Recognition and the evolution of distinctive signatures: when does it pay to reveal identity?

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SUMMARY

A simple evolutionarily stable strategy (ESS) model of identity advertisement is presented, which is applicable to many different situations, ranging from parental recognition of young to recognition of kin by workers in social insect colonies that comprise several genetically distinct lineages. The model assumes that the receiver may respond favourably or unfavourably to the signaller, but that it cannot immediately determine which type of response is appropriate. The signaller, who always benefits by eliciting a favourable response (but is unaware of which type of response is appropriate for the receiver), may choose to reveal or conceal its identity, making the task of discrimination easier or harder for the receiver. The evolutionarily stable outcome of the model depends on the probability that an unfavourable response is appropriate, the relative costs to the receiver of acceptance and rejection errors, and the relative benefits to the signaller of eliciting a favourable response when this is appropriate and when it is inappropriate for the receiver. High costs of acceptance errors to the receiver, and high benefits of appropriate favourable responses to the signaller, favour provision of distinctive identity cues: so, paradoxically, does a high probability that an unfavourable response is appropriate. However, under a wide range of conditions, selection favours the withholding of signature cues, which prevents discrimination by the receiver. Finally, if the signaller must provide some information to elicit a favourable response, but stands to gain more from such a response when it is undesirable, it may do best to provide partial but incomplete information about its identity.

1. INTRODUCTION

Recognition, whether of conspecifics, offspring, mates, neighbours, group members or any other category, involves the communication of information. In outline, a signaller must provide identity or signature cues, (see Halpin 1991), which are perceived by the receiver (although these may be inadvertent cues that have not evolved for the purpose of facilitating recognition). The latter can then integrate this signature information with any contextual information that is available, in order to determine the appropriate response (Reeve 1989; Beecher 1991; Davies *et al.* 1996; Sherman *et al.* 1997). Strangely, while the 'decision problem' faced by the receiver has been the subject of extensive analyses (eg. Reeve 1989; Beecher 1991; Getz 1991; Wiley 1994; Sherman *et al.* 1997), formal models of recognition have largely overlooked the 'communication problem' faced by the signaller (though see Pagel (1997) for a recent exception).

Predicting when it pays signallers to reveal their identity (i.e. to provide distinctive signature cues) is difficult because their interests will sometimes conflict with those of the receiver. Consider, for instance, the problem of parental recognition of eggs and chicks in bird species that engage in intraspecific brood parasitism ('egg dumping'). The parent always stands to

gain by accurately determining whether or not an egg or chick is its own; for the offspring, on the other hand, the provision of distinctive identity cues is beneficial when it is related to the parent, but disadvantageous when it is unrelated (Beecher 1991). If individual progeny can determine their own status, they might adjust their behaviour accordingly, concealing signature information only when they are unrelated to their adoptive parents. If, on the other hand, they share the parents' uncertainty regarding kinship, then it is hard to deduce what strategy will prove best on average.

This same difficulty crops up in many different contexts. Even in species where brood parasitism is absent, for instance, conflicts of interest may arise over the assessment of paternity (provided that males are involved in parental care). If females have the potential to engage in extra-pair mating, then males cannot be certain that the offspring they help to raise are their own. While they would clearly benefit by determining the paternity of their partner's young, the latter may benefit by concealing this information (Davies 1992; Pagel 1997). Other forms of kin discrimination raise similar issues. Colonies of social insects, for instance, frequently consist of a number of genetically distinct lineages. Individuals may stand to benefit by cooperating preferentially with more closely related colony members, but it may not always be to their advantage

to reveal their own identity (Keller 1997). Finally, the problems of recognition are also relevant to interactions between non-kin. Orivel *et al.* (1997), for instance, have recently reported evidence that parabiatic ants can recognize allospecific individuals sharing a nest with them. As with other forms of recognition, this ability depends on the existence of distinctive signature cues (in this case, specific cuticular chemical profiles).

Here, I present a general ESS model of identity advertisement, which is applicable in many different behavioural contexts. The model considers whether a signaller should provide or withhold distinctive signature cues, which allow the receiver to determine what kind of response is appropriate. The model predicts the stable level of signature information provided for a range of different parameter values, taking into account the effects of these values on the expected pay-offs to both signallers and receivers following their various potential courses of action.

