

THE EVOLUTION OF INDIVIDUAL VARIATION IN COMMUNICATION STRATEGIES

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Communication is a process in which senders provide information via signals and receivers respond accordingly. This process relies on two coevolving conventions: a “sender code” that determines what kind of signal is to be sent given the sender’s state; and a “receiver code” that determines the appropriate responses to different signal types. By means of a simple but generic model, we show that polymorphic sender and receiver strategies emerge naturally during the evolution of communication, and that the number of alternative strategies observed at equilibrium depends on the potential for error in signal production. Our model suggests that alternative communication strategies will evolve whenever senders possess imperfect information about their own quality or state, signals are costly, and genetic mechanisms allow for a correlation between sender and receiver behavior. These findings provide an explanation for recent reports of individual differences in communication strategies, and suggest that the amount of individual variation that can be expected in communication systems depends on the type of information being conveyed. Our model also suggests a link between communication and the evolution of animal personalities, which is that individual differences in the production and interpretation of signals can result in consistent differences in behavior.

KEY WORDS: Animal personality, badges of status, behavioral syndromes, disruptive selection, honest signaling, norms of reaction.

Animal communication involves the transfer of information between senders and receivers via ritualized signals (Bradbury and Vehrencamp 1998; Maynard Smith and Harper 2003; Searcy and Nowicki 2005; but see Scott-Phillips 2008). In most communication systems, this information is encoded through a correlation between signal form and the quality or state of the sender (Bradbury and Vehrencamp 1998). For example, male barn swallows, *Hirundo rustica*, of higher quality tend to have longer ornamental tails (Møller 1988), female paper wasps, *Polistes dominulus*, with better fighting ability tend to have more broken facial patterns (Tibbetts and Dale 2004), and male cichlids, *Pundamilia nyererei*, with better immune response tend to have redder flanks

(Dijkstra et al. 2007). How such correlations evolve and are maintained at equilibrium has been the focus of scientific attention for several decades.

The rules by which senders translate quality into signals and receivers choose how to respond to these signals are known as the “sender code” or “signaler strategy,” and the “receiver code” or “receiver strategy” (Bradbury and Vehrencamp 1998; Dugatkin and Reeve 1998). These behavioral blueprints (e.g., Fig. 1) can only be evolutionarily stable if they benefit both parties (at least on average, see Johnstone and Grafen 1993). Otherwise, senders will stop signaling, receivers will stop responding, and communication will eventually break down (Bradbury and Vehrencamp 1998;

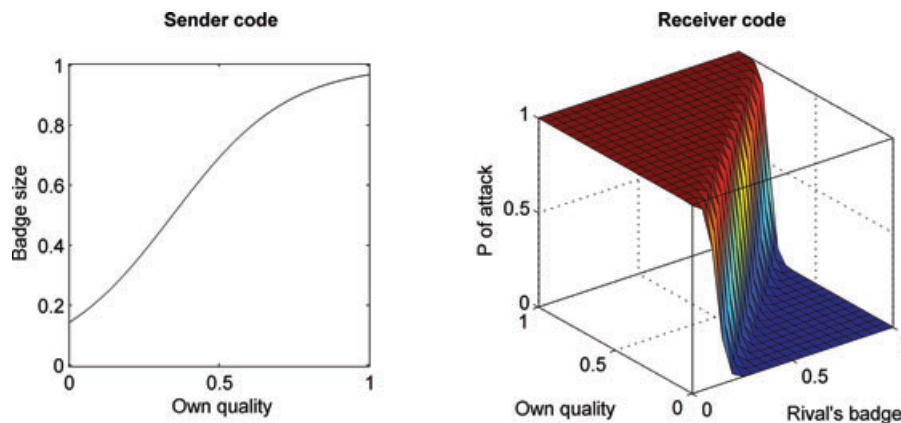


Figure 1. Heritable norms of reaction that define signaling and signal interpretation strategies in our model. During development, an individual produces a badge of size determined by its sender code: $\text{Badge size} = 1/(1 + \exp[a_s - b_s Q])$. In this equation, a_s and b_s are inherited traits and Q is the individual's estimate of its own quality. During the interaction phase, the probability of attacking an opponent upon encounter is determined by the receiver code: $\text{Probability of attack} = 1/(1 + \exp[a_r - b_r Q - c_r B])$. In this equation, a_r , b_r , and c_r are inherited traits, and B is the size of the opponent's badge. This figure depicts the sender and receiver codes corresponding to the trait values $a_s = 1.802$, $b_s = 5.221$, $a_r = -5.340$, $b_r = 47.196$, and $c_r = -43.309$, which are the values that evolved on average in the evolutionary simulations depicted in Figure 2.

Searcy and Nowicki 2005). It follows from this basic argument that signals must be “honest” on average for communication to be stable. More specifically, there needs to be a general agreement on what signals mean (i.e., a standard sender code), and a mechanism to enforce adherence to such standard. The first condition is achieved through the coevolution of sender and receiver behavior, and the second through constraints or selection on senders (for reviews on this topic see Bradbury and Vehrencamp 1998; Maynard Smith and Harper 2003; Searcy and Nowicki 2005). In some systems, communication may be immune to exaggeration because it involves signals that are impossible to fake (Maynard Smith and Parker 1976; Maynard Smith and Harper 2003). For example, the funnel-web spider, *Agelenopsis aperta*, uses ritualized web vibrations to exchange information about body size during agonistic contests. These signals are “honest” because more mass is required to produce more intense vibrations and as a consequence, lighter individuals cannot vibrate the web as intensely as heavier ones (Riechert 1978). In other systems, signals remain honest because senders that adhere to the standard convention do better than those that exaggerate or lie (Maynard Smith 1956; Enquist 1985). Examples of this situation may include communication among relatives or between individuals with common interests (Reeve 1997; Bergstrom and Lachmann 1998; Johnstone 1998). Additionally, honesty can be enforced through quality-dependent costs of signal production, maintenance, or use (Zahavi 1974, 1975; Grafen 1990a; Johnstone 1994; Berglund et al. 1996; Molles and Vehrencamp 2001). Such is the case in widowbirds, *Euplectes jacksoni*, where low-quality males cannot afford to display as intensely as high-quality ones because they suffer from comparatively higher weight loss and mortality (Andersson 1994).

