

Relatedness influences signal reliability in evolving robots

Sara Mitri, Dario Floreano and Laurent Keller

Proc. R. Soc. B 2011 **278**, 378-383 first published online 1 September 2010

doi: 10.1098/rspb.2010.1407

Supplementary data

["Data Supplement"](#)

<http://rspb.royalsocietypublishing.org/content/suppl/2010/08/31/rspb.2010.1407.DC1.html>

References

[This article cites 23 articles, 4 of which can be accessed free](#)

<http://rspb.royalsocietypublishing.org/content/278/1704/378.full.html#ref-list-1>

Subject collections

Articles on similar topics can be found in the following collections

[behaviour](#) (1679 articles)

[evolution](#) (2290 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Proc. R. Soc. B* go to: <http://rspb.royalsocietypublishing.org/subscriptions>

Relatedness influences signal reliability in evolving robots

Sara Mitri^{1,*}, Dario Floreano¹ and Laurent Keller^{2,*}

¹Laboratory of Intelligent Systems, Ecole Polytechnique Fédérale de Lausanne, EPFL, Station 11, 1015 Lausanne, Switzerland

²Department of Ecology and Evolution, University of Lausanne, Biophore, 1015 Lausanne, Switzerland

Communication is an indispensable component of animal societies, yet many open questions remain regarding the factors affecting the evolution and reliability of signalling systems. A potentially important factor is the level of genetic relatedness between signallers and receivers. To quantitatively explore the role of relatedness in the evolution of reliable signals, we conducted artificial evolution over 500 generations in a system of foraging robots that can emit and perceive light signals. By devising a quantitative measure of signal reliability, and comparing independently evolving populations differing in within-group relatedness, we show a strong positive correlation between relatedness and reliability. Unrelated robots produced unreliable signals, whereas highly related robots produced signals that reliably indicated the location of the food source and thereby increased performance. Comparisons across populations also revealed that the frequency for signal production—which is often used as a proxy of signal reliability in empirical studies on animal communication—is a poor predictor of signal reliability and, accordingly, is not consistently correlated with group performance. This has important implications for our understanding of signal evolution and the empirical tools that are used to investigate communication.

Keywords: evolution; communication; reliability; robots; relatedness; kin selection

1. INTRODUCTION

Communication is an important component of animal societies. While signals (defined as behaviours, structures or chemical emissions that affect the behaviour of other organisms, which evolved because of that effect, and that are effective because the receiver's response has also evolved [1,2]) are mainly thought to convey honest information to other individuals, it has been found that unreliable signals used to manipulate the behaviour of others are common [3,4]. Although the reliability of signals of mate quality has been extensively studied (e.g. [5–7]), signals conveying information about the external environment have received comparatively little attention in theoretical and empirical studies. Empirical observations in divergent taxa suggest that honest and reliable communication frequently occurs among highly related individuals [8–11]. This is in line with current social evolutionary theory, which predicts that relatedness is a key component selecting for cooperative behaviour [11–13]. However, because of the lack of quantitative measures of signal reliability in animal communication systems, it has proven difficult to test whether high relatedness is an important factor promoting reliable signalling.

To quantitatively explore how relatedness influences the evolution of signal reliability, we conducted experimental evolution in populations containing 100 groups of eight foraging robots each [14], in which we could manipulate the level of within-group relatedness. The

physical properties of the robots allowed us to study the effect of spatial and visual properties of the system on the evolution of signalling and response strategies. Using this system, we devised a measure of signal reliability, and investigated how this index was influenced by within-group relatedness, which we varied over five experimental treatments.

Experimental trials were conducted by allowing robots to 'forage' for 1 minute in an arena containing a food and a poison source that both emitted red light (figure 1). Robots could distinguish food and poison only at a very close range. The performance of robots was proportional to the amount of time spent in the vicinity of food and negatively proportional to the time spent near poison (see §2). Additionally, robots had the possibility of producing and perceiving blue light, hence potentially allowing them to transmit information about food and/or poison location. Under such circumstances, providing information on the location of food and poison can be beneficial to robots receiving the information, and thus result in higher density and increased competition around the food spot (the space around the food is limited to only six robots). Because such competition could result in robots being pushed away from the food, signalling of a food location constitutes a costly act. Once all robots in the population had been evaluated, the genomes of the 20 per cent of robots with the highest individual performance in the population were selected, subjected to mutation and recombination (i.e. sexual reproduction), and combined to form groups of eight robots for the next generation. This process was repeated for 500 generations of experimental evolution, which was carried out using physics-based computer simulations that precisely model the dynamical properties of real robots. These

* Authors for correspondence (sara.mitri@a3.epfl.ch; laurent.keller@unil.ch).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2010.1407> or via <http://rsob.royalsocietypublishing.org>.