2. AN ESS MODEL OF IDENTITY ADVERTISEMENT

The model focuses on the interaction between a single receiver–signaller pair, such as a parent bird faced with a chick that may or may not be its own, or a worker guard of a social insect colony faced with an intruder that may or may not be a colony member. For simplicity, I assume that the receiver may adopt one of only two responses towards the signaller. The parent, for example, may choose to accept or reject the chick, while the guard may choose to admit or repel the intruder. While the receiver sometimes does best to respond unfavourably, the signaller always benefits by eliciting the same, favourable response. In other words, though the parent does best to reject a chick that is not its own, the chick stands to gain by eliciting acceptance regardless of its identity. Equally, while the guard does best to repel a foreign intruder, the latter benefits by gaining admittance whether or not it truly is a colony member. The probability that the receiver does best to respond unfavourably, i.e. the probability that the chick is not the parent's own, or that the intruder is not a colony member, will be denoted p .

Under the above circumstances, should the signaller conceal or reveal its identity? If it could determine its own status, it would clearly pay to adjust its behaviour accordingly. A chick, for instance, would do best to conceal its identity when in a foreign nest (or when confronting a male that is not its father), but would otherwise benefit by revealing it. Equally, an intruder would stand to gain by concealing its identity when entering a foreign colony, but would otherwise do best to reveal it. But what if the signaller shares the receiver's uncertainty regarding its status (i.e. if it must adopt a strategy that is context independent)?

(a) *Discrete signaller strategies*

To begin with, I will make the simplifying assumption that the signaller must either fully reveal or fully conceal its identity, by providing or withholding individually distinctive signature cues (below, I consider the

more realistic situation in which partial concealment is possible). The former strategy allows the receiver to determine what kind of response is suitable, and thus leads to rejection in the proportion p of cases where this is appropriate (and to acceptance in the remaining proportion $1 - p$ of cases). The latter strategy, by contrast, leaves the receiver completely ignorant of the signaller's identity. In the absence of any information, the receiver is forced to adopt a context-independent response, i.e. to accept or reject the signaller regardless of its actual identity, according to which course of action yields, on average, the highest fitness pay-off.

If the receiver's best decision in the absence of any identity information is to reject the signaller, then the latter clearly does best to reveal its identity. In this way it will ensure acceptance in at least the proportion $1 - p$ of cases where this is the appropriate response for the receiver. By contrast, if the receiver's best decision in the absence of any identity information is to accept the signaller, then the latter does best to conceal its identity. By doing so, it can be certain of acceptance, while to reveal its identity would entail rejection in the proportion p of cases where this is the appropriate response for the receiver.

How can one determine the receiver's best decision in the absence of information? Four possible outcomes of the model may be distinguished, depending on whether the receiver responds favourably or unfavourably, and whether the response adopted is or is not appropriate. The inclusive fitness pay-offs to the receiver in these four cases will be denoted v_{a+} for an appropriate favourable response (e.g. for a parent that accepts its own chick), v_{i+} for an inappropriate favourable response (e.g. for a parent that accepts chick that is not its own), v_{a-} for an appropriate unfavourable response (e.g. for a parent that rejects an alien chick), and v_{i-} for an inappropriate unfavourable response (e.g. for a parent that rejects its own offspring)—the corresponding pay-offs to the signaller will be denoted w_{a+} , w_{i+} , w_{a-} and w_{i-} . The receiver does best to accept a signaller of unknown identity whenever the expected fitness pay-off from doing so is greater than the expected fitness payoff from rejection, i.e. whenever

$$(1 - p)v_{a+} + pv_{i+} > (1 - p)v_{i-} + pv_{a-} \quad (1)$$

Defining a new variable, K , which I shall refer to as the receiver's 'incentive' to respond positively, as

$$K = \frac{(1 - p)(v_{a+} - v_{i-})}{p(v_{a-} - v_{i+})} \quad (2)$$

equation (1) can be more simply expressed as $K > 1$. If this condition is satisfied, the optimal strategy for the signaller is to conceal its identity, which always results in acceptance. If, by contrast, the condition is not satisfied, the optimal strategy for the signaller is to reveal its identity, which results in acceptance if and only if this is the appropriate response for the receiver.

