

The origins of communication in animal populations

August 13, 2003

Meredith Root-Bernstein
Princeton University, Santa Fe Institute
Mentor
David Krakauer
Santa Fe Institute

1 Introduction

The evolution of communication in animal populations has been given many theoretical treatments, ranging from ethological design principles to game theoretic accounts of honesty and deceit (e.g. Gould 1982; Krakauer & Johnstone 1995). However, one issue which has not been paid much attention is the origins of communication. Most models assume the existence of a population which already has a set of communicative signals, and pursue some further dynamics. Other models posit the existence of meaningless signals and allow them to develop a communicative function (e.g. Miller et al. 2002), but this does not appear to be biologically well-informed. We would like to understand how a population initially without signals develops communication. Understanding how communication arises will help biologists appreciate the fundamental nature of communication. Too often the concept of communication is taken for granted, hindering a more thorough understanding of a ubiquitous and intriguing phenomenon.

Some issues related to the origins of communication have been examined in the literature. The classic ethological suggestion is that many signals arise from intention movements and then become ritualized, that is, exaggerated and fixed in performance (Gould 1982). This explanation can account for the forms of many threat and mating displays. There is also a small mercenary army of theories of how receiver bias informs signal design (Endler & Basolo 1998; Rowe 1999). Generally these theories posit some version of the idea that receivers of signals or signal precursors have perceptual biases which signallers attempt to exploit to gain a certain response. These models account for the development of signal form, while other theory, such as Zahavi's handicap principle and models

of deceit, try to account for the development of signal content. Theories and models of content assume the preexistence of form, while theories and models of form assume the preexistence of content. Ideally one would like to assume neither and account for both.

In order to begin to account for the ontogeny of communication, regarding both form and content, one must consider the environment in which a population of animals lives. What the animals may communicate about is limited to what they can perceive; that is, the social and physical environment, or some subset of the environment. Their perceptual capabilities are determined both by adaptation to the current environment and the phylogenetic history of adaptations to past environments (evolution is constrained). Thus social and physical environment will affect the potential content of signals. The form in which animals communicate this potential content will depend both on the behaviours which are preexistent and may be modified for signalling functions, and on the animals' perceptual biases. An animal constantly perceives the external environment and has limited attention (Dukas 2002; Kerr & Feldman 2003; Nakajima 2003). A stimulus which is not difficult to perceive (plays into an animal's perceptual biases and does not require intensive attentional investment to discern), and conveys a higher than average amount of information succinctly is in the animal's interest to exploit. Such a stimulus could be described as a signal.

With these mechanisms in mind we have developed a model of the origins of communication as described in the next section. It should be noted that a very similar model has been developed by Di Paolo (1997). However, our model is somewhat more sophisticated and flexible both in form and in the questions it is able to address. Our model is influenced by the body of models dealing with the evolution of language as developed by Krakauer, Nowak and others (Nowak et al. 1999; Nowak & Krakauer 1999; Nowak et al. 1999; Grassly et al. 2000).

2 The Model

2.1 Set-up of the model

In the basic model we imagine a population of c individuals who live in a spatially inexplicit environment characterized by a number b of objects, or functional groupings of objects, O . These objects might be animate or inanimate. Objects have property vectors P . There are b properties each with a range $(0,1)$. The properties of each object are determined by the OP matrix. There is one OP matrix which determines the properties of all objects in the environment. Properties refer generally to any aspects of the objects which can be perceived by the individuals. Individuals observe an object's properties, and as a result they enter one of b states S . Properties are converted into states through an operation which sums the weighted properties, normalizes the sum to a fraction of the size of the total perceptual window (the sum of the maximum possible values of each weighted property), and rounds up to yield an integer discrete

state:

$$ceiling(S \sum \left[\frac{pi^\alpha}{i^\alpha} \right])$$

Where i is the index of each property value p and alpha determines the relative size of each weight; S is the number of states. This is analogous to a cognitive operation such as summation by which stimuli are processed. The states which result may include internal cognitive, emotional, or physiological conditions. Each state causes the individual to display certain properties P , which are drawn from the same set as the object properties. The state to property mapping is achieved via the *SP matrix*. Each individual has its own *SP matrix*; thus each individual may display different properties when in the same state. The individual who encounters an object and displays a set of properties will be referred to as the "signaller," although he may not be signalling per se. Another individual from the population, the "receiver", then observes the signaller's properties, which in turn put the receiver in a state S via the summation operation. An invariant payoff matrix, the *SO matrix*, determines whether this state is the 'correct response' given the initial object in the interaction. That is, the receiver's state must correspond to the initial object. This process may be summarized for individuals N and N' as follows:

$$\begin{array}{ccccccccc}
 & \textit{OPmatrix} & & \textit{summation} & & \textit{SPmatrix} & & \textit{summation} & & \textit{SOmatrix} \\
 O & \xrightarrow{\quad} & P_O & \xrightarrow{\quad} & S_N & \xrightarrow{\quad} & P_N & \xrightarrow{\quad} & S_{N'} & \xrightarrow{\quad} & O
 \end{array}$$

The sequence of interactions occurs for each individual, who iterates through interacting with each other individual t times, encountering a randomly selected object each time.

2.2 Evolution

The *SP matrix* is initially a random $b \times b$ matrix uniform throughout the population. With each generation each individual's *SP matrix* has a 1% chance of a row mutating and a 1% chance of a column mutating. Thus the mutation of both properties and states has a systemic effect on the organism. Selection occurs on the population so that individuals with higher payoff pass on their *SP matrix* proportionally more to the next generation. Various payoff allocation schemes were explored, and are discussed below. Population size remains fixed. In some cases we also allowed the *OP matrix* to evolve through mutations to columns and rows.

2.3 Redundancy in the model

The model was designed to have a certain amount of redundancy. This allows for non-trivial results. Initially, a random *SP matrix* does not return properties P which map to distinct states S . Thus, individuals may have 5 states, but the 5 property vectors which these appear as may map to only 2 states in the receiver. This is because the summation operation is redundant and degenerate. In order to receive a point for an interaction, the receiver must be able

to match states with objects, and so must be able to attain all of the states available in order to match all the objects available (assuming a diagonal payoff *SO matrix*). The problem which the individuals face is to produce *SP matrices* which yield P which in turn yield a different S each, so that all S are available. However, mutation of the *SP matrix* alone cannot produce a perfectly discriminating interaction. This is because individuals also use the redundant summation operation to interpret the properties P of the objects which they encounter. Consequently there 'appear' to be fewer objects than there are; several objects put an individual into the same state. Only by allowing the *OP matrix* to evolve so that objects produce properties which yield discriminable states can perfect disambiguation and coordination be achieved.

Real organisms distinguish only between categories of objects for which it is "useful" to them to distinguish between; thus some degeneracy and redundancy in perception and cognition is by definition ubiquitous. This is reflected in the *SP matrix* evolution and the summation operation. Mutating the *OP matrix* is equivalent to evolving interspecific communication. For example, many flowers evolved certain properties—ultraviolet bull's eye patterns, runway stripes and scent, for example—to communicate their flower status to bees, allowing the bees to recognise and act upon them efficiently.

3 Behaviour of the model

3.1 Effect of payoff allocation

Most models of evolving populations include only one payoff allocation scheme. We decided to test several to see how they effect the dynamics of the model. The first payoff scheme which we used was that when the receiver received a point, the signaller did also, otherwise neither got a point. This 'mutual benefit' scheme resulted in a step function in population payoff because when a small number of individuals got an adaptive mutation to the *SP matrix*, the entire population benefited (Fig. 1). This kind of behaviour is characteristic of systems in which sets of traits are selected for; in this case, the set is a population of mutually comprehending *SP matrices* (e.g. Cooper & Lenski 2000). We also tried the 'each for himself' scheme, in which both receiver and signaller get a point if their own state matches the appropriate one for the given object. This resulted in an apparent random walk of payoffs and showed much lower scores on average, although the maximum possible aggregate payoff was the same (Figure 2).

