Evolution and maintenance of costly signals across many biological organisms have posed a fundamental challenge in evolutionary biology, since the time of Darwin. Costly signaling theory, originated from Zahavi's handicap principle, and later refined by Grafen, aims to explain the evolution of costly signals by linking them to honest communication. According to this theory, the function of high cost of signals is to guarantee the honesty of signals, as a high production cost makes them expensive to fake. Thus, for example, it is argued, wasteful ornaments in many species such as peacock's tail, which are costly as they are expected to have metabolic cost and increase predation risk, are honest signals which advertise the signal producer's quality as a potential mate. Similarly, begging calls of birds or alarm calls when detecting predator both being costly, for example by increasing predation risk, are honest signals of respectively, need and danger. In the same way, it is argued many costly signals observed in humans, such as wasteful signals of wealth (e.g. conspicuous consumption) foraging strategies and generous donation, or risky behavior in humans, serve a similar function and are honest signals of quality of the producer of the signals.

A seemingly unrelated challenge in evolutionary theory is the evolution of cooperative strategies, despite the cost of cooperation they impose on their bearer. As a result of many attempts devoted to explain the evolution of cooperation, some mechanisms are identified which can promote cooperation. Kin selection is usually appealed to explain cooperation among close relatives, such as in eusocial insects. Group selection can explain cooperation in relatively closed groups. Direct reciprocity can promote cooperation when interactions are repeated, by retaliation against a selfish act. Indirect reciprocity promotes cooperation through mechanisms such as reputation effects. In structured populations, network reciprocity can promote cooperation with certain dynamical rules. Tag based mechanisms promote cooperation by channeling the benefit of cooperative acts towards fellow cooperators. Voluntary participation promotes cooperation, in circumstances where individuals can opt out of the game and resort to a safe income. Punishment, although is not shown to be able to promote cooperation, is known to increase cooperation level, if cooperation is already evolved by another mechanism, or if supplemented by another mechanism to avoid free riding on punishers. Reward is also shown to have positive effects for the evolution of cooperation. Similarly, heterogeneity, such as social diversity, aging, or knowledge of the past can improve cooperation level. In addition, the study of the evolution of cooperation on interdependent networks, and also multigames, have led to interesting insights into the evolution of cooperation.

The fact that cooperative strategies and costly signals coexist in many contexts, has led to conjectures and arguments that costly signaling can provide another road to the evolution of cooperation. This line of thought parallels costly signaling theory, as it is based on the idea that a cooperative act, being costly, can be seen as a costly signal of the cooperator’s quality. In this manuscript, going beyond the premises of costly signaling theory and trying to find a new road to the evolution of cooperation, we raise the question whether co-evolution of costly signals and cooperation is possible due to a purely dynamical phenomena? By considering a population of signal producing individuals, who play a game and decide on their strategy based on the signals they produce, we note
that, signals and strategies form a complex dynamical system, in which both costly signals and costly cooperative strategies can evolve. Costly signals evolve, despite their apparent cost, as they elicit a favorable cooperative strategic response. This strategic response to signals can be quantified in a fitness term which controls the frequency of signals in the population, better than their apparent cost. Similarly, cooperative strategies can evolve, despite the cost of cooperation they impose, due to a large fitness they reach as a result of complex internal dynamics of the system. In the resulting partial cooperative state, agents coordinate in heterogeneous cooperation-defection strategy pairs. That who cooperates and who defects, is determined based on the signals they show by a set of rules. This set of rules emerges from the internal dynamics of the system and can be seen as a set of moral rules which determines legitimate cooperation and defection and supports a partial cooperation state.