(b) *Continuously variable signaller strategies*

The above simple analysis illustrates the basic structure of the model. It is, however, unsatisfactory because

Figure 1. The frequency distributions of perceived dissimilarity between the phenotype of a signaller and the template of the receiver, when the former is desirable and when it is undesirable. If the perceived dissimilarity falls below the receiver's response threshold, the signaller is 'accepted' as desirable and elicits a favourable response; otherwise, the signaller is 'rejected', i.e. it elicits an unfavourable response. The lightly shaded area represents the region of acceptance error, in which the receiver inappropriately adopts a favourable response to an undesirable signaller (a 'false alarm'), while the heavily shaded area represents the region of rejection error, in which the receiver inappropriately adopts an unfavourable response to a desirable signaller (a 'missed detection'). Lowering the threshold (i.e. adopting more stringent response criteria) leads to a reduction in the size of the former area but an increase in the size of the latter. In other words, it is not possible for the receiver to simultaneously minimize the probabilities of false alarms and missed detection; there is a trade-off between the two.

it assumes that the signaller must either fully reveal or fully conceal its identity, so that the receiver is either perfectly informed (and thus able to adopt the appropriate response without error) or left completely ignorant (and thus forced to adopt the same response regardless of the signaller's true identity). To allow for the possibility of partial concealment, it is necessary to consider how the receiver will respond to imperfect information about the signaller's identity.

I shall assume that discrimination involves a process of phenotype matching. That is, the receiver is assumed to have learned the cues characteristic of those signallers to whom it does best to respond favourably, e.g. its own offspring or fellow colony members, forming a template which it can compare with the phenotype of individuals it encounters. A favourable response is elicited if the perceived degree of dissimilarity between the template and signaller phenotype is sufficiently low (figure 1; see Getz 1981; Getz & Chapman 1987; Reeve 1989; Getz 1991).

The signaller is likely to match the receiver's template more closely if it is desirable (i.e. if the receiver does best to respond favourably to it) than if it is undesirable (i.e. if the receiver does best to respond unfavourably to it), but to allow for the possibility of imperfect information, I shall assume that there is

some degree of overlap between the probability distributions of perceived dissimilarity for the two cases. Specifically, I will assume that perceived dissimilarity in either case is normally distributed with variance σ^2 , and with mean d_+ if the signaller is desirable, and d_- if it is undesirable (where $d_+ < d_-$). The expected fitness pay-off to a receiver that responds favourably if perceived dissimilarity falls below a threshold value of t , denoted $v(t)$, is then given by

$$v(t) = \frac{(1-p)}{\sqrt{2\pi\sigma^2}} \left[\int_{x < t} v_{a+} \exp\left(-\frac{(x-d_+)^2}{2\sigma^2}\right) dx + \int_{x > t} v_{i-} \exp\left(-\frac{(x-d_+)^2}{2\sigma^2}\right) dx \right] + \frac{p}{\sqrt{2\pi\sigma^2}} \left[\int_{x < t} v_{i+} \exp\left(-\frac{(x-d_-)^2}{2\sigma^2}\right) dx + \int_{x > t} v_{a-} \exp\left(-\frac{(x-d_-)^2}{2\sigma^2}\right) dx \right] \quad (3)$$

Differentiating, we obtain

$$v'(t) = \frac{(1-p)(v_{a+} - v_{i-})}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(t-d_+)^2}{2\sigma^2}\right] + \frac{p(v_{i+} - v_{a-})}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(t-d_-)^2}{2\sigma^2}\right] \quad (4)$$

Solving for $v'(t) = 0$ yields a unique stationary value, t^* , given by

$$t^* = \frac{d_+ + d_-}{2} + \frac{\sigma^2 \ln K}{d_- - d_+}. \quad (5)$$

It is then easy to show (given $d_+ < d_-$) that $v''(t^*) < 0$, and hence that t^* represents the optimal, fitness-maximizing choice of t for the receiver, which strikes the best balance between the risk of failing to respond to a desirable signaller and responding inappropriately to an undesirable signaller (provided that $\sigma^2 > 0$, even the optimal choice of t cannot rule out the possibility of error completely).

