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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.

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1. 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

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seeker species; for example predator–prey/herbivore–plant systems and predator–prey/pollinator–flower systems.

1.1. 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).

1.2. 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, 2005b; 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.

2. 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.

2.1. 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.1).

Consider a population of flowers (represented by large white or grey circles in Fig. 1), some of which contain a single predator

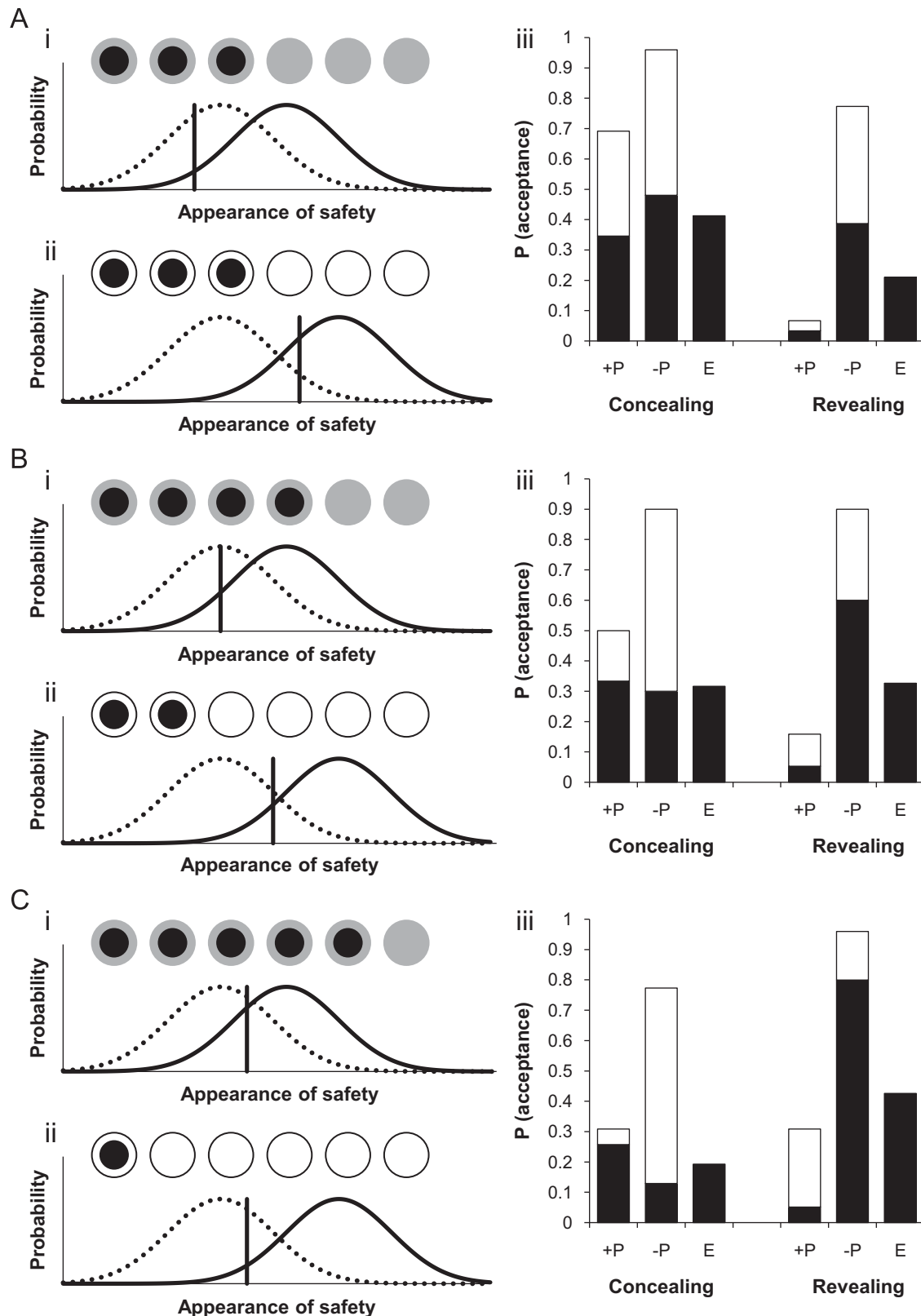


Fig. 1. A graphical description of the model. Rows A–C represent three different distributions of predators between concealing and revealing flowers, with A being a uniform distribution, B being a moderate predator bias towards concealing flowers and C being a large bias. Large grey circles in (i) panels 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.