Unless otherwise noted, all runs used the mutual benefit scheme as the default. We chose this scheme as the default because reflects the observed population dynamics of evolving populations. It is interesting that this is not immediately obvious from the descriptions of the payoff schemes; if anything, the each for himself scheme sounds more biologically realistic.

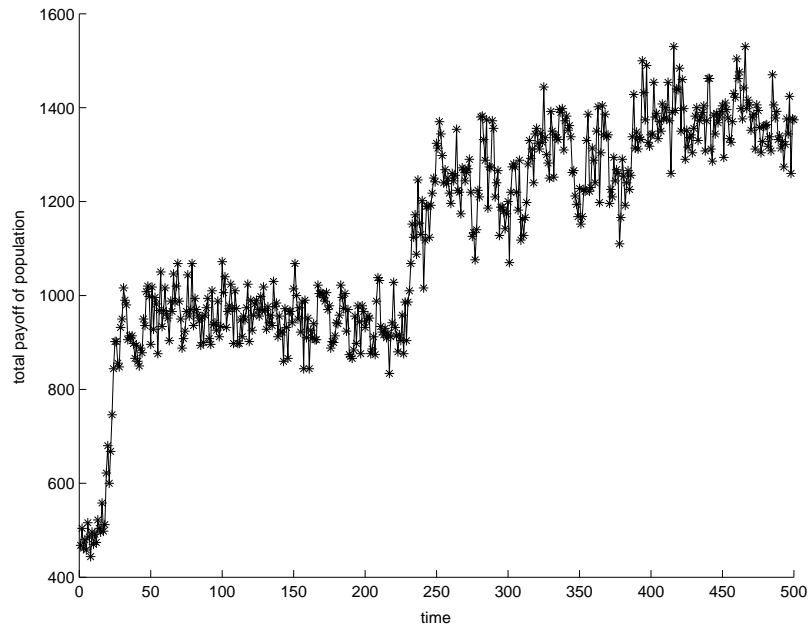


Figure 1: Payoff in the mutual benefit scheme

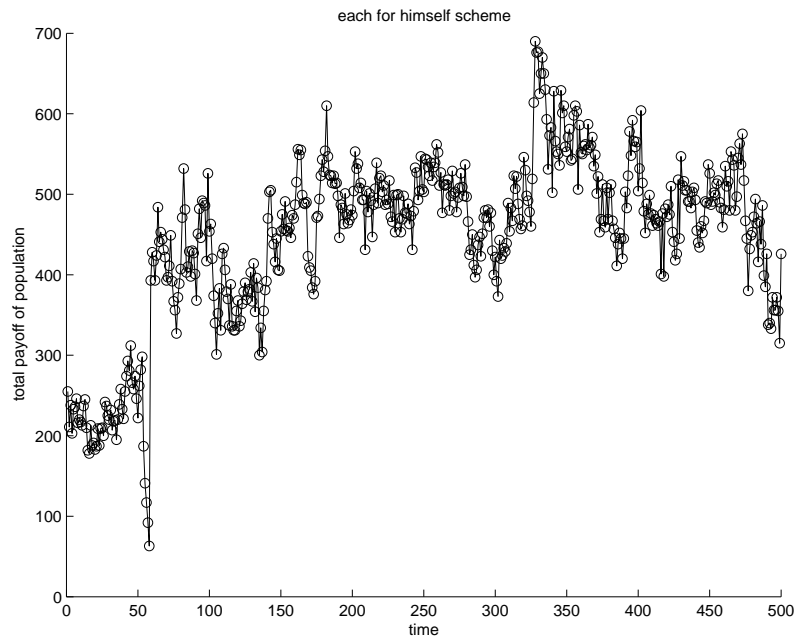


Figure 2: Payoff in the each for himself scheme

3.2 States

Although the individuals in the model are not finite state machines, state is an important variable. The number of reachable states S determines the number of functionally distinguishable objects O in the environment. Figure 3 shows the probability of having states available for use, if there are ten objects and between two and ten states. Note that even with ten states, only states 3-8 are ever used. The probability of having all six of these states available for use is the product of the probabilities and is thus very small. With a random fixed *OP matrix*, a population of 50 individuals with 10 states and a ten-object environment was able to distinguish 4 classes of objects; in other words, it used 4 states. Varying the number of interactions per iteration, t , which varies the selection pressure, had no effect on the number of states used. Increasing the number of iterations twenty fold also resulted in only four states used.