Assuming that the receiver adopts the optimal response threshold defined above, the expected fitness pay-off to the signaller with whom it interacts is equal to

$$\frac{(1-p)}{\sqrt{2\pi\sigma^2}} \left[\int_{x < t^*} w_{a+} \exp\left(-\frac{(x-d_+)^2}{2\sigma^2}\right) dx + \int_{x > t^*} w_{i-} \exp\left(-\frac{(x-d_+)^2}{2\sigma^2}\right) dx \right] + \frac{p}{\sqrt{2\pi\sigma^2}} \left[\int_{x < t^*} w_{i+} \exp\left(-\frac{(x-d_-)^2}{2\sigma^2}\right) dx + \int_{x > t^*} w_{a-} \exp\left(-\frac{(x-d_-)^2}{2\sigma^2}\right) dx \right]. \quad (6)$$

Combining equation (5) and expression (6), we find that expected signaller fitness does not depend on the precise values of d_+ and d_- , but only on the difference between them relative to the value of σ , which will be

denoted $d(= (d_- - d_+)/\sigma)$. This value is a measure of the accuracy with which the receiver can determine whether or not the signaller is desirable. A high value of d indicates that the perceived mismatch between the signaller's phenotype and the receiver's template will tend to be much greater if the signaller is undesirable than if it is desirable, allowing accurate discrimination. A low value of d indicates that the perceived mismatch will tend to be much the same in either case, preventing accurate discrimination. Expected signaller fitness as a function of d , denoted $w(d)$, is given by

$$\begin{aligned}
 w(d) = & \frac{(1-p)}{\sqrt{2\pi}} \left[\int_{x < \frac{\ln K}{d} + \frac{d}{2}} w_{a+} \exp\left(\frac{-x^2}{2}\right) dx \right. \\
 & + \left. \int_{x > \frac{\ln K}{d} + \frac{d}{2}} w_{i-} \exp\left(\frac{-x^2}{2}\right) dx \right] \\
 & + \frac{p}{\sqrt{2\pi}} \left[\int_{x < \frac{\ln K}{d} - \frac{d}{2}} w_{i+} \exp\left(\frac{-x^2}{2}\right) dx \right. \\
 & + \left. \int_{x > \frac{\ln K}{d} - \frac{d}{2}} w_{a-} \exp\left(\frac{-x^2}{2}\right) dx \right] \quad (7)
 \end{aligned}$$

Now, let us assume that the signaller may choose to reveal or conceal its identity to varying degrees, making it easier or harder for the receiver to determine whether or not it should respond favourably. This can be formally represented by the choice of a particular value of d . Choosing a high value corresponds to the provision of distinctive signature cues, which ensure that the degree of perceived dissimilarity between the signaller's phenotype and the receiver's template will be strongly influenced by the signaller's desirability. For instance, a chick that chooses a high value of d chooses to provide a distinctive signature, which ensures that the degree of perceived dissimilarity between its phenotype and the parent's template will tend to be much greater if it is unrelated to the parent than if it is related. Conversely, choosing a low value of d corresponds to concealment of individually distinctive traits, or the production of a generic signature, which ensures that the degree of perceived dissimilarity to the parent's template will tend to be much the same regardless of whether the chick is related or not. We wish to determine the optimal, i.e. fitness-maximizing choice of d for the signaller, assuming that the receiver will adopt the optimal response threshold for the particular value of d that is chosen.

Differentiating equation (7), we obtain the marginal change in signaller fitness with d

$$\begin{aligned}
 w'(d) = & \frac{(1-p)}{\sqrt{2\pi}} (w_{a+} - w_{i-}) \exp\left[\frac{-\left(\frac{\ln K}{d} + \frac{d}{2}\right)^2}{2}\right] \times \\
 & \left(\frac{1}{2} + \frac{\ln K}{d^2}\right) - \frac{p}{\sqrt{2\pi}} (w_{i+} - w_{a-}) \times \\
 & \exp\left[\frac{-\left(\frac{\ln K}{d} - \frac{d}{2}\right)^2}{2}\right] \left(\frac{1}{2} + \frac{\ln K}{d^2}\right) \quad (8)
 \end{aligned}$$

