# **Optimal Investment in Social Signals**

Jean-Louis Dessalles

Telecom ParisTech - LTCI - CNRS UMR 5141

Paris

dessalles@telecom-paristech.fr

www.dessalles.fr

This study is an attempt to determine how much individuals should invest in social communication, depending on the type of relationships they may form. Two simple models of social relationships are considered. In both models, individuals emit costly signals to advertise their "quality" as potential friends. Relationships are asymmetrical or symmetrical. In the asymmetrical condition (first model), we observe that low-quality individuals are discouraged from signaling. In the symmetrical condition (second model), all individuals invest in communication. In both models, high-quality individuals ("elite") do not compete and signal uniformly. The level of this uniform signal and the size of the "elite" turn out to be controlled by the accuracy of signals. The two models may be relevant to several aspects of animal and human social communication.

Keywords: signaling, social selection, honest communication, friendship, social behavior.

## Social signaling

Social signaling is understood here as any signaling behavior that correlates with the establishment and maintenance of social bonds, such as friendship or supportive alliances. This definition applies to several important aspects of animal and human societies (Dunbar, 1996). Social bonds differ however from some other forms of social interactions such as dominance relationships or cooperation. Social bonds can be many-to-one or many-to-many, they can be symmetrical and they are based on an elective process, in which individuals choose their social partners freely. This choice is supposed to be based on social signals that any individual may emit. Social bonding therefore presupposes a *dual competition*: signalers compete to attract social mates, while observers may be in competition to get acquainted with the same individuals.

The issue addressed in this paper is whether individuals are ready to invest in social signals in a context in which attracting friends gives an advantage. More precisely, we want to know how much individuals will invest in the social signaling competition and determine if their investment can be evolutionarily stable.

In recent years, various aspects of animal behavior have been presented as social signals. For instance, it has been proposed that predator mobbing in birds could be a bravery display directed at group mates (Zahavi & Zahavi, 1997, p. 144; Maklakov, 2002). According to Zahavi, animals would engage in costly displays to increase their "prestige" in the group, and therefore to get a higher social status. According to Maklakov, mobbing behavior by Arabian babblers (Turdoides squamiceps) is more intensely performed by subordinate individuals than by dominant breeders. This difference would be more consistent with a signaling, rather than protective, function of mobbing (Maklakov, 2002; but see: Ostreiher, 2003). It could result from the fact that subordinates are more likely to disperse and thus must choose each other to form new coalitions (Maklakov, 2002). Similarly, grooming behavior in primates is known to be correlated with the formation of alliances (Dunbar, 1996; Silk et al. 2006; Mitani, 2009). It is analyzed as a way of signaling the groomer's readiness to form an alliance with the groomee rather than as a mere favor exchange (Dunbar, 1996; Silk et al. 2006). In some hunter-gatherers cultures, sharing meat after a successful hunt may be a social signal (Hawkes, 1991; Bliege Bird & Smith, 2005). Hunting behavior patterns have been shown to be more consistent with signaling than with reciprocal cooperation. Hunters devote more time to hunting overly large prey, despite the lower average calorie return of their strategy, because big catches offer them opportunities to display their hunting skills. Signaling behavior has been invoked to explain other aspects of human behavior, including ritual (Knight, 1998; Palmer & Pomianek, 2007) and language (Knight, 1998; Dessalles, 2009).

Explanations of social behavior in terms of social signaling are not incompatible with cooperation scenarios. Signaling may even make reciprocal cooperation stable (Nesse, 2007; Barclay, 2011).

However, the scope of social signaling is potentially much broader, as it does not require delayed reciprocity. Any social interaction presupposes the existence of a social game, with its benefits and losses. In cooperative games, formally defined as iterated prisoner's dilemmas, roles are symmetrical. When players cooperate, both parties get tangible immediate benefits that are identical in nature. In signaling games, there is no such requirement. For example, the potential benefits and losses of a mobbing individual (status, injuries) and of the audience (choice of the best allies) differ in kind (Maklakov, 2002). Emitters and recipients have different purposes, and there is no requirement that roles be exchanged. Social signaling is asymmetrical in principle (even if it turns out to be sometimes symmetrical in fact).

The Costly Signaling framework (Zahavi, 1975; Grafen, 1990; Zahavi & Zahavi, 1997; Számadó, 1999; Gintis *et al.*, 2001) provides various models that can be applied to social signals. This collection of models includes cases in which signals need not even be costly to be stable (Hurd, 1995; Lachmann *et al.*, 2001; Számadó, 2011). The present study can be understood as an instantiation of some of these abstract models. Social signals, however, have their own peculiarities. For instance, basic assumptions that are made to account for other kinds of signals, such as courtship signals (Grafen, 1990) are not straightforward in the case of social signaling. In particular, Grafen's model presupposes that more intense signals lead to greater benefits for signalers. This is not necessarily true for social signals, as will be illustrated here. Moreover, the collective nature of social networking leads to particular phenomena that may be absent from other signaling systems, such as the coexistence of qualitatively different signaling strategies in a population.

The main problem with social signaling is that it is likely to produce segregation, with a clear separation between signalers and non-signalers. The present study has been motivated by the necessity of finding a plausible context in which *all* individuals invest in costly social signaling. The hope is to build a framework that may then be instantiated to explain behaviors such as primate grooming or human language (Dunbar, 1996), and possibly many other situations that do not obviously appear as evolutionarily stable, such as alarm calls directed at non-kin (Zuberbühler, 2006) or food calls (Chapman & Lefebvre, 1990).

Two simple models will be presented. In each of them, individuals emit costly signals to attract followers, and they benefit from being followed. The first model is a basic recruitment model, probably one of the simplest one may think of. By signaling, individuals may attract a variable number of followers, in a way that is reminiscent of some Web-mediated social networks (Kwak *et al.*, 2010). The model predicts a situation in which only top-quality individuals do send a signal, which is identical for all signalers, whereas all other individuals refrain from signaling. This predicted separation between signalers and non-signalers is systematically observed when simulating a basic recruitment scenario in a population of artifical agents.

Though this first basic model and its binary outcome may correctly represent certain situations in which social signaling is performed only by a minority, it proves inadequate to account for situations in which virtually all individuals in a species invest in social communication. We found that adding a symmetry constraint on social bonds proved sufficient to produce general signaling. The second model, in which all social links are symmetrical, generates stable states in which *all individuals*, even the lowest-quality ones, do invest in social communication. This effect is due to the fact that social competition is now "decentralized".

The present study suggests that social signals differ from what we may expect form standard accounts of signal evolution. In particular, social signals will be shown to be only partially competitive. The next section will briefly compare the present study with some classical approaches to signal evolution. Then two models will be presented in turn, in which social links are supposed to be asymmetrical and symmetrical respectively. We will also consider an augmented version of the second model, based on a "time-sharing constraint", to allow for more realistic social networking. In a further section, a phenomenon that will be called "the banker's suit paradox" will be analyzed. Finally, the relevance of these findings to some particular cases of social signaling will be discussed.