(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 Fig. 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 Fig. 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 Fig. 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 Fig. 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.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 Fig. 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 (Fig. 1, (i) panels) than for revealing flowers (Fig. 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 Figs. 1A(i) and (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.1.2 and A.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.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.

2.2. 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 Figs. 1A–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.2.

Figs. 1A(i) and (ii) show a situation where predators are uniformly distributed between concealing and revealing flowers. As noted above, the criteria indicated in Figs. 1A(i) and (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 Fig. 1A(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 Fig. 1A(ii) can be used as a proxy of the fitness of predators hunting from revealing flowers. A comparison of Figs. 1A(i) and (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 (Fig. 1B(i)). Conversely, pollinators may become more liberal (i.e. shift their criterion to the left) on revealing flowers (Fig. 1B(ii)). Relative to Fig. 1A 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 Fig. 1B(i) than in 1B(ii), the magnitude of this difference is less than in Fig. 1A). 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 Figs. 1B(i) and (ii) with 1C(i) and (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 Figs. 1C(i) and in 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 Figs. 1A–C can be thought of as three possible evolutionarily stable outcomes of this hypothetical predator–prey game. Fig. 1A 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), Fig. 1B is the outcome expected if this cost is intermediate in magnitude, and Fig. 1C is the outcome expected if this cost is very low.

2.3. 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.3).

Panels (iii) of Figs. 1A–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 Fig. 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 Fig. 1 demonstrate this approximation for each of the three (Figs. 1A–C) hypothetical outcomes of the predator–prey portion of the game (see figure caption for details). In the outcome described by Fig. 1A, the concealing strategy has greater fitness than the revealing strategy and should become more common in subsequent generations. In Fig. 1B, the fitness of the two floral colour strategies are essentially equal. In Fig. 1C 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 (Fig. 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.3 and A.4 for more details).

3. 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.

3.1. Predator travel costs

3.1.1. 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 Fig. 1 demonstrates why this was the case. Fig. 1C gives an example of the equilibrium reached for the predator–prey portion 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 Figs. 1C(i) and (ii)). In this example, revealing flowers have greater fitness than concealing flowers (Fig. 1C(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 Figs. 1A and B, and

