

Sexual deception: Coevolution or inescapable exploitation?

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Abstract Sexual deception involves the mimicry of another species' sexual signals in order to exploit behavioural routines linked to those signals. Known sexually deceptive systems use visual, acoustic or olfactory mimicry to exploit insects for predation, cleptoparasitism and pollination. It is predicted that where sexual deception inflicts a cost on the receiver, a coevolutionary arms race could result in the evolution of discriminating receivers and increasingly refined mimicry. We constructed a conceptual model to understand the importance of trade-offs in the coevolution of sexually deceptive mimic and receiver. Four components examined were: the cost of mimicry, the cost to receiver for being fooled, the density of mimics and the relative magnitude of a mimicry-independent component of fitness. The model predicts that the exploitation of non-discriminating receivers by accurate signal mimicry will evolve as an evolutionary stable strategy under a wide range of the parameter space explored. This is due to the difficulty in minimising the costs of being fooled without incurring the cost of falsely rejecting real mating opportunities. In the model, the evolution of deception is impeded when mimicry imposes substantial costs for both sides of the arms race. Olfactory signals that are potentially cheap to produce are therefore likely to be more vulnerable to exploitation than expensive visual ornaments [*Current Zoology* 60 (1): 52–61, 2014].

Keywords Sexual deception, Coevolution, Arms race, Model, Mimicry, Imperfect mimicry

The receivers of mating signals are under strong sexual selection to detect and respond to these conspecific cues. Sexually deceptive species exploit this through mimicry of these species-specific mating signals. In doing so, sexually deceptive mimics take advantage of behaviours tightly linked to the innate perceptual biases of the species they deceive (receivers) (Schaefer and Ruxton, 2009; Schiestl and Johnson, 2013). Signals exploited in sexually deceptive mimicry are most often chemical (Vereecken and McNeil, 2010) but are also known to include visual or tactile mating cues (Lloyd, 1965; Ellis and Johnson, 2010) as well as acoustic mate advertisement (Marshall and Hill, 2009). We currently know of sexually deceptive exploitation of insects in the context of three distinct systems; pollination, predation and cleptoparasitism.

Pollination by sexual deception provides some of the best-known examples we have of the phenomenon. Sexually deceptive plants lure their male mate-seeking insects into receiving or transferring pollen when mating routines are stimulated by the chemical and tactile

cues of the flower (Schiestl et al., 2003; Schiestl, 2005; Ayasse et al., 2011). This intriguing pollination strategy has evolved independently on at least four continents (Africa, Australia, Europe and South America), and is known in several hundred orchid species (Gaskett, 2011). Sexual deception has also recently been discovered in a daisy (Ellis and Johnson, 2010) and an iris (Vereecken et al., 2012) and may be more widespread among plants than presently reported. Sexually deceptive plants are the most studied sexually deceptive systems, with ongoing research on the signals involved in sexual mimicry (Franke et al., 2009; Gaskett and Herberstein, 2010; de Jager and Ellis, 2012; Phillips et al., 2013), the patterns of speciation associated with sexually deceptive lineages (Schlüter et al., 2009; Peakall et al., 2010; Xu et al., 2011; Peakall and Whitehead, 2013), and the genetics underlying floral traits involved in mimicry (Schlüter et al., 2011; Sedeek et al., 2013).

Diverse examples of predation via sexual deception have evolved in several independent lineages. Mimicry in these cases is known to exploit a wide range of sig-

Received Sep. 24, 2013; accepted Nov. 15, 2013.

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nalling modes including chemical, visual and acoustic signals. Bolas spiders lure mate seeking male moth and fly prey through chemical mimicry of species-specific female sex pheromones (Eberhard, 1977; Stowe et al., 1987; Haynes et al., 2002). Much like *Ophrys* orchids, blends of chemicals mimic species-specific chemical mating signals and this facilitates predation on a very specific group of prey (Yeorgan, 1988; Gemeno et al., 2000; Haynes et al., 2002). The predatory katydid *Chlorobalius leucoviridis* mimics the female part of cicada mating call duets in order to deceive males into approaching within striking distance. The katydid's acoustic repertoire is versatile enough to mimic a suite of species-specific wing flick responses used by female cicadas to signal to mate-seeking males (Marshall and Hill, 2009). Similarly versatile, but exploiting visual signals, are *Photuris versicolor* firefly females which mimic the reply flashes used by sympatric congeners for mate-finding (Lloyd, 1965, 1975, 1980, 1984). The species-specific flashes imitated by *P. versicolor* attract males who are then preyed upon. This may however be a flexible entrained mimicry subject to different selective forces than the evolved species-specific signal mimicry inherent to chemical mimicry (Vencl et al., 1994).