The idea that stable communication requires an agreement on what signals mean suggests that selection should favor the evolution of somewhat uniform communication behaviors. Nevertheless, communication codes often exhibit considerable variation in natural systems and regression models typically account for only a relatively small fraction of that variation (e.g., see Fig. 3 in Veiga 1993; or Fig. 2 in Andersson 1994). The unaccounted variance in communication codes could be noise associated with the process of mutation–selection balance (see Hartl and Clark 1997) or with errors in the senders' estimates of own quality or the receivers' perception of signals (Guilford and Dawkins 1991; Johnstone and Grafen 1992; De Jaegher 2003). Noisy codes may also be the consequence of weak selection for higher accuracy because the costs associated with more accurate structures for signal production or perception can often be higher than the benefits of more accurate communication (Bradbury and Vehrencamp 1998, 2000). Additionally, it is also possible that some deviations from average behaviors are strategic attempts to exploit population conventions through “dishonest” signaling (Johnstone and Grafen 1993; Adams and Mesterton-Gibbons 1995; Hurd 1997; Számadó 2000, 2008; Hamblin and Hurd 2007). Such possibility has been explored in theoretical models that have assessed the ability of mutant “cheaters” to persist in populations of honest signalers. These models have shown that if ignoring signals is costly, senders can sometimes get away with exaggeration (Gardner and Morris 1989; Johnstone and Grafen 1993; Számadó 2000; Rowell et al. 2006). The generality of this result remains to be proven given that it is based on highly simplified models of communication in which, for example, signal categories and receiver responses are discrete (in fact, many of these models are variants of a single

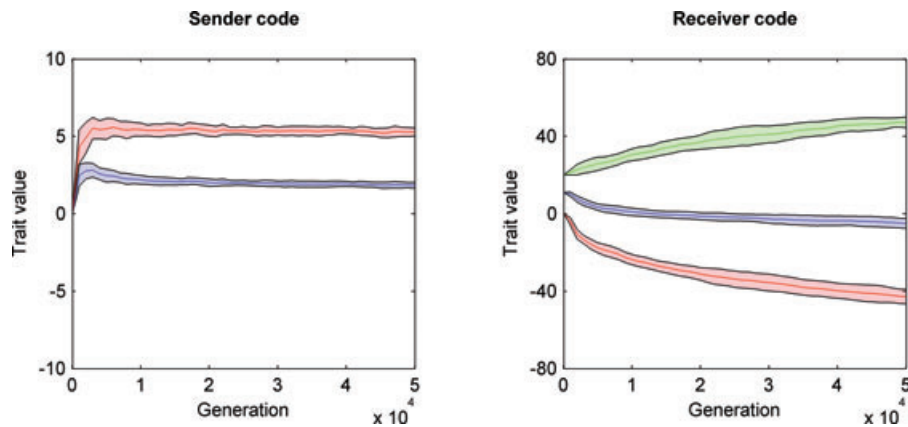


Figure 2. Evolutionary trajectories of the heritable traits in our model. Sender ($a_s = \text{blue}$, $b_s = \text{red}$), and receiver codes ($a_r = \text{blue}$, $b_r = \text{green}$, and $c_r = \text{red}$) in simulation runs where the benefit of winning is $V = 1$ and the cost of losing a fight is $L = -3$. Solid lines represent the mean values for 100 replicate simulation runs and shaded regions represent one standard deviation from the mean. Although the slopes of the receiver code are still undergoing slight adjustments at generation 50,000, communication codes are at this point essentially identical to those observed up to 150,000 generations later (data not shown). Such qualitative stability is a consequence of the already strong effects that changes in quality and badge size have on the probability of attack by generation 50,000, and the fact that even steeper slopes can do very little to alter the overall shape of the receiver code surface at this point.

model proposed by Enquist 1985). Additionally, most models of “cheating” assume that communication is error free and this unrealistic assumption may lead to wrong conclusions about the nature of evolutionary stable strategies (see Johnstone and Grafen 1992).

An intriguing possibility is that some of the variation in communication codes is the product of consistent differences in indi-

vidual behavior known as animal personalities (reviewed by Dall et al. 2004), or behavioral syndromes (reviewed by Sih et al. 2004). This possibility requires a distinction between behavioral polymorphisms and polymorphic communication codes. In the case of the sender code, a behavioral polymorphism can be the product of a shared norm of reaction that leads individuals of similar quality