Allowing the *OP matrix* to mutate, over 500 iterations, in a ten object-ten state system, a population with interactions per iteration $t = 1$ used 7 states, and a population with $t = 10$ used all 8 available states. However, even with 8 states, the population achieved only 49% of the highest possible aggregate payoff, compared to 40% of the highest possible aggregate payoff achieved under the same parameter conditions without *OP matrix* mutation and only 4 states. Figure 4 shows three populations with different numbers of states and their payoffs.

Populations can also have more states than objects; in this case we assume a redundant *SO* payoff matrix, so that some objects have more than one appropriate state. However, in our model it is not possible for one object with only one set of properties P to elicit more than one state in either the signaller or the receiver. Consequently the redundancy of the payoff matrix is not reflected in signal design or evolutionary dynamics. The states which the population achieves through *OP matrix* evolution determine which *SO matrix* payoff correspondences are used. If the number of objects is less than or equal to the number of states most probably obtainable via *SP matrix* evolution, then the population can achieve very close to the maximum possible aggregate payoff; this is because each of the objects can be differentiated by a unique state and a unique set of properties. Fully coordinated communication can be achieved (Fig. 5).

3.3 Signal development

In order to determine whether communication is emerging it is necessary to develop some criteria for recognising a signal as such. Primarily a signal needs to communicate something. Within the framework of the model, this means that for a given object encountered by the signaller, the receiver must be able to enter the appropriate state and receive a point. Thus when the entire population is communicating, maximum possible aggregate payoff should be achieved. This also means that in the long term, the appearances P at maximum possible aggregate payoff should be uniform across the population and over time.

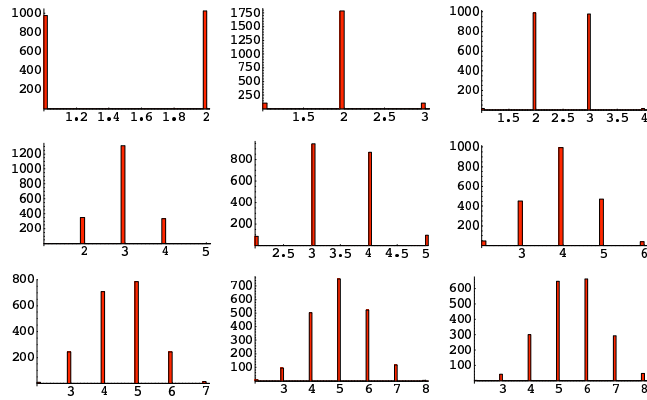


Figure 3: Each distribution shows the probabilities of using each state if you have a random SP matrix, given ten objects and two (upper left) to ten (lower right) states. The probability of having more than one state available is the product of the probabilities shown.