The third known kind of sexual deception is limited to two cases of cleptoparasitic blister beetle larvae (Hafernik and Saul-Gershenz, 2000; Saul-Gershenz and Millar, 2006; Vereecken and Mahe, 2007). The larvae of beetles *Meloe franciscanus* and *Stenoria analis* (family Melidae) cooperatively aggregate and emit hydrocarbon blends mimicking the sex pheromones of their specific solitary bee host. Male bees are attracted and fooled into landing on or near the aggregation, whereupon the larvae attach themselves to the male host for transfer to a female during courtship or copulation. At this point the larvae switch to the female and finally settle in the bee's nest to feed on eggs and pollen provisions in their development to adulthood (Saul-Gershenz and Millar, 2006; Garófalo et al., 2011).

It is important to point out the distinction between these sexually deceptive systems and so-called 'sexual parasites' (Lehtonen et al., 2013) such as the Amazon molly *Poecilia formosa*, the flatworm *Schmidtea polychroa* or the Tassili cypress *Cupressus dupreziana*. These species may 'deceive' other individuals into mating with them before discarding the mating partner's genomic contribution during reproduction. These systems do not necessarily involve evolution of adaptive mimicry in the parasite however, as the mimicry may

simply be a consequence of the hybrid origin of the parasite (e.g. Amazon molly; Dries, 2003), or the parasite and host can be members of the same species (in the case of the flatworm and cypress). The coevolutionary aspects of our article therefore do not apply to many sexual parasites, and interpretation of our results in that context must be treated with caution.

By imposing a cost on the receiver, all of the examples of sexual deception detailed above (pollination, predation and cleptoparasitism) provide sufficient circumstances for the operation of antagonistic coevolution [asymmetric, interspecific arms races according to the classification of Dawkins and Krebs (1979)]. When average receiver fitness is lowered through antagonistic interactions with the mimic, both species "may engage in a coevolutionary arms race of increasing signal discrimination on the part of the dupe, and increasing signal refinement on the part of the mimic" (Stowe, 1988). The opportunity for mimics to impose selection on receivers will be determined primarily by the fitness costs they inflict on the fooled individuals. Secondly, the average fitness cost is determined by the frequency and density of overlap of model/receiver and mimic populations.

The individual fitness cost to being fooled by a sexually deceptive mimic is expected to vary greatly depending on the nature of the exploitative interaction. The individual costs imposed in both the predatory and cleptoparasitic mimicry systems are obviously high—fooled males either lose their remaining lifetime fitness to predation, or lose a single brood of offspring. Antagonistic coevolution has however been deemed as unlikely to be occurring in most sexually deceptive pollination systems due to the perceived low average cost to fooled males (Schiestl, 2005; Gaskett, 2011) and low proportion of the model's range shared with that of the mimic. Despite this, there is evidence for costs to sexually deceived pollinators that may, at high frequencies, be sufficient to exert selection on pollinators. These include male insects preferring mimics over real females (Schiestl, 2004), interfering with mating opportunities for males and females (Wong and Schiestl, 2002; Wong et al., 2004), prematurely ending copulation with a female to inspect a mimic (Coate, 1965), sperm wastage due to ejaculation at the flower (Gaskett et al., 2008; Blanco and Barboza, 2005) and pollinator death after entrapment in the flower (Sargent, 1909; Bernhardt, 1995; Phillips et al., 2013).

It is an important point that in any sexually deceptive coevolutionary arms race scenario, the evolution of dis-

criminating receivers is tempered by a trade-off of two errors. A discriminating mate-seeking signal receiver must minimise the number of erroneous responses to the mimic signaller (false positives), while also minimising erroneous rejections of genuine signallers (false negatives) (Price, 2013; Wiley, 2013). The two errors are very difficult to reduce simultaneously and will incur different consequences for fitness: False negatives result in the loss of a mating opportunity and will generally incur a greater fitness cost than responding to a mimic (Kokko and Heubel, 2011).

For the mimic, the trade-off depends on the cost of the mimicry. The mimic gains fitness by being successful at fooling receivers, but developing the traits required for successful mimicry can be costly. Contrary to the receiver's trade-off, which is an inescapable consequence of choosiness in mate choice, the mimicry trade-off is likely to be strongly dependent on the type of mimicry. Producing complicated visual ornaments, for example, can be very costly, whereas a single chemical compound for olfactory mimicry may be relatively cheap to produce.