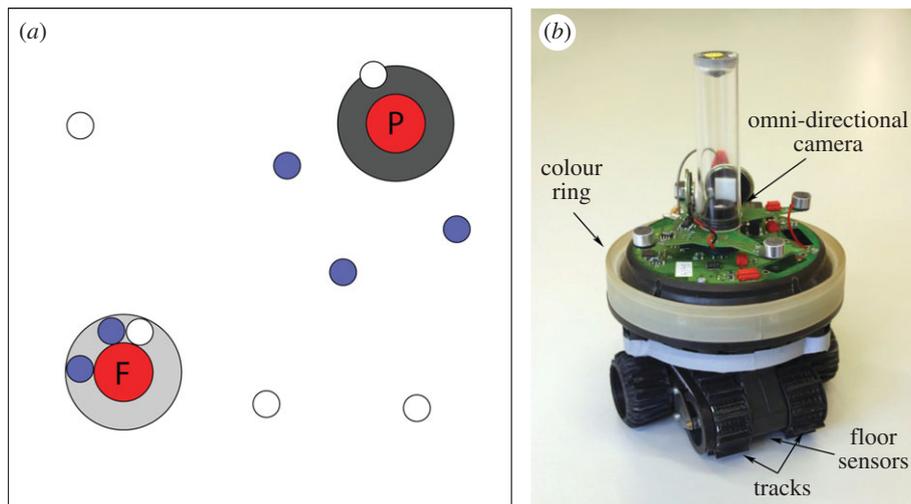


Figure 1. Experimental setup. (a) Food and poison sources, both emitting red light are placed 1 m from one of two opposite corners of the square ($3\text{ m} \times 3\text{ m}$) arena. Robots (small circles) can distinguish the two sources by sensing the colour of the circles of paper placed under each source using their floor sensors when driving over the paper. (b) The robot used for the experiments is equipped with two tracks to drive, an omni-directional (360°) vision camera, a ring of lights used to emit blue light and floor sensors to distinguish food and poison sources. See [14] for details.

selection experiments were repeated in 30 independently evolving populations for each of the five within-group relatedness values.

2. MATERIAL AND METHODS

(a) *Experimental setup*

Each robot was equipped with two tracks that could rotate independently, a 360° camera, a ring around its body that could light up in blue, floor sensors to detect food and poison and a neural controller that determined its behaviour. The neural controller consisted of 11 input neurons connected to three output neurons through 33 ‘synaptic weights’. At each time step, the values perceived by the robot’s sensors (i.e. the amount of blue and red light perceived by its camera and whether it detected that it was on food or poison) were used to activate the 11 input neurons. The activation of the three output neurons (whose values were used to set the speeds of the robot’s two tracks and to emit blue light) was then computed by multiplying each of the values of the input neurons by the corresponding synaptic weight and passing the result through a continuous $\tanh(x)$ function. The 33 synaptic weights were each encoded by one gene consisting of 8 bits representing a value in the range $[-1, 1]$. The genome of a robot (i.e. the 33 genes encoding the values of the 33 synaptic weights) thus determined how it would react to given sensory stimuli (see [14] for more details on the robot hardware, its behaviour and the experimental setup).

(b) *Measuring robot performance*

At each 50 ms time step of the 60 s long trial, a robot gained one performance unit if it was in the vicinity of the food and lost one unit if near the poison. A robot was considered in the vicinity of food or poison if touching the paper disc placed under the food or poison. Otherwise, the robot was counted as being elsewhere in the foraging arena (see also [15]). In the experiments where there was a cost to light emission, the performance of a robot was further reduced by 0.04 units at each time step in which it emitted blue light. The

average performance P of each robot during the 1200 time steps in a trial was

$$P = \frac{t_f - t_p - ce}{1200}, \quad (2.1)$$

where t_f denotes the number of time steps spent by food, t_p the number of time steps spent by poison, e the number of time steps in which the robot emitted blue light and c the cost of light emission per time step (0 or 0.04). The performance of each robot was evaluated as the average of 10 trials conducted on the same group of eight robots.

