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Sex and the Altruist

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Abstract

It has recently been proposed that some forms of altruistic behaviour in nature can be explained by viewing it as a sexually selected signal of quality. The problem contains more depth than at first appears and this report presents one attempt at making the idea more concrete via the construction of evolutionary models. A simple new model of signalling is presented, and an extension is developed incorporating the possibility of altruistic signalling. A discussion follows in which the problem of information loss from the acceptance of altruism is explored, as is behaviour, observed in nature, sufficient to maintain its reliability.

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Introduction

Why should an organism perform an act which is beneficial to another at a personal cost to itself? The aim of this project has been to elucidate a recent explanation for such so-called "altruistic" behaviour which is observed to occur in nature. Its existence is problematic as evolution should be expected to favour selfish individuals.

Rogers [Rog98] has proposed that the existence of certain types of altruistic behaviour can be explained by reference to sexual, as opposed to natural, selection. The idea was stated in general terms and this report presents one attempt at making the idea more concrete via the construction of evolutionary models. Such an approach is a useful one because it necessarily requires any assumptions be made explicit, and thus aids in understanding and reasoning about the ideas.

The following chapters provide the necessary background of signalling theory and sexual selection required to motivate the problem and understand Rogers' proposed solution. A simple new model in which honest signalling is a stable evolutionary outcome is presented and analysed. An extension to this model is then developed which incorporates the possibility of altruistic signalling. A discussion follows in which a disadvantage of altruistic signalling is described. I then show that the rejection of gifts, which is known to occur in nature but lacks any convincing explanation, may evolve because it overcomes exactly this problem.

Chapter 1

Communication in Nature

1.1 The Problem

Organisms in nature face choices, and it is in their genes' interests to make good decisions. On the plains of Africa, a lion catches sight of a potential meal. The meal is staring back. Should the lion expend the time and effort required catch it? Or would it wiser to pass up the opportunity?

Suppose two rival stags encounter each other in the wilderness. Each must assess whether it is worth their while to fight. Should the rival be challenged, or would it be more prudent to avoid a confrontation? The benefits for the victor, in terms of increased mating opportunities, may be huge. However, in both cases, a poor choice risks wasted time and energy or injury.

Even between such seeming antagonists, communication can be to their mutual advantage. If the two stags can asses their chances of prevailing without actually dueling it out, both avoid the possibility of injury. If the gazelle convinces the lion that it can escape, each can avoid an exhausting chase and conserve their energy for more productive ends. In each case, both parties gain. Neither is required to fruitlessly exhaust itself.

If a mechanism which allows them to communicate could evolve, those that made use of it could use their limited resources more cost-effectively. In consequence, they would enjoy a higher chance of survival and reproduction, giving their genes an evolutionary edge. Even if the advantage is small, the action of natural selection over millions of years of evolutionary time would in all likelihood see the adaptation to proliferate.

However, even if such a means of communication could be established, the reliability of the information it provides cannot be guaranteed. Unless the interests of each party coincide completely, which is rarely the case in nature, an incentive to provide false information is created. It is in the interests of weak gazelles to cheat, as they would reap the same benefits as those that were stronger. If this is the case, natural selection will ensure that the cheats are selected for. This is because a weak gazelle will fare worse by adopting a policy of honesty. Everything else being equal, you would eventually expect the entire population to claim that it was fit, irrespective of its true underlying quality.

However, every thing else is not equal because the receivers of the information are also subject to evolutionary pressure. A lion who relied solely on the information provided in such a situation would starve due to a belief that every gazelle could outrun it. The information conveyed has lost its value to the observer and communication would be expected to die out in the population. Those which payed no attention to the information on offer would be selected over those that did. While it is still in the interests of the organisms with valuable information to communicate, there must be some way to ensure honesty if the mechanism of communication is to survive over the long term.

So, in the absence of trust, how can reliable communication take place? In the computing world we rely on cryptographic techniques to identify who is talking to us with relative certainty. However, this essentially boils down to assigning levels of trust amongst various agents. In the final analysis, we can never guarantee that the information we obtain is trustworthy; although the odds can be improved by considerations of reputation, and the costs of any dishonesty being detected.

The problem is made more difficult in nature. Cryptography is not (known to be) available and there is no law imposed from above, so cheaters can prosper and communication becomes worthless. However, organisms do not have to resort to chasing, fighting, etc. They have evolved ways to ensure reliable communication in spite of these difficulties. How they do so is the topic of the next section.

1.2 Zahavi's Theory of Signalling

The gazelle notices the approach of the lion. Instead of running away quietly and at high speed, it typically engages in stotting — leaping into the air and calling out, while making eye contact with the lion [Dug97]. It was such seemingly counter-intuitive behaviour which the Israeli ornithologist Ahmot Zahavi sought to explain when he proposed the theory of costly signalling (or handicap principle) in the late 1970s.

Zahavi showed how such costly and seemingly irrational behaviour could be seen as a means of communication. He postulated a number of conditions that had to be met if the "signal" was to be reliable, and thus evolutionarily stable:

1. A partial intersection of interests between the signaller and observer.
2. A quality of the signaller which is costly to discover.
3. A correlation between the information conveyed by the signal and the quality of interest to the observer.
4. That the cost of dishonesty must outweigh the benefits.

As an example of the first condition: it is in the gazelle's interests to create the impression that it is fit, healthy and able to give the lion a good run for its money if pursued. It is also in the interests of the lion to avoid such sprightly gazelles, as it must spend a lot of effort on the chase: effort which could be more profitably applied to a less risky pursuit.

On the other hand, communication cannot take place if it is not in the interests of both parties involved. If it is never in the interests for an organism to release information, any potential observer will be waiting in vain for a signal. There will be no one at the other end of the line. Additionally, the information provided by the signaller must be honest. If this is not the case, then it is against the interests of a potential observer to rely on it.

The second condition, the existence of a hidden quality of interest, motivates the need for active communication to take place. If the information of interest to the observer is not costly to obtain, there would be no need for the signaller to go to a special effort to get the message across. Qualities such as, for example, foraging ability, fitness levels, freedom from parasites or the fact that a predator has been spotted fall into this category. Each is costly to ascertain without active advertisement: in leu of a signal, the lion must exhaust itself chasing its prey.