Our aim was to model the trade-off in errors for a sexually deceived receiver coevolving with the refinement of sexual mimicry. We ran the model under a range of costs to both the mimic and the receivers to reflect the varied costs associated with the different modes of sexual deception observed in nature.

1 The Model

Our objective was to build a conceptual model of mimic-receiver coevolution in order to better understand some fundamental aspects influencing the evolutionary outcomes in a sexually deceptive system. While we attempt to keep the model relatively simple, we construct it in a modular way in order to simplify additions or amendments.

The fitness of receivers and mimics hinge on the probabilities of false negative (q_1) and false positive (p_2)

decisions, as defined previously. To calculate these probabilities, we need some assumptions about the distributions for the female cue that males assess, as well as the corresponding cue in the deceptive mimic. For our model, we made the assumption that both of these traits follow normal distributions with standard deviation 1. We chose to use this probability distribution as it is commonly encountered in nature, but it is not intended to correspond to a specific type of signal. Instead, we aim to make general inferences about coevolving sexually deceptive systems. The probabilities q_1 and p_2 depend on the distance between the mean of the model and mimic cues, and on the choosiness of receivers. We define the mean of the model cue to be 0, and the corresponding mean in mimics is denoted x . Setting the non-evolving trait to 0 enables the use of the standard normal distribution for p_1 and q_1 , and does not decrease the generality of the model. The evolving traits in the model are the mean of mimicry (x), and receiver choosiness (y). y is defined here as the maximum distance from the model cue mean (0) that the receiver is willing to accept as a mating partner. The required probabilities are then fully defined by x and y . For a visual description of these model parameters, see Fig. 1. The remaining model parameters are shown in Table 1.

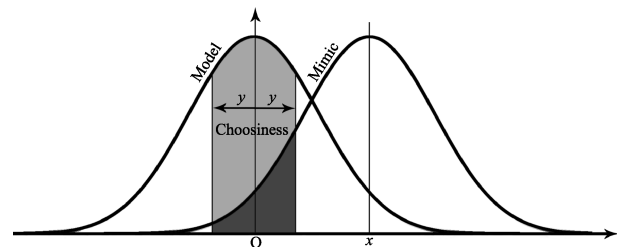


Fig. 1 Description of the coevolutionary model parameters for a sexual mimic and receiver

The two curves depict trait variation in the sexual signal, for which the model mean is set to 0 and the mimic mean defined by x . The trait range within which the receiver will respond is y . The shaded sections correspond to the probability of responding to a real mating partner or a mimic. The total area under each curve is 1.

Table 1 Description of model parameters

Parameter	Description	Value range
y	Male receiver choosiness (maximum detected distance from female trait average value that will be accepted)	$0 \leq y < \infty$
x	Accuracy of mimicry (distance from model, i.e. 0=perfect mimicry)	$-\infty < x < \infty$
r_2	Resources used on 'mating' with a mimic (relative to a real mating), i.e. the cost of responding to a mimic.	$0 \leq r_2 \leq 1$
r_3	Resources used on rejecting a mating opportunity, with a mimic or actual partner (relative to a real mating)	$0 \leq r_3 \leq 1$
a	Mimic density: mimics/(mimics+females)	$0 \leq a \leq 1$
c	Parameter scaling the cost of mimicry (0=no cost)	$0 \leq c \leq 1$
β	Relative contribution of baseline fitness in mimics (route to fitness independent of mimicry)	$0 \leq \beta < \infty$

In the following, we denote the probability density function for a normal distribution (variable t , mean μ and standard deviation ϕ) with $f(t, \mu, \phi)$, and the corresponding cumulative distribution function with $F(t, \mu, \phi)$. Now the probability of accepting a mating with an encountered real female is

$$p_1 = F(y, 0, 1) - F(-y, 0, 1) = \int_{-y}^y f(t, 0, 1) dt$$

$$= \int_{-y}^y \frac{1}{\sqrt{2\pi}} e^{-\frac{t^2}{2}} dt \quad (1)$$

and the probability of rejecting a real female (false negative) is simply

$$q_1 = 1 - p_1 \quad (2)$$

Equivalently, the probability of mating with a mimic (false positive) is

$$p_2 = F(y, x, 1) - F(-y, x, 1) = \int_{-y}^y f(t, x, 1) dt$$

$$= \int_{-y}^y \frac{1}{\sqrt{2\pi}} e^{-\frac{(t-x)^2}{2}} dt = \int_{-y-x}^{y-x} \frac{1}{\sqrt{2\pi}} e^{-\frac{t^2}{2}} dt \quad (3)$$