# Social signals

The problem addressed in this paper is to examine whether social signals can be evolutionarily stable, and how. In the narrow sense adopted in this paper, social signals are part of a social selection process (Nesse,

2007; 2009), as they are used to form or to maintain social bonds. Several models have been proposed in which sending honest signals may be advantageous to the emitter, even when there is a temptation to "lie" with those signals (Grafen, 1990; Számadó, 1999; Lachmann *et al.*, 2001; Számadó, 2011). The general problem is to explain how signals can evolve to be honest indicators of some unobservable *qualities* of the emitter (physical strength, health, social status, attacking determination, bravery, commitment, trustworthiness...) that receivers are interested in. In some models, cost is sufficient to guarantee honesty: each individual signals at a definite level where marginal benefit variation and marginal cost variation balance each other (Grafen, 1990). Under reasonable conditions, these optimal signals are an increasing function of quality. They are therefore *honest*, as the signaler's true quality can be recovered from them. At equilibrium, sending exaggerated signals, for each quality level, would involve a dissuading load for potential cheaters. Under different assumptions, honest signals may remain cheap, because they are costly to fake (Hurd, 1995; Számadó, 1999; Lachmann *et al.*, 2001; Számadó, 2011). Mobbing, if considered as a social signal, would be an example of costly behavior; grooming is costly as well, by the considerable amount of time it requires (Dunbar, 1996); badges of status may be costless but costly when faked (Johnston & Norris, 1993).

The framework adopted here makes hypotheses similar to those generally adopted in the above models. In particular:

- Individuals are supposed to differ by some unobservable quality.
- They may reveal this quality by sending a signal. Their signaling strategy is supposed to be a function of their sole quality.
- Signaling is supposed to be costly in the two models studied here.

However, due to its collective nature, the social signaling game differs from other forms of communication such as courtship displays. In particular:

- Any individual in the population plays both roles, emitter and receiver.
- Sending no signal is an option.
- The return on social signaling investment is indirect, delayed and may be highly non-linear (unlike what one can imagine for simple action–response games).

The second property means that contrary to courtship, the social game is supposed to be optional. In the two models presented below, individuals merely attempt to maximize their benefit. They are not eliminated if they perform poorly. As a consequence, if the probability of attracting friends does not compensate for the cost of the signal, it is in the interest of individuals to remain silent.

The third property is essential for the originality of the present study. Individuals' fitness emerges from a population-level game. Individual fitness is not supposed to be a continuous or monotonous function of signal or quality. Applying standard models to social signals is therefore not straightforward. For instance, Grafen's model requires that the signaler's benefit be an increasing function of the emitted signal (Grafen, 1990). This hypothesis provides the necessary incentive for signalers to bear the cost of signaling. When signals are used to recruit social partners, however, this assumption is not necessarily valid, due to population-level competition. While some individuals may attract many friends, some others may end up alone and get no social profit whatsoever, even if they send non-zero signals. Social bonding is a constant-sum game at the population level. If the best signalers attract many followers, those who cannot match their signals will be followed by no one and will get a zero benefit, whatever the signal they emit.

## First model: Asymmetrical bonds

The model described in this section is a basic recruitment model. It is one of the simplest implementations that can be designed to represent social signal evolution. It is a continuous version of Gintis *et al.*'s (2001) discrete social choice model. Individuals send costly signals to attract followers. When they play the receiver role, they pick the best signalers to follow. Agents are characterized by their quality q. Quality is a private trait. It is only revealed if agents choose to display it by emitting a signal. Let's call s(q) the signal sent by an individual with quality q, and c(q) the associated cost. Agents who are successful in attracting followers get profit  $P_0$  for each of them.

In classical models of social choice (*e.g.* Spence, 1973; Gintis *et al.*, 2001), both quality and signal are binary quantities. Whenever honest signaling emerges, followers can distinguish  $q^+$  (high quality) individuals, who emit signal  $s_0$ , from  $q^-$  (low quality) ones, who remain silent. If honest signaling does not emerge, followers choose whom they follow randomly and no one has any incentive to signal. Gintis *et al.* (2001) showed that the honest signaling condition is met if the proportion p of  $q^+$  individuals remains within limits.

$$P_0/c(q^-) (1)$$

Under the assumption that signals are more costly for low quality individuals:  $c(q^{-}) > c(q^{+})$ , there is a range for *p* in which honest signals are stable: high quality individuals signal their quality, whereas low quality individuals are deterred from signaling.

The purpose of the model described in this section is to show that Gintis *et al.*'s discrete scenario describes a situation that is expected to emerge anyway, even when all quantities, including qualities, vary in a continuum. Let's suppose that the qualities present in the population are evenly distributed over the segment [0,1]. The signal sent by an agent is a continuous function of its quality q. Let's consider the simplest case in which it is a mere proportionality.

$$s(q) = g(q) q, \tag{2}$$

where g(q) represents the individual's investment in communication. This signal can be understood as a "broadcast" signal, as it does not depend on the receiver. A reasonable assumption consists in associating cost, not to signals *per se*, but to investment in signaling. Let's consider the simplest relation and suppose that signalers pay a proportional cost c(q).

$$c(q) = C g(q), \tag{3}$$

where *C* is a constant. This cost represents the burden (in energy, resources, risk or time) required to set up and emit the signal. With this assumption, it is more costly for low quality individuals to send the same signal as high quality individuals. Since c(q) = Cs(q)/q, this expression of cost leaves open the possibility that signals evolve to be honest without being increasingly costly (Hurd, 1995; Számadó, 1999; Lachmann *et al.*, 2001; Számadó, 2011). All quantities, *q*, *s*(*q*), *g*(*q*), *c*(*q*) are supposed to be in the segment [0,1].

By sending s(q), signalers benefit from attracting allies: they get  $P_0$  per follower. We suppose that followers pick the strongest signal when choosing whom they will follow. The problem is to show that g(q) evolves to a definite value for each quality q, so that g is evolutionarily stable.

If there is no restriction on the number of followers per signaler, the whole group follows a handful of top quality individuals. As these individuals are in competition to win the prize of becoming the unique celebrity in the group, they send the maximum signal, provided that  $(N-1)P_0 > C$ , where N is the size of the group.

One (somewhat artificial) way to avoid this winner-take-all outcome is to impose the condition that an individual can have no more than k followers. The consequence is not really different: a fraction 1/k of the population gets k followers, whereas individuals of lesser quality get none. Low quality individuals have therefore no incentive to signal. Let  $\eta$  designate the threshold above which individuals send a signal. Evolution is expected to lead to a situation in which all signalers get their k followers. At this point, they have no incentive to emit more intense signals. If qualities are uniformly distributed, then we must have  $s(q) = s_0$  for  $q \ge \eta = 1-1/k$ . Below that threshold, individuals have no incentive to send non-zero signals, as it would not bring them any follower. The benefit of signalers is

$$B(q) = kP_0 - Cs_0/q.$$
 (4)

Lowest quality signalers  $(q = \eta)$  must send the maximal signal allowed by (2) to avoid being outperformed by worse individuals. Therefore,  $g(\eta) = 1$  and  $s_0 = \eta$ . The corresponding benefit is  $B(\eta) = kP_0 - C$ . If  $kP_0 > C$ , any individual who is able to reach  $s_0$  (even for  $q = \eta$ ) gets a positive benefit from emitting it. The signal stabilizes at a level that only 1/k individuals can reach. The common signal depends only on k and not on benefits and costs.

$$s_0 = \eta = 1 - 1/k.$$
 (5)

As we can see, the continuous case recreates the binary state that was postulated in (Gintis *et al.*, 2001). The population splits up into two groups: higher-quality ones who send the same signal  $s_0$ , and lowerquality ones who send no signal. Even in the less ideal case in which signals are blurred or can be misperceived, the situation still leads to an all-or-nothing signaling behavior. The only difference is that  $s_0$ has a lower value which is likely to be in the following interval (see Supporting material 1).

$$1-2k \leq s_0 \leq 1-1k.$$
 (6)  

$$\int_{(0)}^{(0)} \operatorname{Public}_{g_{a}}$$

(Figure 1B)

**Figure 1.** Continuous version of the classical social signaling model. Agents choose which other agent they follow; the number of followers per agent is limited to 6. (A) shows a snapshot of a single run. Red dots represent 'infants' that are still learning. (B) shows the corresponding sociogram. Individuals are located twice, on the lower and upper horizontal axes, depending on their quality. Social links are represented by lines from the lower to the upper axis.