The next condition necessitates the reliability of the communication. A correlation must exist between the form of signal and the hidden information to which it pertains. If this was not the case, there would be little point in an observer relying on it to infer the underlying quality of the signaller it is interested in. The reason a lion is less likely to chase the stotting gazelle is because stotting requires physical fitness. It is likely to show the weakness of an unfit specimen and such an animal would be wiser to conserve its energy for running.

Of course, the gazelle has other options open to it. It could, for instance, choose to stick out its tongue while performing an elaborate dance. Although costly, requiring time invested to develop the skill, this is beside the point. Not only would the lion need to come closer to appreciate the spectacle, it would remain in the dark as to its primary concern: the stamina of its prey. Thus, there would be selective pressure for lions to ignore such displays.

The fourth and final condition ensures that the signal is adaptive for both parties and thus maintained over evolutionary time scales. Cheating will not be selected for if it is not profitable for a signaller to deceive an observer. This ensures that signallers who cheat cannot invade the population. Conversely, if deception is worthwhile it will occur, devaluing the worth of the signal and creating a disincentive for an observer to pay attention to it.

While initially controversial, Zehavi's theory was largely vindicated by Grafen [Gra90a], who formally modelled it in 1990. It provides a solid foundation for explaining reliable communication in nature. In doing so it provided a way to explain non-adaptive behaviour and form in nature. It was widely held that natural selection, barring the supposed aberration of sexual ornament, would select for efficiency. The existence of wasteful behaviour flew in the face of this assumption and it was not clear as to why it should persist.

The theory of biological signalling shows how bearing a cost can be profitable and thus adaptive. This is the core of the "handicap principle": a self-imposed burden which yields benefits to the individual and, more importantly, their genes. However, the tale does not end here. The handicap principle sheds light on a persistent thorn in the side of evolutionary theory: the evolution of costly preferences for wastage. It to this which we will now turn.

Chapter 2

Sexual Selection

2.1 Distinguished from Natural Selection.

"The survival of the fittest" is the dictum of Darwinian evolution. Yet despite this, there are examples in nature of evolved features which are costly to its bearer. The peacock's tail is the prototypical example: its owner would be better able to survive without it. However, in spite of this, peahens prefer to mate with peacocks possessing the most eye-spots in their train[1]. It is the evolution of such preferences on the part of females for features which are unprofitable for both her mate and her sons that requires explanation. In order to do so, we will need to elaborate on the nature of evolution and natural selection.

Suppose a mutation alters a trait in such a way to increase the probability of survival for an organism which possesses it. The operation of natural selection would expect to see the improved trait shared by the whole population at some point in the future. This is because organisms expressing it should be more likely to produce offspring than other, less endowed, members of their species. All else being equal, there is a greater likelihood that the next generation will see a greater proportion of the population expressing that trait.

The advantage conveyed by a new trait can be seemingly insignificant, even unmeasurable, and yet still be selected for over time. It need only confer a statistical advantage on the new trait over the old. A smaller increase in the probability of survival only means that the rate at which the old trait is displaced will be slower, not that the displacement will not occur. However, it does make it more likely that the trait will die out by chance, due to the length of time in which only a small number of organisms express it. A smaller group has a greater chance of being wiped purely because there is a higher chance that all the members will die out for other reasons.

A straightforward example of the process would be a moth which, due to a mutation, possessed camouflage that fooled its predators slightly more often than other members of its species. Being less likely to be eaten, its progeny and its progeny's progeny, will be at an advantage. By being less likely to be eaten than the others, moths with the trait would be selected for within the population. This would continue until another improvement appeared, or the predators themselves adapted or the whole population possessed the new trait.

However, the phrase "survival of the fittest" does not capture the full picture, both in terms of what it is that is surviving and what it means to be "the fittest". As hinted at above, it would be more accurate to say "survival of the most prolific set of genes". This gene-based focus is the one argued for by Dawkins: the idea that organisms are merely vehicles for the further propagation of the genes that built them. The view has a lot of merit. It

[1] [Cro91] p255

emphasises the fact that it is the genes that replicate and subject to evolutionary pressures, not the organisms themselves. Therefore, it is these which natural selection operates on, not the individual organism. This view is important for understanding the notion of sexual selection which follows.

Throwing the existence of sex into the mix complicates things. While there are organisms which can reproduce asexually, most capable of behavioural communication are sexual. Both types must be approximately adapted to the habitat if they are to propagate their genes. The habitat includes such things as location, climate and other organisms. However, a sexual organism faces an additional hurdle. If it is to reproduce, it needs to attract members of the opposite sex. If it fails to do so, the net effect is the same as if it had drowned or been eaten by a predator in childhood: its genes will be eliminated from the pool.

There are thus two types of selective pressure operating on sexual creatures. Natural selection promotes those which are better at surviving in a given habitat. However, those individuals which make themselves more attractive to the opposite sex effectively give themselves and their progeny a higher rate of reproduction than other members of the species. Sexual selection promotes those which are better at attracting mates. Over time, you would expect the genes that coded for this attractiveness to proliferate within the population in the same way that the genes coding for a trait conducive to survival would do.

It is quite possible for the two selective pressures on a sexual organism to be opposed. That which is adaptive for survival, such as clearer vision, may be maladaptive in the sexual arena. For example, during the mating season, male pelicans (*Pelecanus onocrotalus)* grow large bumps on their beaks which seem to be actively disadvantageous to its owner, as the pelican needs good sight in order to catch fish [Cro91]. At the same time, those same genes may confer great advantage in terms of the number of mating opportunities open to an individual.

Over time, it is the genes that enhance the rate of their own proliferation will be selected for, even where their expression reduces the ability of the organism they designed to survive in its natural environment. This is because evolution operates on the genes themselves via the organism which expresses them and not on the individual itself. As long as the rate of replication is equivalent, evolution is indifferent to the options of burning out in a procreative burst or surviving for longer at a less fertile level.

