Figure 1

Mean + SE number of waggle runs as a function of flower danger. Black bars: mean number of waggle runs when each bee was considered an independent statistical unit. White bars: mean number of waggle runs when each trial was considered the independent unit. Sample sizes are depicted above the bars.

Chapter 3: Figure 1



Chapter 4: Asset-based asymmetries and the willingness to accept predation risk

Manuscript in preparation for publication.

Introduction

Foraging often involves a tradeoff between foraging success and predation risk where options that yield better foraging returns also entail higher predation risks (Lima and Dill 1990). A complete understanding of the foraging behaviour of animals requires understanding how they resolve this tradeoff. The simplest models of optimal foraging in the presence of predation risk suggest that animals simply choose the foraging option that simultaneously maximises foraging gain and minimises predation risk. In particular, Gilliam and Fraser (1987) suggest that animals choose the foraging option that minimises μ/f, where μ is the mortality rate associated with the option and f is the foraging rate associated with the option (note that this criterion is derived for the special case where the forager has access to a refuge with no predation risk or foraging gain, but it serves to illustrate the basic idea). While the Gilliam/Fraser criterion has surprising predictive power given its simplicity (Dahlgren and Eggleston 2000; Gilliam and Fraser 1987; Skalski and Gilliam 2002; Turner and Mittelbach 1990), it does ignore several factors that could affect how foragers resolve the basic tradeoff. These additional factors can be roughly grouped into two categories that correspond to the two variables in the Gilliam/Fraser criterion. First, the cost of mortality (i.e. the relationship between the numerator of the Gilliam/Fraser criterion and expected fitness) may not be constant. Second, the foraging gain associated with a foraging option (i.e. the denominator of the Gilliam/Fraser criterion) may not be constant. I elaborate on both of these factors below.

The cost of death is not a constant

The cost of death is an opportunity cost; a forager that is killed loses all expected future fitness gains (note that 'expected future fitness gains' is often labelled 'reproductive value' (Fisher 1930; Hamilton 1966) or 'assets' (Clark 1994); I use the latter). Foragers can have different assets, and can therefore differ in their willingness to accept predation risk. For example, Clark and Dukas (1994) argued that social and solitary bees differ in vigilance behaviour (higher in solitary bees) because they differ in the amount of expected future fitness gains they would lose (also higher in solitary bees) if killed. In particular, solitary bees have to store a certain amount of food in a cell before they can deposit an egg. If they are killed, they lose the future reproduction potential associated with all the food they have stored in a cell without depositing an egg. For social bees, however, food is converted into reproduction by individuals other than the forager that collected the food. A foraging social bee that is killed does lose future foraging gains, but the future reproductive potential of her past foraging gains are not lost. More generally, foragers can differ in assets if they differ in their expected lifespan in the absence of predation risk (Cartar 1991; Clark 1994; Clutton-Brock 1984; McNamara and Houston 1996). In particular, a forager that will die soon in any case has little to lose and might be expected to accept foraging options that are associated with elevated predation risk.

Foraging gains are not constant

The expected foraging gain associated with a foraging option can depend on the options adopted by other foragers. In particular, if more foragers choose a given option, then that option should be associated with more intense competition and lower expected foraging gains. For example, Fretwell and Lucas (1970) modeled a case where a group of foragers had access to two habitats (i.e. foraging options) that had different resource levels. They demonstrated that the evolutionarily stable distribution of foragers between the two patches should not generally involve all foragers exploiting the better habitat. This is because intraspecific competition reduces the value of the good habitat to the point where it is optimal for a minority of foragers to exploit the poor patch. The same logic applies to cases where different habitats are associated with different levels of predation risk; the level of intraspecific competition in safer habitats can make exploiting more dangerous habitats adaptive for a minority of foragers (habitat selection models are further complicated if habitats vary in intrinsic value to the foragers, and if predators can also choose a habitat (Bouskila 2001; Hugie and Dill 1994; Iwasa 1982; Sih 1998), though I will ignore these factors here) (Grand and Dill 1999; McNamara and Houston 1990; Moody et al. 1996).

Habitat selection problems are more complicated, and more interesting, in cases where individual foragers differ in some way (i.e. when there are asymmetries within the forager population). Many habitat selection models have expanded on Fretwell and Lucas' (1970) classic model by exploring the effect of asymmetries within the forager population or community. For example, asymmetries in the efficiency of exploiting a habitat are predicted to produce a distribution where foragers congregate in the habitats that they are more efficient at exploiting (Possingham 1992; Rodríguez-Gironés and Santamaría 2004; 2006). Similarly, asymmetries in susceptibility to predation are predicted to produce distributions where susceptible foragers congregate in safer patches and less susceptible foragers more heavily exploit dangerous patches (Grand and Dill 1999).

Asset-based asymmetries and frequency dependent foraging gain

As discussed above, several types of asymmetries within the forager population can affect the expected distribution of foragers between habitats that differ in terms of resource availability, predation risk, or both. One type of asymmetry that has not, as far as I know, been modeled is the asymmetry in the assets that different foragers possess. However, foragers will often compete with individuals that have different assets and, therefore, have a different willingness to accept predation risk. Furthermore, in many cases, the nature of this asymmetry should be fairly predictable. Consider, for example, a species of forager with a well defined foraging season that involves several overlapping cohorts of foragers. Assume that the lifespan of a cohort of foragers is limited and well defined (i.e. even in the absence of predation, foragers die after a set period of time). This well defined lifespan assumption means that old foragers have less to lose than younger foragers. On any given bout, relatively young cohorts which have relatively large assets, will be competing with older cohorts which have smaller assets. The interaction of these asymmetries and intraspecific competition could affect the evolutionarily stable willingness of foragers to accept predation risk, the way this willingness changes across the lifespan of a forager, and the way it changes over the season.

Below I describe a model designed to explore these issues. I have based this model on a system where pollinators compete for the resources on flowers, and where some flowers contain flower-dwelling ambush predators that attack visiting pollinators (Balduf 1939; Dukas 2001b; Morse 2007).

The Model

I start by introducing a model for the case where there is one cohort of pollinators (i.e. all individuals have the same expected future fitness, or asset). An analytical solution for a single foraging bout is relatively simple to derive for this case and is described. I then describe a numerical analysis of multiple foraging bouts for one cohort (i.e. all of the foraging bouts in the cohort's lifespan). Finally, this numerical analysis is extended to the case where multiple cohorts, with differing future assets to protect, overlap.

Single cohort/single bout model

Consider a pollinator population consisting of a single cohort of B individuals foraging on F flowers. A proportion, P_p, of these flowers contain flower-dwelling ambush predators. The foraging experience of all pollinators is divided into discrete foraging bouts. The foraging sequence of pollinators is as follows: 1) pollinators approach randomly selected flowers, 2) pollinators assess the approached flower and determine whether or not to land, and 3) if the pollinator does land, she spends some time foraging on the flower depleting the current nectar stores. Each individual pollinator can adopt one of two foraging strategies. Pollinators adopting the risky, R, strategy land on all flowers that they approach, regardless of whether there is a predator present. Pollinators adopting the safe, S, strategy land on all predator-free flowers that they approach but do not land on predator-containing flowers (note that this assumes that pollinators perfectly discriminate between predator-free and predator-containing flowers). Let P_r be the proportion of pollinators that adopt the R strategy and $(1 - P_r)$ be the proportion that adopt the S strategy. Furthermore, let a_r and a_s be the number of flowers that, respectively, an R or S pollinator approaches in a bout. Because S pollinators must spend time approaching flowers they do not land on, they should approach more flowers per bout, but should land on fewer flowers per bout than R pollinators (i.e. $a_s > a_r$ but $(1 - P_p)a_s < a_r$). Let P_L be the probability that an R pollinator is not killed in a given bout (note that I assume that an S pollinator always survives the bout).

Assume that each flower produces V units of nectar per bout. Let a single risky or safe flower receive an expected N_{vr} or N_{vs} visits per bout, respectively. Here 'visits' means the number of pollinators that land on and consume nectar from a flower and does not include bees that approach a flower but do not land on it. It is assumed that the presence of a predator on a flower, and the predation events that occur on that flower, do not affect how much nectar each visitor consumes on that flower. If it is assumed that flowers are completely depleted of nectar with each pollinator visitation, the amount of nectar a bee can expect to gain from a single visit to a risky or safe flower is given by $V/(N_{vr} + 1)$ and $V/(N_{vs} + 1)$, respectively. Note that the simpler gain functions, V/N_{vr} and V/N_{vs}, are not used as they get infinitely large as N_{vr} or N_{vs} approach 0, which is unrealistic and produces unrealistic model results. The gain functions I use implicitly constrain the maximum amount of nectar available on a flower to some reasonable value.

The expected amount of nectar gained by a pollinator adopting R on a given bout is

$$P_L\left(P_p a_r \frac{V}{N_{vr} + 1} + (1 - P_p)a_r \frac{V}{N_{vs} + 1}\right)$$

and the expected nectar gained by an S pollinator is

$$(1 - P_p)a_s \frac{V}{N_{vs} + 1}$$

Two modifications are required to turn these expected-nectar-gain-per-bout formulas into fitness functions for the two strategies. First, N_{vr} and N_{vs} can be described in terms of P_r, in particular $N_{vr} = P_r B a_r / F$ and $N_{vs} = B(P_r a_r + (1 - P_r)a_s)/F$. Second, in order to calculate lifetime fitness, let $W(O)$ be the expected future foraging gains of a pollinator that adopts the optimal strategy in all future bouts. Therefore, the expected fitness of a pollinator adopting the R strategy in a given bout where a proportion, P_r, of pollinators adopt R is

$$W_{P_r}(R) = P_L\left(P_p a_r \frac{VF}{P_r B a_r + F} + (1 - P_p) a_r \frac{VF}{B(P_r a_r + (1 - P_r) a_s) + F} + W(O)\right)$$

and the expected fitness of a pollinator adopting the S strategy in a given bout where a proportion, P_r, of pollinators adopt R is

$$W_{P_r}(S) = (1 - P_p) a_s \frac{VF}{B(P_r a_r + (1 - P_r) a_s) + F} + W(O)$$

Note that $W(O)$ approximates the opportunity cost of death (i.e. asset) discussed above; it is what the pollinator loses if she is killed in the present.

R is a pure ESS (Evolutionarily Stable Strategy; Maynard Smith 1982) if a population, where almost all pollinators in the population adopt R, cannot be invaded by rare S individuals (i.e. the rare S individuals must have fitness that is no greater than the fitness of the common R individuals). Therefore let $P_r \approx 1$ and $(1 - P_r) \approx 0$. For acceptable values of the various parameters (Table 1) R is an ESS when

$$P_L \geq \frac{a_s FV - a_s F P_p V + a_r B W(O) + F W(O)}{a_r FV + a_r B W(O) + F W(O)}$$

Similarly, S is an ESS if a population, where almost all pollinators in the population adopt S, cannot be invaded by rare R individuals. Therefore let $P_r \approx 0$ and $(1 - P_r) \approx 1$. For acceptable values of the various parameters (Table 1) S is an ESS when

$$P_L \leq \frac{a_s FV - a_s F P_p V + a_s B W(O) + F W(O)}{a_r FV + a_r a_s B P_p V + a_s B W(O) + F W(O)}$$

It is also possible to derive the conditions required for a mixed ESS. A mixed ESS will involve stable proportions of R and S bees (or pollinators that adopt R or S with a fixed probability) which can be described by P_r^* and $(1 - P_r^*)$ respectively. At the mixed ESS, the expected fitness of both strategies should be equal so that $W_{P_r^*}(R) = W_{P_r^*}(S)$. This equation can be solved for the P_r^* expected at a candidate mixed ESS. There are two solutions for P_r^*, but one can be rejected as it always produces values outside the range 0-1 (neither solution is shown here for brevity). The other solution does produce sensible values of P_r^*, and this candidate mixed ESS is always stable for acceptable parameter values (i.e. the partial derivative of $W_{P_r^*}(R) - W_{P_r^*}(S)$ with respect to P_r^* is always negative). Note that there is no solution for P_r^* if $W(O) = 0$. It is possible to analyse this model separately for the case where there is no future asset to protect, but for simplicity, I assume that there is always some small, but positive, minimum value of $W(O)$ (Table 1).

Two further extensions to this model that are not included in the analytical solution described above, but are included in the numerical solutions described in subsequent sections, have to do with how P_L, the probability that a pollinator adopting R survives a bout, and the approach parameters, a_r and a_s, are calculated. First, P_L should depend on the number of predators the pollinator encounters, $P_p a_r$, and on the probability that the pollinator survives any given encounter, P_ℓ. In particular, $P_L = P_\ell^{P_p a_r}$. Second, the number of flowers approached by an R, a_r, or S, a_s, pollinator in a bout should depend on the length of the bout, t_b, the time it takes to fly between two flowers, t_f, and the handling time on flowers, t_h. For R pollinators, the equation $t_b = a_r(t_f + t_h)$ can be rearranged to produce $a_r = t_b/(t_f + t_h)$. Similarly, for S pollinators, bout length can be described as $t_b = a_s P_p t_f + a_s(1 - P_p)(t_f + t_h)$, which can be rearranged to produce $a_s = t_b/\left(P_p t_f + (1 - P_p)(t_f + t_h)\right)$. These extensions are not crucial to the analysis, but they do help produce more realistic parameter values.

Single cohort/multiple bout model

The model described in the previous section can be used as a starting point for a dynamic programming (Clark and Mangel 2000; Mangel and Clark 1988) numerical analysis of how the evolutionarily stable proportion of pollinators, P_r^*, changes over the life of a single cohort (base values for the parameters used in most analyses are described in Table 1). This analysis assumes that the cohort forages for some fixed number of bouts, after which all pollinators in the cohort die. The analysis also assumes that the size of the cohort is constant across the lifespan of the cohort, effectively ignoring the effect of predation on population size. This latter assumption is made to minimise the confounding effect of population size (see below) on the asymmetry effect that is the focus of this analysis.

The analysis starts with the final bout in the cohort's life where there is no future asset to protect (as noted above, this involves setting $W(O)$ to a small positive value, rather than to 0). The solution described in the previous section is used to determine P_r^* for this case as well as the expected foraging gains of pollinators in this terminal bout (i.e. $W_{P_r^*}(R)$ if $P_r^* = 1$, $W_{P_r^*}(S)$ if $P_r^* = 0$, and if $0 < P_r^* < 1$, either fitness function describes the expected foraging gain as $W_{P_r^*}(R) = W_{P_r^*}(S)$). This expected foraging gain is then added to $W(O)$ which becomes the future asset for the penultimate bout. P_r^* and the expected foraging gain can then be calculated for the penultimate bout, which allows the calculation of $W(O)$ for the preceding bout. This process can then be repeated until the cohort's first bout is reached (see Clark 1994 for a similar model with no intraspecific competition).

The solid line in Figure 1.a shows the result of this numerical analysis for the base values of all parameters. An examination of the parameter space suggested that, with the exception of ceiling and floor effects, a cohort of pollinators should generally adopt a larger P_r^* in later bouts (I call the pattern of P_r^* across the lifespan of a cohort a Risk Life History Strategy (RLHS)).

Multiple cohort/multiple bout model

In many systems, not all of the foragers on a given bout will be from the same cohort, nor will all foragers have the same asset to protect. Therefore, in this section I expand the model to consider multiple overlapping cohorts. Let i denote a cohort such that, in a given bout, B_i is the number of pollinators in cohort i, P_{r_i} is the proportion of individuals in cohort i adopting R, $W_i(O)$ is the expected future fitness of a pollinator in cohort i, and $W_{i_{\overline{P_r}}}(X)$ is the expected fitness of a pollinator of cohort i that adopts strategy X (R or S) if a proportion, $\overline{P_r}$, of the pollinator population (including all cohorts present in a given bout) adopt R. Furthermore, let $\overline{B}$ be total population size (including all cohorts) in a given bout. The two population parameters can be calculated as $\overline{B} = \sum_i B_i$ and $\overline{P_r} = \sum_i \left(P_{r_i} B_i\right)/\overline{B}$. Therefore, on a given bout, for a given $\overline{P_r}$, the expected fitness of a pollinator of cohort i that adopts R is

$$W_{i_{\overline{P_r}}}(R) = P_L\left(P_p a_r \frac{VF}{\overline{P_r}\,\overline{B}a_r + F} + \left(1 - P_p\right)a_r \frac{VF}{\overline{B}(\overline{P_r}a_r + (1 - \overline{P_r})a_s) + F} + W_i(O)\right)$$

and the expected fitness of a pollinator of cohort i that adopts S is

$$W_{i_{\overline{P_r}}}(S) = \left(1 - P_p\right)a_s \frac{VF}{\overline{B}(\overline{P_r}a_r + (1 - \overline{P_r})a_s) + F} + W_i(O)$$

It is possible to solve for a set of evolutionarily stable P_{r_i}'s (i.e. for the ESS for each cohort present in a given bout) if the values of all parameters are known. As an example consider a bout with two cohorts ($i = \{1,2\}$). There are nine possible ESS combinations: both cohorts adopt R, both adopt S, both adopt a mixed strategy, cohort 1 adopts R and cohort 2 adopts S, etc. All of these ESS combinations must be considered separately. For example, to test whether both cohorts adopting R is an ESS, I test whether $W_{1_{\overline{P_r}}}(R) > W_{1_{\overline{P_r}}}(S)$ and $W_{2_{\overline{P_r}}}(R) > W_{2_{\overline{P_r}}}(S)$ are true when $P_{r_1} \approx 1$ and $P_{r_2} \approx 1$. Similarly, to test whether it is an ESS for cohort 1 to adopt the mixed strategy defined by $P_{r_1}^*$, while cohort 2 adopts the S strategy I solve $W_{1_{\overline{P_r}}}(R) = W_{1_{\overline{P_r}}}(S)$ for $P_{r_1}^*$, while assuming $P_{r_2} \approx 0$. I then test for the stability of this candidate mixed ESS by determining whether the partial derivative of $W_{1_{\overline{P_r}}}(R) - W_{1_{\overline{P_r}}}(S)$ with respect to $P_{r_1}^*$ is negative. I then test whether $W_{2_{\overline{P_r}}}(R) < W_{2_{\overline{P_r}}}(S)$ is true when $P_{r_1} = P_{r_1}^*$ and $P_{r_2} \approx 0$. A similar process can be used to test all nine potential ESS combinations. The process is similar with more than two cohorts except that the number of potential ESS combinations is larger.