Figure 1 shows a typical simulation result for this first social recruitment model. Signal values s(q) are shown in Figure 1A and social links (sociogram) in Figure 1B. As expected, the population splits up into two parts: a silent group  $(q < \eta)$  and a signaling "elite"  $(\eta \le q \le 1)$ . This is an example of a *pooling equilibrium*, *i.e.* a situation in which several groups specialize in emitting different signal levels (Lachmann & Bergstrom, 1998). By making quality binary, models of social choice such as (Gintis *et al.*, 2001) merely postulate the existence of "elite"  $(q^+)$  individuals. In the present model, the fact that only top-quality individuals climb onto the stage is an emergent phenomenon. It occurs despite the fact that qualities and signals take their values from continuous segments. Of course, the segregation in two groups is indirectly due to the artificial limitation to k followers per individual, but the competition among signalers is essential to produce the effect. Its persistence in the presence of noise (see Supporting material 1) is also non trivial. Moreover, as we will see, the decision to signal is no longer a binary one in the second model detailed below, even when the number of followers is artificially limited.

The segregation of top-quality signalers, who benefit from signaling, from lower quality individuals, who are certain to be outcompeted and have no interest in bearing the cost of useless signaling, may be relevant to some contexts (Johnston, 1994; Broom & Ruxton, 2011). It may for instance correctly describe some situations such as dominance displays (Johnston & Norris, 1993) or various forms of cultural signaling in *Homo sapiens* (Bourdieu, 1979). However, this first model and any other recruitment scenario built on the same principle exclude situations of social signaling in which graded signals would be observed. The next model shows that gradually increasing social signals are theoretically possible.

### Second model: Symmetrical bonds

The main motivation of this study was to find a simple scenario of social signaling that does not lead to an all-or-nothing signaling behavior, as basic recruitment models (such as the preceding one) inevitably do. Social signals are not always the prerogative of "elite" individuals. For instance, in primate species such as chimpanzees or baboons, virtually all individuals spend a significant amount of time grooming other individuals of the group, a behavior that has been linked to alliance formation (Dunbar, 1996; Silk *et al.*, 2006; Mitani, 2009). Most human beings advertise their social status and various other qualities by investing in clothing well beyond what is required by purely functional needs (Zahavi & Zahavi, 1997). Most humans devote considerable time to conversational exchange (Mehl *et al.*, 2007), a fact that makes sense if language is involved in coalition formation (Dunbar, 1996). These behaviors, as far as they have a signaling function, are at odds with the model described above, since low-quality individuals are not discouraged from entering the signaling competition. The purpose of the present section is to show that generalized social signaling may be evolutionarily stable.

The problem comes from the "stardom" phenomenon by which a few individuals catch the support of the crowd (Figure 1B). By limiting the number of social relationships an individual can have, as proposed in the preceding section, one merely lowers the signaling threshold, but one does not eliminate it. Excluding signaling "leks" where signalers can be compared, *e.g.* by considering that encounters are rare, is no solution either. It does not eliminate the transition between signalers and non-signalers, but merely blurs it, as lower-quality individuals increase their chances of attracting partners by chance.

The simplest solution that could be found to avoid a signaling threshold involves enforcing symmetry in social relationships. The second model differs from the first one in that partners decide to bind together on a symmetrical basis after having assessed each other's signaling performance. They become acquainted only if they find each other attractive, *i.e.* if they perform better than what the partner's current friend (if any) did.

Let's first consider the simple case in which individuals can make only one friend. When negotiating friendship, individuals do not know each other's quality. They only see the signals displayed by potential partners. Friends may therefore significantly differ in quality, especially at the beginning of the social game when only a few encounters have occurred. After a while, however, individuals have encountered each other several times, and friends end up matched by quality, as shown in Figure 2A. All individuals now have an incentive to invest in signaling, a fact that simulation confirms (Figure 2B). Even low-quality individuals benefit from investing in signaling to attract friends of similar quality. Though individuals would rather have friends of better quality than their own, competition forces them to make do with fellows like them; and by doing so, they leave little chance to individuals of lower quality to rise above their station.

This social assortativeness allows us to make the following assumption: the profit P an individual with quality q gets from being acquainted with a friend of similar quality is a function P(q). The benefit provided by assortative bonding is

$$B_c(q) = P(q) - C s(q)/q.$$
 (7)

As in the first model, both the signal s(q) = g(q)q and the signaling  $\cot c(q) = Cg(q)$  are supposed to be proportional to the investment in signaling g(q). To be an evolutionarily stable strategy (ESS), competitive signaling must be robust to invasion by different strategies. Suppose that a mutant with quality q sends the signal normally sent with quality q+dq. The recruitment of better partners provides P(q+dq), by dint of an augmented  $\cot C s(q+dq)/q$ . The benefit variation  $dB_c = P'(q) dq - C s'(q) dq/q$ must be zero for the equilibrium to be stable, which gives



(Figure 2B)

**Figure 2.** Simulation of the time-sharing model. Individuals follow only one other individual, for comparison with Figure 1. (A) shows a sociogram and (B) shows signal levels depending on quality and cost coefficient. Dotted lines represent model predictions. The model does not include the transition between the two ESS (see Supporting material).

If the profit derivative P'(q) is strictly positive, *i.e.* if friend' quality q is relevant, there is no threshold for signaling (in contrast with the first model): all individuals, including those in the lower quality range, benefit from communicating. In this ESS, individuals emit a competitive signal  $s_c$  that can be deduced from (8) by integrating by parts.

$$s_{c}(q) = [qP(q) - \int_{0}^{q} P(x) dx] / C.$$
(9)

This assortative and competitive situation corresponds to the increasing part of the curves in Figure 2 (details are given in Supporting material 2). In the simulations of Figure 2, the profit function is a mere proportionality: P(q) = Kq, and we expect signals to be a parabolic function of quality. We can see on Figure 2 that there is an excellent match between the model and the simulation. Comparison with Figure 1 shows a major difference, which is that low-quality individuals are now investing in costly social communication.

7

## The time-sharing constraint

One may legitimately consider that a situation in which individuals can make only one friend is somewhat artificial. If, however, individuals are allowed to have many friends without any restriction, everyone ends up to be acquainted with everyone and signals drop down to zero. A natural way to avoid these two extreme cases (being acquainted with only one or with anyone) consists in supposing that friends have a limited amount of time to spend together. This *time-sharing* constraint has symmetry as obvious consequence: if A shares time with B, then B shares equal time with A (social time is supposed to be actively shared, in an exclusive way).