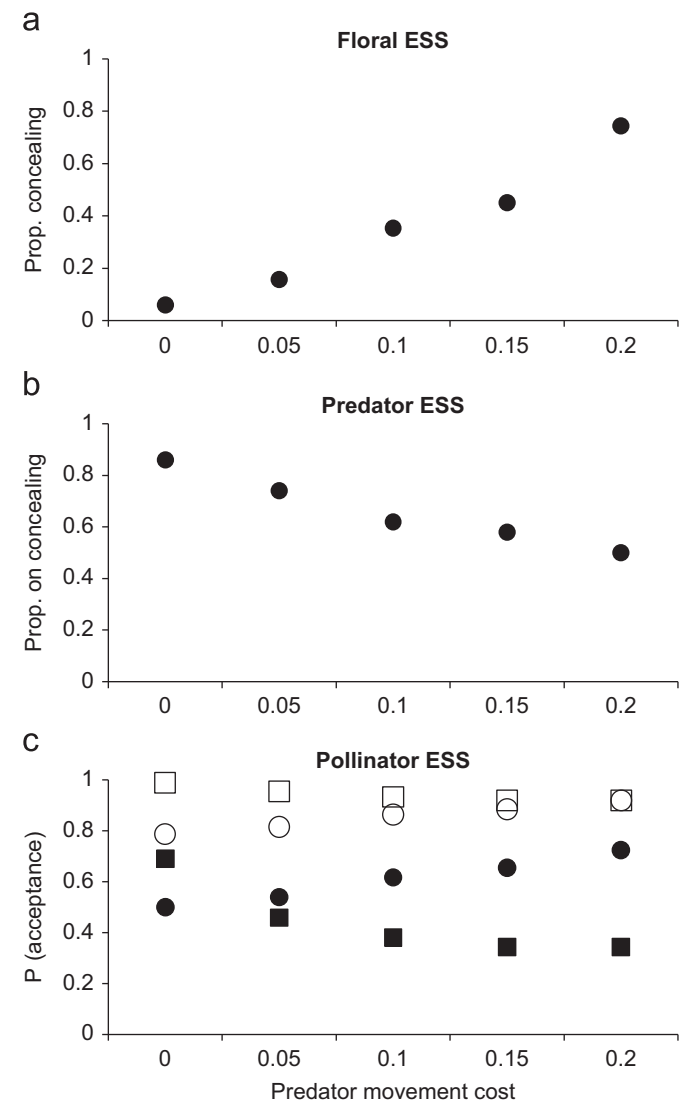


Fig. 2. Effect of predator movement costs. The effect of predator movement costs on the ESS of flowers, predators and pollinators. In all panels, the x-axis shows the range of parameter values tested, with the central point being the base value, and the y-axis shows a measure of the ESS for that player. 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.

Fig. 1A(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).

3.1.2. Result

Fig. 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. Fig. 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. Fig. 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.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 Fig. 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 Fig. 2(i).

It is worth examining Fig. 2(iii) (also Figs. 3A(iii), B(iii), and C(iii)) as it shows the differential fitness trade-offs 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 trade-off can be stated thus: revealing flowers will do very well if not burdened with the presence of a predator but will suffer a