Defining a new variable L , which I shall refer to as the signaller's 'incentive' to advertise, as

$$L = \frac{(1-p)(w_{a+} - w_{i-})}{p(w_{i+} - w_{a-})} \quad (9)$$

we find that for $K < \text{Min}\{1, L\}$, $w'(d)$ is uniformly positive. This implies that an increase in the value of d (allowing for more accurate discrimination by the receiver) always yields an increase in signaller fitness. By contrast, for $K > \text{Max}\{1, L\}$, $w'(d)$ is uniformly negative, indicating that an increase in the value of d always yields a decrease in signaller fitness. In the former case, selection favours provision of individually distinctive cues, while in the latter case, selection favours withholding of such cues.

For $L < K < 1$, and for $L > K > 1$, there exists a unique stationary value d^* given by

$$d^* = \sqrt{-2 \left(\frac{K+L}{K-L} \right) \ln K} \quad (10)$$

In the former case, d^* represents the fitness-maximizing, optimal choice for the signaller, indicating that selection favours the provision of partial but incomplete information about signaller identity. In the latter case, however, d^* represents a fitness minimum. Under these circumstances, selection in fact favours the withholding of distinctive signature cues (as was the case for $K > \text{Max}\{1, L\}$), since the probability of a favourable response tends to 1 as d tends to 0, regardless of whether the signaller is desirable or undesirable.

3. RESULTS

The full model (which allows for varying degrees of concealment) yields three possible kinds of outcome. (1) The signaller may make it as easy as possible for the receiver to determine its identity, which (in the absence of any constraints on its ability to do so) leads to perfect discrimination, with the receiver adopting an appropriate response without error. (2) The signaller may partially conceal (or, equivalently, partially reveal) its identity, so that the receiver can achieve better-than-random discrimination, but will make occasional mistakes. (3) The signaller may make it as hard as possible for the receiver to determine its identity, which (again in the absence of constraints) renders discrimination impossible, and forces the receiver to adopt the same response regardless of the signaller's true identity. This last type of outcome only occurs when the receiver, in the absence of any information about the signaller's identity, does best to respond favourably; it therefore features indiscriminate responsiveness (rather than an indiscriminate failure to respond favourably).

Which outcome is obtained depends on the value of only two parameters: K and L . What do these parameters represent? The former, previously referred to as the receiver's incentive to respond, is a measure of the relative costs and risks of 'false alarms' and 'missed detections' to the receiver (see Wiley 1983, 1994). A high value of K indicates that it is rare to encounter an undesirable signaller, and/or that the cost of mistakenly

Figure 2. Equilibrium outcome of the model, for different values of the parameters K and L . The former may be thought of as the receiver's incentive to respond, the latter as the signaller's incentive to advertise (see main text for a full definition). In the unshaded region, the signaller makes it as easy as possible for the receiver to determine its identity; in the absence of any constraints, this yields perfect discrimination, so that the receiver always responds appropriately. In the lightly shaded region, the signaller partially conceals (or, equivalently, partially reveals) its identity, which results in better-than-random discrimination by the receiver, but with some possibility of error. In the dark shaded region, the signaller conceals its identity to the greatest extent possible; in the absence of any constraints on its ability to do so, the result is that discrimination is impossible and the receiver is forced to respond favourably regardless of the signaller's identity.

adopting a favourable response towards one (a false alarm) is lower than that of failing to respond appropriately to a desirable signaller (a missed detection). Either factor selects for 'adaptive gullibility' on the part of the receiver. A low value of K , on the other hand, indicates that it is common to encounter an undesirable signaller, and/or that false alarms are more costly relative to missed detections, which selects for 'adaptive fastidiousness' on the part of the receiver.