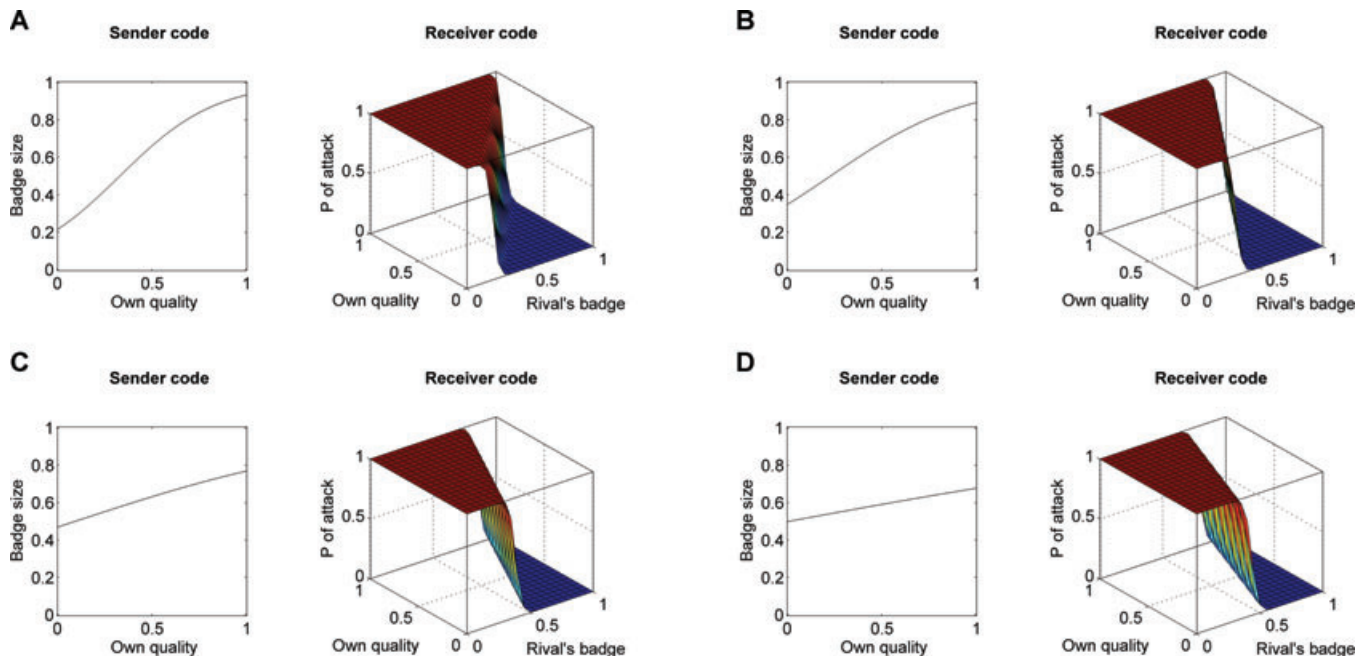


Figure 3. Mean sender and receiver codes predicted by models with different amounts of error in the sender's estimation of own quality. Individual quality varies throughout lifetime in this model and senders are allowed to estimate their current quality before badge production and prior to each interaction. Errors in self-perception are drawn from $N(\mu = 0.5, \sigma = \sigma_E)$. (A) $\sigma_E = 0.05$, (B) $\sigma_E = 0.1$, (C) $\sigma_E = 0.15$, and (D) $\sigma_E = 0.2$.

to produce similar signals and individuals of different quality to produce signals of different intensity. In contrast, a polymorphism in sender codes implies that multiple communication standards (i.e., norms of reaction) coexist within the population and that, as a consequence, individuals of similar quality may produce signals of different intensity. Polymorphic sender codes such as these were recently found in the European barn swallow, *H. rustica*, in which males of similar quality follow different rules for resource allocation during tail production (Muñoz et al. 2008). Similarly, male song sparrows, *Melospiza melodia*, show consistent differences in their responses to playback (Nowicki et al. 2002). The models of “cheating” discussed above provide a first step toward understanding this phenomenon by showing that sender codes that exaggerate quality can indeed persist within a population of “honest” signalers. Nevertheless, the studies on swallows and sparrows suggest that polymorphisms can be more subtle, and that alternative strategies may even include “shy” codes that understate quality instead of exaggerating it. This kind of polymorphic equilibrium was indeed observed by Hamblin and Hurd (2007) in evolutionary simulations inspired by Enquist’s (1985) conventional signaling model. However, the authors point out that these polymorphic outcomes occur only rarely in that model (1.3% of replicates) and that it is possible that they are the product of unstable local attractors (Hamblin and Hurd 2007).

Here, we show that polymorphic sender and receiver codes can in fact be common in natural communication systems, and that the number of communication strategies that coexist at equilibrium depends on the potential for error in signal production. We present a model of animal communication based on a general framework in which sender and receiver codes are represented by heritable norms of reaction (see Fuller et al. 2005) that evolve in individual-based simulations (also known as Genetic Algorithms, see van Doorn et al. 2003a,b). This framework captures some key, yet poorly explored aspects of the inherent complexity of communication such as the heritable and conditional nature of communication strategies, the possibility of individual differences, and the coevolution of sender and receiver codes. Our model is based on a situation in which individuals signal their “quality” (more specifically, their fighting ability) in agonistic interactions with rivals. Each individual is repeatedly confronted with rivals and must repeatedly choose whether to attack or not. Individuals differ in quality and in case of escalation the opponent of higher quality has a higher probability of winning the fight. In a situation like this, signaling quality may be profitable because it can help avoid costly escalation. When talking about signals, we imagine the badges of status of birds and invertebrates (Johnstone and Norris 1993) or the enlarged chelae of crayfish (Bywater et al. 2008). Accordingly, we use the terms “signal intensity” and “badge size” interchangeably in the description of the model.

Individual-based Simulation Model of Communication

We envision communication behaviors as two heritable norms of reaction subject to mutation and natural selection. Individual genotypes are composed of two gene loci that determine the shape of an individual’s Sender Code (a_s , b_s), and three gene loci that determine the shape of its Receiver Code (a_r , b_r , and c_r). When characterizing a strategy by two (or three) parameters, we do not wish to imply that these strategies are encoded in nature by such a specific number of loci. Rather, we use this terminology as a metaphor to relate how one might imagine the genetic determination of norms of reaction.

In our model, the Sender Code tells the individual what signal intensity to express given its own quality and the Receiver Code tells it how to behave in confrontations with rivals. Specifically, the Sender Code (Fig. 1) is modeled as,

$$\text{badge size} = 1/(1 + \exp[a_s - b_s Q]),$$

where a_s and b_s are inherited traits, and Q is the individual’s own quality. This equation implies that the Sender Code can either be flat or can take the form of a logistic curve in which a_s helps determine the point of inflection and b_s determines the slope. Its flexible architecture can describe a wide range of signaling strategies through simple changes in the values of a_s and b_s . For example, badge size may be independent of quality (e.g., always maximum size, always intermediate size, or always minimum size), or may increase or decrease in proportion to individual quality.