According to the time-sharing assumption, the profit one gets from social bonds depends not only on partners' qualities, but also on the amount of time spent with them. Let's suppose that an individual A gets acquainted with several friends  $B_i$ . Friends are ranked by importance, from best friend to mere acquaintance. For the sake of simplicity, the amount of time that A spends with the *i*<sup>th</sup> friend  $(i \ge 1)$  is supposed to be  $\lambda r^i$  (with  $0 \le r \le 1$ ). When negotiating possible friendship, partners therefore are given only limited latitude to adjust the amount of time spent together. The constant *r* measures the equality of friends. For small values of *r*, significantly more time is allotted to best friends (*i* small) than to friends that are farther down the contact list. The constant  $\lambda$  is chosen so that the total amount of time that an individual can devote to social relations is bounded by  $\lambda \Sigma r^i \le 1$ . The profit *P* that A gets from these acquaintances is an increasing function of each  $q_i r^i$ , where  $q_i$  is the *i*<sup>th</sup> friend's quality.

To represent the amount of time that they might share together, two potential partners A and B negotiate a rank *i* in their friendship hierarchy. Signal and time combine to constitute a *social offer*. A's social offer to B amounts to  $\lambda s(q_A) r^i$ , where  $s(q_A)$  is the signal displayed by A, *i* is B's rank offered by A in A's friendship list and  $\lambda r^i$  is the amount of time offered by A to B.

Since friendship is decided based on social offer, two individuals A and B of unequal quality may become acquainted. One possibility is that the less qualified one, B, invests more in signaling than A, so that the signal they emit is similar. Another possibility is that B offers more time than any other more qualified individual C that A has previously encountered and thus comes before C in A's contact list. The ranks  $i_A$  and  $i_B$  that A and B offer to each other are bound to be equal, to implement the idea that  $\lambda r^i$  represents the amount of time A and B will spend together.

In a situation of competition, however, two individuals of unequal quality would get acquainted only thanks to imperfections on the friendship 'market'. When agents are offered the possibility of comparing all would-be friends, *i.e.* when competition is perfect, friends get eventually matched by quality for each friendship level: best friends, second-best friends, and so on. They end up linked to partners with similar social offer and therefore, at equilibrium, with similar quality, as in Figure 2A. Thanks to the time-sharing constraint that limits the availability of high-quality individuals, competition puts lower-quality individuals in a position to form alliances with one another. Anyone who invests in communication can make a profit by attracting friends of comparable quality.

With the time-sharing assumption, the model reproduces the social assortment that was observed when only one friend was allowed. The profit an agent with quality q gets from making several friends of similar quality as its own is still a function P(q) of q, and equations (7)–(9) still hold. Figure 3 illustrates the fact that when individuals are allowed to establish several symmetrical bonds under the time-sharing assumption, we still observe that all individuals, even the lowest-quality ones, invest in costly communication.

The preceding reasoning correctly explains the rising part of the curves of Figures 2-3. One can notice, however, that "elite" individuals spare themselves the trouble of competing with each other. This phenomenon, that we may call "the banker's suit paradox", is described now.



(Figure 3B)

**Figure 3.** Signal level (A) and investment in communication (B) in the time-sharing scenario. The number of friends per individual is limited to 3, for application of formula (17) of supporting material. Parameters are r = 0.6, K = 1,  $L_0 = 0.05$ .

### The banker's suit paradox

An unexpected finding of the second model has been that competitive signaling, where s(q) is increasing, is only one part of the ESS, which concerns lower quality individuals:  $q \in [0, \eta]$ . This competitive strategy coexists with another strategy, where s(q) is constant. We can observe that individuals above a certain quality threshold  $\eta$  all send roughly the same signal  $s_0$  for a given cost coefficient (Figures 2-3). In contrast to the competitive case, social bonding is no longer assortative, as individuals in the "elite club"  $(\eta < q \le 1)$  cannot distinguish from each other. Their profit is therefore  $P(\tau)$  on average, where  $\tau$  is some definite value close to the center of the interval  $[\eta, 1]$ . This uniform signal mode is, understandably, an ESS in this quality range. Individuals who unilaterally signal above  $s_0$  pay an additional cost with no profit, since their partners will be random members of the "elite club" anyway. Those who signal slightly below  $s_0$  make a slight economy but their profit  $P(\eta)$  is dramatically smaller than the normally expected  $P(\tau)$ .

This phenomenon can be dubbed "the banker's suit paradox". As the story goes, all rich bankers wear similar suits, despite the fact that most of them are rich enough to afford magnificent costumes, made of

golden threads. At this level of income, it seems that competition stops after having reached a definite level of elegance. This metaphor can be used to represent natural contexts in which signaling does not produce extravagant signals and arms race seems to stop at a definite signal level. The time-sharing model may help understand how evolution can produce moderate signals. We must imagine that in the banker's story, the way individuals dress has an effect on their social relations. The banker's suit corresponds to the plateau observed in Figures 2-3. The profitable moderation in signaling does not result from some sort of union agreement. It is expected from the existence of a non-competitive ESS in the upper quality range.

In this idealized description, there is no way to determine the couple  $(\eta, s_0)$ . All values of  $s_0$  theoretically lead to an ESS for  $q \in [\eta, 1]$ . In other words, it does not say why bankers would wear dreary suits while aristocrats in the 18<sup>th</sup> century used to dress magnificently. To understand the phenomenon, one must take into account the fact that signals are error-prone. Errors may be due to the production or to the perception of signals (Grafen & Johnstone, 1993; Johnstone, 1994). In the present study, production errors are the inevitable consequence of the fact that agents must learn their optimal investment in communication, and therefore explore alternative values for g(q). As shown in Supporting material 3, the value of the uncertainty, the more intense the competition. When noise affects signals, individuals in the high-quality range are at risk of being confounded with individuals of lesser quality. At equilibrium, this risk just offsets the cost required to distinguish oneself from other members of the "elite".

The "banker's suit" paradox is another instance of *pooling equilibrium*, since a whole class of individuals is sending the same signal (Lachmann & Bergstrom, 1998). In the present model, the uniform signal emerges despite the fact that all quantities (signals, qualities, investments, costs) are gradual. Calculations in Supporting material 3 show that, contrary to results obtained in other signaling contexts (Grafen & Johnstone, 1993), the presence of noise does not discourage low-quality individuals from signaling. Noise has no effect on the competitive signaling strategy. It only affects signaling behavior in the "elite".

The consequence of this analysis is that purely competitive social displays require perfect signals. As soon as displayers do not have perfect control of the signal they emit or as soon as receivers do not have a perfect reading of signal intensities, the "banker's suit" phenomenon is expected to occur. Signals reach a plateau where competition is replaced by leveling. The effect of noise is to dissuade top-quality individuals from investing into efforts that will produce imperceptible social distinctions. Note that signaling noise is inevitable. It may come from imprecision in signal production or in signal reading. But more importantly, noise is generated by the necessary exploration that any adaptive system requires to achieve optimization. In the implementation used here (see Supporting material 1), exploration noise is due to learning. In other implementations of the same experiment using genetic algorithms, exploration noise is generated by mutations. In natural species, each of these four sources of noise: production errors, reading imprecision, learning exploration and genetic mutations can be sufficient causes for producing the "banker's suit" phenomenon.

Note that although uniform signaling in the "elite" ( $\eta < q \le 1$ ) is observed in the two models of this study, the reason for its existence in both cases is different. In the asymmetrical model, the uniform signal was due to an artificial limitation of the number of followers per signaler. In the time-sharing model, a genuine "elite club" emerges. Its members form social relationships among themselves exclusively. In the first model, all individuals that were able to reach the elite signal did emit it. In the second model, many individuals in the lower quality range could signal at the elite level, but are dissuaded from doing so because the net benefit does not compensate for the added cost. The difference comes from the fact that thanks to assortativeness, individuals can benefit from the social system without being part of the "elite".