The parameter L , by contrast, can be thought of as the signaller's incentive to advertise. It is a measure of the relative costs and benefits of advertising identity when a signaller is undesirable to the receiver, and when it is desirable. A high value of L indicates that the signaller is not likely to be undesirable, and/or that the potential cost of advertisement if undesirable is low relative to the potential benefit if desirable. Either factor selects for 'adaptive distinctiveness' on the part of the signaller. A low value of L , on the other hand, indicates that the signaller is likely to be undesirable, or that the potential cost of its advertising when it is undesirable is high relative to the potential benefit

Figure 3. The extent to which, at equilibrium, the receiver can determine whether the signaller is desirable or undesirable, as a function of p (the probability that the signaller is undesirable), for three different values of the ratio $K:L$ (in all cases, $K = 0.9 p/(1-p)$). Accuracy is measured as the probability that the signaller will appear more similar to the receiver's template if it is desirable than if it is undesirable (which ranges from 0.5 to 1). For $L < K < 1$, this probability lies between 0.5 and 1, indicating that the receiver is capable of some discrimination, but that recognition errors will occur.

when it is desirable, which selects for 'adaptive anonymity' on the part of the signaller.

Figure 2 summarizes graphically the predictions of the model for different values of K and L . When $K > 1$ (i.e. $\ln K > 0$), indicated by dark shading in the figure, the signaller should make it as hard as possible for the receiver to determine whether or not it is desirable, regardless of the value of L . The reason for this outcome is that, given the value of K , the receiver does best to respond favourably when lacking any information about the signaller's identity. By concealing all possible signature cues, the signaller can therefore ensure a favourable response.

When $K < 1$, by contrast, the receiver does best to respond unfavourably when lacking any information. The signaller must therefore allow for at least some discrimination by the receiver if it is ever to elicit a favourable response. When $K < L$ (the unshaded region in the figure), the optimal strategy for a signaller is to make it as easy as possible for the receiver to determine what response is appropriate, while if $L < K$ (the lightly shaded region in the figure), the optimal strategy is only partially to reveal identity. In the former region, the receiver is able to acquire perfect information about the signaller's identity, and thus to respond appropriately without error. In the latter region, by contrast, it is able to gain some information and hence to achieve better-than-random discrimination, but will occasionally make mistakes (to the net benefit of the signaller).

Figure 3 looks in more detail at the predicted outcome in the zone of partial information. It shows the level of discrimination possible at equilibrium, measured as the probability that the signaller will be perceived as less similar to the receiver's template

when undesirable than when desirable. The ability to discriminate is shown as a function of p , the probability that the signaller is undesirable, for several different values of the ratio $K:L$. The graph shows that an increase in p , which leads to a corresponding decrease in both K and L , results in the signaller facilitating discrimination to a greater extent. The lower the value of L relative to K (and thus the greater the ratio $K:L$), the larger is the range of values of p over which the signaller does best to partially reveal and partially conceal its identity (rather than completely concealing or completely revealing it).

4. DISCUSSION

Beecher (1991) and Wiley (1994) have both drawn attention to the role of the signaller in the recognition process. Neither, however, incorporates this aspect in their formal analyses. In fact, Beecher (1991) suggests that as regards signalling of identity, 'a simple prediction may not be possible' and 'further empirical studies will prove more fruitful than future modelling'. The above analysis, however, reveals that it is possible to combine both communication and decision problems in a single, unified model of recognition.

The model predicts that the optimal level of information a signaller will provide about its identity depends on the value of only two parameters, K and L , which may be thought of as the receiver's incentive to respond and the signaller's incentive to advertise, respectively. The provision of distinctive signature cues (which allow the receiver to determine whether the signaller is desirable or undesirable) is favoured by low values of K and by high values of L . These correspond to a high cost of acceptance errors relative to rejection errors for the receiver (favouring adaptive fastidiousness), and to a high cost of rejection for the signaller when it is desirable relative to when it is undesirable. In the context of parent-offspring interaction, for example, offspring are more likely to evolve distinctive signature traits that reveal their identity if the cost to parents of mistakenly accepting foreign young is high (e.g. because of intense competition among progeny), or if the cost of mistakenly rejecting their own young is low (e.g. due to a large brood size), because both of these factors lead to adaptive fastidiousness on the part of the parents. Likewise, social insects are more likely to evolve traits indicative of colony membership or kinship if there is a high cost to receivers of admitting alien intruders or aiding non-kin, and/or a low cost of mistakenly rejecting colony mates or relatives.