(c) *Artificial evolution and relatedness*

At the end of each of the 500 generations of selection, the 800 individuals in the population (100 colonies of eight robots) were ranked according to their performance and the best 20 per cent (160 individuals) were selected. From these 160 individuals, genomes were randomly chosen (with replacement) and assorted in pairs to perform crossover (with a probability of 0.2) and mutations (with a probability of 0.01 for each of the genome’s 264 bits) to create 100 new groups of eight robots each. The distribution of newly created individuals among the groups depended on the level of relatedness in a given treatment. Within-group relatedness was defined as the probability of a signal receiver being the signaller’s clone, where we assumed that in any group, it was equally probable for any robot in the group to perceive the signal produced by another robot. Consequently, the mean level of relatedness could be varied by forming robot groups composed of different proportions of clones.

We conducted five sets of experiments, each consisting of 30 experimental replicates with a unique level of within-group relatedness (0, 0.25, 0.54, 0.75 and 1). To form a group of relatedness $r = 1$, one individual was randomly chosen from the pool of the 160 selected individuals, recombined, mutated (according to the probabilities given above) and cloned seven times, to make groups of eight robots with identical genomes. At the other extreme, groups of unrelated robots ($r = 0$) were composed by repeatedly choosing eight different genomes from the pool and assigning

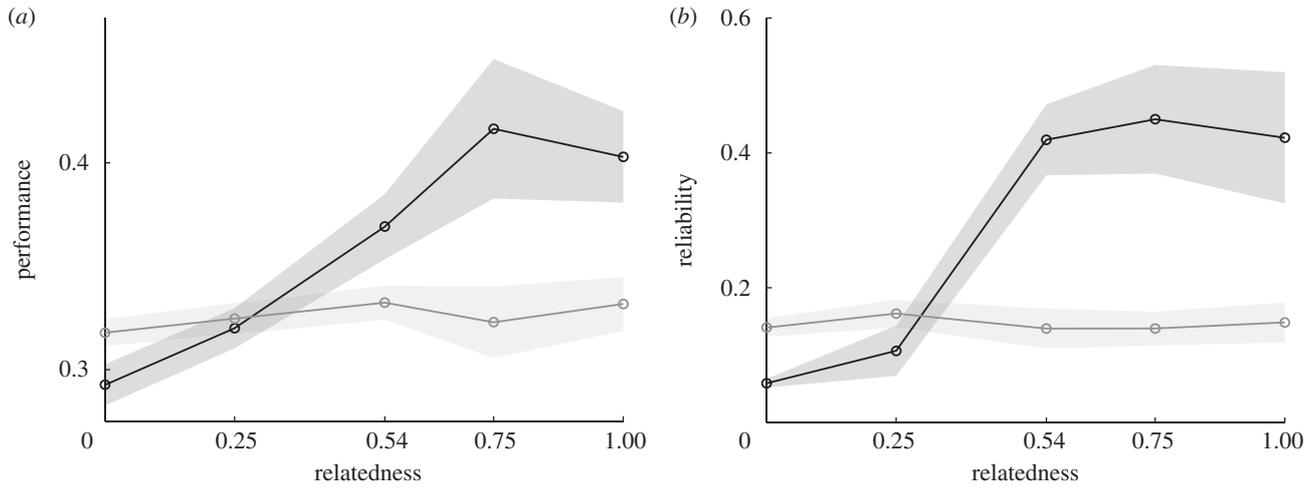


Figure 2. Performance and signal reliability increase with relatedness. (a) Performance and (b) signal reliability at different levels of relatedness for robots that could perceive blue light (black line with circles, normal) and robots that were blind to blue light (grey line with circles, blind). Each point represents the median of 30 independent replicates, where the value of each replicate is the mean of all individuals in the last 20 generations. The grey bands represent the uncertainty about the median. Bands that do not overlap indicate that the medians differ at (approx.) the 5% significance level (see §2 for details).

them to the same group. For intermediate levels of relatedness, $r = 0.25, 0.54$ and 0.75 , different proportions of clones were used to form groups of eight robots (3 : 3 : 2, 1 : 1 : 6 and 1 : 7, for the three levels of relatedness, respectively, see the electronic supplementary material, text S1). Although this group composition differs largely from patterns of group relatedness in most natural populations, social evolution should depend only on the mean relatedness within a group, since the robots have no way of directing interactions towards specific individuals.