$$= \int_{-y-x}^{y-x} f(t, 0, 1) dt$$

and the probability of rejecting a mimic

$$q_2 = 1 - p_2 \quad (4)$$

The alternative forms of Eqs. 1 and 3 are all equivalent, but different forms are useful at different stages of deriving or running the model. Calculation of the probabilities in mathematical software is easiest using the cumulative distribution function. The integral forms, on the other hand, will facilitate determining the partial derivatives of the probabilities.

Using the probabilities derived above, we can calculate the average resource expenditure on a single mating event. Both ‘resource expenditure’ and ‘mating event’ are to be understood in a general sense. Resource expenditure covers the limitations imposed by both time and energy, and a mating event in this context refers to mating with a female, mating with a mimic, as well as rejecting either one. Resource units are scaled such that a real mating requires 1 unit. For parameter definitions, see table 1. Average resource expenditure is

$$r_{mean} = 1(1-\alpha)p_1 + r_2\alpha p_2 + r_3(1-\alpha)q_1 + r_3\alpha q_2 \quad (5)$$

Here, the amount of resources used on each type of mating event is multiplied by the probability of such a mating event. The fitness of a receiver is then proportional to the probability of gaining a real mating, divided by the average resource expenditure on a mating event:

$$w_p = \frac{(1-\alpha)p_1}{r_{mean}} \quad (6)$$

The fitness gradient for y is $\frac{1}{w_p} \frac{\partial w_p}{\partial y}$. A potential

complication arises in differentiating the probabilities q_1 , p_1 , q_2 and p_2 (all of which are in the denominator of Eq. 6). This is much easier than it initially seems, however, as y only appears in the integration limits of equations (1) and (3). Given that integration and differentiation are inverse operations, the task then becomes easy. This, in turn is equivalent to saying that the probability density function is the derivative of the cumulative distribution function. The required partial derivatives of the probabilities p_1 and p_2 are therefore

$$\frac{\partial p_1}{\partial y} = 2f(y, 0, 1) \quad \text{and} \quad \frac{\partial p_2}{\partial y} = f(y, x, 1) + f(-y, x, 1)$$

The derivation of the actual fitness gradient is then straightforward using standard differentiation rules and the partial derivatives given above, and we omit the full equations from this text.

A mimic’s fitness will depend on the probability that a male is fooled into mating with it, i.e. p_2 , but also on whether there is a fitness cost to mimicry. We model this potential cost by multiplying mimic fitness with a cost function denoted $g(x)$. If there is no cost to mimicry, then $g(x)=1$. Otherwise, the lowest value of $g(x)$ must be reached at $x=0$ (i.e. perfect mimicry). A convenient function with these properties is

$$g(x) = 1 - ce^{-\left(\frac{x}{5}\right)^2}$$

where the parameter c ($0 \leq c \leq 1$) determines the magnitude of the cost.

The ancestors of sexually deceptive mimics must have been able to gain fitness (e.g. reproduce or catch prey) without mimicry. Therefore, at the evolutionary origins of sexual deception, an alternative way of gaining fitness must have also been present. The total fitness of the mimic is then composed of a component that is independent of the extent of mimicry, as well as the probability of fooling a receiver. We scale these two fitness components with the parameter β . Finally, both components must be multiplied with the cost function:

$$w_m = (\beta + p_2)g(x) \quad (7)$$

The fitness gradient for the accuracy of mimicry is then $\frac{1}{w_m} \frac{\partial w_m}{\partial x}$.

For deriving the required partial derivative $\frac{\partial p_2}{\partial x}$ we choose a form of Eq. 3 where x only appears in the integration limits, and find that

$$\begin{aligned}\frac{\partial p_2}{\partial x} &= -f(y-x, 0, 1) + f(-y-x, 0, 1) \\ &= -f(y, x, 1) + f(-y, x, 1)\end{aligned}$$

We now have the components needed for calculation of the fitness gradients for both mimic and receiver, where the probability of a false positive (p_2) forms a natural link between the fitnesses of the coevolving organisms. The coevolution of mimicry (x) and choosiness (y) can be tracked from an arbitrary starting point with the fitness gradients $\frac{1}{w_m} \frac{\partial w_m}{\partial x}$ and $\frac{1}{w_p} \frac{\partial w_p}{\partial y}$. For

the figures, we present choosiness as the proportion of rejected real females, i.e. we calculate q_1 from Eq. 2 and plot this value on the y -axis.