2.2 Victims of Fashion?

The situation mentioned above is not uncommon in nature. There are many cases in which some feature is costly to its owner and yet attractive to the opposite sex. The peacock's tail is the prototypical example, as are the male pelican's bumps, mentioned above. Their features are costly to bear. This makes it more difficult to avoid predators, among other things, and yet they are actively sought after by the opposite sex.

The peacock is a victim of sexual selection and its tail is an adaptation to the sexual environment. To have a utilitarian tail drastically lowers their fitness as it effectively prevents them from reproducing. There is therefore selective pressure towards the larger, ornate and more cumbersome variety. However, peahens are products of selection, too. Why should their preference for long tails exist?

The maintenance of the preference, once established, is straight-forward. Once the majority of the population prefers males with long tails, a mother would be putting her sons, and thus her genes, at an evolutionary disadvantage. By making a utilitarian choice, she makes her sons less attractive to the opposite sex. Fisher [Fis30] showed how the process could be started and fuelled in a process of positive feedback, once a majority of the population had a preference for a particular trait. This majority of preference was not necessarily a large proportion of the population; just larger than any other faction [Cro91].

According to Fisher, the peacock's tail is a burden that must be borne in the interests of fashion, a fashion which both sexes are forced to adhere to. Evolution has favoured costly preferences and found itself in a less-than-ideal cul-de-sac from which it cannot escape.

2.3 Zahavi's Solution

The handicap principle is able to shed new light on this conundrum of costly preference. It raises the possibility that, far from being the victims of fashion, females are making sensible decisions when they they choose the largest tail. When viewed as a signal, the fashionable handicap which peacocks are forced to bear is transformed into the means by which reliable information is conveyed.

The essential problem a sexual organism faces is the need to select a mate with good genes. Their choice of partner will directly impact the fitness of their own offspring and thus their inclusive fitness. Natural selection favours genes that can choose wisely. Although this is an issue for both sexes, a poor choice is especially costly for females. This is because, unlike the male, females are limited in the extent to which they can produce offspring.[2] Compared with the male, they must invest more time and energy to produce an equivalent number of offspring. If they make a poor choice, they are burdened with it for longer. It is therefore profitable for the female to spend time and energy assessing a suitor's quality.

This being the case, if the high quality males can find a way to advertise their vigour in a reliable way, they will benefit. Additionally, if females prefer males which exhibit a reliable signal, the male which is able to signal at a level above that of his peers can benefit greatly. There is sexually selected pressure for larger and more costly signals, and so males with even greater handicaps will proliferate in the population. The females which choose based on this signal will be assured of high quality genes.

If the signal takes the form of an elaborate tail, elaborate tails will be sexually selected for. The signal must be costly in order to be reliable and the process will reach an equilibrium at some point, as it cannot go on indefinitely. For instance, the peacock needs to be able to survive as an adult for at least a short period of time in order to mate. This imposes practical limits on the magnitude of the handicap able to be borne. Tail lengths will stabilise at the point where the costs of investing in a longer tail equal the benefits to be gained.

However, there remains the problem of how this situation is maintained over an evolutionary time-scale. When the females are continually selecting the highest quality males, as advertised by the handicap they are able to bear, only the best males in each generation would be able to pass on their genes. The females preferences will be acting as a genetic "sieve", leaving only those males which posses desirable qualities. Within a few generations, all the males in the population would possess the same qualities.

Upon reaching this state, the females have nothing to gain by making any particular choice. All males being of equal worth, there is no incentive to choose and therefore no incentive to signal by bearing a handicap[3]. Expensive tails would expect to be selected against as the females would have nothing to gain by making any particular choice. The tail would have become a pure burden. If elaborate tails are to be explained as a sexually selected signal of quality, the fact that this outcome does not eventuate needs to be explained.

A theory put forward in 1982 by Hamilton and Zuk [HZ82] proposed that a solution to the problem might be found by reference to parasites and pathogens. Due to their short life-

[2] This is Bateman's principle: male fitness is limited by quantity of offspring, female by quality.

[3] the so-called "lek paradox".

cycles, these can evolve at a high rate in response to selective pressure. This means that the genes which grant protection today will not necessarily provide immunity for their bearers tomorrow.

Ridley expresses it thus:

> ... for parasites and their hosts are continually changing their genetic spots to outwith each other. The commoner a particular strain of host is in one generation, the commoner is the strain of parasite that can overcome its defences in the next. And vice versa: whatever strain of host is most resistant to the prevalent strain of parasite will itself be the prevalent strain of host in the next generation. Thus, the most disease-resistant male might often turn out to be the descendant of the least resistant one in a previous generation.[4]

When the females choose the healthiest males in the current generation, they need not be picking the same set of genes as they did in generations past. What was good in the past is not necessarily what is good today. The constant battle between parasites and the individuals on which they rely means there will always be variety within the population and therefore an incentive to choose the healthiest male. The tail is always a useful indicator of quality to the females.

Evidence has tended to support the idea[5]. For example, of 109 species of bird, there was a strong positive correlation between colouration and parasite load. Indeed, the quality of many sexually selected features seems to be very sensitive to their owner's parasite load.

Thus the sexually selected signal has forced the male to communicate valuable information about its level of health and vigour to the females, in whose interests it is to choose the best. The is information that is costly to obtain, in terms of time, energy and the risk of predation. Communication is in the interests of healthy males, and as long as the conditions for honest signalling are met, cheating is not an option. Less fortunate males have no option but to play along as best they can.

What is the significance of this idea that costly preferences, could be signals of quality? It is that sexual preferences for costly traits can be adaptive strategies to adopt. Instead of being an aberration, a consequence of the whims of fashion, it can be in the interests of females to select for those costly traits which relay valuable information to them — information which would otherwise be prohibitive to obtain.

[4] [Rid94] p146

[5] *ibid*

Chapter 3

An Evolutionary Model of Signalling

This chapter describes a model of signalling in which honest signalling is an evolutionarily stable outcome. It has the advantages of:

- Modelling changes in quality and signal level using continuous functions, unlike a discrete game-theoretic model.
- Describing behaviour and fitness in terms of simple linear functions.
- Making explicit assumptions about the nature of an individual's fitness.