The Receiver Code (Fig. 1) is modeled as,

$$\text{probability of attack} = P = 1/(1 + \exp[a_r - b_r Q - c_r B]),$$

where a_r , b_r , and c_r are inherited traits, Q is the receiver’s own quality, and B is the size of the opponent’s badge. This code is a multilogistic surface in which b_r and c_r are the slopes with respect to Q and B , and a_r helps determine the point of inflection. As with the Sender Code, this code is a flexible equation that allows a wide range of strategies for responding to signals. For example, receivers may always attack, never attack, or may be more/less likely to attack depending on their own quality, the size of the opponent’s badge, or both.

We modeled communication strategies as logistic equations because this family of functions can describe a wide range of alternative strategies with only minor changes in a small number of parameters. Furthermore, this type of equation is often invoked in the analysis of field data on communication and is, thus, familiar to empiricists. Field biologists typically use logistic regression models to determine whether the probability of a receiver’s response is affected by the sender’s signals. If the data do not fit a

simple regression model, for example when receiver responses are not monotonically related to one or more of the explanatory variables, researchers often extend these models by adding quadratic or cubic terms (see below).

Our simulations are based on a population of 3000 individuals and cover a time span of 50,000 nonoverlapping generations. At birth, individuals are assigned quality levels (0 = worst, 1 = best), drawn from a truncated normal distribution, $N(\mu = 0.5, \sigma = 0.15)$. Subsequently, they use their personal Sender Codes to produce badges that remain constant throughout life. Following Grafen (1990b), signal costs are modeled as a reduction in survival probability that depends on the individual's own quality and the intensity of the signal. Thus,

$$\text{survival probability} = 1/(1 + \exp[k_1 + k_2(Q - B)]),$$

where Q is the individual's quality, B is the size of the badge, and k_1 and k_2 are scaling constants. Given negative values for k_1 and k_2 , this cost function implies that larger badges will reduce survival probability and that this effect will be stronger in lower quality individuals. An alternative model formulation in which signals are produced every time they are needed and costs are expressed as a reduction in fecundity rather than survival is presented in the Supporting information.

After an initial round of viability selection, survivors interact with each other. Each survivor is allowed to interact with five rivals chosen at random from the pool of other survivors (no mortality occurs at this stage). Upon encounter, rivals use their personal Receiver Codes to decide whether to attack or not. Payoffs are determined as in the well-known Hawk-and-Dove game (Maynard Smith 1982). If only one rival attacks, the attacker gets V whereas the other gets nothing. If both withdraw they both get nothing. When both individuals attack they fight, and the probability of winning depends on relative quality. Thus,

$$\begin{aligned} \text{ego's probability of winning} = \\ 1/(1 + \exp[-k_3(Q_{\text{ego}} - Q_{\text{opponent}})]), \end{aligned}$$

where the Q 's represent individual qualities and k_3 is a positive scaling constant. The winner in a fight gets V and the loser pays a cost of L (with $|L| > V$ following Maynard Smith and Harper 1988).

At the end of each generation, survivors reproduce with a probability determined by the payoffs collected during the interaction phase. Reproduction probabilities are computed by rescaling cumulative payoffs so that the lowest amount is equal to zero and the highest is equal to 1. Offspring inherit the alleles at five gene loci (a_s , b_s , a_r , b_r , and c_r) with mutation probabilities of 0.001 and mutational steps drawn from a normal distribution with mean zero and a standard deviation of 2 (i.e., 2% of the traits' plausible range).

The natural starting point of evolutionary simulations of communication is a population in which signal intensities do not yet convey information on individual quality. However, even in this primordial state individuals should be able to make optimal fighting decisions based on their private knowledge of own quality. To achieve this, we fixed signal intensity to an intermediate value (0.5) and allowed the receiver code to evolve for 50,000 generations. As expected, receiver codes evolved such that the probability of attack was higher for individuals of higher quality. We repeated this process 10 times and then used the mean final values for the five inherited traits as the starting condition. The results reported below are based on $V = 1$, $L = -3$, $k_1 = -3$, $k_2 = -6$, and $k_3 = 10$.

The first model we consider assumes that loci determining communication behaviors are inherited from a single parent (i.e., sex-linked traits or asexual reproduction). In 100 of 100 simulations, communication codes converged rapidly to equilibrium (Fig. 2). As expected from costly signaling theory, the average sender code evolves into a norm of reaction where individuals of higher quality produce larger badges (as in Fig. 1, which reflects the average outcome of the simulation in Fig. 2). The average receiver code at equilibrium is a norm of reaction where the probability of attack increases with own quality but decreases with the size of the opponent's badge (see Fig. 1).

EFFECTS OF PERCEPTUAL ERRORS ON THE EVOLUTION OF ANIMAL COMMUNICATION

It is reasonable to assume that individuals err in their estimation of own quality (Johnstone and Grafen 1992). To study how these errors influence the evolution of communication, we incorporated slight changes in individual quality throughout lifetime by modifying the quality assigned at birth prior to badge production and before each agonistic interaction ($Q_{\text{current}} = Q + e$, where e is drawn each time from $N(\mu = 0, \sigma = 0.05)$). In the simulations described below, individuals were allowed to estimate their current quality every time it was recomputed and the errors in these estimates were drawn from $N(\mu = 0, \sigma_E)$. Additional simulations in which errors were only incorporated either during badge production or during the interaction phase yielded qualitatively identical results (data not shown). We present results for simulations in which $\sigma_E = 0.05, 0.1, 0.15$, and 0.2 . All other details of the model remain unchanged.