We examine the evolutionary effects of four components of the model: the cost of mimicry (c), the cost to receivers of being fooled (r_2), the density of mimics (α) and the relative magnitude of the mimicry-independent component of fitness (β).

2 Results and Discussion

Sexual deception encompasses a wide variation in both the mode of signal mimicry and the costs imposed on the signal receiver (Fig. 2). Our coevolutionary model between mimic accuracy and receiver discrimination predicts that across the broad range of costs to being deceived, stable equilibria (stars in Fig. 2) maintaining sexual mimics can evolve. Frequently, stable equilibria are characterised by accurate mimicry and low receiver choosiness, driven by the trade off between the very costly error of rejecting a real female, and the (in non-predatory systems) less costly error of being fooled by a mimic (Kokko and Heubel, 2011).

In addition to the cost of being fooled, it has been predicted that the frequency of mimicry (determined for example by proportion of range overlap of mimic and model, or ratio of mimic to model) will determine whether or not deception leads to a coevolutionary arms race between mimic accuracy and receiver discrimination (Stowe, 1988). Our model showed that the height of the trajectory was altered by mimic density (not shown) but not the position of the final equilibria. For example, at low mimic densities receiver choosiness remains at lower levels, i.e. the curves in Fig. 2 are vertically flattened, but otherwise change very little (not shown). In other words, mimic density affected only the amplitude of coevolutionary interaction, not the final evolutionary outcome.

In some cases, stable equilibria without mimicry

were reached, i.e. the receiver won the coevolutionary arms race. This was the outcome when the costs to both receiver and mimic are high (Fig. 2, J, K, L). At intermediate costs to mimic and receiver, mimicry is selected for only if it overcomes a certain threshold of similarity to the model signal (Fig. 2, F, G, H). This is an example of positive feedback leading to multiple evolutionary equilibria (Lehtonen and Kokko, 2012). In panels F, G and H, one possible evolutionary endpoint consists of accurate mimicry, and low choosiness in the receiver. A certain amount of initial similarity between the mimic and model is required to start the positive feedback process that leads to this outcome. If mimicry is initially below this threshold accuracy, the system evolves towards the second equilibrium of no mimicry and no choosiness. The latter equilibrium is not visible in the figure, but in all cases where evolutionary trajectories exit the right hand side of the figure, they are leading to the equilibrium of no mimicry.

2.1 Signal modality and the cost of mimicry

Across known examples of sexual deception we see exploitation of a variety of signal modes (e.g. chemical, visual and acoustic). It is likely that different modes of signal influence the costs to the mimic and also the ability for the mimic to evolve accurate mimicry. For example, the production by orchids of elaborate floral morphology replicating a female insect will be both more costly to express and less likely to converge on the model signal than *Photuris* fireflies which alter existing mate-seeking signals to match that of a congener (Lloyd, 1965, 1975).

Our model shows that the cost of signal mimicry is a critical parameter determining the stability of a sexually deceptive strategy. If mimicry is cheap (Fig. 2, A–D), the mimic will win an arms race and accurate mimicry can easily evolve, even if there is a very high cost to the receiver for being fooled (Fig. 2, D). This likely contributes to the observed preponderance of chemical mimicry systems in sexual deception, as there is reason to believe that chemical mimicry might be cheaper than other modes of signalling. For example, *Ophrys* orchids' chemical mimicry is believed to be achieved through modification of cuticular hydrocarbons, presumably involved in other unrelated plant functions (Schiestl et al., 1999; Ayasse et al., 2011). In a biosynthetic pathway producing these hydrocarbons, very subtle molecular modifications could result in exaptation of a cuticle wax to a chemical signal. The fitness cost difference between producing a sexually deceptive chemical signal or the ancestral non-mimic hydrocarbon might therefore be