(d) Data analysis

The total frequency of light emission s was computed as the average number of time steps robots spent emitting light divided by the number of time steps in a trial (1200). To calculate the frequencies of light emission in different areas o of the arena, where $o \in O = \{f, p, n\}$ (f stands for food, p for poison, and n for elsewhere in the arena), the mean number of time steps e_o robots spent emitting light in the vicinity of object o was divided by the mean number of time steps t_o they spent in the vicinity of o .

To quantify the reliability of blue light signals, we devised an index R quantifying whether a robot perceived more blue light in the direction of the food. To do this, we analysed the inputs of each robot's omni-directional visual system if the robot had not yet arrived at the food source and could detect one or more blue light pixels in any direction. This was done by (i) ranking the four quadrants of the robot's visual system by the amount of light perceived at each time step (i.e. the quadrant with the largest amount of blue light was assigned rank $q = 1$, etc. where $q \in Q = \{1, 2, 3, 4\}$) and (ii) computing the ratios φ_q of time steps where the food was located in each of the four quadrant ranks q .

The reliability index R was then calculated using the Shannon entropy [16] (uncertainty) of the probability distribution $X = \{\varphi_1, \varphi_2, \varphi_3, \varphi_4\}$ using the following equation:

$$H(X) = \sum_{q \in Q} \varphi_q \log \varphi_q. \quad (2.2)$$

This entropy value H ranges from $H_{\min} = H(X_{\min}) = 0$, when there is no uncertainty on food location (e.g. blue

light is perceived only in the direction of the food, $X_{\min} = \{1, 0, 0, 0\}$) to $H_{\max} = H(X_{\max}) = 1.39$, when uncertainty on the location of food is maximal (i.e. there is no association between blue light intensity and food location, $X_{\max} = \{0.25, 0.25, 0.25, 0.25\}$). Accordingly, the reliability index R is defined as the difference between the maximum entropy H_{\max} and entropy $H(X)$, normalized by H_{\max} , thus yielding values of R between 0 (when the intensity of blue light provides no reliable information on the location of the food source) and 1 (when the intensity of blue light perceived provides perfectly reliable information on the location of the food source at all time steps):

$$R(X) = \frac{H_{\max} - H(X)}{H_{\max}}. \quad (2.3)$$

Note that the index of reliability is identical to the measure of information used in [15], except that instances in which a robot could perceive no blue light were excluded in the computation of values of φ_q .

To compare performance P , signal reliability R and blue light emission frequencies s between experiments, we calculated the mean values of the 800 individuals over the last 20 generations for each of the 30 independent replicates. These 30 values were used to describe data (mean \pm s.e.) and were compared with non-parametric (Mann–Whitney or Kolmogorov–Smirnov) tests because some of the data did not follow a normal distribution. When comparing the robots' performance in treatments where light emission was costly with treatments where it was not (figures 2–4 and electronic supplementary material, figures S2 and S3), we added a factor $0.04e/1200$ to the robots' performance P . This ensured that we compared their ability to forage, independently of the costs resulting from light emission.

The widths of the grey bands in figures 2 and 3, and also in the electronic supplementary material, figures S2 and S3 were computed using the percentiles of the distributions (identical to boxplot notches in MATLAB). The method represents a visual approximation of significance levels [17].

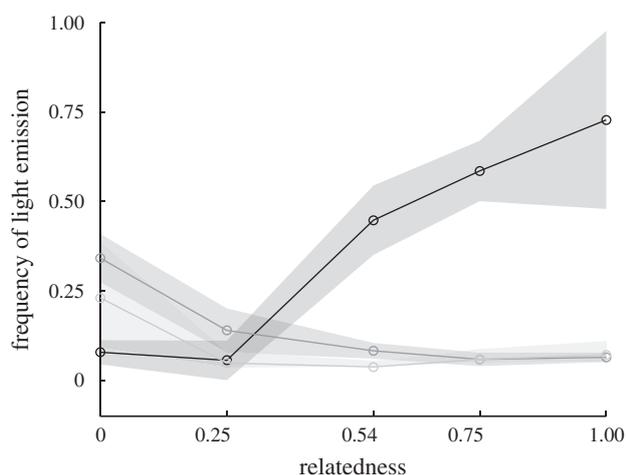


Figure 3. Frequencies of blue light emission in different areas of the arena at different levels of relatedness. Each point represents the median of 30 independent replicates, where the value of each replicate is the mean emission frequency over all individuals in the last 20 generations. For details on the grey bands, see the caption of figure 2 (solid line with black circles, by food; solid line with dark grey circles, by poison; solid line with light grey circles, elsewhere).