Figure 3 shows the average Sender and Receiver Codes at generation 50,000 for 100 replicate simulation runs under the different error levels in the perception of own quality. As expected, communication codes become less sensitive to changes in Q with increasing error in self-perception. Given the results of our previous model, we originally assumed that natural selection would produce a single, yet somewhat different, stable combination of sender and receiver codes at each error level. However, upon

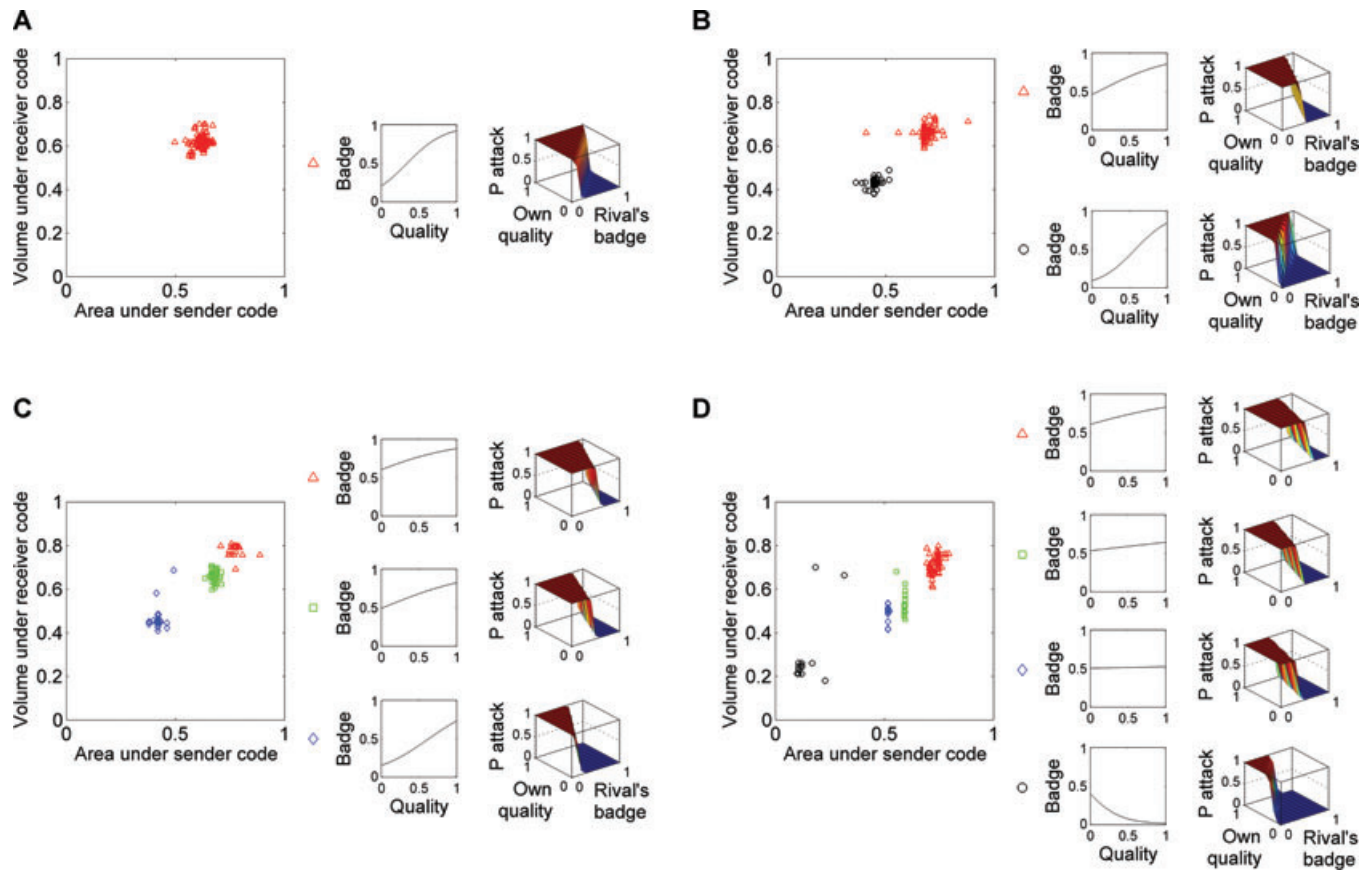


Figure 4. Individual variation in communication strategies predicted by our model of badges of status. To the left, we show the intensity of sender and receiver codes for all individuals in the last generation of representative replicate simulation runs under different values for σ_E . As confirmed through cluster analysis (see data labels), our model predicts the emergence and stable coexistence of fairly distinct communication strategies for $\sigma_E > 0.1$. The striking behavioral differences among strategies are shown to the right in plots of the average sender and receiver codes of individuals of each type. (A) $\sigma_E = 0.05$, (B) $\sigma_E = 0.1$, (C) $\sigma_E = 0.15$, and (D) $\sigma_E = 0.2$.

inspection of the individual distribution of traits in the last generation of the different replicates, we discovered that individual behaviors were strikingly different from the average population codes. To explore the nature of this variation, we summarized each sender code with its average signal intensity (i.e., the area under this curve) and each receiver code with its average probability of attack (i.e., the volume under this surface). Figure 4 depicts these summary statistics for each of the 3000 individuals at the end of a representative simulation run for the different error levels.

Our model shows that imperfect knowledge of own quality leads to the emergence and coexistence of alternative communication strategies. Furthermore, it predicts that the number of alternative strategies that coexist at equilibrium and the pattern of variation observed within each strategy depend on the magnitude of σ_E . When there is no error (i.e., basic model described above) or when the potential for error is low (i.e., $\sigma_E = 0.05$), populations converge into a single, stable combination of sender and receiver codes in every replicate simulation run (Fig. 4A). However, when $\sigma_E = 0.1$ populations exhibit two distinct com-

munication strategies with clear differences in sender and receiver codes (mean \pm SE = 1.86 ± 0.08 clusters per replicate). The first type (depicted as solid triangles in Fig. 4B) is very aggressive. It produces larger badges at all quality levels, and shows a high probability of attack during fights. The second type (depicted as open circles in Fig. 4B) is more conservative. It produces smaller badge sizes and has a lower probability of attacking during fights. The presence of these distinct communication strategies can be detected early on in our simulation (i.e., as early as generation 500) and is maintained until the final generation. Most interestingly, models with even higher σ_E yield populations with a larger number of coexisting personality clusters. For example, populations typically exhibit three distinct communication strategies at $\sigma_E = 0.15$ (mean \pm SE = 2.75 ± 0.09 clusters, Fig. 4C), and even four different strategies at $\sigma_E = 0.2$ (mean \pm SE = 3.21 ± 0.08 clusters, Fig. 4D).