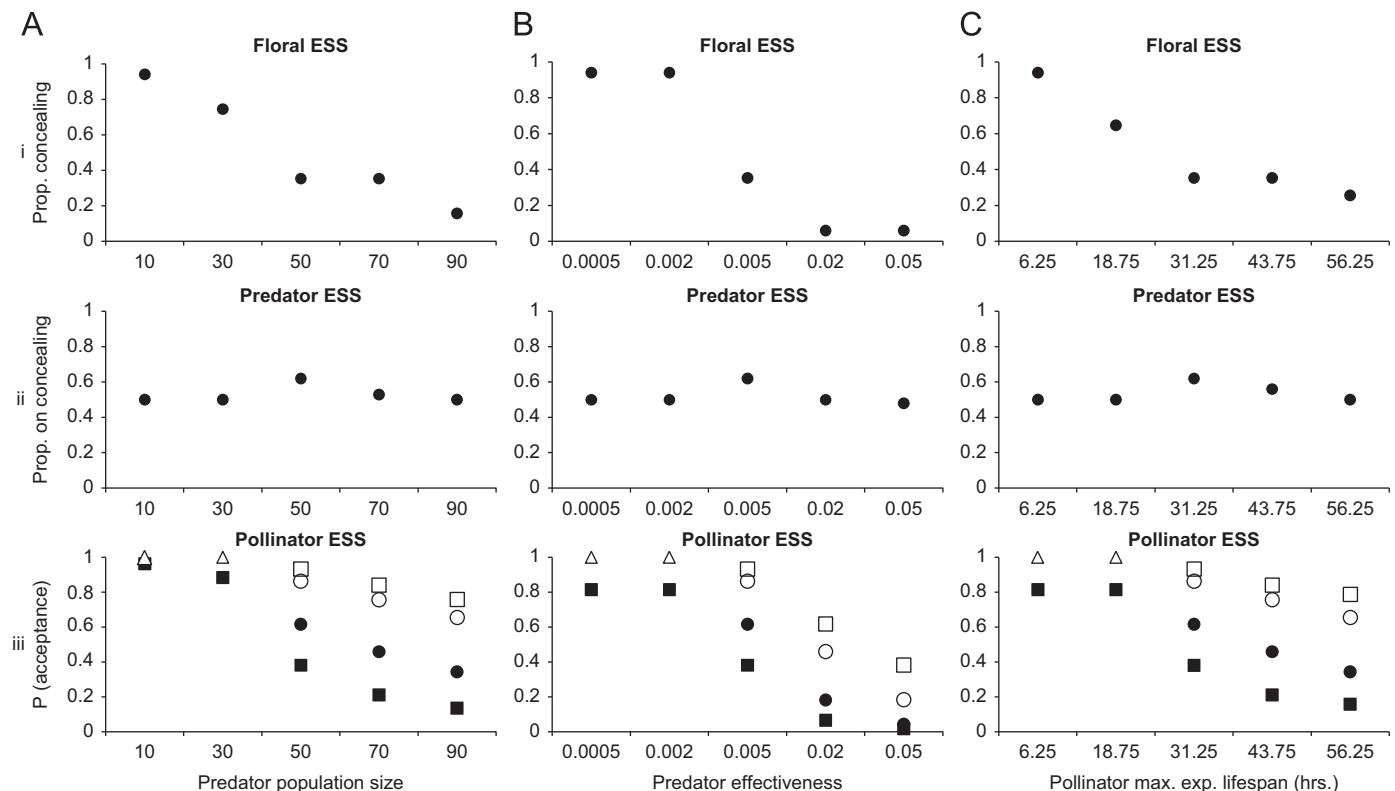


Fig. 3. Effects of predator population size, predator effectiveness, and pollinator lifespan. The effect of predator population size (column A), predator effectiveness (column B), and the maximum expected lifespan of pollinators, in hours, (column C) on the ESS of flowers (row i), predators (row ii) and pollinators (row iii). See Fig. 2 caption for further general details. In the pollinator ESS graphs (row iii), several of the concealing predator-free (\circ), concealing predator-containing (\bullet), and revealing predator-free (\square) values overlap (maximum difference between overlapping points: 0.003). For clarity, these overlapping symbols have been replaced with Δ (i.e. $\Delta = \circ + \bullet + \square$). 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 s.

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 trade-off (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).

3.2. Predator population size

3.2.1. 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.

3.2.2. Result

Fig. 3A(i) shows that, as expected, the evolutionarily stable proportion of concealing flowers is negatively related to the predator population size. Fig. 3A(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. Fig. 3A(ii) suggests that predator population size should have no direct effect on the distribution of predators.

3.3. Predator effectiveness

3.3.1. 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 modelled 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.

3.3.2. Result

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

3.4. Pollinator maximum expected lifespan

3.4.1. 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.

3.4.2. Result

Fig. 3C(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

Fig. 3C(iii) with Figs. 3A(iii) and 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.

4. 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 over-exploitation.

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.

4.1. 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 modelling 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 equilibria 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 specialize on revealing flowers and the risk prone species specialize 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 hide–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.

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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 Tables 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)...

$$B_s = \{\lambda_c; \lambda_r\}$$

$$CS_s = \{CS_c; CS_r\}$$

$$F_s = \{F_c; F_r\}$$

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).

A.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.

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)	10 000, 30 000, 50 000, 70 000, 90 000 ^b
$t_{h,d}$	Pollinator handling time on dangerous flowers	2
$t_{h,s}$	Pollinator handling time on safe flowers	10
t_{fi}	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 Fig. 3C. See the Fig. 3 caption for more details.

Table A2

Summary of the strategy variables used in the model.

Name	Description	Strategy set ^a
B_o	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_o	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_o	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.

A.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.

A.1.2. Flower visitation functions

To determine the fitness of a forager adopting a particular strategy (see Section A.1.3), it is necessary to determine the rate at which the four possible acceptance events (see Section A.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, $B_{\phi foc} = \{\lambda_{c,foc}; \lambda_{r,foc}\}$, as well as the relative frequency of the four flower categories.

The first step is to determine how many flowers a focal pollinator adopting $B_{\phi foc}$ 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 a focal pollinator to approach an arbitrary number of flowers, B_a .