3. RESULTS

(a) Relatedness, performance and signal reliability

Over the 500 generations of selection, the performance of the robots increased at all levels of relatedness (see electronic supplementary material, figure S1). At the end of the selection experiment, the performance of robots was positively associated with within-group relatedness (Pearson's correlation coefficient $\rho = 0.64$, $p < 0.001$, figure 2a). The performance of the robots in these experiments significantly increased between relatedness values 0 and 0.75 (Mann–Whitney tests, all d.f. = 59, $p < 0.05$), but the performance did not differ significantly between relatedness values 0.75 and 1 (d.f. = 59, $p = 0.89$).

To test whether these differences in performance were due to differences in signalling strategies, we conducted an additional experiment where robots were blind to blue light. In this experiment, blue light emission could evolve but it could no longer affect the robots' performance, as it could not be perceived. Consistent with the view that differences in performance were mediated by relatedness altering the robots' communication strategy, there was no significant correlation between relatedness and performance in this experiment ($\rho = 0.12$, $p = 0.15$, figure 2a).

To study the effect of variations in relatedness on the reliability of signalling, we devised an index of signal reliability, which consists of analysing the inputs of each robot's visual system to establish whether robots perceived more blue light in a consistent direction with respect to the direction of the food (see §2). This index could vary between 0 when blue light was equally distributed in all directions relative to the direction of the food (i.e. the signal is completely unreliable) to 1 when blue light was always perceived in a predictable direction relative to the food (i.e. the signal is completely reliable). The reliability index was significantly correlated with

relatedness ($\rho = 0.58$, $p < 0.001$, figure 2b) as well as with performance ($\rho = 0.84$, $p < 0.001$).

At relatedness 0, the reliability of the robots' signals as well as their performance were significantly lower than in the treatment where robots were blind to blue light (Mann–Whitney tests, both d.f. = 59, $p < 0.001$). This is because in the blind treatment the light emitted by robots inadvertently provided some information regarding the location of the food. This was selected against when robots were unrelated and could perceive the signals, thus reducing performance (for a detailed analysis and discussion of this effect see [15]).

To investigate how the signalling strategies of the robots changed with relatedness, we compared the frequency of blue light production in different areas of the arena (near the food, near the poison and elsewhere in the arena) across relatedness treatments in the experiment where robots could perceive blue light. As relatedness increased, there was an increase in the frequency of signalling near the food ($\rho = 0.46$, $p < 0.001$) and a reduction in signalling frequency near poison ($\rho = -0.49$, $p < 0.001$) and elsewhere in the arena ($\rho = -0.36$, $p < 0.001$, figure 3). Thus, groups of highly related robots evolved to emit light by the food more often than in other areas of the arena, allowing other robots to reliably locate the food source [14].

(b) Signal production frequency versus signal reliability

Because measuring signal reliability is difficult under natural conditions, researchers have typically used signal production frequencies as a proxy for signal reliability in a variety of contexts (e.g. signals of need [18,19], sexual signals [20] and cooperative signals [21]). However, it is unclear whether signal production frequencies consistently correlate with signal reliability.