The Model

To see how costly signaling and cooperation can co-evolve, we consider a well mixed population of individuals. At each time step, individuals are paired at random to play a (two-person-two strategy) game. Before each game, each individual produces a signal out of $n$ possible signals. For this purpose, each individual $\alpha$, has a probability distribution $P_\alpha(\sigma)$, for signal production, such that it produces signal $\sigma$ with probability $P_\alpha(\sigma)$. An individual's strategy is determined based on the combination of its own and its opponent's signal. Thus, we show individual $\alpha$'s strategy by $s_\alpha(\sigma_\alpha, \sigma)$. Here, $\sigma_\alpha$ is individual $\alpha$'s signal, and $\sigma$, its opponent's signal (individual $\beta$). Each entry of $s_\alpha(\sigma_\alpha, \sigma)$ can be either C (cooperation) or D (defection). For example, $s_\alpha(\sigma_\alpha, \sigma) = C$ means individual $\alpha$ cooperates if it produces signal $\sigma$, while its opponent produces signal $\sigma$. Signals have costs. We assume signal costs are distributed uniformly at random in the interval $[0, c_{\text{max}}]$. Individuals receive payoff according to the payoff structure of the game, and pay the cost of the signal they have produced. After each round, the population is updated synchronously. That is, individuals reproduce with a probability proportional to their payoff and the new population replaces the old one, such that the population size $N$ remains fixed. The offspring inherit the signal production distribution $P(\sigma)$, and the strategy $s(\sigma, \sigma')$ of their parents. However, with probability $\nu$, a mutation in $P(\sigma)$ occurs, in which case the probability of production of a randomly chosen signal $i$, is increased. This is done by setting $P(\sigma) = (1 - \delta)P(\sigma) + \delta [i]$. Here, $[i]$ is a vector whose $i$th element is 1 and its other elements are zero, and $\delta$ can be considered as the strength of mutation. In the same way, with probability $\nu$, a mutation in strategies occur in which case a randomly chosen entry of the strategy matrix is randomly reset to either $C$ or $D$.

Results

We begin by considering a prisoner's dilemma game (PD). This game is extensively used in studies on the evolution of cooperation\cite{1,2}. See Methods below for payoff and parameter values used in simulations. In Fig. (1a), the fraction of $C$ and $D$ strategies (the mean fraction of $C$ and $D$ entries of the strategy matrix $s_\alpha(\sigma_\alpha, \sigma)$ over the whole population), as a function of time is plotted. As can be seen, a high fraction of cooperative strategies, close to $\frac{1}{2}$, is maintained in the population. The fraction of strategy pairs which are actually played, is plotted in Fig. (1b). Both mutual cooperation (CC) and mutual defection (DD) are maintained and coexist in similar frequencies. However, the strategy pair CD, in which an individual cooperates while its opponent defects is the dominant strategy pair most of the times. This means agents somehow coordinate in asymmetric defection and cooperation. To see how this happens, in the top panel of Fig. (1c), we plot the frequency of two of the signals. As can be seen, the signal frequencies show large fluctuations in time. At each instant of time, some of the signals, are produced with smaller this happens, in the top panel of Fig. (1c), we plot the frequency of two of the signals. As can be seen, the signal frequencies show large fluctuations in time. At each instant of time, some of the signals, are produced with smaller
individuals can achieve high payoff by showing this signal. Consequently, the frequency of signal \( \sigma \) increases when \( C(\sigma) \) strategies are accumulated enough. The individuals who show the signal \( \sigma \) can either cooperate or defect. Obviously, those who show signal \( \sigma \) and defect achieve a higher payoff compared to those who show signal \( \sigma \) and cooperate. This results in higher growth of the former strategies and leads to a high prevalence of the CD strategy pair.