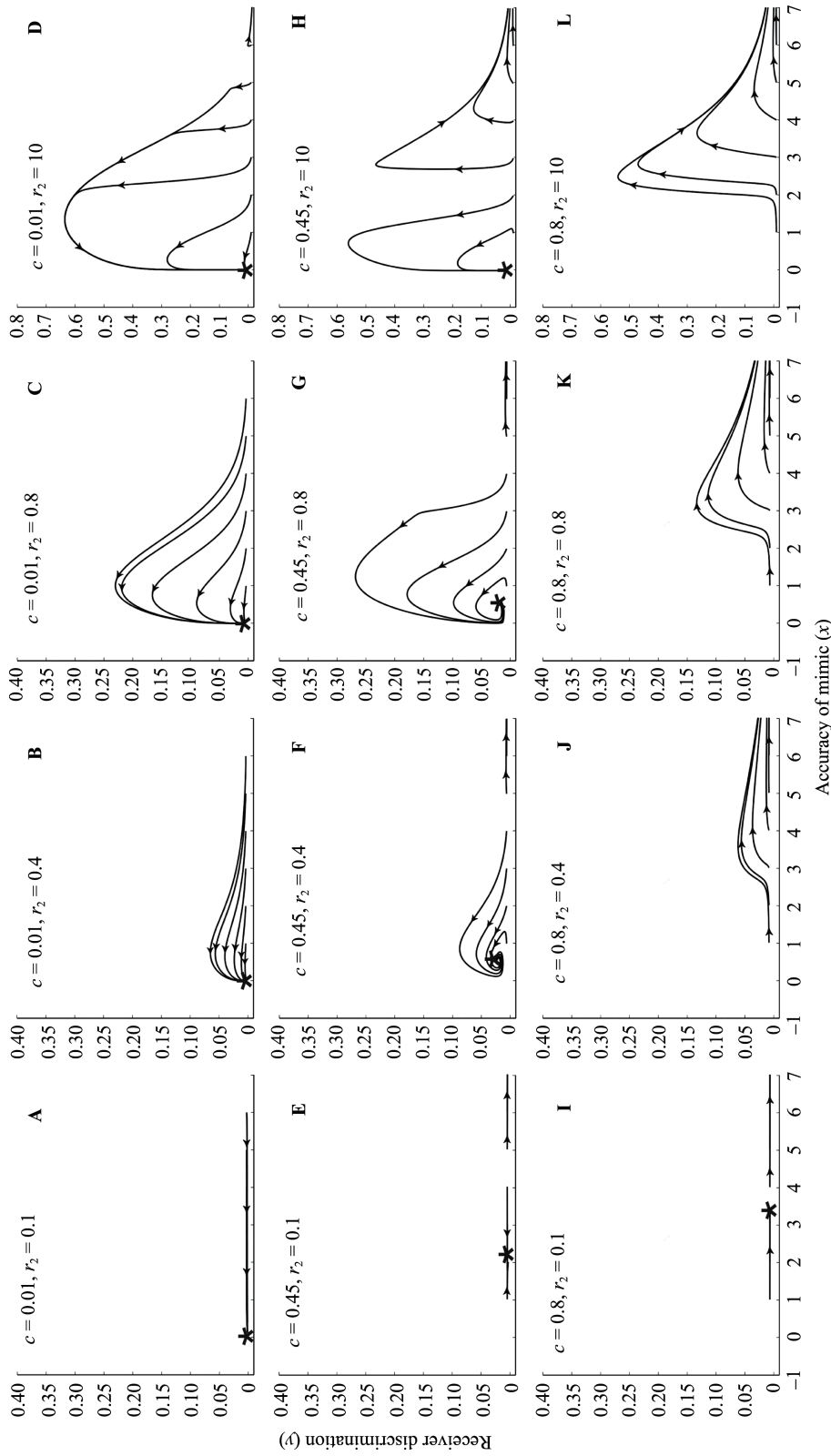


Fig. 2 Interaction of the costs of mimicry (increasing from top row to bottom row), and the cost of being fooled by a mimic (increasing from left to right)
 The x-axis of the individual panels depicts the distance of the mimic signal from the host signal (0=perfect mimicry), while the y-axis corresponds to choosiness of the receiver, measured as the proportion of rejected real mating partners. In most cases, receivers initially evolve intermediate choosiness, but when the mimicry becomes very accurate receivers ‘give up’. Panels **A-C**, **E-G**, **I-J** are plotted with cost parameter r_2 values hypothetically consistent with sexually deceptive pollination, whereas the high cost for panels **D**, **H**, **L** simulate sexually deceptive predation (reflected in different scaling of y-axes in these panels). Stars indicate stable equilibria with mimicry, while trajectories leaving the right side of the panels lead to equilibria with no mimicry and no choosiness. Other parameters used: $r_3=0.1$, $\alpha=0.5$, $\beta=1$.

very small. Furthermore, chemical mating signals exploited by sexually deceptive organisms can be based on only a few key compounds or blends between a few related compounds (Peakall et al., 2010; Ayasse et al., 2011). This limits the number of dimensions in which the signal can vary and makes chemical mimicry of simple olfactory signals particularly vulnerable to accurate mimicry. For example, *Chiloglottis trapeziformis* attracts its wasp pollinator with precise chemical mimicry of just a single compound (Schiestl et al., 2003).