To explore whether signal production frequencies are good indicators of signal reliability in our system, we analysed the frequency of blue light emission in the different treatments. There was no significant correlation between relatedness and signal production frequencies ($\rho = 0.1$, $p = 0.24$). Furthermore, within each relatedness treatment, there was no consistent association between signal frequency and performance. Across the 30 replicates, the correlation between the frequency of signalling and performance was negative for relatedness 0 ($\rho = -0.49$, $p < 0.01$), positive for relatedness 1 ($\rho = 0.88$, $p < 0.001$) and not significant for relatedness levels 0.25, 0.54 and 0.75 (all $p > 0.31$, figure 4a). By contrast, a similar analysis between the index of reliability and performance revealed a significant positive correlation at all levels of relatedness greater than 0 ($r = 0.25$ to $r = 1$, all $\rho > 0.6$, $p < 0.001$, figure 4b). At $r = 0$, light emission was unreliable and resulted in relatively low performance in all experimental replicates and there was thus no significant correlation between the two measures ($\rho = -0.2$, $p = 0.3$). These correlations were significantly higher than the correlations between signal frequency and performance at relatedness levels 0.54 and 0.75 (95% CI of correlations did not overlap). At relatedness 0, 0.25 and 1, there was no significant difference between the two correlations (overlapping 95% CI).

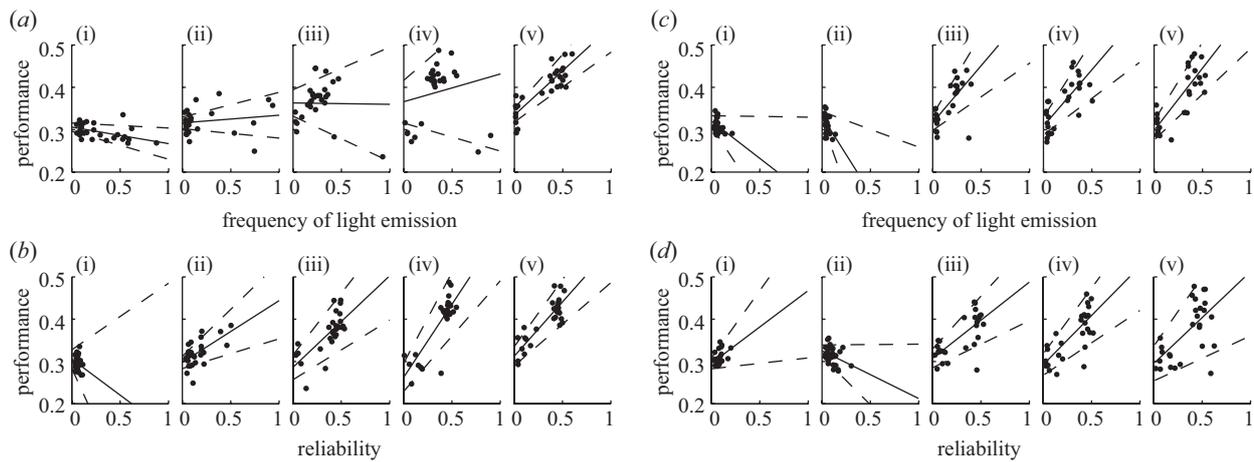


Figure 4. Correlating light emission frequency and signal reliability with performance when light emission was cost-free versus costly. Panels (a) and (c) show the frequency of blue light emission versus performance, while (b) and (d) show signal reliability versus performance of robots at different levels of relatedness, where light emission was cost-free (panels (a) and (b)) or costly (with a cost of 4%, panels (c) and (d)). Each point represents the mean over the last 20 generations for each of the 30 experimental replicates. Solid lines indicate results of a linear regression, while dashed lines show 95% CI. (i) $r = 0$, (ii) $r = 0.25$, (iii) $r = 0.54$, (iv) $r = 0.75$, and (v) $r = 1.0$.

To test whether the lack of consistent correlations between signal production frequencies and performance (figure 4a) may have resulted from the production of blue light being cost-free, we conducted another experiment where the performance of a robot was reduced proportionally to the frequency with which it emitted blue light. These experiments revealed similar associations between relatedness, reliability and performance as in the experiments where light emission was cost-free (compare figures 2 and 3 with the electronic supplementary material, figures S2 and S3). Overall, there was a positive correlation between signal frequency and relatedness over the last 20 generations ($\rho = 0.48$, $p < 0.001$). The correlation between signal production frequency and performance (corrected for the cost of signalling) was positive for three of the five relatedness values (for $r = 0.54$ to $r = 1$, all $\rho > 0.69$, $p < 0.001$) and negative for the other two values (for $r = 0$, $\rho = -0.37$, for $r = 0.25$, $\rho = -0.45$, both $p < 0.05$, see figure 4c). The index of reliability was not significantly correlated with performance at relatedness $r = 0.25$ ($\rho = -0.35$, $p = 0.053$) but was positively correlated for all other relatedness values (all $\rho > 0.41$, $p < 0.05$, figure 4d). In contrast to the experiments where signalling was cost-free, the correlation between signal reliability and performance was only significantly greater than the correlation between signal emission frequency and performance at relatedness 0 (95% CI did not overlap), but was not different at any other relatedness value (95% CI overlapped).