This can be seen as a partial solution to the social dilemma. Instead of sticking in the DD Nash equilibrium, the system reaches a state in which both CC and CD strategy pairs are present. This partial solution to cooperation dilemma performs better than the defective DD Nash equilibrium. However, still worse than the social optimal CC solution. Interestingly however, in a strategic situation where CD performs better than CC, our model suggests that strategic signaling can provide a way to reach a socially optimal state. Turn Taking Dilemma (TTD) which results from PD by imposing the condition \( T + S > 2R \), is suggested as a game which grasps such strategic situations\(^{46,48}\). With this condition, the social optimal is composed of a situation where agents some how manage to coordinate on heterogeneous cooperation-deection. TTD seems to be more difficult than PD to resolve, as it requires agents to solve a coordination task and a cooperation dilemma, at the same time\(^{48}\), and no solution to this dilemma in the case of one shot games is known\(^{49,50}\). Our study shows signaling can provide a way to naturally resolve such dilemmas in a well mixed population with one shot interactions. TTD is not the only strategic context where heterogeneous CD is the socially optimal solution. Prisoner’s dilemma, together with snowdrift (SD), the battle of the sexes (BS), and the leader game, are suggested as the four independent non-trivial archetypal two person, two strategy games\(^{51}\). TTD is suggested as a further refinement of this classification\(^{48,49}\). Among these, TTD, SD, BS and the leader game, all offer contexts where a heterogeneous CD can perform better than (or as good as) a homogeneous strategic pair. In such contexts, individuals need to solve a coordination task to reach a socially optimal state. In TTD and SD, the situation is further complicated as these constitute a social dilemma as well. Signaling, being a natural way to reach a heterogeneous stationary solution, can be appealed to achieve a socially optimal state in all these strategic situations.

As the argument above suggests, even though selection acts on agents, signals and strategies enter a complicated dynamics and can be selected for or against indirectly. To make this statement more quantitative, we define the fitness of a signal as the probability that showing that signal results in cooperation by the opponent. This can be calculated as \( w_{\sigma} = \langle \sum_{\sigma'} \rho_{\sigma} P(\sigma'|\sigma) \rangle \). Here, \( \langle \cdot \rangle \) denotes an average over population, and \( \delta_{\sigma}(\sigma', \sigma) = 1 \) if \( \delta_{\sigma}(\sigma', \sigma) = \text{Card and zero otherwise. It is also possible to define a fitness for strategies. Consider the set of strategies which defect against signal } \sigma. That is all the strategies of the form \( \delta(\sigma', \sigma) = D \), for all possible \( \sigma' \)'s (We denote this set by \( D(\sigma) \)). We define the fitness of such strategies as their expected payoff: \( w_{D(\sigma)} = \langle \sum_{\sigma'} T P_{\sigma}(\sigma'|\sigma) P(\sigma'|\sigma) + \sum_{\sigma'} R P_{\sigma}(\sigma'|\sigma) P(\sigma'|\sigma) \rangle \). The first term is the probability that an agent shows signal \( \sigma \) and cooperates times the temptation \( T \) (as the payoff of \( D(\sigma) \) is \( T \) in this case), and the second term is the probability that an agent shows signal \( \sigma \) and defects times punishment \( P \) (as the payoff of \( D(\sigma) \) is \( P \) in this case).

In the lower panel of Fig. (1c), we plot the average probability that a signal (signal \( \sigma \)) is produced in the population \( \langle P_{\sigma}(\sigma) \rangle \) (red line marked by circles) together with its fitness (blue line marked with squares), as a function of time. As this example for a signal \( \sigma \) shows, the density of a signal \( \sigma \) (top panel) and \( \langle P_{\sigma}(\sigma) \rangle \) both closely follow its fitness \( w_{\sigma} \) possibly with a time lag. To look more closely at the co-evolution of signals and strategies, we calculate the direction of information flow from the density of strategies which defect with a signal to the mean probability of production of that signal, denoted as \( d(w_{D(\sigma)}, \langle P_{\sigma}(\sigma) \rangle) \) and plot it in Fig. (1d) (red squares) for different signals numbered from 1 to n = 20. d always lies between -1 and 1 and a positive d means information flows from its first argument (\( D(\sigma) \)) to the second (\( \langle P_{\sigma}(\sigma) \rangle \)), and vice versa [see Methods below]. In the top panel, the mutation rate of signals is smaller than that of strategies (\( \nu_{s} = 0.05, \nu_{s} = 0.01 \)), and in the lower panel the mutation rate of signals is larger that that of strategies (\( \nu_{s} = \nu_{s} = 0.05, \nu_{s} = 0.5 \)). As can be seen, whichever has the smaller mutation rate drives the other one, such that the variable with larger mutation rate becomes a fast changing variable and \( \sigma \) to the slowly changing variable. In Fig. (1d), the direction of information flow between the fitness and average probability of production of signals \( d(w_{\sigma}, \langle P_{\sigma}(\sigma) \rangle) \) (blue circle), and that between fitness and density of strategies which defect with a given signal \( d(w_{D(\sigma)}, \langle P_{\sigma}(\sigma) \rangle) \) (yellow triangles), for different signals are plotted too. We see that the evolution of the slave variable (the one with larger mutation rate) is derived by its fitness (which in turn is determined by the slowly changing variable).