A numerical analysis, similar to the single cohort/multiple bout model, can be used to examine how the P_{r_i} of all cohorts changes over time. Consider a foraging season with *j* distinct, but overlapping, cohorts. The analysis starts with the final bout of the last cohort to emerge ($i = j$, at which point it is the only cohort present), and follows the protocol described for the single cohort/multiple bout model. The only difference is that when the final bout of the second-last cohort to emerge ($i = (j - 1)$) cohort is reached, the analysis starts using a two cohort model and so on until the first bout of the first cohort is reached.

Model Analysis

Figure 2.b gives an example of how $P_{r_i}^*$ changes across a season that has 10 cohorts with the age structure described in Figure 2.a.
One conspicuous feature of the multiple cohort model shown in Figure 2.b is that different cohorts have different RLHSs (Figure 2.c). These differences could be the result of asset-based asymmetries, which are related to the relative ages of the competing cohorts, and how this asymmetry changes across the lifespan of a pollinator.

As an illustration of how the relative age of competing cohorts might affect $P_{r_i}^*$, consider a case with two cohorts of different ages, denoted by $i = \{old, young\}$. The asset, $W(O)$, of the older cohort should be less than that of the younger cohort. This suggests that $P_{r_{old}}^* > P_{r_{young}}^*$. Moreover, the presence of an older cohort that heavily exploits predator-containing flowers, thereby increasing the intensity of competition on these flowers and reducing competition on predator-free flowers, should further reduce the value of R for the younger cohort, and further reduce $P_{r_{young}}^*$. Similarly, the presence of younger pollinators that are intrinsically less likely to exploit predator-containing flowers should further increase the value of R for the older cohort, and further increase $P_{r_{old}}^*$. In some sense, the intrinsic difference in $W(O)$ of two competing cohorts may push the $P_{r_i}^*$ of the two cohorts apart so that the younger cohort adopts a smaller $P_{r_i}^*$ than it otherwise would have and the older cohort adopts a larger $P_{r_i}^*$ than it otherwise would have. The same logic can be extended to cases with more than two cohorts.

However, this explanation is confounded by the fact that competition intensity (i.e. population size or number of competitors) also changes across the season and that different cohorts experience different lifetime patterns of competition intensity. It is possible that competition intensity, rather than asset-based asymmetries, explains the different RLHSs of different cohorts. Therefore, in the following analysis, I start by considering the effect of the number of competitors a focal pollinator has. I then explore the effect of asset-based asymmetries.

Number of competitors

In Figure 2, all of the cohorts are of equal size, but the population size peaks mid-season when more cohorts are foraging simultaneously (Figure 2.a). It is possible that the fact that each cohort's RLHS differs is due to the fact that each cohort experiences a different pattern of intraspecific competition intensity across its lifespan. The effect of competition intensity can be clearly seen in Figure 1.a where the RLHS of a single cohort changes as a function of cohort size. There are at least two ways in which the lifetime pattern of competition intensity could affect the RLHS of a cohort and could explain Figure 1.a. First, more intense competition reduces the expected foraging gains of all pollinators and can therefore reduce the $W(O)$ for earlier bouts. In other words, an expectation of intense competition in future bouts can reduce expected future fitness of a cohort, which could favour a higher P_r^* in the present. Secondly, it is possible that current population size, or competition intensity, can affect the evolutionarily stable proportion of S and R pollinators independent of its effect on expected future fitness. Figure 1.b demonstrates both of these effects for a single cohort by simulating a temporary surge or drop in the size of the cohort on the tenth bout. This temporary change in the cohort size does affect the value of P_r^* on the focal bout, but it also affects the value of P_r^* on all bouts before the focal bout. The effect on earlier bouts is consistent with P_r^* being negatively correlated with $W(O)$, which is negatively correlated with expected future population size/competition intensity. The short term effect of population size (i.e. the effect on the focal bout 10) is not, however, consistent with the expected future competition argument. In particular, increasing the population size resulted in a decreased P_r^* on the focal bout and vice versa. It is not, however, safe to assume that this is always the short-term effect of population size. For example, Figure 3 shows that for a single cohort on a given bout, increasing the size of the cohort over a given range can cause P_r^* to increase, decrease, or remain unchanged. In fact there are parameter values for which a continuing increase in the cohort size can lead to an increase, then a decrease of P_r^*. Similar patterns are seen for the multiple cohort/multiple bout model.

Asset-based asymmetries and the relative age of competitors

The previous section demonstrated that the effect of population size must be controlled if asset-based asymmetries are to be studied. I controlled for the effect of population size by constructing a series of population age structures where total population size was constant across the lifespan of a focal cohort (i.e. for every bout on which an old cohort died out, a new cohort of equal size was added). I then compared the RLHSs of these cohorts (multiple cohort case) to the RLHS of a cohort that never competes with other cohorts (single cohort case). The population size of the single cohort case was matched to the total population size of the multiple cohort case (i.e. to the total number of pollinators of all cohorts present on a given bout).

Figure 4 represents this comparison for a case where the focal cohort of the multiple cohort case always interacts with one (Figure 4.a), two (Figure 4.b), or three (Figure 4.c) other cohorts. In all cases, when the focal cohort of the multiple cohort case is interacting with more older than younger cohorts, or with the same number of older and younger cohorts, it adopts a smaller $P_{r_i}^*$ than it would have in a comparable single cohort case. Alternatively, later in this focal cohort life, when it interacts with more younger than older cohorts, it adopts a higher $P_{r_i}^*$ than it would have in a comparable single cohort case.

This effect of the relative age of competitors could result in different RLHSs for different cohorts within a season because different cohorts experience different sequences of competitor cohorts. For example (Figure 2.a), cohorts that emerge early in the season interact with no, or few, older cohorts early in life and a large number of younger cohorts late in life. Conversely, cohorts that emerge late in the season interact with a large number older cohorts early in life and few, if any, younger cohorts late in life.

Discussion

The model presented here suggests that the willingness of individual foragers to accept predation risk could be affected by asymmetries in the assets of all of the foragers present. Specifically, the model predicts that foragers with a relatively small asset should be more common on predator-containing flowers than foragers with a larger asset, and that the simultaneous presence of low-asset and high-asset foragers exaggerates this effect. The divergence predicted by asymmetry based habitat selection models (i.e. that a class of forager that is intrinsically more inclined to exploit a given habitat will exploit it more heavily in the presence of a class of foragers that is intrinsically less inclined to exploit that habitat) is often referred to as niche partitioning (Rodríguez-Gironés and Santamaría 2004). In that sense, the current model could be seen as predicting niche partitioning on the basis of age or asset.

This model also replicates previous models that suggest that intraspecific competition intensity (i.e. population size) can affect how forager populations distribute themselves between predator-free and predator-containing habitats (McNamara and Houston 1990). Competition intensity affects the nature of the tradeoff between the greater expected short term foraging gains and the reduced expected long term foraging gains associated with exploiting habitats that contain predators. However, it appears that the way that competition intensity in the present affects the nature of this tradeoff can differ from the way that expected future competition intensity affects this tradeoff. In particular, an expectation of intense competition in future bouts should reduce the asset of a focal forager, and might therefore increase her optimal willingness to accept predation risk in the present bout. However, the intensity of competition in a focal bout can affect a forager's optimal willingness to accept predation risk independent of its effects on expected future foraging gains. These immediate effects of more intense competition can increase or decrease a forager's optimal willingness to accept predation risk. Therefore, in large populations, the immediate effects of high competition intensity could either exaggerate or diminish the effects that the expectation of high future competition intensity has on the distribution of foragers.

This model also demonstrates how life history strategies might differ for different cohorts of individuals from a single population of foragers. In particular, in a population of foragers with a discrete foraging season and overlapping cohorts, different cohorts experience different patterns of age-based asymmetries and competition intensities across their lifespan. This can result in different RLHSs for different cohorts. This suggests that a logical extension to life history theory would be to explore the factors that affect the optimal expression of a trait for a group of animals over a longer time frame than the life of an individual. However, this model relies on two simplifying assumptions. First, the model assumes a well-defined lifespan for all foragers. Second, the model assumes no dilution of predation risk (i.e. the presence of more R foragers does not reduce the per-capita risk to R foragers). Previous models have demonstrated that relaxing both of these unrealistic assumptions can dramatically affect the predicted life history strategies (McNamara et al. 2009) or the expected distribution (Grand and Dill 1999) of foragers. Further work is needed to clarify how the willingness to accept predation risk changes across an individual's lifespan, and across a population's foraging season.

Tables

Table 1: A description of parameters and variables used in the model

Parameter /Variable	Description	Base Value and Constraints
$P_{r_i}^*$	The evolutionarily stable proportion of cohort i adopting the R strategy	The major solution variable
B_i	Number of pollinators in cohort i	750
F	Number of flowers	50 000
P_p	Proportion of flowers that contain a predator	0.005
t_b	Total amount of time foraging per bout	14 400†
t_h	Handling time for a pollinator that lands on a predator free flower	10†
t_f	Time it takes to fly between flowers	10†
a_r	The number of flowers approached by a pollinator adopting the R strategy in a single bout	$a_r = t_b/(t_f + t_h)$
a_s	The number of flowers approached by a pollinator adopting the S strategy in a single bout (note that this includes both the flowers that the pollinator subsequently lands on and those that she rejects)	$a_s = \frac{t_b}{\left(P_p t_f + (1 - P_p)(t_f + t_h)\right)}$ $a_s > a_r$ $(1 - P_p)a_s < a_r$
N_{vr}	The number of pollinators that land and forage on a given predator-containing flower	$N_{vr} = P_r B a_r / F$

N_{vs}	The number of pollinators that land and forage on a given predator-free flower	$N_{vs} = \frac{B(P_r a_r + (1 - P_r) a_s)}{F}$
P_ℓ	The probability that a pollinator adopting the R strategy survives a visit to a single predator containing flower	0.9995
P_L	The probability that a pollinator adopting the R strategy survives an entire bout	$P_L = P_\ell^{P_p a_r}$
V	The amount of nectar produced by a single flower per bout	1

†All time parameters are in the same units. While the specific unit used does not matter, if the unit is assumed to be seconds, then the bout time is four hours

Figures

Figure 1

The evolutionarily stable proportion of pollinators adopting R (P_r^*) over the 12-bout lifespan of a single cohort for base values of all parameters ($B = 750$; solid line), for the case where population size is increased by a factor of 10 ($B = 7500$; dashed line), and for the case where population size is decreased by a factor of 10 ($B = 75$; dotted line). a: Population increase and decrease is in effect on all bouts. b: Population increase and decrease is only in effect on bout 10.

Chapter 4 Figure 1

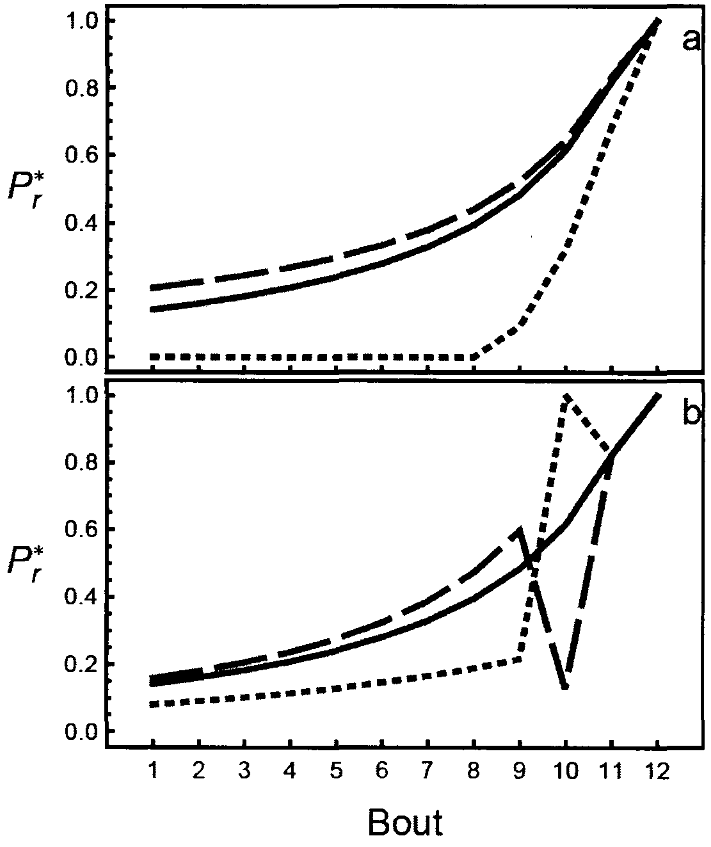


Figure 2

Numerical solution to a multiple bout/multiple cohort problem. a: The age structure used for this analysis. For a given cohort (y axis) the horizontal line shows the bouts (x axis) on which the cohort is present. b: The evolutionarily stable proportion of pollinators of each cohort adopting R (P_r^*) on a given bout in the season. c: The evolutionarily stable proportion of pollinators in three select cohorts adopting R (P_r^*) across their 12-bout lifespan (i.e. the three curves are shifted relative to panel b so that each cohort's first bout overlaps). In all panels, the second cohort of the season is represented by long dashed lines, the fifth cohort by short dashed lines, and the ninth cohort by dotted lines. For simplicity, all other cohorts in a and b are represented by solid lines.

Chapter 4: Figure 2

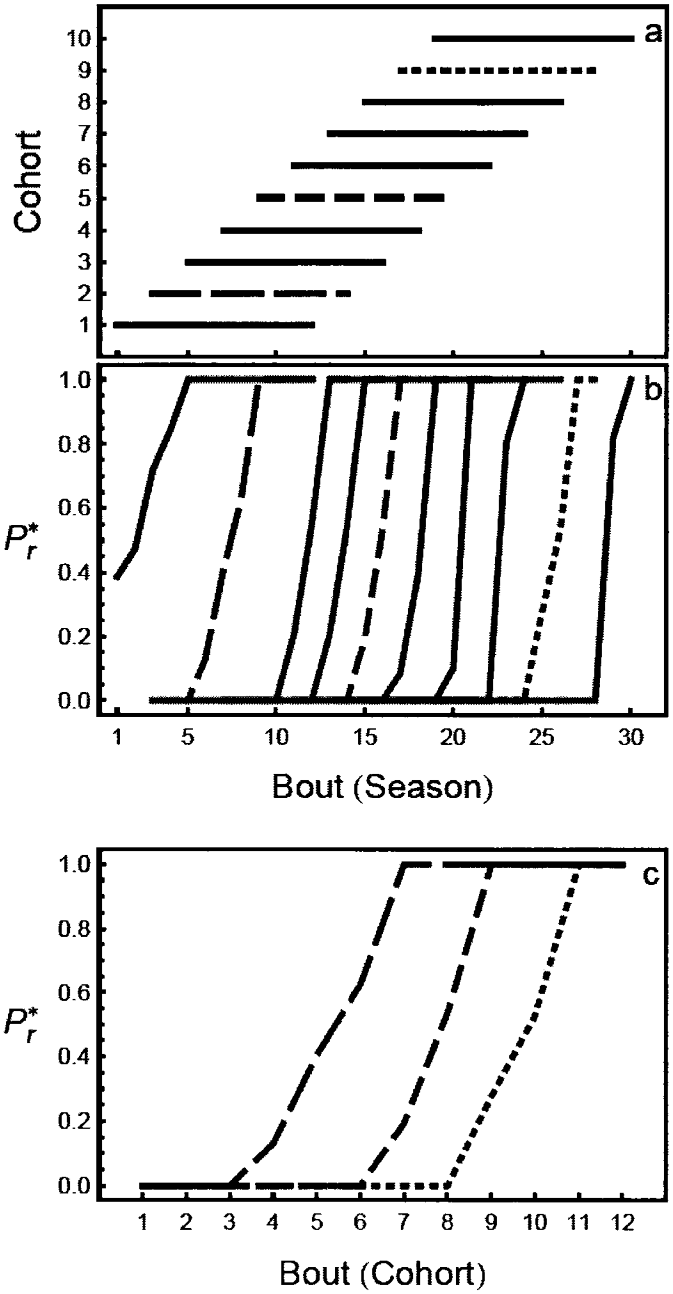


Figure 3

The effect of population size on the evolutionarily stable proportion of pollinators adopting R (P_r^*) in a single bout when only one cohort is present for four values of $W(O)$. Dotted line: $W(O) = 100$; short dashed line: $W(O) = 400$; long dashed line: $W(O) = 700$; solid line: $W(O) = 1000$.