Altogether these data indicate that the frequency of signal production tended to be more frequently positively correlated with performance when there was a cost of signal production, whereas the index of reliability was positively correlated with performance independently of signal production costs. Given that a number of empirical studies have shown that the cost of signal production may be negligibly low (reviewed in [22]), we may expect a lack of association between signal production frequencies and performance in some natural systems, similar to that observed with the robots.

4. DISCUSSION

By applying artificial selection to groups of signalling robots, we have shown that increasing relatedness within groups results in an increase in the reliability of the robots' evolved signalling strategies. These findings can be explained by kin selection theory [11]. In our system, the production of reliable signals increases the likelihood of other robots finding the food, and is thus costly for the signalling robot as it increases the probability of being pushed away from the food. Unrelated robots were therefore selected to produce unreliable signals in order to maximize their direct fitness. By contrast, when robots were related, signalling robots that attracted other robots to the food increased their indirect fitness, thus compensating for the reduction in direct fitness. The gain in indirect fitness was proportional to the average relatedness among robots in a group, which explains the positive correlation between signal reliability and within-group relatedness.

Higher relatedness has also been shown to lead to more reliable signals in natural communication systems [8–11]. For example, barn swallow chicks that beg for food from their parents produce less intense begging displays in groups of siblings than in mixed groups [8]. Similarly, ground squirrels in groups of related individuals are more likely to produce alarm signals than squirrels in groups comprising unrelated individuals [10]. In these two examples, it is notable that two opposing trends in signal frequency are taken to indicate reliable signalling. This apparent contradiction stems from the difference in the benefits of signalling in the two scenarios. In the case of the chicks, louder signalling will lead to larger rewards for the individual signaller and consequently less for its nest-mates, whereas in the case of the squirrels, alarm calls are expected to increase the benefits for other members of the group rather than for the signalling individual alone. An individual squirrel would instead gain more by not producing alarm calls and reaping the benefits of the calls of its conspecifics.

The context in which signals are produced and perceived, such as the distribution of benefits gained

through signalling, or the cost of signal production, are thus expected to largely influence the frequency of signal production and its relation to signal reliability. This suggests that signal production frequencies may not be good predictors of signal reliability under all conditions. Nevertheless, many studies use signal production frequencies to estimate signal reliability (see [4] for a review). An alternative would be to measure signals at the receiving end, as we have shown in this article, resulting in a measure of signal reliability that is independent of such contextual elements. This is, of course, an easier task to accomplish using robots than using animals, because the experimenter can directly access the robots' sensory inputs. Technical advances in neuroscience and molecular genetics should, however, enable similar measurements of perceptual information in living organisms [23–26], making quantitative measurements of signal reliability possible in natural systems.

We thank Michel Chapuisat, Lee Dugatkin, Andy Gardner, Mike Ryan, Claus Wedekind and Stuart West for helpful comments on the manuscript. L.K. thanks Stanislas Leibler who hosted him during his sabbatical at The Rockefeller University. This research has been supported by the Swarmanoid project founded by the Future and Emerging Technologies program (IST-FET) of the European Community under EU R&D contract IST-022 888 and by the Swiss National Science Foundation.