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

In this equation, the first term describes the total amount of time the pollinator has to fly in order to approach B_a flowers ($B_a \times$ the time it takes a pollinator to fly between two flowers, t_{ifl}). The subsequent four terms describe the amount of time spent on each of the four flower categories (number of flowers the pollinator approaches \times probability that the approached flower is of a given category \times probability that a pollinator adopting $B_{\phi foc}$ lands on a flower of that category \times 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...

$$B_a[B_{\phi foc}; CS_{\phi}; F_{\phi}] = F \cdot t_n [F \cdot t_{ifl} + (F_c - CS_c) PCA_c[\lambda_{c,foc}]t_{h,s} \\ + (F_r - CS_r) PCA_r[\lambda_{r,foc}]t_{h,s} + CS_c \cdot PIA_c[\lambda_{c,foc}]t_{h,d} \\ + CS_r \cdot PIA_r[\lambda_{r,foc}]t_{h,d}]^{-1}$$

Note that here I define B_a as a function of the strategies of the focal pollinator $B_{\phi foc} = \{\lambda_{c,foc}; \lambda_{r,foc}\}$, the predators $CS_{\phi} = \{CS_c; CS_r\}$, and the flowers $F_{\phi} = \{F_c; F_r\}$. The predator and flower strategies will be described fully in Sections A.2 and A.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 A.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.

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

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

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

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

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.

$$F_{L,s,c}[B_{\phi mut}; B_{\phi pop}; CS_{\phi}; F_{\phi}] = \frac{1}{F_c - CS_c} [(B - 1) B_{L,s,c}[B_{\phi pop}; CS_{\phi}; F_{\phi}] \\ + B_{L,s,c}[B_{\phi mut}; CS_{\phi}; F_{\phi}]]$$

$$F_{L,s,r}[B_{\phi mut}; B_{\phi pop}; CS_{\phi}; F_{\phi}] = \frac{1}{F_r - CS_r} [(B - 1) B_{L,s,r}[B_{\phi pop}; CS_{\phi}; F_{\phi}] \\ + B_{L,s,r}[B_{\phi mut}; CS_{\phi}; F_{\phi}]]$$

$$F_{L,d,c}[B_{\phi mut}; B_{\phi pop}; CS_{\phi}; F_{\phi}] = \frac{1}{CS_c} [(B - 1) B_{L,d,c}[B_{\phi pop}; CS_{\phi}; F_{\phi}] \\ + B_{L,d,c}[B_{\phi mut}; CS_{\phi}; F_{\phi}]]$$

$$F_{L,d,r}[B_{\phi mut}; B_{\phi pop}; CS_{\phi}; F_{\phi}] = \frac{1}{CS_r} [(B - 1) B_{L,d,r}[B_{\phi pop}; CS_{\phi}; F_{\phi}] \\ + B_{L,d,r}[B_{\phi mut}; CS_{\phi}; F_{\phi}]]$$

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. $B_{\phi pop} = \{\lambda_{c,pop}; \lambda_{r,pop}\}$ is the strategy adopted by the majority of the pollinator population, and $B_{\phi mut} = \{\lambda_{c,mu}; \lambda_{r,mu}\}$ is the strategy adopted by a single mutant pollinator. The mutant strategy can differ from the population strategy on one or both dimensions.

A.1.3. Fitness functions

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 A.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 $B_{\phi foc}$ can be described as...

$$B_{\ell foc}[B_{\phi foc}; CS_{\phi}; F_{\phi}] = MIN \left\{ \frac{t_{exp}}{t_n} \frac{1}{\frac{B_{L,d,c}[B_{\phi foc}; CS_{\phi}; F_{\phi}] + B_{L,d,r}[B_{\phi foc}; CS_{\phi}; F_{\phi}]}{e}} \right\}$$

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 $B_{\phi foc}$ 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 $B_{\phi foc}$ with $B_{\phi pop}$ or $B_{\phi mut}$, 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...