An intuitive interpretation of how distinct “communication styles” emerge is the following. Complementary sender and receiver codes are favored initially because they can help individuals

avoid the costly escalation of fights with stronger opponents (see Bradbury and Vehrencamp 1998, 2000). Once these codes are established they can be easily exploited by mutant strategies that take advantage of the average population behavior. For example, a strategy that signals at slightly higher levels than the average will gain some benefits from bluffing while a strategy that signals at slightly lower levels than the average will benefit from exploiting the signals of others while paying lower signaling costs. These two mutant strategies will be successful when rare but will experience high variability in payoffs as they become more common. Furthermore, their relative frequencies depend on each other because when changes in the number of senders that exaggerate quality are not accompanied by reciprocal changes in the number of senders that understate it (or the other way around), directional selection on the receiver code will lead to changes in the average communication behaviors that will prevent any further exploitation. Given these highly restrictive conditions, we suspect that signaling polymorphisms such as these will be rare or highly unstable (see Supporting information). The emergence and coexistence of alternative types may be facilitated by errors in self-perception because mutant strategies similar to the ones described above can also exploit uncertainties regarding an individual's ability to win a fight. In error-prone systems, overestimation of fighting ability can lead to extra signaling costs and fights with stronger opponents. Similarly, underestimation of own quality can lead to missed opportunities for acquiring resources. These costly mistakes have a negative impact on fitness and can be exploited by

bluffing strategies that invest more heavily into signaling and are more likely to attack. However, as the average signal intensity in the population increases, the high signaling costs required for bluffing begin outweighing the benefits of this strategy. Under these conditions, risk-averse individuals that invest little into signals and attack only under optimal conditions (i.e., when they are strong and the opponent appears to be weak) can have a similar fitness to the more aggressive types. At equilibrium, the relative frequency of each type depends upon the costs of signaling and the benefits of bluffing (Fig. 5).

ANALYTICAL MODEL OF THE COEXISTENCE OF PERSONALITY TYPES

We explored the role of frequency-dependent selection on the coexistence of communication strategies more formally with a simplified analytical model (for a detailed description of this model see Supporting information). In this model, individuals can be strong or weak and can produce a badge or not. Conservative individuals only produce a badge when strong and only attack when strong and their opponent does not have a badge. Aggressive individuals always produce a badge and always attack, unless they are weak and the opponent has a badge. Moderate individuals produce a badge with probability 1.0 when strong and with probability 0.5 when weak. These same individuals always attack when strong, never attack when weak and their opponent has a badge, and attack with probability 0.5 when weak and their opponent does not have a badge. This simplified model shows that

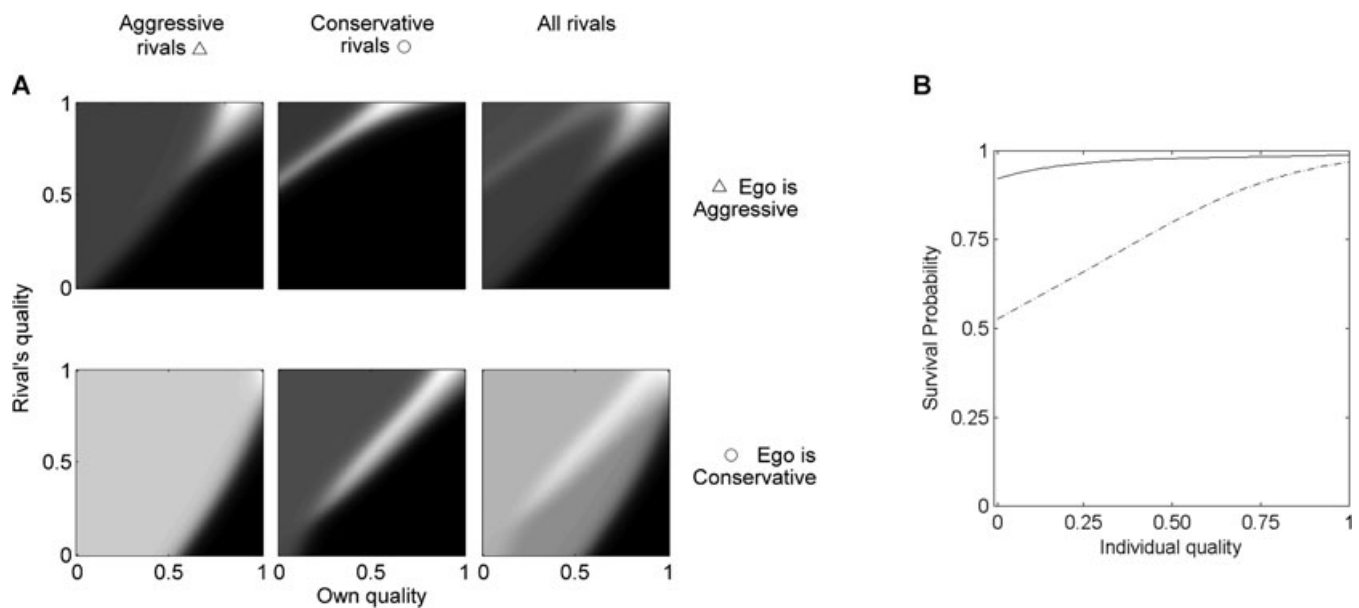


Figure 5. (A) Expected payoffs and (B) survival probabilities of alternative communication strategies at $\sigma_E = 0.1$. As in Figure 4B, aggressive individuals are depicted with triangles (broken line in B) and conservative individuals with open circles (solid line in B). Payoffs for Ego are computed against rivals of different qualities and with different communication strategies (darker regions imply higher payoffs). Although aggressive individuals obtain more resources in confrontations with rivals, conservative ones show much higher survival probability.