Chapter 4: Figure 3

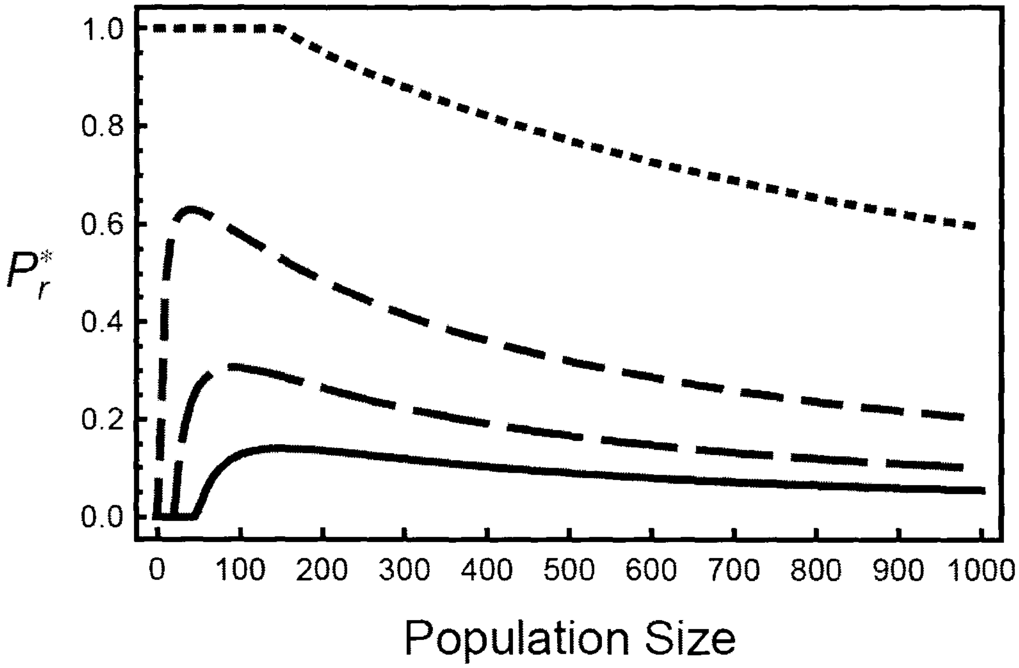
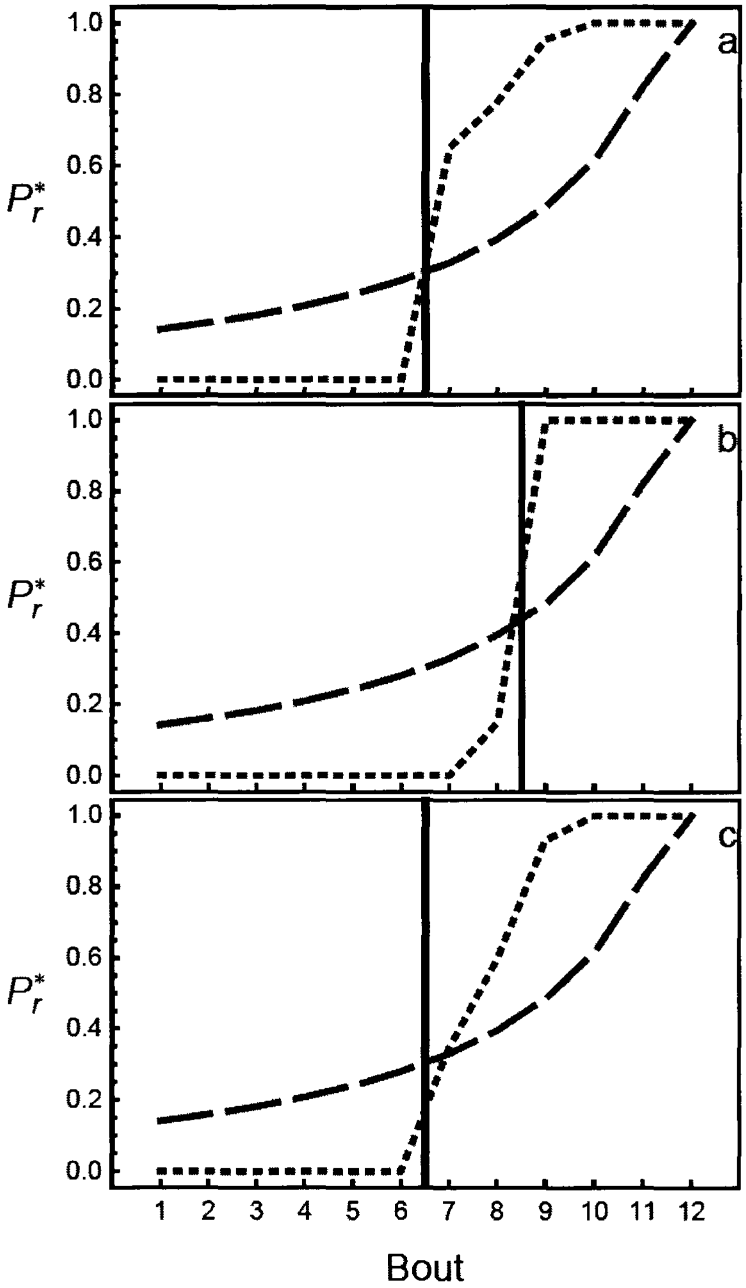


Figure 4

A comparison of the evolutionarily stable proportion of pollinators adopting R (P_r^*) over the 12-bout lifespan of individual cohorts for a cohort that interacts with no other cohorts (dashed line; single cohort/multiple bout model), and a cohort that does interact with other cohorts (dotted line; multiple cohort/multiple bout model). For the multiple cohort case, the age structure of the season is constructed so that for the focal cohort, the number of cohorts present and the total population size is stable across bouts. In all cases, the total number of pollinators present on a given bout is 750 (Table 1). In all panels, the solid vertical line represents the point at which the focal cohort of the multiple bout case becomes one of the relatively older cohorts. a: In the multiple bout case there are two separate cohorts present on all bouts, the number of pollinators in each cohort is 750/2, to the left of the solid vertical line the focal cohort interacts with one older cohort, and to the right of the line it interacts with one younger cohort. b: In the multiple bout case there are three separate cohorts present on all bouts, the number of pollinators in each cohort is 750/3, to the left of the solid vertical line the focal cohort interacts with either two older (bouts 1-4) or one older and one younger (bouts 5-8) cohort(s), and to the right of the line it interacts with two younger cohorts. c: In the multiple bout case there are four separate cohorts present on all bouts, the number of pollinators in each cohort is 750/4, to the left of the solid vertical line the focal cohort interacts with either three older (bouts 1-3) or two older and one younger (bouts 4-6) cohorts, and to the right of the line it interacts with either one older and two younger (bouts 7-9) or three younger (bouts 10-12) cohorts.

Chapter 4: Figure 4



Chapter 5: Background evolution in camouflage systems: a predator-prey/pollinator-flower game

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Abstract

A common predator or anti-predator strategy involves camouflage based on background matching. In some systems, the background is an organism whose fitness is affected by the predator-prey interaction. In these cases, the phenotype of the background species may evolve to affect the degree of background matching in the predator-prey interaction. For example, some flower species (the background) are inhabited by camouflaged ambush predators that attack visiting pollinators. These flowers have a fitness interest in the outcome of the predator-prey interaction because flowers depend on pollinator visitations for reproduction. Therefore, floral colour might evolve relative to predator colour so as to influence the detectability of resident predators. I have created a three-player game, based on Signal Detection Theory, to model the co-evolution of predator and prey/pollinator behavioural strategies with floral colour. This model makes two general predictions. 1) Constraints on predator distributions favour the evolution of flowers that match the predators' colour because they prevent predators from overexploiting these flowers. 2) Factors that produce less discriminating pollinators also favour the evolution of flowers that match the predators' colour because these pollinators are willing to land on these flowers even if the safety of the flower is in doubt.

Introduction

Predator-prey interactions involving background-matching-based camouflage consist of three components. The first component is the background upon which the predator-prey interaction occurs. The second is the predator or prey species that hides on the background (colloquially, hiders). The third component is the predator or prey species (colloquially, seekers) that attempt to determine whether there are any hider individuals on a given piece of background. The ability of hiders to avoid detection depends on how its phenotype interacts with the background, within the seeker's perceptual system. In this paper I will assume that camouflage operates via a colour matching mechanism. This means that the seekers' ability to detect the presence of a hider individual is negatively related to the similarity of the hider's colour to that of the background, as perceived by the seekers' visual system. It is important to note that camouflage does not need to be based on a background-matching mechanism (Cuthill et al., 2005; Fraser et al., 2007; Hanlon et al., 1999; Merilaita and Lind, 2005; Rowland et al., 2008; Schaefer and Stobbe, 2006; Sherratt et al., 2005) and can involve dimensions other than vision (Chittenden and Saito, 2006; Dettner and Liepert, 1994; Ruxton, 2009).

Most evolutionary studies of camouflage systems have focused on the hider and/or seeker species. For example it has been shown that the phenotypes of hider species are cryptic within the perceptual system of seeker species (Chittka, 2001; Downes and Shine, 1998; Théry and Casas, 2002; Théry et al., 2005). Conversely, it has been proposed that the evolution of perceptual abilities or behavioural strategies of seeker species can be affected by the need to detect camouflaged hider individuals (Downes and Shine, 1998; Dukas and Clark, 1995; Ings and Chittka, 2008; 2009; Morgan et al. 1992). The studies that have focused on the background usually deal with how heterogeneous or changing backgrounds affect the predator-prey interaction (Chiao and Hanlon, 2001; Hanlon et al., 1999; Kettlewell, 1955, 1956; Merilaita et al., 1999; Merilaita, 2003). Few researchers have considered the evolution of the background in camouflage systems (but see Lev-Yadun et al., 2004). This focus makes sense as often the background is an abiotic substrate, or has no fitness interest in the outcome of the predator-prey interaction (in fact, according to some definitions the key feature of camouflage, as opposed to mimicry, is a background that is an "uninteresting object or form" (Vane-Wright, 1976) or that is "non-living or inanimate" (Starrett, 1993)). However, there are systems where the fitness of the species adopting the background role is affected by the outcome of the predator-prey interactions of the hider and seeker species; for example predator-prey/herbivore-plant systems and predator-prey/pollinator-flower systems.

Predator-Prey/Herbivore-Plant Systems

Plants are the substrate upon which many predator-prey interactions occur, and can act as the background on which predator or prey species are camouflaged. When the prey species is also an herbivore of the plant species, then the plant species has a fitness interest in the outcome of the predator-prey interaction. There are two different forms such a system can take. First, there are cases where ambush predators wait on foliage and attack visiting herbivores. In this case, the presence of a predator positively affects plant fitness by deterring or killing herbivores. There is, however, a conflict between the predators and the plants. From the plants' perspective, the deterrent value of a predator is greatest when the predator is poorly camouflaged. Predators, however, do better if they are well camouflaged and herbivores are not deterred from visiting their ambush sites. The colour of the plant species, relative to the colour of the predator species, may partially be an outcome of the resolution of this conflict. Secondly, there are systems where herbivores spend significant amounts of time on the plants and predators search for herbivores on these plants. Here, plant adaptations that disrupt herbivore camouflage might be expected (Lev-Yadun et al., 2004). The evolution of plant strategies in predator-prey/herbivore systems has been studied (Dicke and van Loon, 2000; Dicke et al., 1990; Turlings et al., 1990), though rarely in a camouflage context (but see Lev-Yadun et al., 2004). Therefore, for the rest of this paper I will focus on predator-prey/pollinator-flower systems, as the evolution of flowers in response to predator-prey interactions has received less attention (Dukas, 2001b).

Predator-Prey/Pollinator-Flower Systems

Pollinators depend on flowers as a food source, and the reproductive success, and therefore the fitness, of flowers depend on visits by pollinators. There are, however, flower-dwelling ambush predators that kill (Balduf, 1939; Dukas, 2001b; Morse, 1979) and deter (Abbott, 2006; Dukas, 2001a; Dukas and Morse, 2003, 2005; Elliott and

Elliott, 1994; Knight et al., 2006; Muñoz and Arroyo, 2004; Reader et al., 2006; Robertson and Klemash Maguire, 2005; Suttle, 2003 but see Dukas and Morse, 2005; Elliott and Elliott, 1991; Morse, 1986; Reader et al., 2006; Wilkinson et al., 1991) pollinators, and can negatively affect plant fitness (Knight et al., 2006; Muñoz and Arroyo, 2004; Suttle, 2003 but see Dukas and Morse, 2005; Wilkinson et al., 1991). Furthermore, the colour of these predators generally match floral colour as perceived by pollinator visual systems, either because predators change their colour so as to better match a flower or because predators select flowers with matching colours (Balduf, 1939; Chittka, 2001; Elliott and Elliott, 1991; Greco and Kevan, 1994; Heiling et al., 2005a; Morse, 2007; Théry and Casas, 2002; Théry et al., 2005 but see Heiling et al., 2005a, 2005b for an example where non-matching may be adaptive). Therefore, in this system the predators adopt the role of hiders, the pollinators adopt the role of seekers, and the flowers adopt the role of the background that has a fitness interest in the outcome of predator-prey interactions. It is plausible that floral colour should evolve relative to predator colour, but it is not immediately obvious how it should evolve. On the one hand, if the colour of a flower is similar to the predators' colour, the presence of a predator is less likely to have a negative fitness impact on the flower because the pollinators are less likely to detect and avoid the predator and the flower. On the other hand, predators may prefer to hunt on these camouflage facilitating flowers and the increased frequency of predators and decreased probability of the detection of predators may mean that pollinators are generally reluctant to visit these flowers, which would decrease the fitness of these flowers.

Given this uncertainty, I have developed a three-player game theoretical model that attempts to describe how floral colour might co-evolve with pollinator and predator behavioural strategies. This model considers two floral colour strategies. The colour of concealing flowers is relatively similar to the predators' colour, aiding predator camouflage. The colour of revealing flowers is relatively dissimilar to the predators' colour making it easier for pollinators to determine whether or not a flower contains a predator. In this model, predator strategies determine how predators distribute themselves between concealing and revealing flowers, and pollinator strategies determine the level of predation risk that pollinators accept on concealing and revealing flowers. Note that while I present this model in terms of a predator-prey/pollinator-flower game, I am actually attempting to explore the more general hider-seeker-background problem. I have chosen a specific system primarily because a concrete example simplifies the model description and provides a basis for parameterisation. The hope is that this model, and its predictions, can easily be applied to other hider-seeker-background systems.

Model Description

This section describes, in a general way, how this model is structured and analyzed. This description is primarily verbal and graphical. Throughout this section, I refer to the relevant portions of Appendix A, where the math behind this model is described. It should be possible to understand the basics of the model using only this section, but those who want more details should make use of the appendix. I describe the model by introducing the strategies and fitness functions of the three players sequentially. First I describe Signal Detection Theory which is used to define the strategy of the pollinators and to determine the evolutionarily stable strategy adopted by pollinators in any given situation. Second, I describe the factors that determine how predators in this model distribute themselves between concealing and revealing flowers and explain the dynamics of the predator-prey portion of the game. Third, I describe how the predator-prey game affects the fitness of the two floral strategies which can be used to explain how floral colour evolves in the predator-prey/pollinator-flower model.

Pollinators

The presence of predators on flowers means that, for the pollinators, there is a trade-off between foraging success and mortality risk. In particular, a pollinator that is unwilling to land on any flower that might contain a predator will have a low mortality risk but will also have low foraging returns as she will waste time rejecting flowers that are actually safe. Alternatively, a pollinator that only rejects flowers that definitely do contain a predator will enjoy high foraging returns but will suffer from high mortality risk and will have a relatively short expected lifespan. The optimal strategy of pollinators in such a situation becomes essentially a question of how certain they must be that a flower contains a predator before they reject the flower. This situation is well described by Signal Detection Theory (Ings and Chittka, 2008; Sherratt, 2002), and this section will explain how Signal Detection Theory is used to describe the behaviour of the pollinators (see also Appendix A, section 1).

Consider a population of flowers (represented by large white or grey circles in Figure 1), some of which contain a single predator (represented by small black circles). Some flowers have a colour that is similar to the predator's colour (concealing flowers represented by large grey circles that contrast minimally with black predators in i panels) and other flowers have a colour that is distinct from the predator's colour (revealing flowers represented by large white circles that contrast strongly with black predators in ii panels). The experience of pollinators in this model can be separated into discrete trials. A trial begins when a pollinator leaves the previous flower and spends some flight time approaching the focal flower. I assume that pollinators must approach a randomly selected flower before identifying it as concealing or revealing. This means that pollinators encounter predator-containing concealing flowers, predator-free concealing flowers, predator-containing revealing flowers, and predator-free revealing flowers in proportion to their relative frequency. I also assume that pollinators never misidentify a flower as concealing or revealing once she has approached it. At this point, the pollinator makes a decision as to whether or not to act as though the focal flower contains a predator. If the pollinator accepts the flower, she lands on it. If there is no predator present, the pollinator spends some time foraging, gaining some nectar reward and reducing the amount of nectar available to the next visitor. If there is a predator present, the pollinator gains no reward and is killed by the predator with some probability related to the predators' hunting efficiency. I assume that the amount of time that a pollinator spends on a flower where she has escaped from a predator's attack is less than the amount of time she spends on a predator-free flower. If the pollinator rejects the focal flower, she does not land and does not deplete the amount of nectar available on the flower.

The signal detection aspect of the trial occurs after a pollinator has approached a flower and identified it as concealing or revealing, and involves deciding whether or not the flower contains a predator. The i panels of Figure 1 are relevant to the case where the focal flower is concealing and the ii panels are relevant to the case where the focal flower is revealing. The x-dimension for the overlapping distributions in Figure 1 is a measure of how safe a flower appears, or how much it looks like it does not contain a predator. In reality this dimension would be measured in units related to some concrete perceptual dimension, in this case perhaps something about colour contrast, but the specifics are not important. Predator-free flowers, on average, score higher on this dimension than predator-containing flowers do. However, noise in the pollinators' perceptual system or variation in the physical qualities of the visual scene (e.g. shifting light conditions) means that the probability that a given concealing or revealing flower is perceived at any given point along this dimension is best described by two Gaussian probability distributions. The dashed distributions in the i and ii panels of Figure 1 show the probability that a predator-containing flower is perceived at any given point along this dimension by a pollinator. The solid distributions show the probability that a predator-free flower is perceived at any given point along this dimension.

The ideal way for a pollinator to decide whether to act as though the flower contains a predator, or to act as though it is safe, is to adopt a pair of criteria, one for when assessing concealing flowers and one for when assessing revealing flowers. In Figure 1 these criteria are represented by solid vertical lines in the i and ii panels. If a flower is perceived as falling to the left of the criterion on the x-dimension, the pollinator assumes that the flower contains a predator and does not land. If a flower is perceived as falling to the right of the criterion, the pollinator assumes that the flower is safe and lands on the flower. The placement of this criterion determines the value of four conditional probabilities (see also Appendix A, section 1.1). The probability that a pollinator correctly chooses to avoid a flower that actually does contain a predator is the area to the left of the criterion in the dashed distribution. Conversely, the probability that this pollinator incorrectly chooses to land is the area to the right of the criterion in the dashed distribution. Similarly, the probability that a pollinator incorrectly chooses to avoid a flower that does not contain a predator is the area to the left of the criterion in the solid distribution, and the probability that this pollinator correctly chooses to land is the area to the right of the criterion in the solid distribution.

The optimal placement of the criterion for a given flower type (i.e. concealing or revealing) depends on three factors (note that the criteria shown in Figure 1 are intended to represent the optimal or evolutionarily stable placement of the criterion for an exemplary set of parameter values). First, it depends on the proportion of flowers of that type that contain a predator. Pollinators should adopt a more conservative (rightward shifted) criterion on a flower type if the frequency of predators on that flower type is high. An example of this effect will be seen in the next section where predator strategies are discussed.

Second, the optimal criterion placement depends on how difficult it is for a pollinator to detect the presence of a predator on a flower. By definition, it is more difficult for pollinators to detect predators on concealing flowers than on revealing flowers. From a Signal Detection Theory perspective, this reduced detectability of predators on concealing flowers is caused by the fact that the two distributions are closer together and overlap more for concealing flowers (Figure 1, i panels) than for revealing flowers (Figure 1, ii panels). The consequence of this relative spacing of the distributions is that a leftward shift in the criterion that results in a fixed increase in the probability of correctly accepting safe flowers causes a greater increase in the probability of incorrectly accepting dangerous flowers when the focal flower is concealing than when it is revealing. In other words, on concealing flowers there is more of a trade-off between the risk of incorrectly avoiding a predator-free flower and the risk of incorrectly landing on a predator-containing flower. All else being equal, pollinators should adopt a more liberal criterion (i.e. a leftward shifted criterion so that the pollinator is more likely to accept a predator-containing flower) on concealing flowers and a more conservative criterion on revealing flowers. The reason for this is that on revealing flowers, pollinators adopting a conservative criterion can correctly reject most predator-containing flowers without incorrectly avoiding too many predator-free flowers (compare Figure 1.A.i and 1.A.ii).