### Discussion

In the two models presented here, costly signals are displayed to recruit friends. The first model is a continuous version of a basic recruitment model (Gintis *et al.*, 2001). The main achievement of this study is to show that under minimal assumptions (symmetrical links), we can observe a situation in which all individuals invest in social communication. A basic implementation of Costly Signaling principles (first model) produces a binary outcome, in which individuals choose to signal or not to signal depending on their quality. Just by adding a symmetry constraint based on time-sharing (second model), we can observe that low-quality individuals benefit from spending resources in communication. This phenomenon is due

to the emergence of social assortment in the second model. Social assortment is itself the indirect consequence of the *time-sharing* assumption, which limits the social availability of top-quality individuals. The time-sharing constraint has been introduced as a natural way of enforcing symmetry in social relationships. It requires that friends spend time together on a symmetrical basis. Its main consequence is that individuals in the lower quality range now have some hope of finding available friends. Social signaling is no longer hopeless for them as it was in the first model.

The social assortment predicted by the second model can be observed in various contexts. It is observed among grooming female baboons, where unrelated grooming partners tend to have similar ranks in the hierarchy, despite the fact that females prefer high-ranking partners and attempt to groom with them (Silk *et al.*, 2006). A hypothesis, mentioned by these authors, is that competition restricts females' access to high-ranking partners, and forces them to settle for partners who are close to their own rank. A similar pattern is observed in *Homo sapiens*, where friends show strong bias toward similarity in social characteristics such as education or occupational prestige (Verbrugge, 1977). It is interesting to note that the time-sharing assumption is verified, both for baboon grooming and for human relationships (Dunbar, 1996): in both species, stronger relationships suppose more time spent together.

An important restriction of the time-sharing assumption is that time is supposed to be shared actively, not through passive tolerance. This means that the amount of time devoted by A to B is the same as the amount of time devoted by B to A. One possible mechanism for active time sharing is offered by the fission-fusion process (Kummer, 1997; Sueur *et al.*, 2011). In a fission-fusion schema, individuals must choose with which other individuals they will spend time next, at various time scales ranging from hours to months. The reasons for splitting are generally related to subsistence constraints, for instance when food or water is available in small patches that cannot sustain large groups. On the other hand, there may be several reasons why individuals must be careful about selecting their company when the large group splits. One of them is the possibility of pooling information, as a way to take better collective decisions (Kummer, 1997; Sueur *et al.*, 2011). Another one is protection: by spending time with strong or alert companions, individuals may avoid being harmed by predators or by conspecifics. When the large group splits, it is crucial for individuals who want to benefit from information pooling or from protection to select the best available companions.

To implement the social advantage of sharing time with competent individuals, we consider that when two individuals become acquainted, each of them benefits from the competence of the other, but only in proportion of the time shared. This translates into to the following profit function, which was used in the simulations of the time-sharing model.

$$P = 1 - \prod_{i} (1 - K r^{i} q_{i}).$$
<sup>(10)</sup>

*K* is a constant smaller than 1. The product  $\Pi_i (1 - K r^i q_i)$  is computed over all of the individual's friends. In the fission-fusion schema, the product represents the probability of taking bad decisions or of getting harmed. The presence of the *i*<sup>th</sup> friend during a fraction  $r^i$  of the time contributes by  $K r^i q_i$  to reducing this probability. We can see that profit *P* is an increasing function of the friends' competence and of the time spent with them. The simulations of the time-sharing model (Figures 2-3) use this expression of *P*.

A major result of the time-sharing model is the existence of an ESS with two distinct parts that emerge below and above the cut-off quality  $\eta$ . Below  $\eta$ , signals are competitive and gradual. They reveal the true quality of performers. In the first model, signaling evolved to be binary (either zero or a constant  $s_0$ ). By contrast, in the time-sharing model, gradual signals emerge as a natural consequence of signaling competition. The second component of the ESS, which corresponds to what we called the banker's suit paradox, is observed above  $\eta$ . There, individuals are no longer competing. They all send the same signal, which means that the highest quality individuals save on signaling. This phenomenon, in contrast with other signaling scenarios (e.g. Lachmann & Bergstrom, 1998; Broom & Ruxton, 2011), is not the consequence of any discreteness that would preexist either on the sender's or on the receiver's side. The threshold  $\eta$ , above which individuals stop competing, emerges despite the fact that all quantities take continuous values. The phenomenon is due to the fact that above a certain signal level, distinguishing oneself from some other less competent individuals is no longer profitable. In the presence of noise, the cost of distinction exceeds the cost of being misjudged. It is more profitable for individuals above  $\eta$  to spare the cost of competition, even if the price to pay is to get acquainted with individuals of lesser quality. Interestingly, the transition  $\eta$  between the two components of the ESS could be, in principle, located anywhere. Its precise location is controlled by the amplitude of the noise which, by blurring signals, determines the risk faced by uniform signalers (see Supporting material 3). A corollary of this result is that high precision in signals leads to fierce competition in the "elite".

### Conclusions

This study is an attempt to determine how much individuals should invest in social communication, depending on the type of relationships they may form. Individuals advertise their quality by displaying signals, and choose their friends based on those signals. In the first, unrestricted model, in which social links can be asymmetrical, the population splits up into two groups, the signalers and the non-signalers. Only top-quality individuals benefit from climbing onto the stage that emerges from the signaling game. This model extends known results about the stability of honest social communication (Gintis *et al.*, 2001) to the continuous case.

A second model has been designed to avoid the binary segregation between signalers and non-signalers. In this second model, social links are made symmetrical in a natural way: friends are supposed to spend time together. Under this time-sharing assumption, friends choose each other not only according to signals, but also by considering the amount of time they are ready to share together. With this simple assumption, two new phenomena occur. First, contrary to what is observed in the unrestricted model, all individuals in the time-sharing model invest in signaling. This competition, in the lower quality range, leads to honest signals, from which true quality can be inferred. Second, we observe that above a certain quality threshold, individuals stop competing and uniformly send the same signal. The competitive strategy and the uniform strategy are both evolutionarily stable.

The time-sharing model is developed theoretically and is implemented in a simulation program. We observe from the simulation that both competitive signaling and uniform signaling systematically emerge and match the predictions of the idealized model. The model predicts observations in the competitive mode with no free parameter. Concerning the uniform mode, all relations between the cost coefficient, the learning exploration, the maximum number of friends and the signal level are predicted as well (see Supporting material 3). The model indicates that maximal signals are determined, not only by cost and profit, but also by signal precision (in production or perception).

The phenomena highlighted by the time-sharing model are robust and are observed for a wide range of parameter values. In particular, the introduction of a bottom quality or of overlap in the time shares devoted to friends does not affect the main results of this study. The model should nevertheless be adapted to reflect specific situations, for instance by modifying the profit function or by introducing additional parameters. Some contexts may for instance require additional costs associated with social time (Bergstrom, Kerr & Lachmann, 2006; Barclay, 2011) or with the number of friends (Dunbar, 1996; Sueur *et al.*, 2011).

The time-sharing model offers a new theoretical tool that may be used to explain some behaviors observed in nature. It may be relevant to any context in which signaling is necessarily associated with shared time. Grooming among primates is obviously a good candidate (Dunbar, 1996; Silk *et al.* 2006; Mitani, 2009). Aspects of human conversation may also be potentially explained using the time-sharing model (Dunbar, 1996). The model may also shed new light on some seemingly altruistic signals, such as alarm calls directed at non-kin (Zuberbühler, 2006) or food calls (Chapman & Lefebvre, 1990).