The work in this chapter was done in collaboration with Marcus Frean.

3.1 The Model

The model comprises of two distinct populations, the signallers and the observers. Each signaller i has a certain amount of quality q_i varying between zero and one, some of which it can choose to spend on signalling. The strength of its signal is calculated from the linear equation

$$s_i = S_i^0 + (S_i^1 - S_i^0)q_i \tag{3.1}$$

That is, S_0^i is the signal level adopted if $q = 0$, and S_1^i is that adopted if $q = 1$. Between these two extremes we assume a smooth linear transition and the two parameters together describe its signalling strategy. The parameters and signal level can range between $[0, 1]$.

When $S_i^0 = S_i^1$, the signaller is dishonest, that is, it signals at the same level regardless of its underlying quality. The greater the difference, the greater the honesty of the signal. This means that it is easier for an observer to distinguish different signal levels, in order to deduce a signaller's underlying level of quality. Figure 3.1 shows an example of an honest signalling strategy.

Each observer j can in turn assign to each signaller an "alliance strength" a_{ij}, based on its signal level:

$$a_{ij} = A_j^0 + (A_j^1 - A_j^0)s_i \tag{3.2}$$

Similarly, the alliance parameters A_j^0 and A_j^1 of individual j describe the observer's preferences. Note that both equations allow for an individual to assume counter-productive strategies, such as signalling at a high level when of low quality, or choosing the signaller which signals the least.

Once an observer j has assigned a preference a_{ij} to an individual signaller i, its strength is normalised with respect to its preferences for all other signallers. This captures the fact

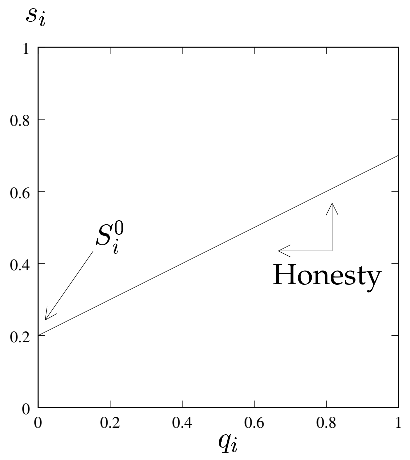

Figure 3.1: A graphic representation of the signalling function.

that the observer has a limited number of resources available and must make good decisions if its genes are to prosper, reflecting the position of female organisms in the real world.

$$p_{ij} = \frac{a_{ij}}{\sum_k a_{kj}} \tag{3.3}$$

The utility of such decisions is measured by two fitness equations for each type of individual, respectively. The fitness w of signaller i is calculated by

$$w_i = (q_i - cs_i)n_i \quad \text{where } n_i = \sum_j p_{ij} \tag{3.4}$$

In other words, it is a product of its remaining quality after signalling and the sum strength of the alliances it achieves. If this is negative the individual is assigned an effective fitness of zero: it has signalled itself to death. The constant c establishes the relative cost of signalling at a given level and is assumed to be unity hereafter, unless stated otherwise.

The term $(q_i - cs_i)$ can be thought of as probability of surviving as an adult for a given amount of time, and n_i the number of alliances or matings achieved. Achieving a low alliance level lowers your fitness, even if the individual is of high quality. This reflects the real world: genes with a low rate of replication will be selected against.

The observer's fitness function is determined by:

$$\text{Observer fitness } v_j = \sum_i p_{ij} q_i \tag{3.5}$$

This is the sum of the qualities of the signallers, weighted by its chosen alliance strength.

The dynamics of the model are as follows:

- The population size is fixed.
- Roulette wheel selection of strategies is employed to select the next population, based on the fitness each individual achieved. A small amount of noise is added to each strategy parameter.
- A random quality is assigned to every signaller from the range $[0, 1]$: we model the evolution of strategies, but not of quality per se. We want to establish the fitness of the

strategies, and thus the genes that code for them, when expressed over generations in many different individuals[1].

3.2 Analysis

The following is an analysis of the model described above. Its aim is to show that it pays an observers to ally with an honest signaller and that the strategy of honest signalling is a profitable outcome across all levels of quality. We begin with the observers and deal with an arbitrary observer. We assume a homogeneous observer population for simplicity, and therefore represent equation 3.5 without an index j:

$$v = \sum_i p_i q_i \quad \text{where} \;\; p_i = \frac{A_0 + (A_1 - A_0)s_i}{Z}$$

The normalisation Z can be reduced to

$$\begin{aligned} Z &= \sum_k A_0 + (A_1 - A_0)s_k \\ &= NA_0 + (A_1 - A_0)N\overline{s} \\ &= N\Big(A_0 + (A_1 - A_0)\overline{s}\Big) \end{aligned}$$

where N is the size of the signalling population. So,

$$\begin{aligned} v &= \frac{1}{N\Big(A_1\overline{s} + A_0(1-\overline{s})\Big)} \sum_i A_0 q_i + (A_1 - A_0)s_i q_i \\ &= \frac{N\overline{q}A_0 + (A_1 - A_0)\sum_i s_i q_i}{N\Big(A_1\overline{s} + A_0(1-\overline{s})\Big)} \end{aligned}$$

We now derive and simplify $\frac{\partial v}{\partial A_1}$ in order to establish the change in fitness experienced by an observer given a change in the parameter A_1:

$$\begin{aligned} \frac{\partial v}{\partial A_1} &= \frac{\sum_i s_i q_i}{Z} - \frac{(N\overline{q}A_0 + (A_1 - A_0)\sum_i s_i q_i)N\overline{s}}{Z^2} \\ &= \frac{1}{Z}\left[\sum_i s_i q_i - \frac{(N\overline{q}A_0 + (A_1 - A_0)\sum_i s_i q_i)\overline{s}}{A_0 + (A_1 - A_0)\overline{s}}\right] \\ &= \frac{1}{Z}\left[\Big(\sum_i s_i q_i\Big)\left[1 - \frac{\overline{s}(A_1 - A_0)}{A_0 + (A_1 - A_0)\overline{s}}\right] - \frac{N\overline{q}\,\overline{s}A_0}{A_0 + (A_1 - A_0)\overline{s}}\right] \\ &= \frac{1}{Z}\left[\Big(\sum_i s_i q_i\Big)\frac{A_0}{A_0 + (A_1 - A_0)\overline{s}} - \frac{N\overline{q}\,\overline{s}A_0}{A_0 + (A_1 - A_0)\overline{s}}\right] \\ &= \underbrace{\frac{1}{Z} \times \frac{A_0}{(A_0 + (A_1 - A_0)\overline{s})^2}}_{\geqslant 0} \times \underbrace{\left[\frac{1}{N}\sum_i s_i q_i - \overline{q}\,\overline{s}\right]}_{cov(q,s)} \end{aligned}$$