Third, the optimal placement of the criterion depends on the magnitude of the costs associated with incorrect acceptance and rejection events and the magnitude of the benefits associated with correct acceptance and rejection events. For example, if the costs of incorrectly accepting a predator-containing flower are high (e.g. certain death), then the pollinators should adopt a conservative criterion and thus accept only flowers that are almost certainly safe. The effect of these costs and benefits on the optimal placement of the criterion is more complex than in standard signal detection models. In particular, the benefit received from a correct acceptance trial depends on the amount of nectar available on the focal flower, but this amount depends on the criterion adopted by all other pollinators on the focal flower type (concealing or revealing; see also Appendix A, sections 1.2 and 1.3). For example, if all other pollinators adopt a liberal criterion on the focal flower type, it is likely that many pollinators have previously landed on the focal flower and little nectar will be available. Less intuitively, the criterion other pollinators adopt on the non-focal flower type also affects the amount of nectar reward available on the focal flower. For example, if pollinators adopt a conservative criterion on the non-focal flower type, they will rarely actually land on non-focal flowers. The time these pollinators do not spend on non-focal flowers is time that they can spend approaching focal flowers. This increased encounter rate with focal flowers means that pollinators will land on more focal flowers per unit time and will, therefore, reduce the amount of nectar rewards that can be expected on the focal flower. Note that the way that the criterion adopted by other pollinators affects the reward expected by the focal pollinator depends on how quickly the flowers replenish their nectar stores (Ohashi and Thomson, 2005; Possingham, 1989). If flowers replenish very quickly, then whether or not the previous pollinator actually landed on the flower has little effect on the reward expected by the current pollinator because the flower is likely to have replenished its nectar store in the intervening time period. If the flowers take longer to replenish their nectar stores, intraspecific competition will be more intense and the behaviour of other pollinators will have a greater impact on the optimal strategy of the focal pollinator. Therefore, the optimal strategy for a pollinator to adopt depends on the strategy adopted by all other pollinators. This means that it is necessary to search for an evolutionarily stable placement of the criteria in order to describe the expected behaviour of the pollinators for a given set of parameter values. I developed an algorithm that systematically searches the pollinator strategy set in order to identify the strategy that, if adopted by the majority of pollinators, has greater fitness than a rare mutant adopting any other strategy. This uninvadable strategy is the pollinators' ESS (Evolutionary Stable Strategy) and is used to describe how all pollinators actually behave for a specific set of parameter values (see also Appendix A, section 1.4). Note that as is typical in Game Theory models, I do not describe the mechanism that determines what strategy the pollinator population adopts. This mechanism could be an optimal learning process that allows the pollinator population to approach the ESS within a single generation. Alternatively the mechanisms could involve a set of genes that affect the placement of the criteria so that a population of pollinators approaches the ESS over evolutionary time. To study whether either of these mechanisms, or some combination of the two, could produce a population that adopts the ESS would require a learning or evolutionary dynamics model that is beyond the scope of the current paper.

Predators

To explain the selective pressures affecting how predators distribute themselves between concealing and revealing flowers, and the dynamics of the predator-prey portion of the game, this section works through an example illustrated by panels i and ii of Figure 1.A, B, and C. Note that the example illustrated here describes an algorithm for finding the evolutionarily stable solution to the predator-prey portion of this game. This algorithm is described in more detail in Appendix A, section 2.

Figure 1.A.i and 1.A.ii show a situation where predators are uniformly distributed between concealing and revealing flowers. As noted above, the criteria indicated in Figure 1.A.i and 1.A.ii are meant to represent the ESS for the pollinators for an example set of parameter values and for this uniform predator distribution. If the strategy that the pollinators will adopt is known, the relative fitness of predators hunting from concealing or revealing flowers can be approximated. The area to the right of the criterion in the dashed distribution in Figure 1.A.i is the

probability that a pollinator incorrectly accepts a predator-containing concealing flower. This probability is positively related to the number of prey encountered by predators hunting from concealing flowers. Therefore this probability is assumed to be proportional to the hunting success of predators on concealing flowers and can be used as a proxy for their fitness. Similarly, the area to the right of the criterion in the dashed distribution in Figure 1.A.ii can be used as a proxy of the fitness of predators hunting from revealing flowers. A comparison of Figures 1.A.i and 1.A.ii shows that for this predator distribution, predators on concealing flowers have greater fitness than predators on revealing flowers. The predators that are currently on revealing flowers would have greater hunting success if they were on a concealing flower, but shifting to an unoccupied concealing flower will only be optimal if the expected fitness benefit associated with this increased hunting success outweighs the cost of the shift. The cost of this shift should depend on how far the predator has to move to find an unoccupied concealing flower and on the cost per unit distance. If the potential gain is large enough, and the cost is small enough, the model predicts that one predator will shift to the more productive flower type (when predators start from a uniform distribution, this will generally be a shift from a revealing flower to a concealing flower). This change in the frequency of predators on the two flower types may cause a change in the behaviour of the pollinators. In particular, the pollinators will likely become more conservative on concealing flowers (i.e. shift their criterion to the right) in response to the increased frequency of predators on concealing flowers (Figure 1.B.i). Conversely, pollinators may become more liberal (i.e. shift their criterion to the left) on revealing flowers (Figure 1.B.ii). Relative to Figure 1.A where predators were uniformly distributed, the fitness advantage that predators on concealing flowers have over predators on revealing flowers has been reduced by this change in predator distribution and pollinator behaviour (note that while the area to the right of the criterion in the dashed distribution is still larger in Figure 1.B.i than in Figure 1.B.ii, the magnitude of this difference is less than in Figure 1.A). This change in the predator distribution will also increase the cost associated with switching from a revealing flower to a concealing flower. This is because a predator would have to spend a longer time searching for an unoccupied concealing flower, as these flowers have become less common. Although the benefit to a predator of switching from revealing to concealing flowers is reduced, and the cost of switching is increased by the prior movements of other predators, it may be that it is still advantageous for one predator to switch. If another predator does switch, then the criteria adopted by pollinators will likely shift in the same direction as discussed above (compare Figures 1.B.i and 1.B.ii with 1.C.i and 1.C.ii). After this second shift in predator distribution and pollinator behaviour, predators on concealing and revealing flowers have similar hunting success (area to the right of the criterion in the dashed distribution is the same in Figure 1.C.i and in Figure 1.C.ii). At this point, there is no reason to expect any further changes in predator distribution or in the placement of the criteria adopted by pollinators, regardless of how cheap movement is for predators.

Panels i and ii of Figures 1.A, B, and C can be thought of as three possible evolutionarily stable outcomes of this hypothetical predator-prey game. Figure 1.A is the outcome expected if the costs of predator movement are high (recall that the cost of switching to an alternate flower type is a combination of the cost of movement and how far the predator can expect to move in its search), Figure 1.B is the outcome expected if this cost is intermediate in magnitude, and Figure 1.C is the outcome expected if this cost is very low.

Flowers

In the previous sections, plants were not considered active players in this game. In this section, instead of considering concealing and revealing flowers as just two passive co-existing colour variants, I will consider them as two floral strategies that can evolve (see also Appendix A, section 3).

Panels iii of Figures 1.A, B, and C demonstrate how the fitness of concealing and revealing flowers depend on the evolutionary stable outcomes of the predator-prey game represented by the i and ii panels. I assume that the reproductive success of a flower is positively related to the number of pollination visits it receives. As discussed above, the areas to the right of the criterion in the dashed distributions in Figure 1 are the probabilities that a pollinator incorrectly chooses to land on a predator-containing flower and the areas to the right of the criterion in the solid distributions are the probabilities that a pollinator correctly chooses to land on a predator-free flower for cases where the focal flower is concealing (i panels) or revealing (ii panels). Therefore, the fitness of the concealing strategy can be approximated by the average of the probability that a pollinator lands on a predator-containing concealing flower and the probability that a pollinator lands on a predator-free concealing flower, weighted by the relative frequency of predator-containing and predator-free concealing flowers. A similar analysis can be done to approximate the fitness of the revealing strategy. Panels iii of Figure 1 demonstrate this approximation for each of the three (Figure 1.A, B, and C) hypothetical outcomes of the predator-prey portion of the game (see figure caption for details). In the outcome described by Figure 1.A, the concealing strategy has greater fitness than the revealing strategy and should become more common in subsequent generations. In Figure 1.B, the fitness of the two floral colour strategies are essentially equal. In Figure 1.C it is the revealing strategy that has greater fitness.

The evolutionarily stable proportion of concealing flowers predicted by this model can be determined by examining the relative fitness of the concealing and revealing strategies for a range of cases with different proportion of concealing flowers (Figure 1 shows just one of these cases where there are equal proportions of concealing and revealing flowers). The model can predict that all flowers will be concealing (a pure concealing ESS), that all flowers will be revealing (a pure revealing ESS), or that there will be some stable mix of concealing and revealing flowers (a mixed ESS) (see Appendix A, section 3 and 4 for more details).

Model Results

I have selected a set of biologically plausible base parameter values (Table A1 in Appendix A) as a common starting point for each individual analysis. Each analysis described below involves testing the effect of changing the value of one parameter while keeping all other parameters constant.

Predator travel costs

Rationale: An earlier version of this model assumed that there were no constraints on predator movement. This meant that predators would always distribute themselves between the two flower types so as to equalize the fitness of predators on concealing and revealing flowers. This version of the model predicted that all flowers would be revealing (i.e. a pure revealing ESS) for all parameter values tested. An inspection of Figure 1 demonstrates why this was the case. Figure 1.C gives an example of the equilibrium reached for the predator-prey potion of this game when predator movement is unconstrained. As can be seen, predators have adopted a distribution where they have equal expected fitness on the two flower types (i.e. the area to the right of the criterion in the dashed distributions is equal in Figure 1.C.i and 1.C.ii). In this example, revealing flowers have greater fitness than concealing flowers (Figure 1.C.iii). In particular, while predator containing flowers of both types do equally well (the fitness of predator containing flowers is proportional to the fitness of their resident predator and all predators have equal fitness in this situation), predator free revealing flowers do better than predator free concealing flowers. This is a general outcome if predators can always distribute themselves so as to equalize fitness, and in the absence of constraints on predator movement this model predicts that concealing flowers will not exist for any set of parameter values.
If the movement of predators between flowers is constrained, however, predators may not always distribute themselves so as to equalize fitness on the two flower types. Distributions adopted by constrained predators are described in Figure 1.A and 1.B, and Figure 1.A.iii suggests that such predator distributions can produce cases where the concealing strategy has a greater expected fitness than the revealing strategy. I consider a case where predator movement is constrained by a movement cost (as described above).

Result: Figure 2.i confirms that not only does the existence of movement costs allow for the existence of concealing flowers, the greater this cost, the greater the evolutionarily stable proportion of concealing flowers expected. Figure 2.ii shows that when predator movement costs are low, predators heavily exploit concealing flowers, but that this exploitation decreases as the cost of searching for unoccupied concealing flowers increases. Figure 2.iii shows that the probability that a pollinator accepts any concealing flower increases as predator movements costs increase and the proportion of concealing flowers that contain predators decreases. Conversely, the pollinators' acceptance rates for revealing flowers decreases over this range, due to the increased proportion of revealing flowers that contain a predator. This means that the pollinators' acceptance rates for predator containing concealing and revealing flowers converge as the predators movement costs approach 0. Unexpectedly, these acceptance rates flip when the predator movement cost equals 0 so that the incorrect acceptance rates on the two flowers are not equal (recall that above I argued that in the absence of movement costs, predators would distribute themselves so as to equalize their fitness on the two flower types, which is equivalent to equalizing incorrect acceptance rates on the two flower types). It seems likely that the failure of these incorrect acceptance rates to equalize reflects nothing more than noise introduced by the analysis. See Appendix A, section 5 for further details, but in short, the fact that the model considers a finite number of flowers, predators, and a non-continuous set of pollinator criteria, means that it is not always possible for predators to reach a distribution that results in equal incorrect acceptance rates. This problem can also be exaggerated when there is a predator distribution, near the evolutionarily stable predator distribution, for which there is no evolutionarily stable pair of criteria for the pollinators. This was the case for the data point in Figure 2.iii where the predator movement cost was 0. It should be noted that for the most part, these incorrect acceptance rates were equalized for other proportions of concealing flowers that were tested, including at the evolutionarily stable proportion shown in Figure 2.i.

It is worth examining Figure 2.iii (also Figures 3.A.iii, 3.B.iii, and 3.C.iii) as it shows the differential fitness tradeoffs concealing and revealing flowers experience. In all cases (with the exception of the anomalous case where there is no movement cost discussed in the previous paragraph), the predator-free revealing flowers enjoy among the greatest fitness (i.e. the greatest pollinator acceptance rates) while predator-containing revealing flowers suffer the lowest fitness. The presence of a predator also has a negative fitness impact on concealing flowers, though the magnitude of this impact tends to be smaller than for revealing flowers. However, predator-free concealing flowers generally achieve lower fitness than predator-free revealing flowers. Therefore the tradeoff can be stated thus: revealing flowers will do very well if not burdened with the presence of a predator but will suffer a large fitness cost otherwise, whereas concealing flowers suffer a fitness cost by nature of being concealing but are not as burdened as greatly by the presence of a predator. It is this tradeoff (i.e. sometimes the average fitness of the concealing strategy will exceed that of the revealing strategy) that allows for the counterintuitive evolutionarily stable existence of concealing flowers (counterintuitive because it is natural to think of the flowers' fitness interests as being aligned with the pollinator and not with the predator).

Predator population size

Rationale: Predator population size is a particularly interesting parameter within the current model because it highlights some less-than-obvious similarities between predator-pollinator-flower systems and mimic-model systems. Sherratt's (2002) signal-detection/game-theory model predicts that when aposematic models are rare relative to their mimics, the mimics should evolve to match the models phenotype more closely (See Harper and Pfennig, 2007 for data consistent with this prediction). The reason for this is that when the unpalatable model is rare, predators should be willing to attack anything that looks even slightly dissimilar to the model. Therefore, only mimetic phenotypes that closely match the model's phenotype are favoured. It is well recognized that mimicry and camouflage are related concepts (Starrett, 1993; Vane-Wright, 1976). While the current system is generally thought of as an example of camouflage, it is possible to think of the function of the flowers' colour in terms of mimicry of the predator. The only real difference is that in mimicry systems the focus is on how good the mimicry is, whereas in the current system the strategy set is broader, ranging from mimicry (the concealing strategy) to the opposite of mimicry (the revealing strategy). If this analogy is valid, we might expect to replicate Sherratt's (2002) result so that when the predator (model) is rare, the concealing strategy (good mimic) is common and vice versa. Furthermore, we might expect this to be true for similar reasons; namely that predator rarity favours less discriminating pollinators which favours the concealing strategy.

Result: Figure 3.A.i shows that, as expected, the evolutionarily stable proportion of concealing flowers is negatively related to the predator population size. Figure 3.A.iii suggests why this is the case. As expected, when predators are rare, pollinators are relatively indiscriminate and accept all flower types at high rates. The cases where the predator population size is 10 or 30 are particularly informative. Note that all concealing and predator-free revealing flowers are accepted at virtually the same high rate. The only flowers that are avoided at any significant rate are predator-containing revealing flowers, where the presence of a predator is conspicuous. It is not surprising, therefore, that the concealing strategy is at a selective disadvantage for low predator population sizes. When predators become more common, pollinators are less likely to accept any flower. This reduction in acceptance rates is more pronounced for some flower types than others so that the four acceptance probabilities diverge at higher predator population sizes. This allows for cases where the revealing strategy has greater expected fitness than the concealing strategy, even if predator-containing revealing flowers have the lowest fitness of any flower type. Figure 3.A.ii suggests that predator population size should have no direct effect on the distribution of predators.

Predator effectiveness

Rationale: The effect of predator population size, discussed above, suggests that this model replicates one prediction of a mimicry model (Sherratt, 2002). A second prediction of the mimicry model is that mimics should match the phenotype of aposematic models more closely when the model is less well defended (See Darst and Cummings, 2006; Lindström et al. 2006 for data consistent with this prediction). The basis of this prediction is similar to the model abundance prediction; when models are less well defended, predators are willing to attack anything that does not look exactly like the model and therefore, a high level of mimicry is required if the mimic is to avoid attack. It seems plausible that the current model will also replicate this second prediction for a similar reason, namely that when predators are less dangerous, pollinators should be willing to land on any flower where the presence of a predator is not immediately obvious, so floral mimicry of predators (concealing strategy) prevents pollinators from detecting and avoiding the presence of a predator without the risk that pollinators will avoid all concealing flowers. I modeled the danger of a predator in terms of predator effectiveness, which is the probability that a pollinator will be captured if she lands on a predator-containing flower.

Result: A comparison of Figure 3.B with 3.A demonstrates that the effect of predator effectiveness on all three players is similar to the effect of predator density.

Pollinator maximum expected lifespan

Rationale: Flower dwelling ambush predators are generally rare relative to the number of flowers and pollinators present in the system (Morse, 1986). This means that most of the flowers that a pollinator encounters will not contain a predator. Therefore, adopting a conservative criterion may entail a high opportunity cost associated with incorrectly rejecting many safe flowers, particularly safe concealing flowers. It may not be adaptive to accept this opportunity cost if the pollinator has a short expected lifespan. This is because the pollinator is unlikely to encounter many predators in her short lifetime, even if she does adopt a liberal criterion. In this case, adopting a liberal criterion does not have much of an effect on the expected lifespan of the pollinator, and may increase her expected lifetime foraging gain. If pollinators could expect to live for a long time, in the absence of predation by flower dwelling ambush predators, then two related factors may make them more cautious. First, the fact that they visit more flowers in their longer lives means that they should expect to encounter more predators. Therefore adopting a liberal criterion could significantly shorten their expected lifespan. Second, longer lived pollinators have more future foraging gains to lose if they are killed (Clark, 1994). Taken together, this suggests that the criteria that maximize expected lifetime foraging gains will be more conservative for relatively long-lived pollinators. The maximum expected lifespan of pollinators (based on sources of mortality other than the ambush predator considered in this model) may, therefore, affect the evolution of floral colour strategies via its effects on the criteria adopted by the pollinators.