Though the present study has been conceived to represent how social links such as friendship are formed, it may provide insight into other types of relationships such as mating. Figures 1 and 2 illustrate situations in which followers can choose only one followee. With slight modifications, the model could represent mating choices of signaling males by females. The first model would illustrate the case in which a male can breed with k females, whereas the second model would be relevant to situations in which both genders invest in signaling and must spend equal time on breeding. A conjecture, inspired by the second model, would be that couples in the second case would be matched according to quality. As already mentioned, however, the models should be modified to cover these situations, by introducing gender distinction and by imposing a strong penalty on lonely individuals.

The time-sharing model may also provide new insight into various human forms of social signaling. We mentioned hunting, clothing and language. The model may be relevant to the analysis of Web communities, such as open source software development communities (Stewart & Gosain, 2001), Wikipedia developers (Auray, Poudat & Pons, 2008) or social networks (Kwak *et al.*, 2010), for which

costly signaling accounts have been proposed (Donath, 2007). As far as affiliations or references are bilateral on these networks, the model may contribute to explaining contributors' general altruism, in relation with the construction of online reputation.

## References

Auray, N., Poudat, C. & Pons, P. 2008. Democratizing scientific vulgarization - The balance between cooperation and conflict in French Wikipedia. Observatorio 1(3):185-199.

Barclay, P. 2011. Competitive helping increases with the size of biological markets and invades defection. J. Theor. Biol. 281:47-55.

Bergstrom, C. T., Kerr, B. & Lachmann, M. 2008. Building trust by wasting time. In: Zak P. J. (Ed.). Moral markets: The critical role of values in the economy, 142-153. Princeton University Press, Princeton, NJ, USA.

Bliege Bird, R. & Smith, E. A. 2005. Signaling theory, strategic interaction, and symbolic capital. Curr. Anthr. 46(2).

Bourdieu, P. 1979. La distinction - Critique sociale du jugement. Les Editions de Minuit, Paris.

Broom, M. & Ruxton, G. D. (2011). Some mistakes go unpunished: the evolution of "all or nothing" signalling. Evolution, 65 (10), 2743-2749.

Chapman, C. A. & Lefebvre, L. 1990. Manipulating foraging group size: Spider monkey food calls at fruiting trees. Anim. behav. 39:891-896.

Dessalles, J.-L. 2009. Why We Talk (2<sup>nd</sup> edition). Oxford University Press, Oxford, UK.

Donath, J. 2007. Signals in social supernets. J. Comput. Mediat. Commun. 13(1).

Dunbar, R. I. M. 1996. Grooming, gossip, and the evolution of language. Harvard University Press, Cambridge MA, USA

Gintis, H., Smith, E. A. & Bowles, S. 2001. Costly Signaling and Cooperation. J. Theor. Biol. 213:103-119.

Grafen, A. 1990. Biological signals as handicaps. J. Theor. Biol. 144:517-546.

Grafen, A. & Johnstone, R. A. 1993. Why we need ESS signalling theory. Philosophical Transactions of the Royal Society B 340:245-250.

Hawkes, K. 1991. Showing off: tests of another hypothesis about men's foraging goals. Ethol. Sociobiol. 11:29-54.

Hurd, P. L. (1995). Communication in discrete action\_response games. J. Theor. Biol., 174, 217-222.

Johnstone, R. A. & Norris, K. 1993. Badges of status and the cost of aggression. Behav. Ecol. Sociobiol. 32:127-134.

Johnstone, R. A. (1994). Honest signalling, perceptual error and the evolution of all-or-nothing displays. *Proceedings of the Royal Society of London B* 256, 169-175.

Knight, C. 1998. Ritual/speech coevolution: a solution to the problem of deception. In: Hurford J. R., Studdert-Kennedy M. & Knight C. (Eds.). Approaches to the evolution of language: Social and cognitive bases, 68-91, Cambridge University Press, Cambridge, UK.

Kummer, H. 1997. In quest of the sacred baboon: A scientist's journey. Princeton University Press, Princeton NJ, USA.

Kwak, H., Lee, C., Park, H. & Moon, S. 2010. What is Twitter, a social network or a news media ? Proceedings of the 19th International World Wide Web (WWW) Conference, 591-600, Raleigh NC: ACM.

Lachmann, M. & Bergstrom, C. T. 1998. Signalling among relatives - II. Beyond the Tower of Babel. Theor. Popul. Biol. 54:146-160.

Dessalles, J-L. (2014). Optimal Investment in Social Signals. Evolution, 68 (6), 1640-1650.

Lachmann, M., Számadó, S. & Bergstrom, C. T. 2001. Cost and conflict in animal signals and human language. Proc. Natl. Acad. Sci., USA 98(23):13189-13194.

Maklakov, A. A. 2002. Snake-directed mobbing in a cooperative breeder: Anti-predator behaviour or selfadvertisement for the formation of dispersal coalitions?. Behav. Ecol. Sociobiol. 52:372-378.

Mehl, M. R., Vazire, S., Ramírez-Esparza, N., Slatcher, R. B. & Pennebaker, J. W. 2007. Are women really more talkative than men? Science 317:82.

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. Animal behaviour, 77:633-640.

Nesse, R. 2007. Runaway social selection for displays of partner value and altruism. Biol. Theory.:143-155.

Nesse, R. 2009. Social selection and the origins of culture. In: Schaller M., Norenzayan A. & Heine S. J. (Eds.). Evolution, culture and the human mind, 137-150, Psychology Press, New York NY, USA.

Ostreiher, R. (2003). Is mobbing altruistic or selfish behaviour? Anim. behav., 66 (1), 145-149.

Palmer, C. T. & Pomianek, C. N. 2007. Applying signaling theory to traditional cultural rituals - The example of Newfoundland mumming. Hum. Nat. 18:295-312.

Silk, J. B., Altmann, J. & Alberts, S. C. 2006. Social relationships among adult female baboons (*papio cynocephalus*) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61:183-195.

Spence, M. 1973. Job market signaling. Q. J. Econ. 87(3):355-374.

Stewart, K. J. & Gosain, S. 2001. An exploratory study of ideology and trust in open source development groups. Proc. 22nd Intern. Conf. on Information Systems (ICIS-2001), 507-512.

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D. & et al., . Collective decision-making and fission-fusion dynamics: A conceptual framework. Oikos.

Számadó, S. (1999). The validity of the handicap principle in discrete action-response games. J. Theor. Biol. 198(4):593-602.

Számadó, S. (2011). The cost of honesty and the fallacy of the handicap principle. Anim. Behave. 81:3-10.

Verbrugge, L. M. 1977. The structure of adult friendship choices. Soc. Forces. 56(2):576-597.

Zahavi, A. 1975. Mate selection - A selection for a handicap. J. Theor. Biol. 53:205-214.

Zahavi, A. & Zahavi, A. 1997. The handicap principle. Oxford University Press, New York NY, USA.

Zuberbühler, K. 2006. Alarm calls. In: Brown K. (Ed.). Encyclopedia of language and linguistics (2nd ed.), 143-155, Elsevier, Oxford, UK.

## Supporting material 1

#### Asymmetrical relations

The first model implements social relationships in the simplest way by representing them with unidirectional social links, as in (Gintis *et al.*, 2001).