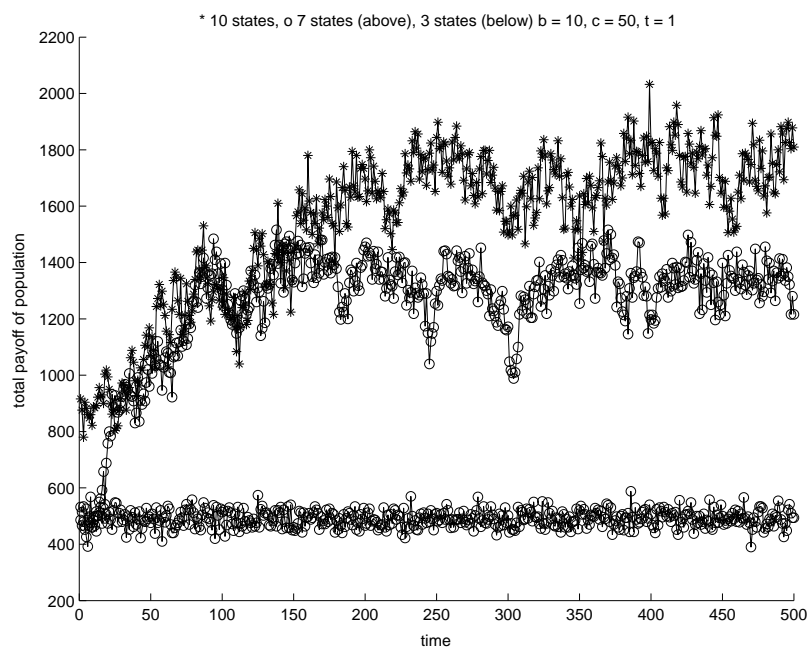


Figure 4: * have 10 states, o above have 7 states, and o below have 3 states. The highest possible aggregate payoff is 4900.

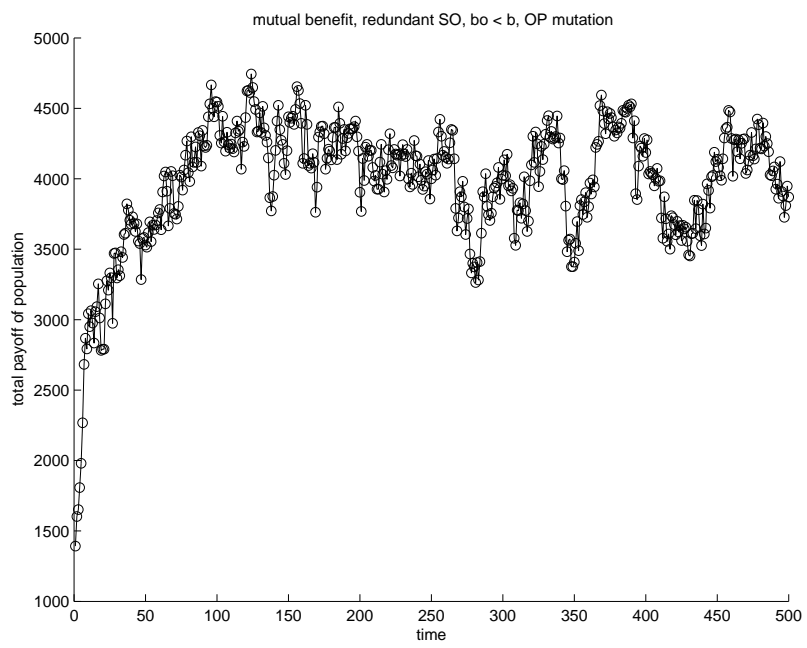


Figure 5: Payoff with four objects and ten states reaches close to the maximum possible aggregate payoff, 4900.

Because the summation operation is redundant, it is possible to have multiple property arrays which all 'look' the same to the summation function. Consequently one could have multiple signals which all 'look' the same at maximum possible aggregate payoff. However, drift would probably result in one dominant signal.

We were not able to run a simulation in which the population achieved maximum possible aggregate payoff, even given the number of states actually available to them. Nor did it appear that any of the populations were converging on similar solutions. See, for example, Figure 6. This shows the properties displayed by each individual when confronted with an arbitrary object, in two different conditions. There are no solutions in common between any of the conditions.

3.4 Spatial model

In order to investigate the effects of space and movement on the evolution of communication, we developed a spatial version of the model. The spatial model differed from the nonspatial model in that the individuals and objects existed on a two dimensional torus (to eliminate edge effects from movement), and had interaction radii within which they could interact with objects and individuals. Objects and individuals could diffuse in a random walk over the torus. We found that when interactions between individuals are constrained by movement, small local communities which only communicate with each other form. Typically individuals communicate best within their local community (Figure 7). This pattern occurs for both large and small interaction radii. In the large interaction case this is equivalent to the non-spatial model because everyone interacts with everyone else. Thus "dialects" form with or without spatial constraints during the evolution of communication.