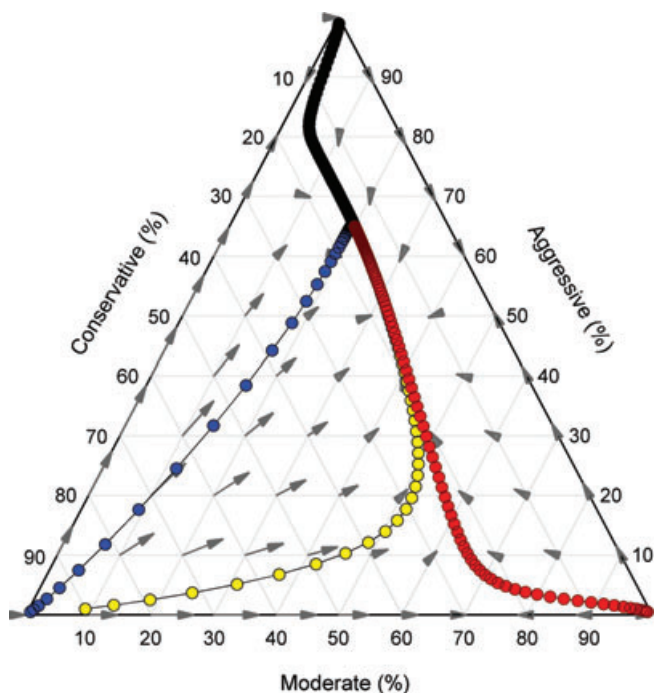


Figure 6. Evolutionary dynamics of the frequency distribution of Aggressive, Moderate, and Conservative types. These three idealized conventions were modeled after the communication strategies observed in our individual-based simulations (see Supporting information). For the parameters chosen, the system settles at a polymorphic equilibrium with the following frequencies: Aggressive = 0.65, Moderate = 0.20, and Conservative = 0.15.

no single strategy is immune to invasion by the others and that, as seen in the individual-based simulations, the system will converge toward an equilibrium with a majority of aggressive individuals (Fig. 6).

EFFECTS OF BEHAVIORAL FLEXIBILITY ON THE EVOLUTION OF COMMUNICATION

The equations used to describe communication codes in our model may impose some arbitrary constraints on the evolution of these behaviors (Dieckmann et al. 2006). For example, simple logistic equations are monotonic and, thus, maximum badge size or maximum probability of attack can only occur at extreme values of *Q* and/or *B*. To test whether the evolution of personality clusters is related to the functional form of the norms of reaction, we included quadratic terms in the evolving communication codes. In this version of our model, communication codes are defined as,

$$\text{badge size} = 1/(1 + \exp [a_s - b_s Q - c_s Q^2]),$$

probability of attack =

$$1/(1 + \exp [a_r - b_r Q - c_r Q^2 - d_r B - e_r B^2]),$$

where *Q* is the individual’s own quality, and *B* is the rival’s badge. The quadratic terms in these equations allow these codes to reach a maximum or a minimum at intermediate values of *Q* and/or *B*.

Modeling communication codes with these alternative equations yield qualitatively identical results to those reported above. For example, at $\sigma_E = 0.05$, populations converge into a single stable strategy and, at $\sigma_E = 0.1$, they exhibit two distinct personality clusters (mean \pm SE = 1.77 \pm 0.06 clusters, Fig. S2). The clusters observed in this case are equivalent to those achieved using simple logistic equations (compare Fig. 4B with Fig. S2). Identical results are obtained when communication codes include both a quadratic and a cubic term (data not shown).

EFFECTS OF GENETIC ASSUMPTIONS ON THE EVOLUTION OF COMMUNICATION

The genes affecting communication behaviors may also be located in autosomes and thus, may be exposed to recombination during sexual reproduction. We studied the effects of recombination on the evolution of signals by modifying our algorithm for reproduction. Individuals are also haploid in this model, but each offspring receives alleles from two parents. Sexual partners are selected from the pool of survivors at the end of each generation based on the payoffs collected during the interaction phase (probability of breeding is computed as above and communication codes are modeled as simple logistic equations).

Communication evolves quickly when loci segregate independently under different probabilities of recombination, *R* (*R* = 0.1, 0.25, and 0.5), and the average Sender and Receiver Codes at equilibrium are qualitatively identical to those of models without recombination. However, under the simple form of recombination implemented in this model there is no emergence of alternative communication strategies. For example, all replicates with $\sigma_E = 0.15$ show a single stable combination of Sender and Receiver Codes equivalent to the strategy observed in models with no sender error and no recombination (see Fig. 1).

The loss of personality clusters in the model with recombination is due to a lack of mechanisms that allow a correlation between traits. Adaptive norms of reaction rely on specific combinations of slopes and points of inflection and the values for these parameters are very different in aggressive than in conservative codes. When traits segregate independently, the point of inflection of a conservative code may be recombined with the slope of an aggressive one leading to a maladaptive norm of reaction that resembles neither of the parental phenotypes. Because of the possibility of such maladaptive combinations, selection favors standard trait values at each locus that yield successful communication behaviors no matter how they are recombined during reproduction.

An alternative way to model sexual recombination is to envision all the parameters that define each norm of reaction as different expressions of a single gene locus (or as traits with high linkage disequilibrium). We explored this possibility with a model in which recombination leads to offspring that receive all

the parameters for the sender code from one parent and all the parameters for the receiver code from another. As in the model with full recombination, this model yields a single communication strategy at $R = 0.1, 0.25,$ and 0.5 . Once again, the lack of personality clusters can be attributed to selection for standard behaviors that are not penalized by recombination. If alternative strategies were to evolve in this system, cross-strategy recombination would be penalized because offspring with aggressive sender codes and conservative receiver codes would have low survival and a reduced ability to accumulate resources. Similarly, offspring with the opposite combination would have a higher probability of being attacked and would engage more often than others in escalated fights.