REFERENCES

- Keller, L. & Surette, M. 2006 Communication in bacteria: an ecological and evolutionary perspective. *Nat. Rev. Microbiol.* **4**, 249–258. (doi:10.1038/nrmicro1383)
- Scott-Phillips, T. 2008 Defining biological communication. *J. Evol. Biol.* **21**, 387–395. (doi:10.1111/j.1420-9101.2007.01497.x)
- Maynard Smith, J. & Harper, D. 2003 *Animal signals*. Oxford, UK: Oxford University Press.
- Searcy, W. A. & Nowicki, S. 2005 *The evolution of animal communication: reliability and deception in signaling systems*. Princeton, NJ: Princeton University Press.
- Johnstone, R. A. & Grafen, A. 1992 The continuous Sir Philip Sidney game: a simple model of biological signalling. *J. Theoret. Biol.* **156**, 215–234. (doi:10.1016/S0022-5193(05)80674-5)
- Maynard Smith, J. 1991 Honest signalling: the Sir Philip Sidney game. *Anim. Behav.* **42**, 1034–1035.
- Zahavi, A. 1997 *The handicap principle: a missing piece of Darwin's puzzle*. New York, NY: Oxford University Press.
- Boncoraglio, G., Caprioli, M. & Saino, N. 2009 Fine-tuned modulation of competitive behaviour according to kinship in barn swallow nestlings. *Proc. R. Soc. B.* **276**, 2117–2123. (doi:10.1098/rspb.2009.0085)
- Cheney, D. L. & Seyfarth, R. M. 1985 Vervet monkey alarm calls: manipulation through shared information? *Behaviour* **94**, 150–166. (doi:10.1163/156853985X00316)
- Dunford, C. 1977 Kin selection for ground squirrel alarm calls. *Am. Nat.* **111**, 782–785. (doi:10.1086/283206)
- Hamilton, W. D. 1964 The genetical evolution of social behaviour. *J. Theoret. Biol.* **7**, 1–52. (doi:10.1016/0022-5193(64)90038-4)
- Lehmann, L. & Keller, L. 2006 The evolution of cooperation and altruism: a general framework and a classification of models. *J. Evol. Biol.* **19**, 1365–1379. (doi:10.1111/j.1420-9101.2006.01119.x)
- West, S. A., Griffin, A. S. & Gardner, A. 2007 Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**, 415–432. (doi:10.1111/j.1420-9101.2006.01258.x)
- Floreano, D., Mitri, S., Magnenat, S. & Keller, L. 2007 Evolutionary conditions for the emergence of communication in robots. *Curr. Biol.* **17**, 514–519. (doi:10.1016/j.cub.2007.01.058)
- Mitri, S., Floreano, D. & Keller, L. 2009 The evolution of information suppression in communicating robots with conflicting interests. *Proc. Natl Acad. Sci. USA* **106**, 15 786–15 790. (doi:10.1073/pnas.0903152106)
- Shannon, C. E. 1948 A mathematical theory of communication. *Bell Syst. Tech. J.* **27**, 379–423, 623–656.
- McGill, R., Tukey, J. & Larsen, W. 1978 Variations of box plots. *Am. Statist.* **32**, 12–16. (doi:10.2307/2683468)
- Cotton, P. A., Kacelnik, A. & Wright, J. 1996 Chick begging as a signal: are nestlings honest? *Behav. Ecol.* **7**, 178–182. (doi:10.1093/beheco/7.2.178)
- Redondo, T. & Castro, F. 1992 Signalling of nutritional need by magpie nestlings. *Ethology* **92**, 193–204. (doi:10.1111/j.1439-0310.1992.tb00959.x)
- Zahavi, A. 1975 Mate selection—a selection for a handicap. *J. Theoret. Biol.* **53**, 205–214. (doi:10.1016/0022-5193(75)90111-3)
- Wauters, A. & Richard-Yris, A. 2003 Maternal food calling in domestic hens: influence of feeding context. *C. R. Biol.* **326**, 677–686. (doi:10.1016/S1631-0691(03)00128-8)
- Bergstrom, C. T. & Lachmann, M. 1998 Signaling among relatives. III. Talk is cheap. *Proc. Natl Acad. Sci. USA* **95**, 5100–5105. (doi:10.1073/pnas.95.9.5100)
- Chittka, L. & Brockmann, A. 2005 Perception space—the final frontier. *PLoS Biol.* **3**, e137. (doi:10.1371/journal.pbio.0030137)
- Cummings, M. E. 2007 Sensory trade-offs predict signal divergence in Surfperch. *Evolution* **61**, 530–545. (doi:10.1111/j.1558-5646.2007.00047.x)
- Ryan, M. J. 1990 Sensory systems, sexual selection, and sensory exploitation. In *Oxford surveys in evolutionary biology*, vol. 7, pp. 157–195. Oxford, UK: Oxford University Press.
- Stuart-Fox, D., Moussalli, A. & Whiting, M. J. 2007 Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *Am. Nat.* **170**, 916–930. (doi:10.1086/522835)