$$B_{g,mult}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}] = \frac{1}{t_n} \cdot \left[(B_{L,s,c}[B_{\sigma,mult}; CS_{\sigma}; F_{\sigma}] \cdot \left\{ \frac{n_{max}}{F_{L,s,c}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}]} \right\} \text{ if } F_{L,s,c}[\dots] > 1 \right) + \left(B_{L,s,r}[B_{\sigma,mult}; CS_{\sigma}; F_{\sigma}] \cdot \left\{ \frac{n_{max}}{F_{L,s,r}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}]} \right\} \text{ if } F_{L,s,r}[\dots] > 1 \right) \right]$$

for pollinators adopting the mutant strategy, and

$$B_{g,pop}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}] = \frac{1}{t_n} \cdot \left[(B_{L,s,c}[B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}] \cdot \left\{ \frac{n_{max}}{F_{L,s,c}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}]} \right\} \text{ if } F_{L,s,c}[\dots] > 1 \right) + \left(B_{L,s,r}[B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}] \cdot \left\{ \frac{n_{max}}{F_{L,s,r}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}]} \right\} \text{ if } F_{L,s,r}[\dots] > 1 \right) \right]$$

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

$$B_{W,mult}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}] = B_{g,mult}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}] \cdot B_{\ell,mult}[B_{\sigma,mult}; CS_{\sigma}; F_{\sigma}]$$

for pollinators adopting the mutant strategy, and

$$B_{W,pop}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}] = B_{g,pop}[B_{\sigma,mult}; B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}] \cdot B_{\ell,pop}[B_{\sigma,pop}; CS_{\sigma}; F_{\sigma}]$$

for pollinators adopting the population strategy.

A.1.4. Identifying pollinator ESSs

A pollinator strategy, $B_{\sigma,candidate}$, is an ESS, $B_{\sigma,ESS} = \{\lambda_{c,ESS}; \lambda_{r,ESS}\}$, if it is the case that when the majority of the population adopts the candidate strategy, $B_{\sigma,pop} = B_{\sigma,candidate}$, there is no mutant strategy, $B_{\sigma,mult} \neq B_{\sigma,candidate}$, that a single pollinator could adopt where $B_{W,mult}[\dots] > B_{W,pop}[\dots]$. 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_{σ} , and flowers, F_{σ} , are known. All possible strategies that a focal pollinator could adopt, $B_{\sigma,foc}$, 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 $B_{\sigma,mult}$ that invalidates the inequality $B_{W,mult}[\dots] > B_{W,pop}[\dots]$. If no such mutant strategy can be found, $B_{\sigma,candidate}$ is considered an ESS.

There are combinations of parameter values and predator and floral strategies for which no ESS 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 A.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 $B_{W,mult}[\dots] > B_{W,pop}[\dots]$ 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 $B_{W,mult}[\dots] > B_{W,pop}[\dots]$ was true for similar CS_{σ} and F_{σ} values.

A.2. Predators

The strategy of the predator population at any given point in time is defined by $CS_{\sigma,curr} = \{CS_{c,curr}; CS_{r,curr}\}$, 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

$$CS_{W,c}[B_{\sigma,ESS}[CS_{\sigma,curr}; F_{\sigma}]] = PIA_c[\lambda_{c,ESS}]$$

and the fitness of predators on revealing flowers is

$$CS_{W,r}[B_{\sigma,ESS}[CS_{\sigma,curr}; F_{\sigma}]] = PIA_r[\lambda_{r,ESS}]$$

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

Starting with $CS_{\sigma,curr}$, 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, $CS_{\sigma,curr+1c} = \{CS_{c,curr} + 1; CS_{r,curr} - 1\}$, or a predator that is currently on a concealing flower could move to an unoccupied revealing flower, $CS_{\sigma,curr-1c} = \{CS_{c,curr} - 1; CS_{r,curr} + 1\}$ (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

$$CS_{g,r \rightarrow c}[B_{\sigma,ESS}[CS_{\sigma,curr+1c}; F_{\sigma}]; B_{\sigma,ESS}[CS_{\sigma,curr}; F_{\sigma}]] \\ = CS_{W,c}[B_{\sigma,ESS}[CS_{\sigma,curr+1c}; F_{\sigma}]] - CS_{W,r}[B_{\sigma,ESS}[CS_{\sigma,curr}; F_{\sigma}]]$$