The results of the recombination models described above show that the emergence of alternative communication strategies relies on mechanisms that enable the stability of adaptive norms of reaction and a correlation between sender and receiver behavior. At a very basic level, these requirements can be met with high linkage disequilibrium between all traits or with sex-linked loci for communication behaviors. We hypothesized that alternative communication strategies could also emerge more generally whenever mechanisms that allow a correlation between sender and receiver behavior are in place. As a starting point, we tested this hypothesis with a new model in which traits segregate independently and an additional trait, m , modulates the expression of the points of inflection in both the Sender and the Receiver code. As all traits in this model, m is inherited from a single parent and is subject to mutation and natural selection. Phenotypic values for the points of inflection are then calculated as $a_s = a'_s + m$, and $a_r = a'_r + 1.5 m$, where a'_s and a'_r are alleles inherited from the parents (the difference in the effect of m is to account for differences in the typical magnitudes of a_s and a_r , see Figs. 1 and 2). Thus, negative values for m increase aggressiveness (i.e., lead to higher investment in signals and higher probabilities of attack), whereas positive ones do the opposite. Although this model is admittedly crude, it allows us to explore how a simple mechanism that enables correlation between sender and receiver behavior influences the evolution of individual variation in communication strategies. As in the case with full recombination, populations evolve standard trait values at the five communication loci. Nevertheless, these populations exhibit a polymorphism in m that effectively yields alternative strategies resembling those of the asexual model (e.g., when $\sigma_E = 0.15$: mean \pm SE = 2.46 ± 0.09 clusters, Figs. S3 and S4).

Discussion

We conclude that individuals within a population may employ vastly different communication strategies and that these strategies will coexist via frequency-dependent selection (see Számádó 2000). Our model predicts that alternative communication strate-

gies will evolve whenever (1) senders possess imperfect information about their own quality or state, (2) signals are costly, and (3) genetic mechanisms allow for a correlation between sender and receiver behavior. The first two criteria generate an opportunity for strategies that differ in risk-taking behavior to derive similar payoffs (as in Wolf et al. 2007), and the last criterion allows adaptive combinations of sender and receiver behaviors to persist in spite of being different from the average population behavior.

There are several potential sources of error in natural systems that could act alone or in combination to yield errors of comparable magnitude to the ones required for the emergence of polymorphisms in our model (i.e., $\sigma_E > 0.05$). For example, there is potential for error in individual judgment and for arbitrary biases to emerge when prior-experiences are not representative of the whole population of rivals (e.g., see Whitehouse 1997). Errors are also possible when self-assessment relies on noncognitive mechanisms. For example, testosterone levels are highly correlated with fighting ability and may be a good physiological indicator of individual quality (Oyegbile and Marler 2005; Wingfield 2005). However, because hormones can be mobilized very rapidly within the body with important consequences on behavior (e.g., Sachs and Leipheimer 1988), testosterone titers, and consequently fighting ability, could be very different between the time of signal production and the time of signal use. This problem is particularly evident in signals such as the badges of status, which are produced weeks or months before they are actually used. Such time lag allows this and other processes to affect individual quality in the interim. Additionally, uncertainty regarding the probability of winning a fight can have similar effects to those of an error in self perception. Such uncertainty will occur whenever the outcome of fights is not solely determined by relative differences in fighting ability, such as when strategic advantages, random events, or even personal motivation may influence the probability of winning.

The relationship between the errors in perception of own quality and the number of personality clusters in our model suggests that we can expect the amount of individual variation in communication systems to depend on the type of information being conveyed. For example, systems in which signals reflect an individual's perception of relative quality are likely to show highly polymorphic codes because senders are unlikely to have perfect information about the quality of their rivals. On the other hand, signals of individual ability, current condition, or foraging ability, are likely to exhibit less polymorphism because senders can estimate these variables more precisely. One possible method to detect and account for polymorphic communication codes in field studies is to compare signal/response intensity for individuals of similar quality at different quality levels. If communication codes are polymorphic, signals/responses should show discrete clusters at each quality level and the number of clusters should be

consistent across a broad range of quality levels (except perhaps at the extremes because individuals of very high or very low quality might behave in the same way regardless of the code they follow, see Figs. 4, S2, and S3).

The possibility of individual differences in communication strategies has important conceptual implications for empirical studies. The first one is that a single regression line may not be appropriate for describing sender or receiving codes in most natural systems. Whenever multiple coding schemes coexist within a population, field data will appear overdispersed if fitted to a single model, and the evolutionary importance of communication may be drastically underestimated. A second implication is that judging signal “honesty” as the magnitude of the residual from the average population code (a common practice in communication studies) can be oversimplifying and misleading. In our simulations, every alternative strategy is “honest” in the sense that high-quality individuals produce more intense signals than lower quality ones. Nevertheless, it is the differences across strategies that create the impression of “deception”: moderate signals will appear overstated to conservative individuals but understated to more aggressive types. Thus, the concept of signal “honesty” can be highly misleading in the analysis of dyadic interactions but is still useful as a reminder that senders are playing against the field (i.e., that individual communication codes are selected against the average population behaviors).

A third implication is that the evolution of communication strategies is deeply tied to the evolution of stable differences in individual behavior known as animal personalities. It is becoming increasingly clear that adaptive explanations for animal personalities are not only possible but likely (Dall et al. 2004; Reale et al. 2007; Wolf et al. 2007, 2008), and that the degree and structure of variation in personality can have strong effects on evolutionary processes (McNamara et al. 2004). The communication strategies that emerge in our model lead to stable differences in signaling behavior and aggressiveness. Hence, our model provides an adaptive explanation for the coexistence of animal personalities: when individuals produce and perceive signals in consistently different ways, they will also show consistent differences in behavior.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Mean sender and receiver codes predicted by our alternative formulation of the model of badges of status with different amounts of error in the sender's estimation of own quality.

Figure S2. Individual variation in communication strategies in a representative replicate simulation run with quadratic logistic communication codes and $\sigma_E = 0.1$.

Figure S3. Individual variation in communication strategies in a representative replicate simulation run with sexual reproduction, recombination rate of 0.5, and $\sigma_E = 0.15$.

Figure S4. Histogram of trait values for the *m* locus in the replicate simulation run of the sexual recombination model depicted in Figure S3.

Figure S5. Mean sender and receiver codes predicted by our model of dynamic signals (e.g., crest erection in birds) with different amounts of error in the sender's estimation of own quality.

Supporting Information may be found in the online version of this article.

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