Thus,

$$sign\Big(\frac{\partial v}{\partial A_1}\Big) \;=\; sign\Big(cov(q,s)\Big)$$

[1] A more ambitious approach would be to attempt to model both at once!

The covariance between q and s represents the average level of honesty within the population. This shows that A_1 should rise if signalling is honest. Performing a similar analysis on the parameter A_0, we have:

$$v = \frac{N\overline{q}A_0 + (A_1 - A_0)\sum_i s_i q_i}{N(A_1\overline{s} + A_0(1-\overline{s})) = Z}$$

$$\begin{aligned}
\therefore \frac{\partial v}{\partial A_0} &= \frac{N\overline{q} - \sum_i s_i q_i}{Z} - \frac{\Big(N\overline{q}A_0 + (A_1 - A_0)\sum_i s_i q_i\Big)N(1-\overline{s})}{Z^2} \\
&= \frac{1}{Z} \times \left[N\overline{q} - \sum_i s_i q_i - \frac{N(1-\overline{s})(N\overline{q}A_0 + (A_1 - A_0)\sum_i s_i q_i)}{N(A_0 + (A_1 - A_0)\overline{s})}\right] \\
&= \frac{1}{Z^2} \times N\overline{q}A_0 + N\overline{q}(A_1 - A_0)\overline{s} - (\sum_i s_i q_i)A_0 - \\
&\quad (\sum_i s_i q_i)(A_1 - A_0)\overline{s} - N\overline{q}A_0 - (A_1 - A_0)\sum_i s_i q_i + N\overline{s}\,\overline{q}A_0 + \overline{s}(A_1 - A_0)\sum_i s_i q_i \\
&= \sum_i s_i q_i[\overline{s}(A_1 - A_0) - (A_1 - A_0) - \overline{s}(A_1 - A_0) - A_0] + N\overline{q}A_1\overline{s} - N\overline{q}A_0\overline{s} + N\overline{s}\,\overline{q}A_0 \\
&= -A_1(\sum_i s_i q_i + N\overline{q}\,\overline{s}) \\
&= -NA_1(\sum_i s_i q_i - \overline{q}\,\overline{s})
\end{aligned}$$

And, similarly,

$$sign\Big(\frac{\partial v}{\partial A_0}\Big) = sign\Big(-cov(s,q)\Big)$$

achieving the result that A_0 should fall with honesty and discernment increase.

We now establish that it is profitable for the signallers to be honest, i.e that it is adaptive to signal at a level appropriate to their quality. The result we are leading up to is shown in figure 3.2. We assume discerning choosers (e.g. $A_1 = 1$, $A_0 = 0$), which allows us to take a signaller's alliances are proportional to the level of its signal ($n_i \propto s_i$). We thus have

$$w_i \propto (q_i - cs_i)s_i$$

and want to determine how a change in S_0 affects the fitness w for a signaller overall fitness of quality q, given that the observers are choosy:

$$\begin{aligned}
\frac{\partial w_i(q)}{\partial S_0} &= s(\frac{\partial q}{\partial S_0} - c\frac{\partial s}{\partial S_0}) + (q - cs)\frac{\partial s}{\partial S_0} \\
&= (q - 2cs)(1-q) \\
&= q - q^2 - 2cs + 2csq \\
&= q - q^2 - 2c\Big[S_0 + \Delta S_q\Big] + 2c\Big[S_0 + \Delta S_q\Big]q \quad \text{where } \Delta S = S_1 - S_0 \\
&= q - q^2 - 2cS_0 - 2c\Delta S_q + 2cS_0 q + 2c\Delta S_q^2 \\
&= q^2(2c\Delta S - 1) + q(1 - 2c\Delta S + 2cS_0) - 2cS_0 \\
&= q^2(2cS_1 - 2cS_0 - 1) + q(1 - 2cS_1 + 4cS_0) - 2cS_0
\end{aligned}$$

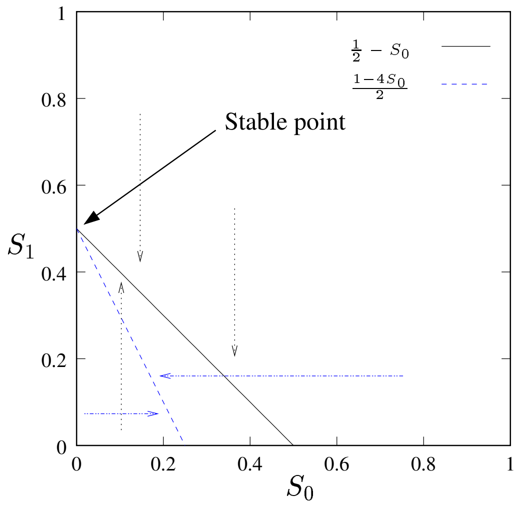

Figure 3.2: These lines are the stationary points of $\frac{\partial w}{\partial S_1}$ and $\frac{\partial w}{\partial S_1}$, respectively. Given discerning observers, the system is expected to tend towards $(0, \frac{1}{2})$ as the point of maximum fitness.