*N* agents differing by their quality  $q \in [0,1]$  interact and establish social links. Each agent emits a signal s(q) = g(q)q and bears the corresponding cost Cg(q), where  $g(q) \in [0,1]$  represents the agent's investment in signaling (note: all non-discrete quantities belong to the segment [0,1]; in figures, they are displayed in percentages, between 0 and 100). An agent gets reward  $P_0$  for each attracted follower. Each agent can accept a maximum of k followers. In the absence of noise, the best N/k individuals are followed by the whole population. In the presence of noise, the quality threshold  $\eta$  above which individuals are likely to be followed is smaller that (1-1/k). For individuals in the "elite group" (above  $\eta$ ), displaying the same signal  $s_0$  is an ESS, whereas it is in the interest of low-quality individuals (below  $\eta$ ) to send no signal. To understand why, we must consider how learning is implemented.

#### Learning

Agents learn g(q) through trial and error by exploring around the current value and the best value encountered so far. The mechanism used is a basic exploration/exploitation method. The learning agent adopts a new value for g(q) that realizes a compromise between three terms:

- The past value of g(q) that provided the highest benefit. Memory span is limited to M past learning episodes.
- An additive perturbation of g(q) of amplitude *L*. The value of the exploration term *L* decreases linearly until the agent reaches 'adulthood', where it stays at a bottom value  $L_0$ .
- g(q') for neighboring abilities q'.

Agents 'die' when they reach a maximum age. They are replaced by another agent with same quality q but with a random value for g(q). After a definite number of steps, the overall shape of g is supposedly reached. All new agents are now born adult (*i.e.* their learning exploration equals  $L_0$ ), as a way to lower the temperature of the learning system.

Five parameters determine the values of M and  $L_0$ , the relative contribution of the best memorized solution, the influence of neighbors, and the age of adulthood. In the first model (asymmetrical links), the influence of neighbors is set to a small value and individuals never reach adulthood. This makes convergence slower, but it allows the system to evolve a sharp discontinuity in  $g(\eta)$ .

#### Uniform signaling with asymmetrical relations

The optimal investment g(q) for an individual A with quality q corresponds to the lowest signal  $s_0$  that proved sufficient to attract k followers at least once in the M past trials. On average, A will emit  $s_0$  if the probability of getting k followers with  $s_0$  is larger than 1/M. We can conclude that  $s_0$  is independent of q. If  $kP_0 > C$ , the benefit given by equation (4) is positive. All individuals that can reach  $s_0$  will emit it. It constitutes therefore an ESS.

This reasoning does not determine the value of  $s_0$ . In the absence of noise,  $s_0 = \eta = 1-1/k$ . In the presence of learning noise, no individual is certain to get followers. If the average amplitude of the learning noise for g(q) is  $L_m = \alpha L_0$ , then the probability of attracting k followers when sending signal s decreases from 1 for  $s = s_0 + \alpha L_0$  to 0 for  $s = s_0 - \alpha L_0$ . Let's consider a uniform approximation of the probability density of s for each quality q.

$$s = s_0 + \rho \alpha L_0 q \quad \text{with } \rho \in [-1, 1]. \tag{11}$$

15

The individuals that successfully attract *k* followers are the *N/k* individuals that happen to emit the highest signals. Their signals are located in the upper part of the trapezoid defined by (11) when  $q \in [\eta, 1]$ . Let  $s^-$  be the minimum signal required to belong to the *N/k* successful signalers. As can be easily verified<sup>1</sup>,

$$\bar{s} = s_0 + (1+\eta)\alpha L_0 (1/2 - 1/(k(1-\eta))).$$
(12)

Individual with quality close to  $\eta$ , the smallest quality that allows to reach  $s_0$ , will maximally invest in signaling:  $g(\eta) = 1$  and  $s(\eta) = \eta = s_0$ . For them to have a chance to be followed, we must have  $s^- < s_0$ , and therefore,

$$\eta > 1 - 2/k. \tag{13}$$

This is the condition announced in formula (6). Note however that the preceding reasoning concerns very few individuals, located near  $\eta$ . The real value of  $\eta$  may therefore significantly fluctuate above the lower bound given by (13). If the learning excursion  $\alpha L_0$  is not too small,  $\eta$ -individuals may forget about  $s_0$ . They will stop signaling, and  $\eta$  will increase. The converse situation is controlled by the probability of the "mutation" from 0 to  $s_0$ , which itself depends on  $\alpha L_0$ . Even when M,  $L_0$  and the ratio of 'children' are fixed,  $\eta$  is expected to vary due to the occurrence of accidental events, when individuals below the current value of  $\eta$  happen to attract followers and remember their success during M time steps.  $s_0$  and  $\eta$  may then diminish for a time due to these lucky events. Simulations indeed show that  $\eta$  is well-determined at each point in time, but significantly fluctuates above 1-2/k through time.

#### Simulations

A population of N = 100 agents, with qualities uniformly distributed over [0, 1], plays the social game a number of times. Agents learn to optimize their investment in signaling g(q) (agents make typically 100 encounters on average per learning step). Individuals last for 200 time steps, before being reinitialized with the same quality. When playing the social game, agent A is allowed to encounter and compare 5 randomly chosen individuals. The one with the strongest signal is compared with A's former champion, and A chooses which individual to follow. Individuals memorize their scores during the last M = 10 time steps. A new value  $g_1$  of g(q) is computed based on the most profitable value in this time window (60%) and on neighboring values (40%) (only immediate neighbors are considered). Then a random positive or negative value (exploration) is added to  $g_1$ . Its maximal amplitude decreases from 1 for newborns to  $L_0 =$ 0.03 for adults (values of g(q) are brought back to [0,1] if necessary). In the asymmetrical model, the new value  $g_2$  resulting from this random addition contributes 95% of the final value of g(q), together with  $g_1$ (5%). Infancy lasts for 20% of lifetime.

### Supporting material 2

#### **Time-sharing**

The time-sharing model differs from the unrestricted model in the way social links are established. At each step, a pair (A,B) of agents is selected and negotiates a possible friendship, according to the following rule. Agent A (with quality  $q_A$ ) makes a social offer  $\lambda s(q_A) r^i$ , where  $i \ge 1$  is the rank offered by A to B in its friendship shortlist (with  $0 \le r \le 1$ ). Agent A starts by offering the most favorable rank i=0, but A may then increase i if B's return offer is smaller than what A's current friend at rank i offered in a previous encounter. B follows the same rule, but never offers a rank i that is lower (*i.e.* better) than the rank previously offered by the partner. If A and B come to an agreement, their mutual social time offer

<sup>&</sup>lt;sup>1</sup> Expression (12) is only valid if  $s^- < s_0 + \eta \alpha L_0$ .

corresponds to the same  $i^{\text{th}}$  place (which is the maximum, *i.e.* the worst, of the two offered ranks) in their contact list.

Agents compute the benefit P obtained from having friends. The following function has been used to compute the social profit that an agent gets from being acquainted with friends with abilities  $q_i$ .

$$P = (1 - \Pi(1 - K r^{i} q_{i})).$$
(14)

This function, which has a probabilistic interpretation (see discussion), increases linearly for small values of the  $q_i$ , and saturates, if r is not too small, when the qualities of close friends (first values of rank i) get close to 1.