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

$$CS_{g,c \rightarrow r}[B_{\sigma,ESS}[CS_{\sigma,curr-1c}; F_{\sigma}]; B_{\sigma,ESS}[CS_{\sigma,curr}; F_{\sigma}]] \\ = CS_{W,r}[B_{\sigma,ESS}[CS_{\sigma,curr-1c}; F_{\sigma}]] - CS_{W,c}[B_{\sigma,ESS}[CS_{\sigma,curr}; F_{\sigma}]]$$

The costs associated with these moves can be described by

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

for revealing to concealing moves and

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

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

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

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

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

To determine the evolutionarily stable distribution of predators, $CS_{\sigma,ESS} = \{CS_{c,ESS}; CS_{r,ESS}\}$, 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 $CS_{\sigma,ESS}$ is the uniform predator distribution, but if so, then the algorithm changes $CS_{\sigma,curr}$ 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 $CS_{\sigma,ESS}$.

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 A.1.4 it was noted that there are instances where there is no pollinator ESS. If this algorithm encounters a $CS_{\sigma,curr}$ for which no pollinator ESS exists, it effectively skips over this distribution by testing the movement conditions with $CS_{\sigma,curr+2c}$ rather than $CS_{\sigma,curr+1c}$. 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, $CS_{cost,c \rightarrow r}[CS_{\sigma,curr}; F_{\sigma}]$, 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 practise, 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: 10).

A.3. Flowers

The strategy of a flower population is defined by $F_{\sigma,curr} = \{F_{c,curr}; F_{r,curr}\}$, 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

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

for predator-free concealing flowers,

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

for predator-free revealing flowers,

$$F_{W,d,c}[B_{\sigma,ESS}[CS_{\sigma,ESS}[F_{\sigma,curr}]]] = PIA_c[\lambda_{c,ESS}]$$

for predator-containing concealing flowers, and

$$F_{W,d,r}[B_{\sigma,ESS}[CS_{\sigma,ESS}[F_{\sigma,curr}]]] = PIA_r[\lambda_{r,ESS}]$$

for predator-containing revealing flowers. Here $B_{\sigma,ESS}$ is described as a function of $CS_{\sigma,ESS}$, which is described as the strategy of the current flower population, $F_{\sigma,curr}$. 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

$$F_{W,c}[B_{\sigma,ESS}[CS_{\sigma,ESS}[F_{\sigma,curr}]]] = \left(\frac{F_{c,curr} - CS_{c,ESS}}{F_{c,curr}} F_{W,s,c}[B_{\sigma,ESS}[CS_{\sigma,ESS}[F_{\sigma,curr}]]] \right) + \left(\frac{CS_{c,ESS}}{F_{c,curr}} F_{W,d,c}[B_{\sigma,ESS}[CS_{\sigma,ESS}[F_{\sigma,curr}]]] \right)$$

and the expected fitness of a revealing flower is

$$F_{W,r}[B_{\sigma,ESS}[CS_{\sigma,ESS}[F_{\sigma,curr}]]] = \left(\frac{F_{r,curr} - CS_{r,ESS}}{F_{r,curr}} F_{W,s,r}[B_{\sigma,ESS}[CS_{\sigma,ESS}[F_{\sigma,curr}]]] \right) + \left(\frac{CS_{r,ESS}}{F_{r,curr}} F_{W,d,r}[B_{\sigma,ESS}[CS_{\sigma,ESS}[F_{\sigma,curr}]]] \right)$$

The algorithm to determine the ES relative frequency of the two flower strategies, $F_{\sigma,ESS} = \{F_{c,ESS}, F_{r,ESS}\}$, 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, $F_{W,c}[\dots] > F_{W,r}[\dots]$, then the concealing strategy is a pure ESS and we would expect the vast majority of flowers to be concealing. Conversely, if $F_{W,c}[\dots] < F_{W,r}[\dots]$ 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 Fig. 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 A.5 of this appendix).

A.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).

A.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 A.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 practise, 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 trade-off 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.

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