Result: Figure 3.C.i shows that the evolutionarily stable proportion of flowers adopting the concealing strategy is negatively related to the pollinators maximum expected lifespan. A comparison of Figure 3.C.iii with Figures 3.A.iii and 3.B.iii shows that the reason for the effect of pollinator lifespan is similar to the reason for the effect of predator population size and predator effectiveness. In all cases, indiscriminate pollinators that adopt liberal criteria (short pollinator lifespan, small predator populations, or ineffective predators) favour the concealing floral strategy, and discriminating pollinators adopting conservative criteria (long pollinator lifespan, large predator populations, or effective predators) favour the revealing strategy.

Discussion

The co-evolution of predator-prey strategies has been well studied (Bouskila, 2001; Brown et al., 2001; Hugie and Dill, 1994; Iwasa, 1982; Mitchell and Lima, 2002; Sih, 1998 but see Lima, 2002). Similarly, the co-evolution of floral and pollinator strategies have been well studied, including at least one signal detection model (Lynn et al., 2005). The novel aspect of the current model has to do with how floral strategies evolve in the presence of flower-dwelling ambush predators. Therefore, the most interesting, and potentially the most testable (see Ings and Chittka, 2009 for a laboratory setup that would be well suited to testing many of these predictions), predictions of this model are predictions about when we would expect floral colour to be similar to the predators' colour (i.e. high proportion of concealing flowers predicted) and when we would expect floral colour to differ from the predators' colour (i.e. low proportion of concealing flowers predicted). The analysis of this model has identified two major factors that may affect the evolution of floral colour.

The first factor is the constraints on the distribution of predators. In the absence of sufficient constraints, a tragedy of the commons (Hardin, 1968; Rankin et al., 2007) seems to exist, where the predator population overexploits concealing flowers, which makes pollinators reluctant to visit any concealing flower, which causes the extinction of the concealing strategy (note that the existence of concealing flowers on which predators are well camouflaged is the common resource in this analogy). The tragedy can be alleviated by constraints that prevent overexploitation. The most obvious constraint on the distribution of predators is the cost associated with moving from one flower to another. The fact that the cost of movement for flower-dwelling ambush predators can vary by age or species (Kevan and Greco, 2001) presents an opportunity to test this prediction. The effect of predator travel costs on predator distribution can also be thought of in terms of the habitat selection literature. The predator-prey portion of this game is effectively a predator-prey habitat selection game model (Bouskila, 2001; Brown et al., 2001; Hugie and Dill, 1994; Iwasa, 1982; Sih, 1998). The effect of predator movement costs in this model replicate the effect seen in habitat selection models, namely that increased predator travel costs result in more uniform distributions of predators across habitats/patches (Bernstein et al., 1991). This more uniform distribution results in relatively greater predator exploitation of low quality patches (revealing flowers in my model, low prey-density patches in traditional models) and less exploitation of high quality patches (concealing flowers or high prey-density patches). The tragedy found in the current model does not, however, seem to exist in the model of Bernstein et al. (1991), or if it exists it is of the opposite form (i.e. in the presence of high movement costs, the predator population as a whole might benefit if some predators from low quality patches moved to higher quality patches, but the selfish interest of each individual predator prevents this from happening). While Bernstein et al. (1991) do not consider prey movement, the difference between our models that produces this difference in outcome seems to be in terms of whether or not the population of patches itself can evolve. Unlike my model, most traditional habitat selection games would probably not consider high quality patches becoming less common over generations due to overexploitation.

The second factor that the model predicts may affect the evolution of floral colour is how discriminating pollinators are with respect to determining whether or not a flower is safe. In general, the model predicts that indiscriminate pollinators, who are willing to accept a flower unless the presence of a predator is obvious, will favour a high proportion of concealing flowers and vice versa. Several parameters seem to affect how discriminating pollinators are. Low predator population size means that incorrect acceptance events are unlikely and therefore can produce indiscriminate pollinators. Similarly, ineffective predators and short pollinator lifespan reduce the cost of incorrect acceptance events and may also produce indiscriminate pollinators. The density of many flower-dwelling ambush predators may frequently be so low that a pollinator will encounter few predators in their relatively short foraging lifespan (Morse, 1986). Furthermore, flower-dwelling ambush predators may be relatively ineffective predators (Dukas and Morse, 2003, 2005; Morse, 1979, 2007). All of this suggests that the concealing strategy may be common among flowering plants, or perhaps more accurately, it might be that there is little selective pressure for floral colour to evolve to be distinct from the colour of the predators. Other parameters that were not included in this model should also affect how discriminating pollinators are, and therefore might affect the evolution of floral colour. One example that is particularly relevant to pollination systems is eusociality. The negative impact of death on the inclusive fitness of a eusocial pollinator should be less than the impact on the fitness of a solitary pollinator (Clark and Dukas, 1994). It may be, therefore, that eusocial pollinators are less discriminating and favour the evolution of concealing flowers, and solitary pollinators are more discriminating and favour the evolution of revealing flowers.

Model extensions

Many aspects of this model have been simplified, either to increase the generality or the tractability of the model. Some of these simplified aspects are interesting enough to be targets of future modeling efforts. For example, in the current model, I have ignored the fact that predator colour can change over time. The revealing strategy may actually be part of an evolutionary chase where predator colour evolves to be more similar to the colour of flowers and floral colour evolves to be less similar to the colour of the predators. The observed similarity between floral and predator colour may be an outcome of the strength of the selective pressures on flowers and predators, as well as the speed at which flowers and predators can evolve. Furthermore, there are predator species that can change colour over short periods of time so as to better match the current background (Chittka, 2001; Morse, 2007; Théry and Casas, 2002; Théry et al., 2005). The revealing strategy will only be a meaningful concept in systems where the ability of individual predators to match their background is limited and there are possible floral colours that cannot be perfectly matched by the predator.

In this model, the colour of concealing and revealing flowers remained constant in all analyses (more accurately, the difference in the degree to which the colour of concealing and revealing flowers contrasted with the colour of predators remained constant). There are factors, not included in the current model, which could result in different evolutionary dynamics depending on the amount of colour contrast between concealing and revealing flowers. For example, if the colours of concealing and revealing flowers are relatively similar, the assumption that pollinators always know which type of flower they have approached would be invalid. In particular, a second signal detection process would be involved, where pollinators would have some control over the rate at which they correctly classify or misclassify concealing and revealing flowers. In this case, some concealing flowers could benefit from being mistaken for revealing flowers and some revealing flowers could suffer from being mistaken for concealing flowers. Furthermore, the degree of colour separation may affect pollinator behaviour with respect to colour constancy and to innate or learned colour preferences (Waser, 1986). Both of these factors could bias the placement of the pollinators' criteria for reasons that have nothing to do with predation risk. In the presence of such biases and if the colour of concealing and revealing flowers are very different, few individual pollinators may forage on both flower types. The evolutionary dynamics of such systems, and the equilibriums reached may, therefore, depend heavily on whether novel mutant floral colours tend to be similar or very different from the non-mutant colour (which would likely depend on the genetic and developmental mechanisms that control colour in this species).

Additionally, there are several other species that interact with the three discussed here in ways that might affect the solution to the game. For example, second order predators (or parasitoids) that prey on the ambush predators described in this model provide an additional selective advantage for predator camouflage. If the predators and the prey of the focal predators have sufficiently different perceptual systems, the colour that maximizes camouflage against their predator may not be the colour that maximizes their camouflage against their prey and vice versa. This should affect the evolution of the ambush predator's colour (Théry and Casas, 2002; Théry et al., 2005), but could also affect the evolution of floral colour. Similarly, the presence of multiple pollinator species might affect the predictions made by this sort of model. In particular, it is plausible that some pollinator species would accept higher levels of predation risk (i.e. adopt more liberal criteria) than other pollinator species, due to species differences in the cost of incorrectly accepting predator-containing flowers (e.g. species differences in expected lifespan or likelihood of being captured by the predator). This intrinsic species difference could, in turn, lead to niche partitioning (Possingham, 1992; Rodríguez-Gironés and Santamaría, 2004, 2006) where the risk averse pollinator species specialise on revealing flowers and the risk prone species specialise on concealing flowers. This could affect the distribution of predators and the evolution of floral colour.

Finally, while I have focused on the predator-prey/pollinator-flower system, there are other systems where the background has a potential fitness interest in the outcome of an interaction involving camouflage (e.g. the predator-prey/herbivore-plant systems discussed in the introduction). It should be possible to apply the basic ideas, and predictions, of this model to other comparable hider-seeker-background systems, and it is quite possible that some other system will prove to be better suited for empirical work on the evolution of backgrounds.

Appendix A: Mathematical supplement to model description

This appendix is not intended to be a standalone document; it is intended a supplement to the description of the model provided in the body of the paper. All appendix sections are referenced in the body of the paper and provide the mathematical basis behind the descriptions being given at that point in the paper.

For the purpose describing this of this model, I consider the system where the predator is a crab spider and the pollinator is a bee. This is done solely as a convenience when naming strategy variables, and related functions, as there is a glut of variables that would naturally use the letter *P* (predator, pollinator, prey, plant). Therefore, the predator variables will use *CS* (crab spider), the prey/pollinator variables will use *B* (bee) and the plant variables will use *F* (flowers). These variables will be clarified by the use of subscripts. Two exceptions to this naming scheme will be that, instead of beginning with *B*, terms beginning with *P* will be used for all probability or proportion variables and terms beginning with λ will be used to describe the criterion adopted by pollinators (these exceptions maintain consistency with standard naming conventions). Parameters will generally use their own naming systems. See Table A1 and A2 at the end of this appendix for a description of all parameters and strategy variables, as well as base values for the parameters, the range of values tested for selected parameters, and the breadth of the strategy sets.

In order to emphasize which players' strategies affect a function, and to enhance readability, I show the strategies, and not the various parameters, that are arguments of a given function. I use variables of the following form to describe the strategy for each player (variants of these variables are described throughout this appendix)...

$$B_{\mathscr{s}} = \{\lambda_c; \lambda_r\}$$
$$CS_{\mathscr{s}} = \{CS_c; CS_r\}$$
$$F_{\mathscr{s}} = \{F_c; F_r\}$$

for the strategy adopted by pollinators (criterion adopted on concealing and revealing flowers, respectively), predators (number of predators on concealing and revealing flowers, respectively), and flowers (number of concealing and revealing flowers, respectively), respectively. These strategies will be described in more detail in the appropriate sections.

I use the following convention throughout this appendix. Flower type refers to the colour or strategy of a flower. Therefore there are two flower types (concealing and revealing). Flower category refers to both the type of flower and whether or not it has a resident predator. Therefore there are four flower categories (predator-containing concealing, predator-free concealing, predator-containing revealing, and predator-free revealing).

Section 1: Pollinators

In general, the subsections in this section describe how the strategies adopted by focal and non-focal pollinators affect various functions relevant to a focal individual's fitness.

1.1 SD probability functions: These probabilities are defined by the areas under the relevant curves to the left or right of the criterion (λ). Therefore they are calculated by integrating the Gaussian function from the criterion to positive or negative infinity. The acceptance probabilities are more useful than rejection probabilities and therefore only acceptance probabilities are discussed hereafter. There are two relevant correct acceptance probabilities (i.e. the probability of choosing to land on a flower that is, in fact, safe),

$$PCA_c[\lambda_c] = \int_{\infty}^{\lambda_c} N[\mu_{s,c}]$$

$$PCA_r[\lambda_r] = \int_{\infty}^{\lambda_r} N[\mu_{s,r}]$$

and two relevant incorrect acceptance probabilities (i.e. the probability of choosing to land on a flower that does contain a predator),

$$PIA_c[\lambda_c] = \int_{\infty}^{\lambda_c} N[\mu_{d,c}]$$

$$PIA_r[\lambda_r] = \int_{\infty}^{\lambda_r} N[\mu_{d,r}]$$

where $N[\mu]$ refers to the formula for a Gaussian with a mean of μ. For simplicity, all Gaussians are assumed to have a standard deviation of 1. The floral colour strategy is denoted by subscript *c* for the concealing strategy, or *r* for the revealing strategy. The floral predator state is denoted by subscript *s* for safe, predator-free, flowers, or *d* for dangerous, predator-containing, flowers. Therefore, there are four relevant Gaussian distributions; $N[\mu_{d,c}]$ is the distribution for dangerous (predator-containing) concealing flowers, $N[\mu_{s,c}]$ is the distribution for safe (predator-free) concealing flowers, $N[\mu_{d,r}]$ is the distribution for dangerous revealing flowers, and $N[\mu_{s,r}]$ is the distribution for safe revealing flowers. For convenience, I set $\mu_{d,c} = \mu_{d,r} = 0$. Since relative spacing of d and s flowers should be greater for revealing flowers than concealing flowers, I let $\mu_{s,r} > \mu_{s,c}$. Note that these probabilities are conditional on the pollinator encountering the appropriate flower category. The actual probability that any given trial will end with one of these acceptance events depends also on the relative proportion of the four flower categories.

1.2 Flower visitation functions: To determine the fitness of a forager adopting a particular strategy (see section 1.3), it is necessary to determine the rate at which the four possible acceptance events (see section 1.1) occur for a focal pollinator and for the population as a whole. From a focal pollinators perspective, this is determined by the strategy that she adopts, which is defined as the pair of criteria adopted on the two flower types, $B_{s,foc} = \{\lambda_{c,foc}; \lambda_{r,foc}\}$, as well as the relative frequency of the four flower categories.

The first step is to determine how many flowers a focal pollinator adopting $B_{s,foc}$ will approach (including flowers that are subsequently landed on and those that are rejected) in an arbitrary amount of time (assuming that the pollinator is not killed by a predator in this time period). To do this, I start by calculating the amount of time, *t*, that it takes for to focal pollinator to approach an arbitrary number of flowers, B_a.

$$t = \left[B_a \cdot t_{ifi}\right] + B_a \frac{F_c - CS_C}{F} PCA_c\left[\lambda_{c,foc}\right] t_{h,s} + B_a \frac{F_r - CS_r}{F} PCA_r\left[\lambda_{r,foc}\right] t_{h,s} + B_a \frac{CS_c}{F} PIA_c\left[\lambda_{c,foc}\right] t_{h,d} + B_a \frac{CS_r}{F} PIA_r\left[\lambda_{r,foc}\right] t_{h,d}$$

In this equation, the first term describes the total amount of time the pollinator has to fly in order to approach B_a flowers (B_a X the time it takes a pollinator to fly between two flowers, t_{ifi}). The subsequent four terms describe the amount of time spent on each of the four flower categories (number of flowers the pollinator approaches X probability that the approached flower is of a given category X probability that a pollinator adopting $B_{s,foc}$ lands on a flower of that category X length of the handling time on a flower of that category ($t_{h,s}$ and $t_{h,d}$ for safe and dangerous flowers respectively)). There are no rejection probabilities in this equation because there is no handling time associated with rejected flowers. Rearranging for B_a produces …

$$\begin{aligned}
&B_a\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right]\\
&= F\cdot t_n\left[F\cdot t_{ifi} + (F_c - CS_c)PCA_c\left[\lambda_{c,foc}\right]t_{h,s}\right.\\
&+ (F_r - CS_r)PCA_r\left[\lambda_{r,foc}\right]t_{h,s} + CS_c\cdot PIA_c\left[\lambda_{c,foc}\right]t_{h,d}\\
&\left.+ CS_r\cdot PIA_r\left[\lambda_{r,foc}\right]t_{h,d}\right]^{-1}
\end{aligned}$$

Note that here I define B_a as a function of the strategies of the focal pollinator $B_{\mathscr{s},foc} = \{\lambda_{c,foc};\lambda_{r,foc}\}$, the predators $CS_{\mathscr{s}} = \{CS_c;CS_r\}$, and the flowers $F_{\mathscr{s}} = \{F_c;F_r\}$. The predator and flower strategies will be described fully in sections 2 and 3. Also note that I have set the arbitrary length of time, t_n, to be the length of time it takes a fully depleted flower to completely replenish its nectar stores (I assume that flowers will stop producing nectar if they already hold some maximum volume of nectar, n_{max}). The reason for this decision will become obvious in section 1.3.

Given the number of flower a focal pollinator approaches in t_n, it is possible to calculate the expected number of flowers, of each of the four categories, that the focal pollinator will land on in t_n units of time.

$$B_{L,s,c}\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right] = PCA_c\left[\lambda_{c,foc}\right]\frac{(F_c - CS_c)\,B_a\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right]}{F}$$

$$B_{L,s,r}\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right] = PCA_r\left[\lambda_{r,foc}\right]\frac{(F_r - CS_r)\,B_a\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right]}{F}$$

$$B_{L,d,c}\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right] = PIA_c\left[\lambda_{c,foc}\right]\frac{CS_c\cdot B_a\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right]}{F}$$

$$B_{L,d,r}\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right] = PIA_r\left[\lambda_{r,foc}\right]\frac{CS_r\cdot B_a\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right]}{F}$$

where $B_{L,fps,fcs}$ is the expected number of times the focal pollinator lands on flowers adopting floral colour strategy, fcs, and floral predator state, fps. Note that the number of lands on a given flower category depends not only on the criterion the focal pollinator adopts on that flower type, but the criterion adopted on the alternate flower type. This effect is mediated by the fact that B_a depends on both criteria. For example, a pollinator that adopts a liberal criterion on revealing flowers will land on many of the revealing flowers she approaches. The time she spends on these revealing flowers is time she cannot spend searching for flowers. Therefore, she will approach fewer flowers in t_n units of time, meaning that she will encounter and land on fewer concealing flowers than she would if she adopted a more conservative criterion on revealing flowers.

It is now possible to calculate the expected number of visitors a focal flower of each of the four categories will receive in t_n units of time.

$$\begin{aligned}
&F_{L,s,c}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]\\
&\qquad=\frac{1}{F_c-CS_c}\Big[(B-1)\,B_{L,s,c}\left[B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]\\
&\qquad+B_{L,s,c}\left[B_{\mathscr{s},mut}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]\Big]\\
&F_{L,s,r}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]\\
&\qquad=\frac{1}{F_r-CS_r}\Big[(B-1)\,B_{L,s,r}\left[B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]\\
&\qquad+B_{L,s,r}\left[B_{\mathscr{s},mut}\,;CS_{\mathscr{s}};F_{\mathscr{s}\mathscr{s}}\right]\Big]\\
&F_{L,d,c}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]\\
&\qquad=\frac{1}{CS_c}\Big[(B-1)\,B_{L,d,c}\left[B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]+B_{L,d,c}\left[B_{\mathscr{s},mut}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]\Big]\\
&F_{L,d,r}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]\\
&\qquad=\frac{1}{CS_r}\Big[(B-1)\,B_{L,d,r}\left[B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]+B_{L,d,r}\left[B_{\mathscr{s},mut}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]\Big]
\end{aligned}$$

where $F_{L,fps,fcs}$ is the expected number of visitors a flower adopting floral colour strategy, fcs, and of floral predator state, fps receives. $B_{\mathscr{s},pop}=\{\lambda_{c,pop}\,;\lambda_{r,pop}\}$ is the strategy adopted by the majority of the pollinator population, and $B_{\mathscr{s},mut}=\{\lambda_{c,mut}\,;\lambda_{r,mut}\}$ is the strategy adopted by a single mutant pollinator. The mutant strategy can differ from the population strategy on one or both dimensions.