#### Competitive Signaling

Below threshold  $\eta$ , competition for entering others' "contact list" leads to assortativeness. If the number k of friends per agent is limited, we get the following polynomial functions.

$$k=1:$$
  $s(q) = K q^2 / (2C).$  (15)

$$k = 2: \qquad s(q) = \left(-2K^2r \, q^3/3 + K \, q^2(1+r)/2\right)/C. \tag{16}$$

$$k = 3: \qquad s(q) = (K(1+r+r^2)q^2/2 - 2K^2r(1+r+r^2)q^3/3 + 3K^3r^3q^4/4)/C. \qquad (17)$$

The parabolic shape predicted by (15) can be observed on Figure 2B.

Benefit in the competitive mode depends on the profit function, but not on the cost coefficient C.

$$B_c = \int_0^q P(x) \, dx \,/\, q. \tag{18}$$

In other words, signal levels adapt to guarantee a constant distribution of benefits to individuals, regardless of the cost.

#### Simulations

Since continuous curves are expected, learning coefficients differ from their values in the first model. Neighboring values contribute 70% to  $g_1$ , and  $g_2$  (which is  $g_1$  plus learning exploration) contributes 80% of the final value. After 60% of the total simulation time, renewed individuals are born 'adult', *i.e.* their maximal learning exploration is  $L_0$ . Agents make some 500 individual encounters before each learning event. Each point of the curves in Figures 2-3 is the average of 30 simulation runs.

### Supporting material 3

#### Uniform signaling in the time-sharing model

In the uniform mode of the time-sharing model, all individuals above quality  $\eta$  send the same signal  $s_0$ . Since they cannot distinguish from each other based on their performance, they get acquainted with a random member of the  $[\eta, 1]$  "elite club". On average, their profit is  $P(\tau)$ . If we use a linear approximation of P, then  $\tau \approx (1+\eta)/2$ . The benefit  $B_u$  of elite individuals depends on their quality q and on the cost coefficient C.

$$B_u = P(\tau) - C \, s_0 / q. \tag{19}$$

Signaling above  $s_0$  increases cost without providing any additional profit, since the better signaler will get paired with an elite individual anyway. Signaling below  $s_0$  allows to spare on the cost, but profit drops down from  $P(\tau)$  to  $P(\eta)$ . Based on this reasoning, one can see that  $s_0$  is an ESS for  $q \in [\eta, 1]$ , whatever its

value. Simulations, however, always converge to a definite value of  $s_0$ . To explain the phenomenon, we must take into account the inevitable blurring of  $s_0$  introduced by learning.

The variability of the signal emitted by agents with ability q depends on the amplitude  $\alpha L_0 q$  of learning, where  $L_0$  is the maximum variation of g(q) (for 'adults') in one learning step, starting from the best previously encountered value. The constant  $\alpha$  is introduced to approximate the effects of cumulative exploration through several learning steps. An agent in the "elite club"  $[\eta, 1]$  emits  $(s_0 + \rho \alpha L_0 q)$ , where  $\rho \in [-1, 1]$ . Its probability of getting acquainted with another agent of the same quality range, and thus of getting social profit  $P(\tau)$  on average, decreases from 1 for  $\rho = 1$  to 0 for  $\rho = -1$ , where it gets  $P(\eta)$  instead of  $P(\tau)$ . A linear approximation gives the following expression for the benefit.

$$B_{u}(\rho) = (1+\rho) P(\tau)/2 + (1-\rho) P(\eta)/2 - C \left(s_{0} + \rho \alpha L_{0} q\right) / q.$$
<sup>(20)</sup>

 $dB_u/d\rho$  must be zero, otherwise  $s_0$  would not be stable. We get:

$$dB_{u}/d\rho = P(\tau)/2 - P(\eta)/2 - C\alpha L_0,$$
(21)

$$P(\tau) - P(\eta) = 2C\alpha L_0. \tag{22}$$

This relation defines threshold  $\eta$ . This value of  $\eta$  corresponds to the limit between the competitive mode and the uniform mode. We can write that  $B_u$  and  $B_c$  are equal in  $\eta$ .

$$(P(\tau) + P(\eta))/2 - C s_0/\eta = \int_0^{\eta} P(q) \, dq \,/\eta.$$
(23)

This relation defines  $s_0$ .

Figure 4 shows the observed and computed values of the uniform signal  $s_0$  depending on noise amplitude  $L_0$  in (A) and on the equality factor r in (B-C). The only free parameter of the model,  $\alpha$ , has been set to 1.2. The model's predictions are nearly perfect in (A) and (B). One should note that the uniform signal level  $s_0$  decreases when the uncertainty about signals ( $\alpha L_0$ ) increases (Figure 4A). This indicates that harsh competition in the "elite" [ $\eta$ , 1] requires precision, and is pointless otherwise.

When the maximum number of friends per individual is not limited or has a significant value (k = 10 in Figure 4C), signaling only exists when friends are given unequal amount of time (equality factor r < 0.6). The model predicts the decrease, but not the sudden drop that can be seen on Figure 4C. The difference with experimental values comes from the imperfection of the friendship market. When r is close to one, individuals have to select the best 10 partners they can claim. The limited number of encounters does not allow them to achieve this selection and many bonds are due to chance. Spending energy in signaling becomes useless if one is likely to be selected anyway.

Note that the preceding calculus of  $s_0$  presupposes its constancy. We can observe on Figures 2 and 3 that signals in the "elite" [ $\eta$ , 1] are slightly increasing. This makes sense, as in our implementation, the signal excursion  $\pm \rho \alpha L_0 q$  is wider for top-quality individuals. Both the probability and the amplitude of the risk of being misjudged are larger for them. They must slightly increase their signal to compensate for that risk.

#### Competitive–Uniform transition

We would expect a sharp transition in  $\eta$  between  $s_0$  and the competitive signal  $s_c$ . Such a transition is not to be observed, however, as individuals having their quality in some interval  $[\theta, \eta]$  (with  $\theta < \eta$ ) will adopt yet another strategy. This intermediary component of the ESS consists in uniformly emitting signal  $(s_0 - \sigma)$ . The benefit in this component is

$$B_u(\rho) = (1+\rho) P(\eta)/2 + (1-\rho) P((\theta+\eta)/2)/2 - C (s_0 - \sigma + \rho \alpha L_0 q)/q.$$
(24)

By making  $dB_u/d\rho = 0$ , we get

$$(P(\eta) - P((\theta + \eta)/2)) = 2C \ \alpha L_0.$$
(25)

18

This gives a minimum value for  $\theta$ , given the constraint that  $B_u > B_c$  in  $\theta$ . In Figures 2 and 3, transitions in the model's predictions (dotted lines) are located in  $\theta$ . The preceding reasoning can be iterated for various couples ( $\sigma_i$ ,  $\theta_i$ ), which explains the smooth transition that can be observed between the competitive and the uniform mode.



(Figure 4A)



(Figure 4B)



(Figure 4C)

**Figure 4.** Uniform signal values. The figure shows  $s_0$  depending on the amplitude of learning exploration (A) and on the friend equality factor (B-C). Dotted lines show model predictions. The number of friends per individual is limited to k = 2 in (A-B) and to k = 10 in (C). (K = 1; b = 0;  $\alpha = 1.2$ ; r = 0.6 in (A) and  $L_0 = 0.05$  in (B) and (C)).

Dessalles, J-L. (2014). Optimal Investment in Social Signals. Evolution, 68 (6), 1640-1650.

Dessalles, J-L. (2014). Optimal Investment in Social Signals. Evolution, 68 (6), 1640-1650.