2.2 The cost of being fooled

The costs of being sexually deceived vary greatly. For example, insects fooled into inspecting and displaying mating routines at a flower (de Jaeger and Ellis, 2013) bear far smaller fitness costs than sexually deceived moths preyed upon by the bolas spider (Stowe et al., 1987). Our model shows that for systems in which deception is very cheap for the receiver, discrimination or choosiness is unlikely to evolve even in intermediate evolutionary stages (Fig. 2. A, E, I). Lack of choosiness, in turn, means that there is little selective pressure driving the mimic towards very accurate signal mimicry (Fig. 2. A, E, I).

On the other hand, systems that incur a great cost to the receiver (such as sexually deceptive predation) show very different coevolutionary trajectories (Fig. 2 D, H, L). Not surprisingly, great costs drive the evolution of discriminating receivers. Our model predicts that stable sexually deceptive predation (i.e. costs are very high to the receiver) can evolve if mimicry is cheap for the mimic (Fig. 2, D), or under higher costs of mimicry if the mimic signal is initially relatively close to the model signal (Fig. 2, H). This initial signal accuracy could certainly be the case in at least two out of the three known sexually deceptive predation systems. *Photuris* fireflies make use of the flashing visual signals they use for mate attraction to also prey on their congeners (Lloyd 1965, 1975, 1980, 1984). The cost of mimicry is therefore likely to be a minimal additional investment on top of the costs already invested in mate-seeking flash signalling. The accuracy in signal mimicry is also likely to be quite high due to the recent common ancestry of the receiver and deceiver lineages. The costs of chemical emission in bolas spiders is unknown but given that spiders have the metabolic machinery in place to drive their own intraspecific pheromone communication (Gaskett, 2007), co-opting this system for predation might also represent a minor additional investment. As discussed above, the limited dimensions of simple olfactory signals favour accurate mimicry. It is difficult to say what costs might be involved in acoustic mimicry

mimicry by the predatory katydid (Marshall and Hill, 2009), but this system might be the most tractable for empirically measuring the costs of deception through techniques such as respirometry (Withers, 2001).

2.3 The evolution of discriminating receivers

In most scenarios that promote the evolution of discriminating receivers (Fig. 2 B–D, F–H) it is worth noting that discrimination is only a transient state, and receivers ‘give up’ when mimics evolve to high accuracy. The reason for this is that when mimicry is very accurate, it becomes impossible to reject a significant proportion of mimics without also rejecting a significant proportion of mating partners. The burden of false negatives, relative to benefits of discrimination becomes too high and discrimination is selected against. Mimicry, on the other hand, keeps evolving towards ‘perfect’ mimicry, unless the costs are too high. Therefore, in most of our model outcomes, combinations of intermediate mimicry and choosiness are not stable.

The coevolutionary trajectories described in our model suggest that even in systems that look today like one-sided exploitation, there may have been intermediate stages in the past where discrimination coevolved with mimic accuracy. What might these intermediate stages look like? One potential example is *Gorteria diffusa*, a species of daisy that shows remarkable variation in floral morphology, including sexually deceptive forms with raised black petal spots (Ellis and Johnson, 2010). Male Bombyliid flies show wide variation in their response to sexually deceptive forms and deceived males appear to learn to discriminate mimicked signals from real females (De Jager and Ellis, 2013). The system appears to be purely visual and tactile and therefore might conceivably lie further from the model trait values than more precise chemical mimicry seen in other sexually deceptive pollination systems. *Gorteria* might therefore not yet have evolved an accurate enough mimicry to win out against the evolution of discriminating receivers.

For discriminating receivers to persist as a stable outcome of the arms race, the costs of mimicry must be sufficient to halt the evolution of mimicry at an intermediate stage, which would also allow discrimination to stabilize at an intermediate level. For this to happen, mimics must be limited in their options of gaining fitness. If an alternative, mimicry-independent route to fitness exists and allows equally high fitness returns ($\beta=1$, Fig. 2), high costs of mimicry simply make mimics channel their resources away from mimicry (Fig. 2, H, J–L). However, if the alternative route to fitness is diminished ($\beta=0.25$, Fig. 3), the outcome is different.