The fact that selection can (over a wide parameter range) promote such concealment indicates that the 'communication problem' faced by the signaller is of considerable importance in the evolution of recognition systems. One cannot simply assume that discrimination will evolve whenever it would be of benefit to receivers; it is also necessary to determine whether the provision of signature cues would be beneficial to signallers. Kin discrimination, for example, is not an inevitable consequence of kin selection; in some circumstances, indiscriminate altruism may prevail, simply because

selection favours those individuals that conceal their identity (Keller 1997).

Both parameters, K and L , also decrease as the probability that the signaller is undesirable increases. The more commonly a receiver encounters undesirable signallers, the lower its incentive to respond; equally, the more likely a signaller is to prove undesirable, the lower its incentive to reveal its identity. Despite the latter effect, the net result is that the stable level of information transferred will tend to increase as encounters between receivers and undesirable signallers become more likely (see figure 3). Signallers may be less 'willing' to reveal their identity when they are more likely to prove undesirable, but the greater fastidiousness of receivers under these circumstances forces them to do so. Offspring, for instance, are more likely to evolve distinctive signature traits when brood parasitism or extra-pair mating (both of which increase the risk of raising foreign young) are common; equally, social insects are more likely to advertise their identity if encounters with alien intruders are frequent.

This last result highlights the importance of treating recognition as an evolutionary game, in which both the signaller and the receiver can change their behaviour as the relevant parameters change. As far as I am aware, the present model is the first to adopt this approach. As mentioned in the introduction, previous analyses of recognition have largely focused on the decision problem faced by receivers (Reeve 1989; Davies *et al.* 1996; Sherman *et al.* 1997), assuming a fixed level of uncertainty regarding the signallers' identity. These studies show how the relative frequencies of interaction with desirable and undesirable signallers, and the fitness consequences of acceptance and rejection errors, interact to determine the level of adaptive fastidiousness or gullibility shown by receivers. They do not, however, attempt to deal with the 'communication problem' faced by signallers.

Conversely, a recent analysis by Pagel (1997) of paternity advertisement, which does explicitly examine whether selection will favour offspring that reveal or that conceal their identity (i.e. their parentage), excludes consideration of the parental decision problem. Consequently, his study suggests that advertisement of identity is less likely when the frequency of encounter with undesirable signallers is higher (i.e. when more offspring are the product of extra-pair mating), the opposite prediction to that of the present model. When signallers often prove undesirable, they do have a lower incentive to reveal their identity (because this will lead to rejection more often), but receivers also have a lower incentive to respond. As discussed above, the present model, which considers both parties simultaneously, shows that this greater fastidiousness of receivers forces signallers to reveal their identity despite their lower incentive to do so. Advertisement of identity is, surprisingly, more likely when signallers often prove undesirable.

To conclude, it is worth pointing out that many aspects of identity advertisement remain to be investigated. In the present model, I first assumed that signalling was cost-free, i.e. that there are no constraints on the level of information that signallers

choose to provide. In reality, either advertisement or concealment may be costly (Pagel 1997), and the scope of both may be limited (e.g. it may be impossible to completely conceal identity, because too many aspects of an individual's phenotype provide clues to its genotype). It would be interesting to incorporate such constraints in the analysis. Secondly, I assumed that receivers have only two discrete behavioural options. This is appropriate for some situations, e.g. where a parent must choose to accept or reject an egg or a chick, or where a social insect guard must choose whether to admit or repel an entrant into its colony. In other cases, however, there will be a continuum of possible responses.

A final limitation of the present model is its exclusive focus on a single signaller/receiver pair. In many situations, each signaller is either directly or indirectly in competition with others for a favourable response. Parental decisions regarding egg or chick rejection in birds, for instance, involve choice among a number of signallers, as do female decisions regarding mate selection (though in the latter case competing males may not be simultaneously present). Under these circumstances, the optimal level of information provision for an individual signaller depends on the strategy of its competitors, thereby introducing a new level of complexity. Equally, in the context of mate choice, the optimal response threshold for one receiver may depend on the strategies of others (since females are indirectly in competition for desirable mates). Reeve (1989) has developed frequency-dependent decision models which consider how receivers should behave when their fitness depends on the distribution of response thresholds in the population; similar analyses incorporating the signallers' communication problem could yield intriguing results.

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