The fact that signals evolve according to their fitness has far reaching consequences; It implies costly signals can evolve, despite having a large apparent cost, as long as they reach a large enough fitness as a result of internal dynamics of the system. Furthermore, this argument implies that signal fitness can explain signal densities better than their apparent cost. This is indeed the case. When the time average density of the signals (\( \rho_{\sigma} \)) is plotted as a function of apparent normalized signal cost \( \tau \) (apparent signal cost divided by the mean payoff of the individuals from the games), as in the inset of Fig. (2a) (for different signals numbered from 1 to n), a puzzling picture emerges: not only costly signals are produced, despite the fact that they offer no direct benefit and impose a large cost on the signal producer, but also signal density seems almost unrelated to the signal cost (it was the same sort of puzzle which made Darwin to feel sick: “The sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick” (Letter to Asa Gray, 3 April [1860])). However, when the time average density of the signals is plotted as a function of the time average payoff they accrued (to the signaler) (\( w_{\sigma}^{a} \)), as in Fig. (2a), a strongly increasing function appears, which shows signal densities are determined by their fitness.

This theory is not restricted to the structure of the prisoner’s dilemma game. To see this, we consider all the nontrivial two person two strategy games PD, SD, BS, and the leader game together with the TTD. In Fig. (2b) to Fig. (2e), we perform similar experiments but for respectively, TTD, SD, BS, and the leader game. We see that in all the cases, when the time average frequency of the signals is plotted against apparent cost, a puzzling picture emerges in which signals with large cost are produced. Furthermore, their densities seem to have little or no
Figure 2. Costly signaling. (a) to (e) Time average density of signals produced in the population $\langle \rho_s \rangle$, as a function of their payoff $\langle w^p_s \rangle$, averaged over the same time period for five different game structures. Insets show $\langle \rho_s \rangle$, as a function of normalized cost $c$ (cost divided by mean payoff). When signal densities are plotted against apparent cost, a puzzling picture emerges: not only costly signals are produced, but also signals show little or no dependence on their cost. However, by plotting the signal density against their payoff, a strong pattern emerges: signal densities are distributed as an increasing function of their payoff.

Table 1. Trend test between time average density of signals $\langle \rho_s \rangle$, and normalized apparent cost $c$, and between $\langle \rho_s \rangle$, and time average payoff of signals $\langle w^p_s \rangle$, in different games. From top to down, Spearman’s rank correlation coefficient between $\langle \rho_s \rangle$ and $c$, and between $\langle \rho_s \rangle$, and $\langle w^p_s \rangle$, p value of the Spearman test between $\langle \rho_s \rangle$ and $c$, and between $\langle \rho_s \rangle$, and $\langle w^p_s \rangle$, and finally, p value of the Mann-Kendall test between $\langle \rho_s \rangle$ and $c$, and between $\langle \rho_s \rangle$, and $\langle w^p_s \rangle$. Here, an average over a window of length 5000 time steps is taken. In all the cases both tests strongly support a trend between payoff and density of signals, but in the case of TTD and SD, fail to establish a trend between the apparent cost and density of signals. In all the cases, the trend between density and fitness is significantly stronger compared to the trend between apparent cost and density.