We assume quality is random for individuals, but are interested in the evolution of the *gene* coding for the behaviour, averaged over the individuals it finds itself in. We therefore integrate over q:

$$\begin{aligned}
\int_q \frac{\partial w_i(q)}{\partial S_0} dq &= \left[\frac{q^3}{3}\right]_0^1 (2cS_1 - 2cS_0 - 1) + \left[\frac{q^2}{2}\right]_0^1 (1 - 2cS_1 + 4cS_0) - \Big[q\Big]_0^1 2cS_0 \\
\therefore \frac{\partial w}{\partial S_0} &= \frac{(2cS_1 - 2cS_0 - 1)}{3} + \frac{1 - 2cS_1 + 4cS_0}{2} - 2cS_0 \\
&= \frac{4cS_1 - 4cS_0 - 2 + 3 - 6cS_1 + 12cS_0 - 12cS_0}{6} \\
&= \frac{-2cS_1 - 4cS_0 + 1}{6} \\
&= -\frac{c}{3}(S_1 + 2S_0 - \frac{1}{2}c)
\end{aligned}$$

This sees $\frac{\partial w}{\partial S_0} = 0$ at

$$S_1 + 2S_0 = \frac{1}{2}c$$

For example, if $S_0 = 0$ then $S_1 \longrightarrow \frac{c}{2}$, ie it pays to increase S_1 and thus honesty at this point (given $c = 1$). Performing the same analysis on parameter S_1, we have:

$$\begin{aligned}
\frac{\partial w_i(q)}{\partial S_1} &= (q - 2s)\frac{\partial s}{\partial S_1} \left(\tfrac{\partial s}{\partial S_1} = q\right) \\
&= (q - 2s)w \\
&= (q - 2(S_0 + \Delta S q)) \\
&= q^2 - 2qS_0 - 2\Delta S q^2 \\
&= (1 - 2\Delta S)q^2 - 2S_0 q
\end{aligned}$$

$$\int_q \frac{\partial w_i(q)}{\partial S_1} dq = \left[\frac{q^3}{3}\right]_0^1 (1 - 2\Delta S) - 2S_0 \left[\frac{q^2}{2}\right]_0^1$$

$$\begin{aligned}\therefore \frac{\partial w}{\partial S_1} &= \frac{1-2\Delta S}{3} - \frac{2S_0}{2} \\ &= \frac{1}{3}(1 - 2S_1 + 2S_0 - 3S_0) \\ &= \frac{c}{3}(\frac{1}{c} - 2S_1 - S_0)\end{aligned}$$

So, $\frac{\partial w}{\partial S_1} = 0$ at

$$\begin{aligned}2S_1 + S_0 &= \frac{1}{c} \\ S_0 &= \frac{1}{c} - 2S_1\end{aligned}$$

Setting $S_1 = \frac{1}{2}$ to find point of $\frac{\partial w}{\partial S_0} = 0$ at, we have $S_0 \longrightarrow 0$. Therefore, assuming choosy observers and a signalling cost of 1, the system should tend to a stable point at $(0, \frac{1}{2})$, as shown in figure 3.2.

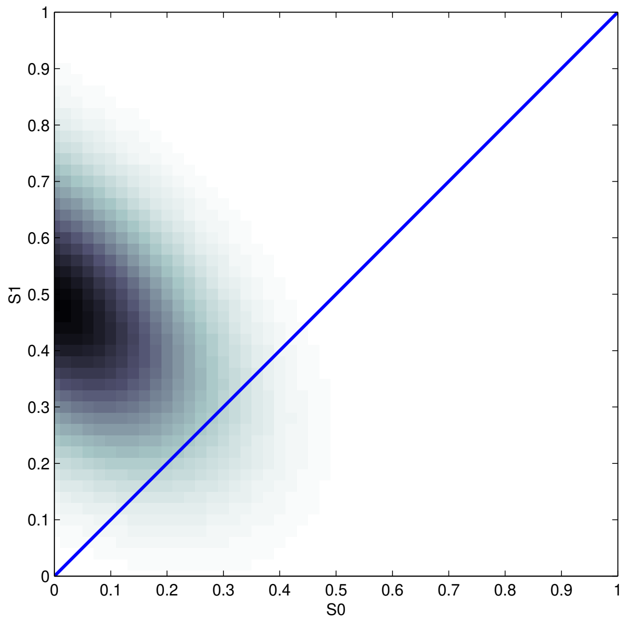

Figure 3.3: Signaller fitness, assuming discerning observers, integrated over quality. Darker shading indicates higher fitness. Signallers will tend towards honesty. Compare this with figure 3.2

The plot of fitness for a signaller at different values of its signalling parameters is shown in figure 3.3. The line $S_0 = S_1$ describes completely uninformative signalling. The graph shows that the population of signallers should tend towards honest signalling, given that the observers preferentially choose high quality signallers.

In figure 3.4 we can see a typical run showing the development of honest signalling strategies. Initially, the average observer strategy prefers non-signalling, creating a disincentive to signal. Around the 5000th generation, however, observers start to prefer signallers and a positive feedback loop is created. Honest signalling develops, as indicated by the difference between S_1 and S_0. Following this, S_0 settles close to zero and S_1 cycles close to $\frac{1}{2}$.

This is exactly the strategy predicted by the preceding analysis It is exactly that achieved in figure 3.4, where S_1 cycles close to 0.5 with S_0 remaining close to zero. Note that, while there is an incentive to signal at a high level, the average strategy does evolve towards dishonesty. It does not pay the lower quality individuals to signal beyond their means.