4 Discussion

4.1 The evolution of states

In this model we evolve both states and signals. These are linked through the mechanisms of perception; we use states as a shorthand for the end result of some perceptual-cognitive-emotional-physiological set of processes. The most disambiguated communication resulting in the highest fitness occurs when the organisms have more states than there are objects in the environment. This seems counterintuitive. What are the extra states for, or is there a biological justification for supposing their existence? The answer to this question may be understood in the following way. Suppose I have ten objects and ten states. At my most keenly perceptive, I can distinguish six classes of objects and react to them in six different ways (six states are used out of ten). If I develop some more subtlety in my perception or in my internal state possibilities, I can distinguish, say, eight classes of objects. I go on adding subtlety to my perception or state

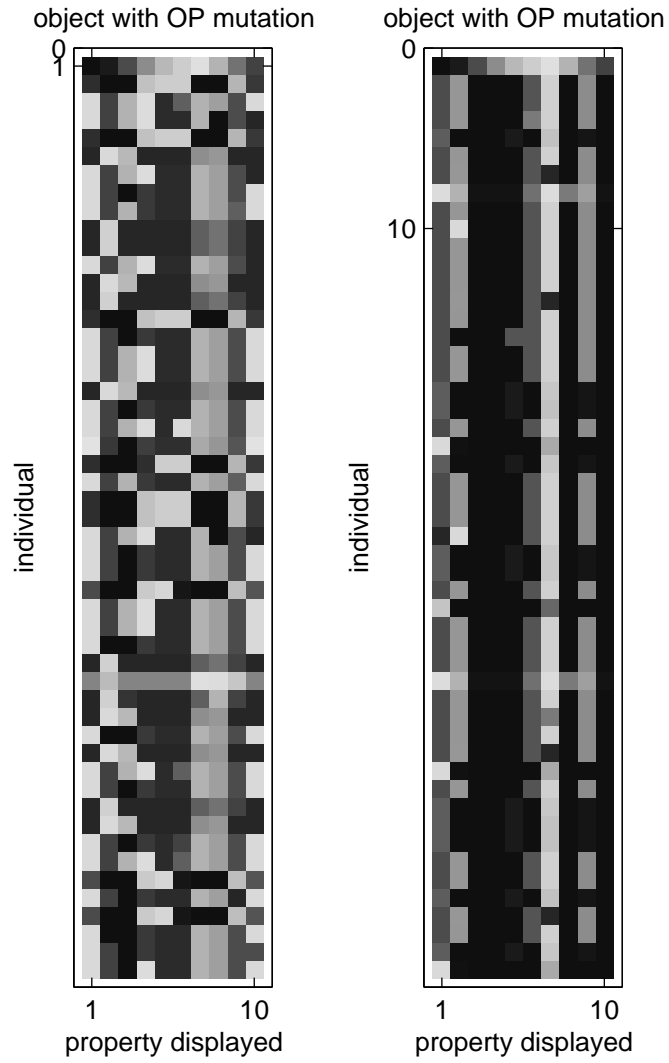


Figure 6: Each colored square indicates a P value. Individuals in two different conditions were shown object 7 and displayed a P vector represented by the rows of the figures.

space until I can distinguish all ten objects— but I now have many more than ten states, some of which are never elicited by any object properties. These states in some sense are only potential states—states which I might be able to achieve but haven't evolved to experience. They might be understood as epiphenomena of the state space which I have evolved to use in response to my environment and the selection pressure to communicate. But note that in this model although the evolution of the state repertoire is linked to intraspecific communication, the comprehension part of the loop, in which the receiver must find the appropriate state to match the original object, is not vital to the evolution of state repertoire. It is simply the *OP matrix* evolution, the evolution of *interspecific* signals, which determines the state repertoire. Thus we see receiver psychology at work between species in order to coordinate behaviour with the environment and vice versa.

4.2 The evolution of communication

In modeling the evolution of communication one wants to avoid presupposing the form and content of the potential signals as much as possible. We constrained form by the range of properties available and content by the range of objects and states and the ways in which they had to be matched to receive points. However, we found that there were many varieties of result which could be produced within these constraints due to degeneracy in the model and evolution to avoid it.