The idea that costly signals can help cooperation to flourish had been considered before based on game theoretic arguments. According to this idea, if there are different qualities of individuals to advertise, and if cost and benefit of signals and strategies satisfy certain conditions, in game equilibrium, cooperation can evolve as a costly and honest signal of one’s quality. Such a view is in parallel with costly signaling theory in that it links costly signals to honest communication. In contrast, the mechanism introduced here, shows that costly signals and costly cooperative strategies can co-evolve, in different strategic contexts as modeled by different game structures and under general and broad conditions, due to a purely physical and dynamical phenomena.
The evolution of costly dishonest signals, for example fighting signals and signals of strength\textsuperscript{52–55}, or signals of need in sibling conflict\textsuperscript{56}, has posed a challenge for costly signaling theory, on the basis of which, some criticism have been raised against costly signaling theory\textsuperscript{52}. The dynamical scenario introduced here, instead, shows the evolution of costly signals results from density dependent effects in cost and benefit of signals, and seems to be a simple mechanism which can be argued to be at work in many contexts where costly signals are produced, irrespective of the truthfulness of the signals. This explanation of the evolution of costly signals contrasts costly signaling theory, in that it suggests the evolution of costly signals can have nothing to do with the honesty of communication, and occurs under rather general conditions, as long as individuals decide upon their strategies based on the signals they produce.

One might wonder what advantage costly signals offer? Returning to the top panel of Fig. (1c), we see a key to the answer of this question. Due to having a large cost, individuals tend to produce costly signals less often. Being less frequent, strategies which cooperate with them impose lower fitness cost (compared to the strategies which cooperate with cheap more frequent signals), and thus increase in frequency. This in turn increases the fitness of costly signals in spite of their high cost, and thus increases their frequency, and at the same time increases cooperation level in the system. When increased in frequency, the advantage of costly signals is undermined as the strategies which cooperate with them start to diminish. The competition of agents to maximize their payoff can be considered as a signaling war, or an evolutionary arms race between signals and strategies\textsuperscript{52}, through which both costly signaling, and cooperation emerges.

### Methods

**Overview of the model.** In our model, at each time step agents are randomly paired to play the game. Each pair of individuals \(\alpha\) and \(\beta\) produce signals, respectively, \(\sigma_\alpha\) and \(\sigma_\beta\), according to their signal production probabilities and decide about their strategy based on the signals. That is, individual \(\alpha\) plays strategy \(s_i(\sigma_\alpha, \sigma_\beta)\), and individual \(\beta\) plays strategy \(s_j(\sigma_\beta, \sigma_\alpha)\). Individuals gather payoff according to the payoff structure of the game and pay the cost of the signals they produce. After playing the game, individuals reproduce according to their net payoff, such that the population size \(N\) remains constant. In other words, each individual in the next generation is the offspring of an individual \(\alpha\) in the past generation with probability \(\frac{w_\alpha}{\sum w_i}\). Here, \(w_\alpha\) is the net payoff of individual \(\alpha\) (in case an agent’s net payoff becomes negative, it is set to zero. This makes sure that the corresponding agent does not contribute any offspring to the next generation). The offspring inherit the signal production probability \(P(\sigma)\) and the strategy matrix \(s(\sigma_1, \sigma_2)\) of their parent. However, mutations can occur. With probability \(\nu\), a mutation in signal production probability occurs in which case the probability that the offspring produces a randomly chosen signal \(i\) increases. This is done by setting \(P_i(\sigma) = (1 - \delta \sigma) P_i(\sigma) + \delta \sigma [i]\). Here, \([i]\) is a vector whose \(i\)-th element is 1 and its other elements are zero, and the subindices \(o\) and \(p\) refer respectively, to offspring and parent. With probability \(\nu\), a mutation in strategy occurs in which case a randomly chosen entry of the strategy matrix of the offspring is set randomly equal to either \(C\) or \(D\).

#### Simulations.

The simulations start with random assignment of strategies to individuals. That is, each entry of the strategy matrix of each individual is set independently at random to either \(C\) or \(D\). The initial signal production probability distribution of each agent \(\alpha, P_\alpha(\sigma)\) is chosen independently of others, and uniformly at random such that the normalization condition holds. That is, \(P_\alpha(\sigma) = \frac{f_\alpha(\sigma)}{\sum f_\alpha(\sigma)}\), where \(f_\alpha(\sigma)\) for \(\alpha = 1..N\) and \(\sigma = \sigma_\alpha, \sigma_o\) are random numbers, chosen uniformly at random in the interval \([0, 1]\). The base parameter values used in the simulations (unless otherwise specified) are as follows: \(\nu_0 = 0.05, \nu_\sigma = 0.05, \delta \sigma = 0.1, N = 400, \epsilon_{max} = 0.1\). Games and their payoffs are given in Table (2). Direction of information flow plotted in Fig. (1d) is defined as \(d(x, y) = \frac{I(x, y) - H(x) - H(y)}{I(x, y) + H(x) + H(y)}\), where \(I(x, y)\) stands for the conditional mutual information\textsuperscript{57}. Time series used are run for 50000 time steps. Time averages in Fig. (2) are taken over a time window of length 5000 time steps starting from \(t = 10000\) in the simulations. Trend tests used in Table (1) are performed on the same data.