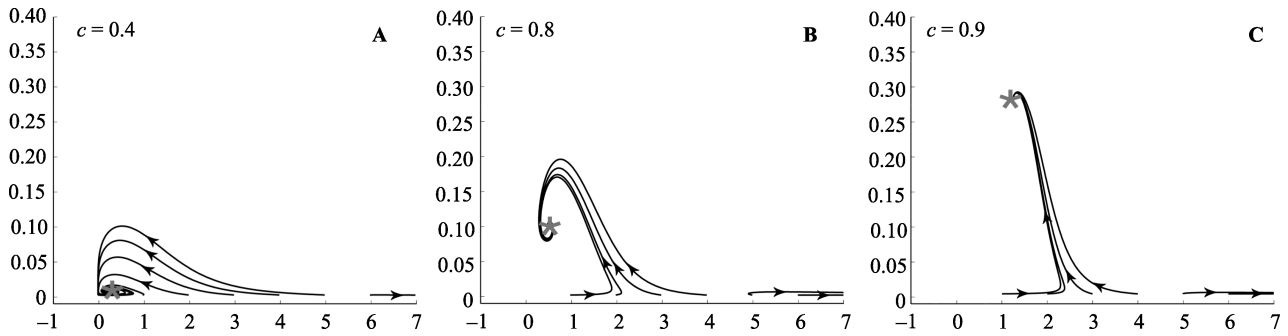


Fig. 3 The effect of an increasing cost of mimicry, when the mimic's alternative route to fitness is diminished

A combination of costly mimicry (increasing c from left to right) and reduced alternative fitness pathways ($\beta=0.25$ for all panels) enables the evolution of stable intermediate values of both mimicry (x-axis) and choosiness (y-axis). Equilibria are indicated as in Fig. 2. Other parameters used: $r_2=0.9$, $r_3=0.1$, $\alpha=0.5$.

This can be understood as an example of the ‘life-dinner principle’ (Dawkins and Krebs, 1979); if mimicry-dependent fitness is more akin to a lifetime benefit than the benefit from a dinner (low β in our model), mimicry can be maintained even in the face of relatively high costs. However, in this scenario the costs force mimicry to remain at an intermediate level, which in turn allows intermediate discrimination to be maintained in receivers. This suggests that imperfect mimicry, and intermediate rates of mimic rejection by receivers should be found in systems where mimicry is costly (e.g. visual or tactile mimicry), and where mimics have become reliant on sexual deception to such an extent that they are unable to easily revert back to alternative ways of gaining fitness.

3 Conclusions

We modelled the trade-off of two errors and costs of mimicry to show that this antagonistic coevolutionary interaction makes sexual deception a stable strategy under a wide range of parameters. We found few parameter sets that resulted in equilibrium between discriminating receivers and mimicry (Fig. 3). Most arms race scenarios modelled resulted in the receiver “giving up” and stable exploitation by accurate sexual mimics (Fig. 2).

One possible path to escape from exploitation could exist via coevolution of model mating signals and receivers to elaborate beyond the exploited trait space. We did not allow coevolution of the model's signal but under an expanded model models might be allowed to track receiver choosiness and mimics could in turn track the changes in signals they exploit. Another potential expansion of our model would be to allow the lower and upper bounds of receiver choosiness to vary independently rather than equally around a mean signal value.

Further empirical work is required to assess evidence for and against receiver discrimination or coevolution, especially in predatory systems. In numerous independently evolved sexually deceptive lineages we have evidence of learned avoidance of sexual mimics (Alcock, 2000, Ayasse et al., 2000; Bower, 1996; de Jager and Ellis, 2013; Peakall, 1990; Schiestl, 2004; Whitehead and Peakall, 2013; Wong et al., 2004; Wong and Schiestl, 2002), however we do not know if this is an adaptive response to deception or an independent and inherent mating behaviour. Future studies focusing on selection acting on behaviour and cognition in receivers and quantifying the costs of mimicry and deception will provide substrate for validation of our model and reveal the forces underlying complex adaptation in sexual mimicry.

Acknowledgments The authors would like to thank Mikael Mökkönen, Leithen M'Gonigle and two anonymous reviewers for comments that improved the manuscript.

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