<u>1.3 fitness functions:</u> The number of times that a focal pollinator visits a safe concealing, safe revealing, dangerous concealing or dangerous revealing flower depends on the strategy she adopts as well as the relative frequency of the four flower categories (which depends on the strategy adopted by the predator and flower populations as described below), but it does not depend on the strategy adopted by the rest of the pollinator population (see description of B_L functions in section 1.2). Therefore, the rate at which predators are encountered, and thus the

expected lifespan of the focal pollinator, is independent of the strategy adopted by other pollinators (Note that I make the simplifying assumption that an increased number of pollinators visiting risky flowers does not dilute the risk for any individual pollinator). The expected lifespan of a focal pollinator adopting $B_{\mathscr{s},foc}$ can be described as ...

$$B_{\ell,foc}\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right] = MIN\left\{\begin{matrix} t_{exp} \\ \dfrac{t_n}{B_{L,d,c}\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right] + B_{L,d,r}\left[B_{\mathscr{s},foc};CS_{\mathscr{s}};F_{\mathscr{s}}\right]}\dfrac{1}{e} \end{matrix}\right\}$$

where *e* describes the predators' effectiveness (probability of capturing a landing pollinator). The upper term, t_{exp}, is the pollinators maximum expected lifespan, and the lower term is the expected length of time until a pollinator adopting $B_{\mathscr{s},foc}$ gets killed by a predator. The model takes the lower of these two values as the expected lifespan of a pollinator. Note that the model assumes that regardless of age, a pollinator of any age can expect to live for and additional t_{exp} units of time if she is not killed by a predator. This assumption would be consistent with a case where pollinators experience no senescence and experience a fixed risk of mortality from inclement weather or from a secondary predator (i.e. not the predator considered in this model). The expected lifespan of a pollinator adopting the population or mutant strategy are both calculated using this equation, substituting $B_{\mathscr{s},foc}$ with $B_{\mathscr{s},pop}$ or $B_{\mathscr{s},mut}$, respectively.

Unlike expected lifespan, the expected rate at which nectar is collected by a focal pollinator does depend on the strategy adopted by all other members of the population, as well as on her own strategy and the relative frequency of the four flower categories. This is because the rate at which other pollinators visit the four flower categories determines the amount of intraspecific competition that is expected on a given flower. Making the simplifying assumptions that a pollinator never gets nectar from a visit to a dangerous flower (even if she survives), that a pollinator that visits a safe flower collects all of the nectar currently stored in that flower, and that the number of pollinators adopting the population and mutant strategies are stable (i.e. killed pollinators are replaced with a pollinator adopting the same strategy), the expected rate of nectar gain can be described as ...

$$\begin{aligned} B_{g,mut}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right] &= \frac{1}{t_n} \\ &\cdot \Bigg[\Bigg(B_{L,s,c}\left[B_{\mathscr{s},mut}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right] \\ &\cdot \begin{cases} \dfrac{n_{max}}{F_{L,s,c}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]} & if\ F_{L,s,c}[\dots] > 1 \\ n_{max} & if\ F_{L,s,c}[\dots] \le 1 \end{cases}\Bigg) \\ + \Bigg(B_{L,s,r}\left[B_{\mathscr{s},mut}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right] &\cdot \begin{cases} \dfrac{n_{max}}{F_{L,s,r}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}\mathscr{s}}\right]} & if\ F_{L,s,r}[\dots] > 1 \\ n_{max} & if\ F_{L,s,r}[\dots] \le 1 \end{cases}\Bigg)\Bigg] \end{aligned}$$

for pollinators adopting the mutant strategy, and

$$\begin{aligned} B_{g,pop}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right] &= \frac{1}{t_n} \\ &\cdot \Bigg[\Bigg(B_{L,s,c}\left[B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right] \\ &\cdot \begin{cases} \dfrac{n_{max}}{F_{L,s,c}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]} & if\ F_{L,s,c}[\dots] > 1 \\ n_{max} & if\ F_{L,s,c}[\dots] \le 1 \end{cases}\Bigg) \\ + \Bigg(B_{L,s,r}\left[B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right] &\cdot \begin{cases} \dfrac{n_{max}}{F_{L,s,r}\left[B_{\mathscr{s},mut}\,;B_{\mathscr{s},pop}\,;CS_{\mathscr{s}};F_{\mathscr{s}}\right]} & if\ F_{L,s,r}[\dots] > 1 \\ n_{max} & if\ F_{L,s,r}[\dots] \le 1 \end{cases}\Bigg)\Bigg] \end{aligned}$$

for pollinators adopting the population strategy. This derivation incorporates intraspecific competition by the use of a set of conditional statements of the following form; if a flower receives more than one visitor in the time that it takes a fully depleted flower to completely replenish its nectar stores, t_n, then those pollinators on average share the n_{max} units of nectar equally, but if there is less than one visitor in this time period, then each visit results in the pollinator collecting n_{max}, the maximum amount of nectar a flower can hold.

The functions describing the pollinators expected lifespan and expected rate of nectar gain can be combined to give the expected lifetime nectar gain of pollinators adopting the mutant or population strategies. I use expected lifetime nectar gain as a proxy for the fitness of a pollinator strategy, which can be described by

$$B_{W,mut}\left[B_{\mathscr{s},mut}\,; B_{\mathscr{s},pop}\,; CS_{\mathscr{s}}; F_{\mathscr{s}}\right] \\ = B_{g,mut}\left[B_{\mathscr{s},mut}\,; B_{\mathscr{s},pop}\,; CS_{\mathscr{s}}; F_{\mathscr{s}}\right] \cdot B_{\ell,mut}\left[B_{\mathscr{s},mut}\,; CS_{\mathscr{s}}; F_{\mathscr{s}}\right]$$

for pollinators adopting the mutant strategy, and

$$B_{W,pop}\left[B_{\mathscr{s},mut}\,; B_{\mathscr{s},pop}\,; CS_{\mathscr{s}}; F_{\mathscr{s}}\right] \\ = B_{g,pop}\left[B_{\mathscr{s},mut}\,; B_{\mathscr{s},pop}\,; CS_{\mathscr{s}}; F_{\mathscr{s}}\right] \cdot B_{\ell,pop}\left[B_{\mathscr{s},pop}\,; CS_{\mathscr{s}}; F_{\mathscr{s}}\right]$$

for pollinators adopting the population strategy.

1.4 Identifying pollinator ESSs: A pollinator strategy, $B_{\mathscr{s},candidate}$, is an ESS, $B_{\mathscr{s},ESS} = \{\lambda_{c,ESS}; \lambda_{r,ESS}\}$, if it is the case that when the majority of the population adopts the candidate strategy, $B_{\mathscr{s},pop} = B_{\mathscr{s},candidate}$, there is no mutant strategy, $B_{\mathscr{s},mut} \neq B_{\mathscr{s},candidate}$, that a single pollinator could adopt where $B_{W,mut}[\ldots] > B_{W,pop}[\ldots]$. It is unlikely that an analytical solution for the ESS could be produced, so I developed an algorithm to systematically search for an ESS given a set of parameter values and given that the strategies adopted by predators, $CS_{\mathscr{s}}$, and flowers, $F_{\mathscr{s}}$, are known. All possible strategies that a focal pollinator could adopt, $B_{\mathscr{s},foc}$, can be represented as a two dimensional strategy space, where a strategy is defined as a point, $\{\lambda_{c,foc}; \lambda_{r,foc}\}$, in this space. The algorithm requires that the boundaries of the space are well defined, and that the space is divided into discrete segments (as a compromise between precision and computational time, I have set the boundaries as +/-5 standard deviations from the means of the dangerous distributions, $\{\mu_{d,c}; \mu_{d,r}\}$, in both dimensions, and set the size of the segments to 0.1 standard deviations). The algorithm considers each point in this space as a candidate ESS. For each candidate ESS, the algorithm searches the strategy space for a $B_{\mathscr{s},mut}$ that invalidates the inequality $B_{W,mut}[\ldots] > B_{W,pop}[\ldots]$. If no such mutant strategy can be found, $B_{\mathscr{s},candidate}$ is considered an ESS.

There are combinations of parameter values and predator and floral strategies for which no ES pollinator strategy is identified by this algorithm.

It is unclear whether these cases reflect the fact that there are actually areas of parameter space for which no ESS exists, or whether they are an artefact of bounded and low resolution strategy space used in the algorithm. Preliminary investigations suggested that the number of no-ESS cases is reduced when the resolution of the strategy space is increased, suggesting that the artefact possibility is at least partially true. It is also possible that no ESS is found in cases where a mixed ESS is favoured (note that the algorithm does not allow for mixed ESSs). The way I deal with these no ESS cases is described in section 2. There are also combinations of parameter values and predator and floral strategies for which multiple ESSs are identified. This happens much less frequently than the no-ESS result, and the multiple ESSs seem to always occur in a short line (two or three adjacent points) at one edge of the strategy space. This suggests that this is an artefact of the fact that the algorithm uses a bounded strategy space. When this happens, the algorithm uses the average of these multiple points as the estimate of the ESS.

The speed of this algorithm can be greatly increased by noting that it is not always necessary to compare every possible mutant strategy for every candidate ES population strategy. In particular, as soon as one mutant strategy is found that can invade a population adopting the candidate strategy, the candidate can be rejected. The speed of the algorithm can be further increased by focusing the search for the mutant strategy that could invade a given candidate strategy on locations of the strategy space where the condition $B_{W,mut}[\ldots] > B_{W,pop}[\ldots]$ is more likely to be true. This can be achieved by focusing on mutant strategies that are not at the extremes of the strategy space, or are near the locations in the strategy space where $B_{W,mut}[\ldots] > B_{W,pop}[\ldots]$ was true for similar CS_{s} and F_{s} values.

Section 2: Predators

The strategy of the predator population at any given point in time is defined by $CS_{s,curr} = \{CS_{c,curr}\,; CS_{r,curr}\}$, which describes how many predators are currently on concealing and revealing flowers, respectively. The expected fitness of a predator is assumed to be proportional to its hunting success, which is assumed to be proportional to the probability that a pollinator chooses to land on the predator's flower. Therefore the fitness of predators on concealing flowers is given by

$$CS_{W,c}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]\right] = PIA_c\left[\lambda_{c,ESS}\right]$$

and the fitness of predators on revealing flowers is

$$CS_{W,r}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]\right] = PIA_r\left[\lambda_{r,ESS}\right]$$

where $B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right] = \{\lambda_{c,ESS};\lambda_{r,ESS}\}$ is the strategy adopted by all pollinator individuals when the population is adopting the ESS (see section 1.4 and note that here $B_{\mathscr{s},ESS}$ is described as a function with arguments describing the current predator and flower strategies).

Starting with $CS_{\mathscr{s},curr}$, we can consider two possible movements that individual predators could make; a predator that is currently on a revealing flower could move to an unoccupied concealing flower, $CS_{\mathscr{s},curr+1c} = \{CS_{c,curr}+1; CS_{r,curr}-1\}$, or a predator that is currently on a concealing flower could move to an unoccupied revealing flower, $CS_{\mathscr{s},curr-1c} = \{CS_{c,curr}-1; CS_{r,curr}+1\}$ (note that I assume that predators never share a flower). The gains associated with these moves can be described by the difference between the long-term fitness the predator could expect if she moved (taking into account that the modified distribution of predators might alter the pollinators' ESS) and the long-term fitness she would expect if she stayed on the current flower type. The gain expected by a revealing flower-dwelling predator that moves to a concealing flower would be

$$\begin{aligned}CS_{g,r\to c}&\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr+1c};F_{\mathscr{s}}\right];B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]\right]\\&= CS_{W,c}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr+1c};F_{\mathscr{s}}\right]\right] - CS_{W,r}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]\right]\end{aligned}$$

and the gain expected by a concealing flower-dwelling predator that moves to a revealing flower would be

$$\begin{aligned}CS_{g,c\to r}&\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr-1c};F_{\mathscr{s}}\right];B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]\right]\\&= CS_{W,r}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr-1c};F_{\mathscr{s}}\right]\right] - CS_{W,c}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]\right]\end{aligned}$$

The costs associated with these moves can be described by

$$CS_{cost,r\to c}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right] = \left(\frac{F}{F_c - CS_c}\right)\cdot k$$

for revealing to concealing moves and

$$CS_{cost,c\rightarrow r}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]=\frac{F}{F_r-CS_r}\cdot k$$

for concealing to revealing moves. These functions are the product of the distance a predator can expect to travel before she finds an unoccupied flower of the desired type and the cost incurred per unit distance travelled, *k*. This expected distance is in units of the average distance between two randomly selected flowers and is calculated as a sampling with replacement problem (i.e. if a predator randomly picks a flower and approaches it, accepting it if it is of the desired type and unoccupied and moving on otherwise, what is the expected number of approaches before she reaches her target?). *k* can also be considered a scaling parameter that converts the expected cost into the same units as the expected gain. In particular, *k* is the gain that would be required from a switch in order to offset the cost of moving the average distance between two randomly selected flowers.

Therefore, a single revealing flower-dwelling predator should move to an unoccupied concealing flower if

$$CS_{g,r\rightarrow c}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr+1c};F_{\mathscr{s}}\right];B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]\right]-CS_{cost,r\rightarrow c}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]>0$$

and a concealing flower-dwelling predator should move to an unoccupied revealing flower if

$$CS_{g,c\rightarrow r}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr-1c};F_{\mathscr{s}}\right];B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]\right]-CS_{cost,c\rightarrow r}\left[CS_{\mathscr{s},curr}\,;F_{\mathscr{s}}\right]>0$$

To determine the evolutionarily stable distribution of predators, $CS_{\mathscr{s},ESS}=\left\{CS_{c,ESS};CS_{r,ESS}\right\}$, I have developed an algorithm that starts with predators uniformly distributed across the two flower types (i.e. for a given relative number of concealing and revealing flowers, the proportion of predators that are on concealing, rather than revealing, flowers is the same, rounded to the nearest integer, as the proportion of flowers that are concealing, rather than revealing), and proceeds to determine how many predators should move from one flower type to the alternate type. The first step is to determine (as described above) whether either a revealing-to-concealing or a concealing-to-revealing move is favoured from a uniform predator distribution. If not, then $CS_{\mathscr{s},ESS}$ is the uniform predator distribution, but if so, then the algorithm changes $CS_{\mathscr{s},curr}$ in the appropriate way. This step is repeated until a distribution is found where no further predator movement is favoured, which is considered to be $CS_{\mathscr{s},ESS}$.

A few points should be noted about the implementation of this algorithm. From a starting point where predators are uniformly distributed across the two flower types, the concealing-to-revealing move was almost never favoured for the parameter values tested. This makes sense as concealing flowers are intrinsically better hunting sites for predators. Furthermore, once it is determined that a revealing-to-concealing move is favoured from the uniform starting point, it is not necessary for the algorithm to check whether the concealing-to-revealing move is favoured in subsequent steps. This is because an adaptive revealing-to-concealing move followed by an adaptive concealing to revealing move would imply that it is adaptive for a predator to leave a revealing flower, search for an unoccupied concealing flower, then immediately leave the concealing flower and search for an unoccupied revealing flower. Such a predator would pay the cost of two moves and would end with the same long term hunting success that she started with, which clearly cannot be adaptive. Finally, in section 1.4 it was noted that there are instances where there is no pollinator ESS. If this algorithm encounters a $CS_{\mathscr{s},curr}$ for which no pollinator ESS exists, it effectively skips over this distribution by testing the movement conditions with $CS_{\mathscr{s},curr+2c}$ rather than $CS_{\mathscr{s},curr+1c}$. This is equivalent to asking whether it is adaptive two predators to simultaneously move from one flower type to the other. The cost of the move, $CS_{cost,c\rightarrow r}\left[CS_{\mathscr{s},curr}; F_{\mathscr{s}}\right]$, for each of these two predators is calculated as the average of the cost incurred by the first to move and the cost incurred by the second to move. If there is no pollinator ESS for a case where two predators move, the algorithm asks whether it is adaptive for three predators to simultaneously move, or four predators and so on until a solution is found. In practice, a solution was usually found with only a few simultaneous moves (three or fewer in 87% of cases, five or fewer in 96% of cases), but in rare cases more simultaneous moves were required (observed maximum: ten).

Section 3: Flowers

The strategy of a flower population is defined by $F_{\mathscr{s},curr} = \{F_{c,curr}\,; F_{r,curr}\}$, which describes the number of flowers that are concealing or revealing, respectively. The expected fitness of a flower is assumed to be proportional to the number of pollinator visitations it receives. Therefore the fitness of the four categories of flowers can be described as

$$F_{W,s,c}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right] = PCA_c\left[\lambda_{c,ESS}\right]$$

for predator-free concealing flowers,

$$F_{W,s,r}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right] = PCA_r\left[\lambda_{r,ESS}\right]$$

for predator-free revealing flowers,

$$F_{W,d,c}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right] = PIA_c\left[\lambda_{c,ESS}\right]$$

for predator-containing concealing flowers, and

$$F_{W,d,r}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right] = PIA_r\left[\lambda_{r,ESS}\right]$$

for predator-containing revealing flowers. Here $B_{\mathscr{s},ESS}$ is described as a function of $CS_{\mathscr{s},ESS}$, which is described as the strategy of the current flower population, $F_{\mathscr{s},curr}$. This is done to emphasize the order of analysis in this algorithm. The ES flower strategy is determined based on the ES predator strategy for a range of flower strategies, the ES predator strategy is, in turn, determined by the ES pollinator strategy for a range of predator strategies. The ES strategy of any player is actually determined by the strategies adopted by all players, but showing the full range of functional dependence would be cumbersome.