Although we did not see the development of communication in the form which we expected, it is difficult to determine what this means. One possibility is that there are many local maxima in the evolutionary trajectory which the simulations get stuck at, which are characterized by suboptimal communication. It is also possible that with certain initial conditions it is extremely difficult if not impossible to solve both the *OP matrix* and the *SP matrix* simultaneously. This would also result in suboptimal communication. Finally, it is possible that as there are many possible solutions, local interaction communities in both the spatial and nonspatial models each arrive at different optimal communications, with the result that as a whole the population does not appear to have developed a unique signal. We do not have a measure of how long it takes to solve both matrices together on average, so it is difficult to distinguish between the latter two possibilities.

It is notable that in our model all the signals or proto-signals are multimodal and multicomponent (Rowe 1999). This is reflective of some forms of communication in reality, but not all. However, it implies that multimodality and multicomponentality may have evolved in order to fully stimulate receivers in distinctive ways which will yield distinctive states in the receiver. Our model also implies that signals should be "evenly spaced" in the perceptual window in order to yield distinct states when received. Another result of this receiver bias manipulation is that groups of populations in an environment which all interact will all be trying to manipulate each other as objects in the environment, and thus we may see that certain interspecific signals are conserved while certain intraspecific signals are similar across several of the species. In fact, many interspecific and intraspecific signals are conserved; for example, warning calls,

aposematism, and calls following the M-S rules (dominance and subordination signals, generally) (Morton & Page 1992) are very similar across and between species. Generalized rules of signal design have been looked for and not found (Dawkins 1993), but the idea of mutual perceptual manipulation may provide a basis for developing such a theory.

4.3 Future directions

At this stage there is still much exploration of the model to be done. We would also like to add noise to some of the properties to see how the population differentially uses noisy and non-noisy channels. Another possibility is to allow objects to evolve away from being perceptible, i.e. towards camouflage. It would be desirable to be able to control the community structure of the space, for example by making the objects clumpily distributed or by adding communicative barriers. Finally, making the individuals into finite state automata would link this model to many others which use communicating finite state automata to solve coordination problems (Miller et al. 2002; Miller & Moser 2003).

5 Bibliography

Cooper, V S, Lenski R E. 2000. The population genetics of ecological specialization in evolving *Escherichia coli* populations. *Nature*. 407, 736-739.

Dawkins, M S. 1993. Are there general principles of signal design? *Philosophical Transactions: Biological Sciences*. 340, 251-255.

Dukas, R. 2002. Behavioural and ecological consequences of limited attention. *Philosophical Transactions of the Royal Society of London B*. 357, 1539-1547.

Endler, J, Basolo A L. 1998. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution*. 13, 415-420.

Gould, J L. 1982. *Ethology: the mechanisms and evolution of behavior*. New York: W W Norton & Company.

Grassly, N C, Haesler, A v, Krakauer, D C. 2000. Error, population structure and the origin of diverse sign systems. *Journal of theoretical biology*. 206, 369-378.

Kerr, B, Feldman, M W. 2003. Carving the cognitive niche: optimal learning strategies in homogenous and heterogeneous environments. *Journal of theoretical biology*. 220, 169-188.

Krakauer D C, Johnstone R A. 1995. The evolution of exploitation and honesty in animal communication: A model using artificial neural networks. *Philosophical Transactions: Biological Sciences*. 348, 355-361.

Miller, J H, Butts, C T, Rode, D. 2002. Communication and coordination. *Journal of Economic Behavior and Organization*. 47, 179-195.

Miller, J H, Moser, S. 2003. Communication and coordination. Santa Fe Institute Working Paper.

- Morton, E S, Page, J. 1992. *Animal Talk: Science and the voices of nature*. Random House.
- Nakajima, T. 2003. Probabilities of encounters between objects in biological systems 2: cognizer view. *Journal of theoretical biology*. 221, 39-51.
- Nowak, M A, Krakauer, D C, Dress, A. 1999. An error limit for the evolution of language. *Proceedings of the Royal Society of London B*. 266, 2131-2136.
- Nowak, M A, Plotkin, J B, Krakauer, D C. 1999. The evolutionary language game. *Journal of Theoretical Biology*. 200, 147-162.
- Nowak, M A, Krakauer, D C. 1999. The evolution of language. *Proceedings of the National Academy of Sciences USA*. 96, 8028-8033.
- Rowe, C. 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*. 58, 921-931.