#### Trend tests.

The Mann-Kendall test is computed as follows. To examine whether time average signal densities \((\rho_i)\) is an increasing (or decreasing) function of another variable, for example normalized signal costs \(c_{\sigma_i}\), we first order signal densities according to their cost starting from the signal with lowest cost. Denoting the ordered signal densities by \(y_i\) for \(i = 1..n\), the Mann-Kendall statistics is defined as

\[
S = \sum_{i=1}^{n} \sum_{j=i+1}^{n} \text{sgn}(y_j - y_i),
\]

where \(\text{sgn}(x) = -1\) if \(x < 0\), and \(\text{sgn}(x) = 0\) if \(x = 0\). The p value of the test is defined as the probability that a value as extreme as \(S\) is reached under the null hypothesis that no trend exists. For large samples \((n \geq 10)\), the Mann-Kendall standardized \(Z\) statistics, as a normal approximation to \(S\) is computed as follows, \(Z_{MK} = \frac{S - 1}{\sqrt{\frac{n(n-1)(2n+5)}{24}} - \frac{n-1}{2} - \frac{\sum_{p=0}^{n} t_p (t_p - 1) (2t_p + 5)}{24}}\). Here, \(n\) is the size of the sample (i.e. number of signals), \(g\) is the number of tied groups in the sample, and \(t_p\) is the size of the tied groups.

| R | S | T | P | R | S | T | P |
|---|---|---|---|---|---|---|---|
| PD | 0.6 | 0.8 | 0.2 | TTD | 0.6 | 1.4 | 0.2 |
| BS | 0.4 | 0.6 | 0.2 | leader | 0.4 | 0.6 | 0.2 |

Table 2. Games and their payoffs. R is the payoff to mutual cooperation, T payoff to defection against a defector, S payoff to cooperation with a defector, and P the payoff of mutual defection.
pth tied group (a tied group is a set of equal data points in the sample, and the size of a tied group is the number of data points belonging to that group). The p value of the test can be calculated using $Z_{MK}$ as the probability that a value as high as $r$ is reached under the null hypothesis that no trend exists. This can be determined by referring to statistical tables in statistic textbooks or softwares. See, for example[^59], for further details.

The Spearman rank correlation coefficient between two variables $x$ and $y$, $r(x, y)$, is defined as the Pearson’s correlation between rank ordered variables. That is, to calculate the Spearman rank correlation coefficient between $x$ and $y$, first their values are converted to their ranks, resulting in the rank ordered variable $Rx$ and $Ry$ and then the Pearson’s correlation is calculated as the covariance of the rank variables divided by their standard deviations, $r(x, y) = \frac{\text{cov}(Rx, Ry)}{\sigma_{Rx} \sigma_{Ry}}$. When the ranks of all the variables are distinct (which holds in our case as the variables are real numbers and the probability of ties is almost zero), this can be calculated using the simple formula

$$ r = 1 - \frac{6 \sum_{i=1}^{n} d_i^2}{n(n^2 - 1)} $$

where, $d_i$ is the difference between ranks of $x_i$ and $y_i$. The p value of the test, defined as the probability that a value as high as $r$ is observed under the null hypothesis that no trend exists, is calculated using the variable $t = r \sqrt{\frac{n-2}{1-r^2}}$, by taking the fact into account that $t$ is distributed approximately according to student’s t distribution. This can be determined by referring to statistical tables in many statistic textbooks or software packages. See for example[^59] for further details.

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