Note that these fitness functions assume that predator-free and predator-containing flowers get the same fitness benefit from a pollinator visitation. It seems likely that predator-containing flowers should get less benefit from a pollinator visitation because these visits are relatively short and because the death of a pollinator precludes pollen export (note that this suggests that the effects on male and female fitness components may differ). It is not obvious, however, what the effect of the presence of a predator should be, as it will depend on the mechanics of pollen transfer in the system. In this model, allowing predator-containing flowers to get less fitness benefit from a visit reduces the predicted frequency of concealing flowers but does not change the qualitative pattern of results.

The fitness of a floral colour strategy is simply the mean of the fitness for predator-containing and predator-free individuals of that strategy, weighted by the relative frequency of predator-free and predator-containing individuals. Therefore, the expected fitness of a concealing flower is

$$\begin{aligned} & F_{W,c}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right] \\ & \quad = \left(\frac{F_{c,curr} - CS_{c,ESS}}{F_{c,curr}} F_{W,s,c}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right]\right) \\ & \quad + \left(\frac{CS_{c,ESS}}{F_{c,curr}} F_{W,d,c}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right]\right) \end{aligned}$$

and the expected fitness of a revealing flower is

$$\begin{aligned} & F_{W,r}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right] \\ & \quad = \left(\frac{F_{r,curr} - CS_{r,ESS}}{F_{r,curr}} F_{W,s,r}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right]\right) \\ & \quad + \left(\frac{CS_{r,ESS}}{F_{r,curr}} F_{W,d,r}\left[B_{\mathscr{s},ESS}\left[CS_{\mathscr{s},ESS}\left[F_{\mathscr{s},curr}\right]\right]\right]\right) \end{aligned}$$

The algorithm to determine the ES relative frequency of the two flower strategies, $F_{\mathscr{s},ESS} = \{F_{c,ESS}; F_{r,ESS}\}$, starts by considering a case with a small, but non-zero, proportion of concealing flowers, P_c and determines and records the fitness of the two floral colour strategies. It then increments P_c by some set value and repeats the process. This is repeated for the full range $0 < P_c < 1$ (actual range used, 0.01-0.99, with 11 evenly spaced values). There are four simple outcomes that could occur. If for all tested P_c values, $F_{W,c}[\ldots] > F_{W,r}[\ldots]$, then the concealing strategy is a pure ESS and we would expect the vast majority of flowers to be concealing. Conversely, if $F_{W,c}[\ldots] < F_{W,r}[\ldots]$ is always true, then the revealing strategy is a pure ESS. The last two simple outcomes involve the fitness of the concealing and revealing strategies intersecting at a single P_c value, $P_{c,intersect}$ (the algorithm does not actually identify the exact intersection point, it just estimates the location of $P_{c,intersect}$ as being half way between two of the P_c values that were actually tested). If $F_{W,c}[\dots] > F_{W,r}[\dots]$ when $P_c < P_{c,intersect}$, but $F_{W,c}[\dots] < F_{W,r}[\dots]$ when $P_c > P_{c,intersect}$, then there exists a single mixed ESS involving P_c proportion of concealing flowers. Conversely, if the concealing strategy has a fitness advantage over the revealing strategy when common, but is at a disadvantage when rare, then an unstable solution exists at $P_{c,intersect}$ and both pure strategies are ESSs (this outcome was never observed). More complex outcomes involving intersections at multiple P_c values are also possible. Such an outcome would suggest multiple solutions, some stable and some unstable, for a given set of parameter values. None of the results shown in Figure 2 involve this form of complex solution, but such solutions do occur for reasonable parameter values. It seems likely, however, that these complex solutions are artefacts of noise produced by the low resolution of the analysis (see section 5 of this appendix).

Section 4: Algorithm for analyzing predator-pollinator-flower game

To analyze this model, I produced an algorithm that systematically searched the three-player strategy space for an ESS for any given set of parameter values. The elements of this algorithm have been discussed above but are consolidated in this section. The steps involved in this algorithm are described below (the relevant section of this appendix are given in parentheses).

1) Assume a population of flowers with some small proportion of concealing flowers and large proportion of revealing flowers (3).
2) Assume predators are uniformly distributed across concealing and revealing flowers so that the proportion of concealing flowers that contain a predator is the same as the proportion of revealing flowers that contain a predator (2).
3) Determine the pollinators' evolutionarily stable placement of the criteria for this relative frequency of concealing flowers with this distribution of predators (1.4).
4) Determine the cost that a predator would incur switching from a concealing to a revealing flower or from a revealing to a concealing flower (2).

5) Determine the pollinators' evolutionarily stable placement of the criteria if one predator switched to a revealing flower or to a concealing flower and determine how much the long term hunting success would increase for the switching predator (1.4, 2).
6) By comparing the outcomes of step 4 (cost of switching) and 5 (expected gains from switching), determine whether it would be adaptive for a predator to make a concealing-revealing or revealing-concealing shift. If so, assume that one predator makes the adaptive shift (2).
7) Repeat steps 3-6 with the modified predator distribution. Repeat until it is not adaptive for any predator to shift to the alternate flower type. This distribution of predators, and the criteria adopted by the pollinators for this distribution represents the evolutionarily stable outcome of the predator-prey portion of the game for this proportion of concealing flowers (2).
8) Record the fitness to the concealing and revealing floral strategies (3).
9) Increment the proportion of concealing flowers and repeat steps 2-9 until there is a large proportion of concealing flowers and small proportion of revealing flowers (3).
10) Determine the evolutionarily stable proportion of concealing flowers (3).
11) Determine the evolutionarily stable distribution of predators and evolutionarily stable placement of the pollinators' criteria for that proportion of concealing flowers (1.4, 2).

Section 5: Resolution of analyses and precision of results

The algorithm used to analyze this model can be thought of as a systematic search of a four-dimensional strategy space (one dimension for each player's strategy with an extra dimension for pollinators as their strategy involves two independent criteria) for a set of strategies that is evolutionarily stable for all players. Each of these dimensions needs to involve a finite number of discrete points, which introduces issues of resolution and precision of results.

Section 1.4 discussed some of the issues related to the resolution of the pollinator strategy space. Note that because the pollinator strategy space is two-dimensional, and because the same boundaries and resolution are used for both dimensions, increasing the resolution or expanding the boundaries of this space exponentially increases the number of criterion pairs that have to be considered.

The resolution of the predator dimension of the four-dimensional strategy space is defined by the number of predators considered. Theoretically, the results of the model should not be affected by changes to the size of the predator population, as long as the pollinator and flower population size are also changed to keep the predator/pollinator and predator/flower population size ratios constant. In practice, increasing the population sizes (i.e. increasing resolution) should increase the precision of the analysis. This is because the algorithm only considers the movement of whole predators, and because the behaviour of pollinators is largely defined by the proportion of concealing or revealing flowers that contain a predator. There might be a case where there is a proportion of predator containing flowers of a given type that is the actual predator ESS, but where no distribution of predator achieves this exact proportion. Increasing population sizes will reduce the amount to which the predicted distributions over or undershoots the actual ES proportion. However, increasing population size also increases computation time as the algorithm has to consider the move of more predators before it approaches the ES distribution of predators. Note that the over/undershoot problem is especially pronounced when the proportion of flowers that is concealing is high or low as the movement of a single predator has a large effect on the proportion of the rarer flower type that contains a predator which in turn can have a large effect on the criterion adopted by pollinators on this flower type.

The resolution of the flower dimension of the four-dimensional strategy space is determined by the number of P_c values between 0 and 1 the algorithm considers. A mixed ES flower strategy is estimated as the midpoint between two tested P_c values. Therefore, the estimate of the ES flower strategy is more precise if more values are tested.

The fact that the precision of the results are not perfect can introduce noise and artefacts into the results. The resolution I have chosen for each dimension is based on a tradeoff between precision and computation time. Preliminary testing suggested that increasing the resolution in any single dimension does little to improve the precision of the analysis, and that significant gains would only come from increasing the resolution of all dimensions. This would have dramatic effects on computation time.

Tables

Table A1: Summary of the parameters used in the model

Name	Description	Base/tested values [a]
$\mu_{d,c}$	Mean of the dangerous concealing distribution	0
$\mu_{d,r}$	Mean of the dangerous revealing distribution	0
$\mu_{s,c}$	Mean of the safe concealing distribution	0.8
$\mu_{s,r}$	Mean of the safe revealing distribution	1.8
B	Number of pollinators	250
CS	Number of predators	10, 30, 50, 70, 90
F	Number of flowers	500
e	Predator effectiveness (probability that a pollinator will be killed if she lands on a dangerous flower)	0.0005, 0.0016, 0.005, 0.016, 0.05
k	Cost incurred per unit distance moved by a predator	0, 0.05, 0.1, 0.15, 0.2
n_{max}	Maximum volume of nectar a flower can hold	1
t_{exp}	Pollinator maximum expected lifespan (expected time till death of a pollinator if she is not killed by the predator considered in this model)	10000, 30000, 50000, 70000, 90000 [b]
$t_{h,d}$	Pollinator handling time on dangerous flowers	2
$t_{h,s}$	Pollinator handling time on safe flowers	10
t_{ifi}	Amount of time it takes a pollinator to fly between flowers	5
$t_n\ (t)$	Length of time it takes a fully depleted flower to completely replenish its nectar stores	1000

[a] Base values are given for all parameters. For parameters where a range of values were tested, as described in the results section of the text, these tested values are shown (In these cases, the base value is third value of the five values listed).

[b] These are in the same units as all other time parameters in this model. While the time unit is not specified by the model, these values are converted into hours on the x axis of Figure 3.C. See the Figure 3 caption for more details.

Table A2: Summary of the strategy variables used in the model

Name	Description	Strategy set [a]
B_s	Strategy adopted by a pollinator focal (foc), mutant (mut), or population of (pop) predators	
λ_c	Pollinator criterion adopted on concealing flowers	-5 to +5 in steps of 0.1
λ_r	Pollinator criterion adopted on revealing flowers	-5 to +5 in steps of 0.1
CS_s	Distribution of strategies adopted by the predator population	
CS_c	Number of predators on concealing flowers	0 to *CS* in steps of 1
CS_r	Number of predators on revealing flowers	0 to *CS* in steps of 1
F_s	Distribution of strategies adopted by the flower population	
F_c	Number of concealing flowers	
F_r	Number of revealing flowers	
P_c	Proportion of flowers that are concealing	0.01-0.99 in steps of 0.098

[a] Strategy sets describe the range of values that the given strategy variable was allowed to adopt.

Figures

Figure 1: A graphical description of the model.

Rows A, B, and C represent three different distributions of predators between concealing and revealing flowers, with A being a uniform distribution, B being a moderate predator bias towards concealing flowers and C being a large bias. Large grey circles in i panels represent concealing flowers and large white circles in ii panels represent revealing flowers. Small black circles on the flowers in i and ii panels represent predators. The overlapping distributions describe the psychophysics of predator detection by pollinators assessing concealing (i panels) or revealing (ii panels) flowers. The solid vertical line overlaying the overlapping distributions represents an example of the pollinators' evolutionarily stable criterion for a given distribution of predators. iii panels describe the fitness of the two floral colour strategies for a given predator distribution. +P represents flowers that contain a predator and –P represents predator-free flowers. The heights of the +P and –P bars represent the probability that a pollinator accepts a given concealing or revealing flower, which is a proxy for floral fitness. The height of the shaded sections of +P and –P bars describes the relevant acceptance probabilities multiplied by the probability that a random flower adopting that colour strategy does or does not contain a predator, respectively. The height of the E bar describes the floral colour strategies' expected fitness and is the average of the shaded sections of the +P and –P bars (i.e. the average probability that a pollinator accepts a randomly selected concealing or revealing flower). See text for further details.

Chapter 5: Figure 1

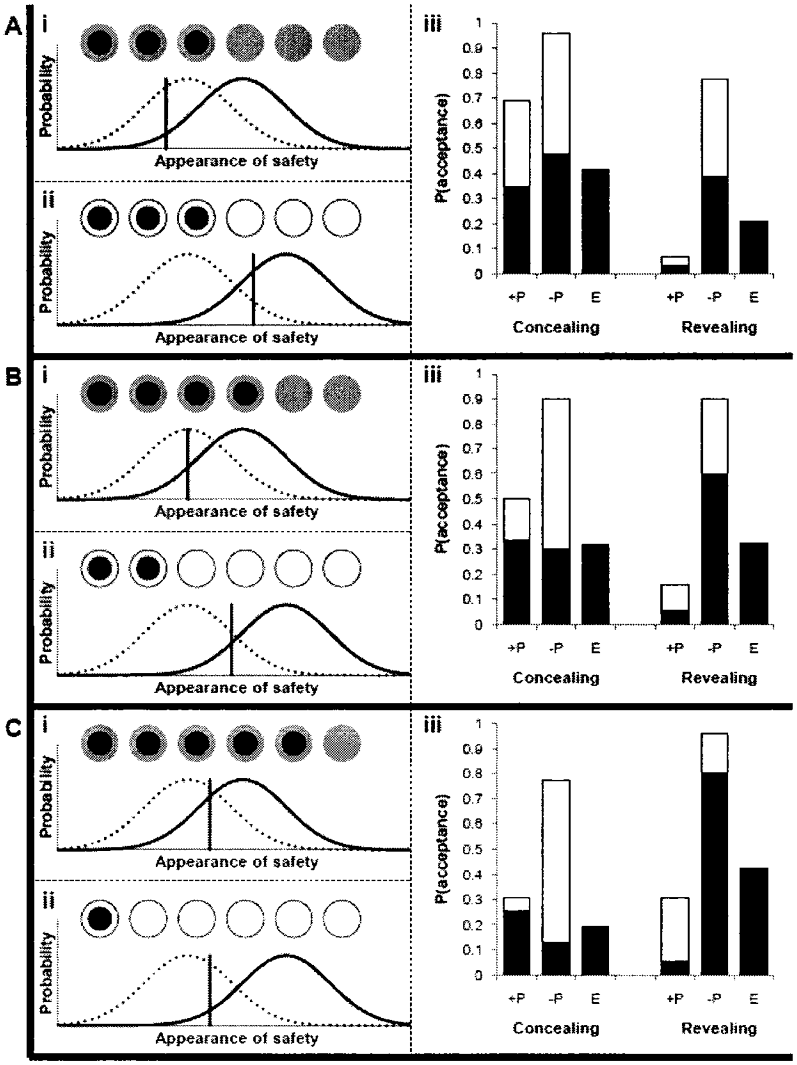


Figure 2: Effect of predator movement costs.

The effect of predator movement costs on the ESS of flowers, predators and pollinators. In all panels, the x-axis shows the range of parameter values tested, with the central point being the base value, and the y-axis shows a measure of the ESS for that player. Row i shows the predicted evolutionarily stable proportion of flowers adopting the concealing strategy. Row ii shows the evolutionarily stable proportion of predators that are on concealing flowers for the case where there are an equal number of concealing and revealing flowers. Row iii shows the evolutionarily stable probability that a pollinator will accept (acceptance probability is directly related to the placement of the criterion) a concealing predator-free (○), concealing predator-containing (●), revealing predator-free (□), or revealing predator-containing (■) flower, also for the case where there is an equal number of concealing and revealing flowers. The predator and pollinator results in rows ii and iii are given for the case where there is an equal number of concealing and revealing flowers, rather than the evolutionarily stable mix of concealing and revealing flowers shown in row i, in order to simplify interpretation of the results.

Chapter 5: Figure 2

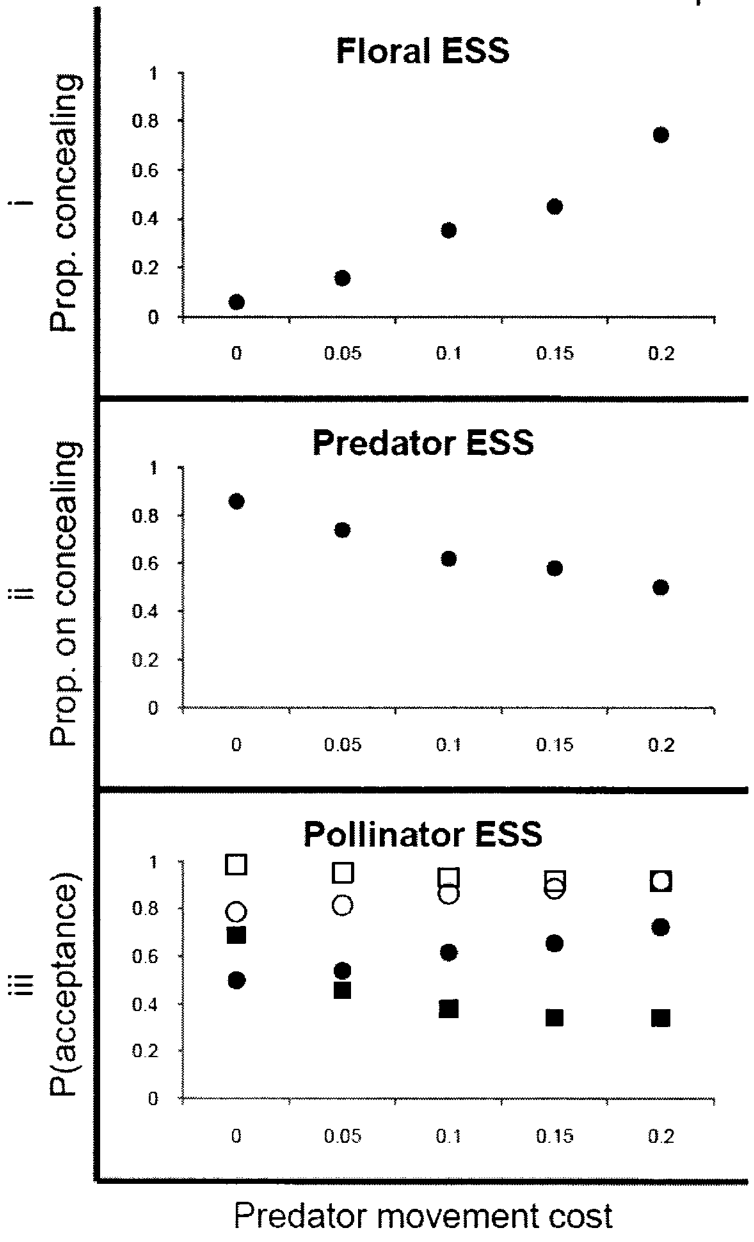
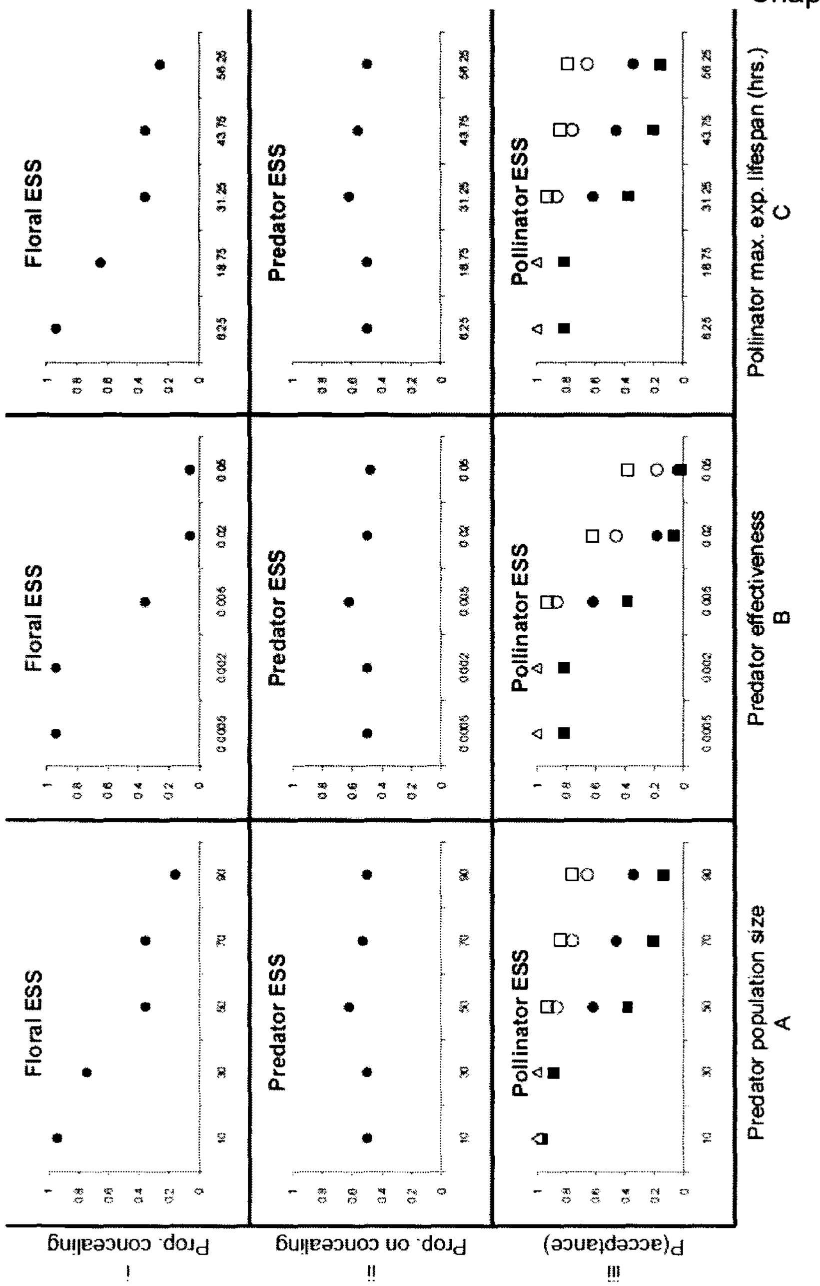