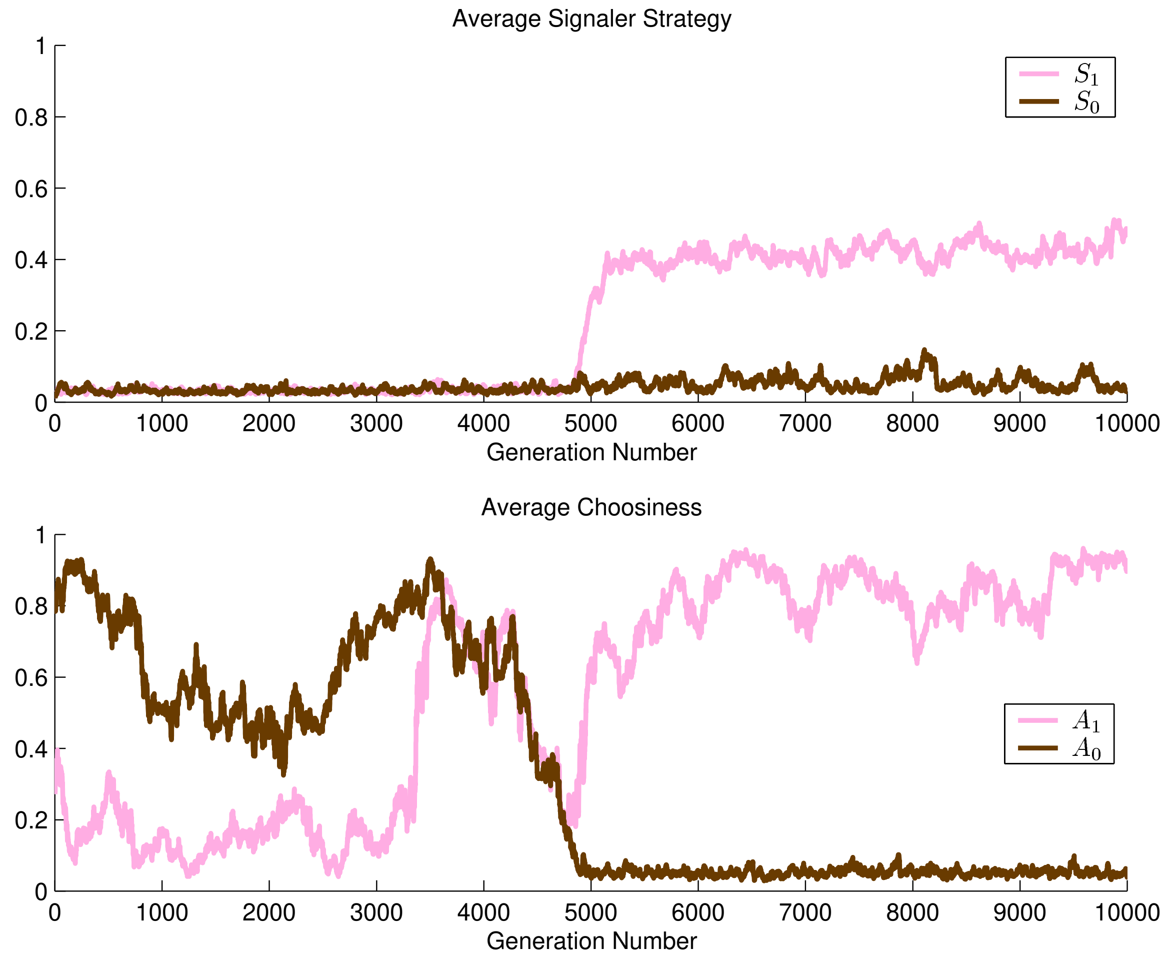

Figure 3.4: The development of honest signalling, occurring around the 5000th generation. Note that honesty is maintained: S_0 does not rise to meet S_1.

Chapter 4

Sex and the Altruist

altruism *n.* • **1** regard for others as a principle of action. **2** unselfishness; concern for other people.

Concise Oxford Dictionary

4.1 Biological Altruism

Contrary to the natural world's image as a place where only the strong survive and in which it is a case of every dog, dolphin or donkey for themselves, many examples exist of animals actively helping one-another out. Such behaviour is dubbed "altruistic" by biologists. For example [Dug97]:

Alarm Calling. Considered the "Quintessential example of altruism" by Dugatkin. Animals, including a number of avian species, often take part in alarm calling activity. This involves emitting a loud call and warning other members of the group when a predator has been spotted. It appears to be a dangerous activity: willow tits produced alarm calls more often when a hawk was 40 versus 10 meters away [AH90].

Mobbing. In his studies of the Arabic Palestine Babbler, Zahavi describes how the birds band together to communally harass snakes that enter their territory. It is a dangerous activity for the individual, as witnessed by their wariness [ZZ97].

Food Sharing. Zahavi's babblers also engage in food sharing: upon finding food, the altruist looks for another to give it to. This behaviour occurs even when the altruist is itself hungry [ZZ97].

Allogrooming. Literally "grooming another". This involves grooming of places which the recipient cannot reach itself, such as the back of the neck. Studies of Impala (*Aeptyceros melampus*), suggest that it reduces the parasite load of the recipient which is likely to be greatly beneficial [HH92]. The grooming itself also appears to carry cost.

Blood Sharing. In vampire bats (*Desmodus rotundus*), females regurgitate blood meals to nest-mates that have been unable to find a meal. The food sharing is a matter of life and death for the recipient as individuals will starve without a meal of blood every 60 hours.

The evolutionary forces which have selected for these behaviours are not immediately obvious. Why should an animal perform personally costly acts for another's benefit? It turns out that altruism without profit cannot persist over evolutionary time in nature.

While extreme, the following example illustrates the core problem. Imagine that, due to a mutation, a monkey with a propensity for some rather personally costly behaviour is born. Upon reaching adulthood, it appraises the local lion population to determine which is the most in need of a meal. It then approaches its choice, lies down in front of it and allows itself to be eaten. This is altruism in its purest form: making the ultimate sacrifice for the benefit of another. However, as it stands, the behaviour and the genes that code for it cannot be expected to persist for long in the population.

The same argument applies to such selfless altruism when it occurs in a less extreme form. In helping another at no advantage to either itself or its genes, an organism puts itself at an evolutionary disadvantage. Natural selection favours the proliferation of those genes most able to proliferate. Over evolutionary time, an organism which helps another without profit is committing evolutionary suicide as surely as if it had run out and placed itself in the lion's jaws.

The existence of altruistic acts in nature is therefore puzzling. In order to persist, the act of altruism must involve some payoff to the genes that code for it. Altruism when used in a biological setting is thus a technical term, because it is ultimately selfish — if not for the individual, then for its genes. The nature of the payoff and, more importantly, how is it maintained needs to be explained.