Figure 3: Effects of predator population size, predator effectiveness, and pollinator lifespan.

The effect of predator population size (column A), predator effectiveness (column B), and the maximum expected lifespan of pollinators, in hours, (column C) on the ESS of flowers (row i), predators (row ii) and pollinators (row iii). See Figure 2 caption for further general details. In the pollinator ESS graphs (row iii), several of the concealing predator-free (○), concealing predator-containing (●), and revealing predator-free (□) values overlap (maximum difference between overlapping points: 0.003). For clarity, these overlapping symbols have been replaced with Δ (i.e. Δ=○+●+□). Note that the maximum expected lifespan of foragers is the expected lifespan excluding mortality inflicted by the models focal predator. Furthermore, it is measured in terms of foraging time, not raw survival time. All time variables in this model are assumed to be measured in the same units, but the unit is not specified (see Appendix A and Table A1 therein). For simplicity, the maximum expected lifespan in hours shown in column C are calculated by assuming the amount of time it takes a pollinator to fly between flowers is 11.25 seconds.

Chapter 5: Figure 3



Chapter 6: Discussion

This thesis has explored two related questions. First, how do/might pollinators detect and respond to the presence of flower-dwelling ambush predators ("do": Chapters 2 and 3; "might": Chapters 4 and 5)? Secondly, given that the presence of predators affects the foraging behaviour of pollinators, how might pollinator, predator, and floral traits co-evolve (Chapter 5)? I believe that this thesis is a significant step towards answering both of these questions, though as is expected for such a complex system, much work remains to be done. In this chapter, I discuss these contributions and future research prospects for each of the content chapters individually. I then discuss issues, insights, and research prospects that only become apparent when these content chapters are compared and contrasted with each other.

Contributions and prospects

Chapter 2

This chapter reinforced the idea that evidence of past predation events can act as a cue of the presence of cryptic predators and went some way towards discounting the alternate hypothesis that the avoidance of dead conspecifics is simply an avoidance of competition risk. This chapter, along with other studies with consistent findings (Dukas 2001a; Reader et al. 2006), suggests that the basic effect (bees avoid flowers that contain dead bees) is very robust. Of particular note is evidence that both the release of specific chemicals (necromones) by corpses and the avoidance of these chemicals by live individuals is phylogenetically ancient (Yao et al. 2009). In particular, the production and avoidance of specific necromones (oleic and linoleic acids) likely predates the divergence of crustaceans and insects (or less plausibly, there has been convergent evolution). The existence of necromones supports the interpretation of Chapter 2, experiment 2 that scent is a major component of the avoided cue. The phylogenetic conservation of these necromones implies that the observed avoidance behaviour probably did not evolve within the pollination context, and that it did not necessarily evolve solely in response to challenge posed by cryptic ambush predators (note that the authors propose that disease avoidance, along with predator avoidance, could be a reason why the avoidance of necromones is adaptive). Nonetheless, this ancient avoidance behaviour likely remains adaptive in pollination systems that contain flower-dwelling ambush predators. Furthermore, it is possible that this trait has been evolutionarily modified to make it more adaptive within the pollination context. For example, it is plausible that the aversive nature of necromones interacts with the attractive nature of cues of floral quality. Similarly, the aversive nature of necromones should interact with the temporal persistence of these scents in different pollination systems (possibly a function of the permeability of the focal petals or leaves) and the frequency at which predators move to a new location (likely a function of the predators' movement costs and the lifespan of a single flower or umbel). Note that the existence of alarm pheromones (Balderrama et al. 1996) in some pollinator species highlights the fact that necromones may not be the only olfactory component of the avoided stimuli, and that the avoidance behaviour observed in this chapter could well be partially explained by adaptations that arose within a pollination context.

Chapter 3

This chapter proposed and demonstrated a novel way in which some pollinator species might reduce their exposure to cryptic flower-dwelling ambush predators. In particular, this experiment demonstrated that in a species that actively recruits hivemates to high quality foraging sites, the presence of a cue of predation risk (the same cue used in Chapter 2) results in reduced levels of recruitment. Note that, as discussed in Chapter 3, a similar mechanism may be involved in the avoidance of predators in a non-pollination system (Nonacs 1990), the avoidance of intraspecific aggression (Franks et al. 2007), and the avoidance of poisonous foods (Galef 1985). Social learning about predation risk (and other types of risk) is usually assumed to take the form reviewed by Griffin (2004) where a naïve individual associates a cue that another individual has encountered a predator (e.g. a fear display) with a cue that indicates where this encounter took place (e.g. a food scent), and subsequently avoids the latter cue. What this chapter demonstrates is not this classic form of social learning about predation risk which is why the terms implicit social learning, or modulation of social learning are more appropriate. Nonetheless, it is plausible that this classic form of social learning about predation risk also occurs as a single experienced forager could display both of the required cues. In particular, a forager can display both cues that she has encountered evidence of predation risk (alarm pheromones) and cues that indicate where this encounter took place (floral scents). In honeybees, this classic form of social learning could occur in two ways. Honeybee colonies contain receiver bees that interact with returning foragers and collect their nectar. Receiver bees are known to preferentially unload nectar containing preferred floral scents (Gruter and Farina 2009). This means that foragers with these preferentially scented nectars are unloaded by more receivers, which makes these foragers more likely to dance and recruit hivemates to the foraging site (Gruter and Farina 2009; Seeley 1996). Therefore, receiver bees could associate alarm cues on returning foragers with a floral odour and refuse to unload nectar that contains this floral odour. This would discourage dancing by the focal foragers and reduce recruitment to dangerous sites. Alternatively, potential recruits could be the individuals that associate the two cues. These individuals could refuse to utilise the information provided in the dance of a bee that exhibit alarm cues, and further refuse to attend to any future experienced forager that is carrying the floral odours associated with the dangerous site. Note that the first possibility involves social learning by receiver bees, the second involves social learning by potential recruits, and the two possibilities are not mutually exclusive. In my opinion, exploring this possibility of a classic form of social learning would be the most interesting future line of research resulting from Chapter 3.

Chapter 4

Chapter 4 is, as far as I know, the first model to simultaneously consider the effects of age, population age structure, and intraspecific competition on the distribution of foragers with respect to predation risk. In particular, Chapter 4 introduces several novel factors that might affect the habitat selection strategies of animals. While Chapter 4 primarily addresses the minor emphasis of this thesis (exploring how pollinators might respond to the presence of flower-dwelling ambush predators), it has the potential to help address the major emphasis (exploring the three-way co-evolution of predator, pollinator, and floral traits). In particular, this model could be expanded to explore predator-pollinator-flower co-evolution in two ways. First, the current model could be used to estimate the expected visitation rate at predator-containing and predator-free flowers over the course of a season. From this, it might be possible to make predictions about how the intensity of the indirect negative fitness effect of predators (i.e. the amount to which the visitation rate at predator-containing flowers is less than at predator-free flowers) changes over the season for various sets of parameter values. More intense indirect negative fitness effects should result in more intense selection pressure on floral traits. Therefore, this model might provide some insights as to the seasonal nature of floral adaptations that are related to the presence of flower-dwelling ambush predators. Second, this chapter describes an optimality model for pollinator behaviour. This is, in effect, one third of a potential game theory model that could describe the co-evolution of predator, pollinator and floral traits. Such a modeling effort would require a description of the predator and floral traits that co-evolve with the pollinators' willingness to land on predator-containing flowers. As the optimal pollinator willingness to land on a predator-containing flower is partially determined by the expected amount of nectar on that flower, an obvious floral trait to consider is nectar production rate. If flowers differ in nectar production rate, then the predator strategy could be defined in terms of a distribution between flowers with high and low nectar production rates. From the flowers' perspective, the tradeoff is similar to the one described in Chapter 5. A flower that has a high nectar production rate may get a high pollinator visitation rate, even if a predator is present. However, such a flower might also attract predators. Such a model would be challenging to produce, but could provide some interesting insights on how nectar production rate evolves in response to the presence of predators and the age structure of pollinator populations.

Chapter 5

While this chapter emphasized the generality of the hider-seeker-background model, it is also a significant advancement within the confines of the predator-prey/pollinator-flower system as it is the first model to consider how floral traits should evolve in the presence of a flower-dwelling ambush predator species. Much of the future work, of a theoretical nature, that derives from this chapter should involve considering how other species and factors affect the evolutionarily stable outcomes predicted by the model (this is discussed at length in the discussion of Chapter 5). However, what would be more useful are follow up studies of an empirical nature. Both comparative and laboratory studies should prove to be useful for understanding how floral colour co-evolves with predator and pollinator behavioural strategies. The comparative studies could test the predictions of the model by comparing the observed colour contrast between predators and flowers in a set of pollination systems that differ in some key parameter (e.g. predator travel costs or predator population density). For tractability, initial laboratory studies should probably focus on only one of the three players. As discussed in the introduction, understanding, and correctly modeling, the foraging behaviour of the pollinators is extremely important as the pollinator acts as a linchpin in the three species co-evolutionary dynamic. Fortunately, the laboratory setup of Ings and Chittka (2008; 2009) provides a convenient way to study the pollinators foraging strategy in the presence of cryptic predators. Ings and Chittka's setup involves a field of artificial flowers (any colour could be used so that concealing and revealing flowers are possible) that may or may not contain a model predator. When a bumblebee lands on a flower that contains a model predator, it is trapped by foam pincers, which simulates a failed predation attempt. This basic setup could be used to "artificially evolve" (Sherratt and Beatty 2003) the floral and predator strategies in response to observed pollinator behaviour (Note that to have intraspecific competition affect the pollinators' behaviour in a natural way, the nectar replenishment mechanism of these artificial flowers would have to be modified to something like that used by Ohashi et al. (2008)).

Content chapters: comparisons and contrasts

Contrasting predator avoidance mechanisms in Chapters 2, 3, and 5

Chapter 2 and 3 describe predator avoidance strategies that are very different from that modelled in Chapter 5. This raises the possibility that the actual anti-predator adaptations observed in the former two chapters might interfere with the co-evolutionary dynamic modelled in the latter chapter. In particular, for there to be concealing and revealing flowers, there must be floral traits that affect the detectability of predators. The existence of indirect anti-predator pollinator adaptations might, in effect, make the flower powerless to affect predator detectability. This concern might actually be valid for the social modulation of predation risk shown in Chapter 3. Even if a predator is perfectly camouflaged (i.e. the flower is perfectly concealing), pollinators that survive failed attacks by the predator can still reduce the long term visitation rate at predator containing flowers by reducing recruitment effort. This suggests that the idea of a concealing or revealing strategy may be less meaningful. However, this social modulation has only been shown in one pollinator species (*Apis mellifera*), and is only possible in species where the location of quality patches is actively communicated (honeybees are the best known, but not the only, example of a bee species with recruitment behaviours (Dornhaus and Chittka 1999; Nieh 1998)). At first, Chapter 2 might seem to pose a similar problem. Concealing and revealing floral colourations may mean little if pollinators focus primarily of the presence or absence of dead conspecifics. Furthermore, flowers would appear to be limited in their ability to conceal the presence of these corpses. Nonetheless, the previous discussion of the temporal persistence of cue of past predation events (Chapter 2, and this chapters Contributions and research prospects section for Chapter 2) poses one possible resolution. Flowers could differ in the length of time that a cue of past predation events persists. For example, if this cue is olfactory as suggested by Chapter 2 and Yao et al. (2009), then flowers that differ in permeability to scent might differ in cue persistence. If pollinators and predators can discriminate between flowers with greater or lesser scent persistence times, the problem becomes very similar to the one discussed in Chapter 5 (i.e. long persistence flowers are comparable to revealing flowers, short persistence flowers are comparable to concealing flowers). If, however, pollinators and predators cannot discriminate between long and short persistence flowers, then it seems likely that short persistence will be favoured. This is because short persistence flowers will avoid a significant reduction in visitation rates after a predation event without being generally attractive to predators or repulsive to pollinators. There could also be other floral traits (i.e. other than permeability) that affects the persistence of cues of past predation events. For example, the structure of a flowering plant could make it more or less likely that a corpse will fall to the ground after the predator is done feeding.

Contrasting assumptions in Chapters 4 and 5

As is typical for models, Chapters 4 and 5 make many simplifying assumptions. It is interesting to note one way that these chapters made contrasting assumptions, which emphasised different aspects of the problem. On the one hand, Chapter 4 assumes that pollinators can perfectly discriminate between predator-containing and predator-free flowers, but that some pollinators still land on predator-containing flowers because predators do not always interrupt foraging (i.e. pollinators have some expectation of reward from these flowers). On the other hand, Chapter 5 assumes that predators always interrupt foraging (i.e. landing on such a flower has no benefits) but some pollinators still land on predator-containing flowers because predator-containing and predator-free flowers are not perfectly discriminable. The contrast in these assumptions highlights the existence of two distinct, but interacting, tradeoffs faced by pollinators. Chapter 4 focused on the fact that pollinators often face a tradeoff between competition intensity and predation risk. Therefore, this chapter allowed predator-containing flowers to be an exploitable resource and minimised the complicating effect of predator crypsis. Chapter 5 focused on the fact that pollinators often face a tradeoff between correct acceptance (landing on predator-free flowers) and incorrect acceptance (landing on predator-containing flowers) rates. Therefore, this chapter assumed that there was no reward to be had on predator-containing flowers in order to create a well defined incorrect acceptance event (note that empirical signal detection studies would also be complicated if the supposed incorrect-acceptance event was occasionally beneficial or "correct"). The two extremes described by these two assumptions might exist is some systems. The Chapter 4 assumption is consistent with a large umbel (e.g. milkweed, where a resident predator is incapable of monopolising the entire surface area) and a poorly disguised predator (or some clear cue of predator presence as in Chapter 2). The Chapter 5 assumption is consistent with a case where there is a reasonably well hidden predator on a small umbel or flower (e.g. wild rose). However, it is likely that most systems fall somewhere between these two extremes. In particular, predator-containing and predator-free flowers will generally not be perfectly discriminable, and predators will not always interrupt foraging. This means that there is a possibility that the competition intensity/predation risk and correct acceptance/incorrect acceptance tradeoffs could interact within a given system. Further work is needed to understand the effect of such an interaction on pollinator foraging behaviour.

Conclusions

This thesis can be considered as a step towards understanding the evolutionary effects flower-dwelling ambush predators have on pollination systems. This is not the first step as many of the individual components of this system are already well understood. For example, the foraging behaviour of a flower-dwelling ambush predator, the crab spider *Misumena vatia*, has been particularly well studied (Morse 2007). Similarly, the way that pollinators respond to the presence of cues of predation risk on flowers has been studied (Reviewed extensively in previous chapters). And finally, the possibility that predators have an indirect negative fitness effect on flowering plants has been empirically explored (Dukas and Morse 2005; Knight et al. 2006; Muñoz and Arroyo 2004; Suttle 2003; Wilkinson et al. 1991). However, I believe that this thesis, particularly Chapter 5, provides a framework for a future body of research that studies the predator-prey/pollinator-flower system in a more holistic way. Above, I have emphasised future lines of study that derive from the content chapters of this thesis. However, I would like to end by emphasising that the major gap in our current knowledge of predator-prey/pollinator-flower systems has to do with the nature of floral adaptations that arise in response to the presence of flower-dwelling ambush predators. I suspect that the most profitable and interesting future work in this system will involve examining how various floral traits affect the intensity of the indirect negative fitness effect that predators have on plants. Such studies should begin to demonstrate what floral adaptations might exist, and what the nature of the three species co-evolutionary dynamics might be, in this system.

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