4.2 Ensuring Payoffs

The following is a sampling of the main theories which have been invoked to elucidate on this point: group selection, kin selection and the theory of reciprocity. However, none is a panacea for explaining all observed behaviour and group selection in particular is problematic.

4.2.1 Group Selection

Group selection and is the original explanation for altruistic behaviour. It applies to animals which live in a social group and states that the altruist benefits because the group to which it belongs will have a greater chances for survival, as a whole, than on that does not. This being the case, it is posited that altruistic groups will come to dominate the population.

The primary objection to this line of argument stems from the fact that natural selection operates at the level of the individual. If the interests of the group and those of the individual come into conflict, it will be those of the latter that will prevail at the expense of the former. Consider a group in which the majority are altruists. An individual which accepts the benefits of altruism without contributing to the wellfare of the group will be at a selective advantage. It will enjoy a greater rate of survival than the altruists because it is being carried on the latter's shoulders.

In consequence, even if an altruistic group can be established, it will not be stable because cheating is a profitable option for the individual. This has been dubbed the "free-rider" problem. Note that the existence of a "police force" to enforce behaviour beneficial to the group does not solve the problem when posed in this basic form. Policing is itself an altruistic act as it is not profitable for the punisher *as an individual* — imposing a cost on another is costly in terms of both time and energy.

4.2.2 Kin Selection

This next theory looks for the selective payoff at the genetic level. In a nutshell, a gene or set of genes will enjoy a selective advantage if they can affect a net increase in their rate of replication by helping copies of themselves in other individuals. As long as this net benefit exists, the behaviour can persist — even if it is at an individual cost.

If this strategy is to be effective, the genes must be able to somehow "recognise" copies of themselves in another individual. Siblings have a good chance of sharing genes and the relationship is a relatively easy one to determine. For example, "he that hatched in my nest", or "she that belonged to my litter". However, kin selection does not explain all instances of altruistic behaviour, because not all instances of altruistic behaviour are between kin.

4.2.3 Reciprocity

The theory of reciprocity can fill this gap. This is biological altruism at its most self-interested. Its creed is encapsulated in the phrase "I'll scratch your back if you scratch mine": quite literally in the case of reciprocal allogrooming mentioned above [Dug97]. The altruist receives a payoff for its behaviour if and when the original benefactor returns the favour. This reciprocation can be of real benefit: the altruist may have fallen on hard times or is simply not able to perform the service for itself (for example, grooming the back of its neck).

However the free-rider problem in the form of non-reciprocation still exists. Game theory shows how the altruist can avoid it by adopting a strategy which ensures that it cannot be exploited [Axe84]. Called Tit-for-Tat, the strategy is to initially co-operate and from thenonwards do what your partner did last. By doing so, an altruist can reap the full benefits of cooperation with another altruist, while preventing free riders from being able to exploit it. This places the altruists at an evolutionary advantage.

It would seem that a combination of kin-selection and reciprocal altruism can show how organisms which perform selfless acts can ensure a payoff for their selfish genes and thus prosper. However, according to Gilbert, this is not the case. He posits that it is not clear how reciprocity can account for acts that benefit the whole group, ie altruism which is asymmetric, or entirely one-way. For example, territorial defense, or allopreening which is not reciprocated [Rog98].

4.3 Altruism as a Signal for Sexual Selection

Recently, an alternative way for the biological altruist to obtain a return on its investment has been suggested. If altruistic behaviour is a sexually selected signal of quality, like the peacock's tail, then the payoff need not come from the recipient nor be directed towards kin.

Does altruism qualify as a reliable signal? It seems that it does. Firstly, it is necessarily costly to perform. Zahavi's babblers give food to others, even while hungry and without expectation that the favour will be reciprocated. They stand guard for long hours, and give alarm calls [ZZ97]. Such activities cannot be performed without the altruist giving something of itself. Also, as detailed in section 2.3, a coincidence of interest exists between the high quality males and females. It is arguable that the performance of such altruistic acts are inextricably linked to the qualities that females are interested in, such as general fitness or parental ability.

However, the real beauty of this theory stems from the fact that the free rider problem is avoided without resort to reciprocity, and that the altruism need not be restricted to kin. It is itself an adaptation to the sexual environment. The result is that, while it may pay a free-rider to shirk responsibility in the short term, the long term consequence of such behaviour for the genes that encode it is oblivion.

Chapter 5

Helping the Competition

5.1 One-Shot Altruism

The first step on the path towards a model of altruistic signalling is one in which a single altruistic transaction can occur per generation. This was achieved by extending the model presented in chapter 3 to incorporate the effects of altruistic behaviour on other signallers. Will choosers prefer altruistic signals over conventional ones?

5.1.1 Description of the Model

Following a suggestion, a new signalling function a new signalling function was introduced which modelled the level of altruism for a given signaller i:

$$g_i = G_0 + (G_1 - G_0)q_i \tag{5.1}$$

As a result of this gifting, the quality of each signaller is enhanced by the mean level of received altruism, or gifting, within the population. This quantity describes the modified ability of a given signaller to survive in its environment by taking into account the net help it receives from others. Its new quality is:

$$q_i^* = q_i - g_i + \overline{g} \tag{5.2}$$

Conventional signalling can then occur, making use of this enhanced fitness. The signal level of individual i is:

$$s_i = S_0 + (S_1 - S_0)q_i^* \tag{5.3}$$

We want to give each observer the chance to use either g or s, or a mixture of both. To do this, each observer has a single preference function, as before:

$$obs_j(x_i) = A_j^0 + (A_j^1 - A_j^0)x_i \tag{5.4}$$

The strength of an alliance between an observer j and signaller i is determined by both the conventional and altruistic signals, weighted by the parameter α. This is the relative attention an observer pays to the two types of signal.

$$a_{ij} = \alpha \times obs(s_i) + (1 - \alpha) \times obs(g_i) \tag{5.5}$$

Notice that $\alpha = 1$ means altruistic signalling is completely ignored. Signaller fitness is as before, but now incorporates q_i^*, the ith individual's altruism-enhanced quality:

$$w_i = (q_i^* - cs_i)n_i \tag{5.6}$$

This can be justified if the factor $(q_i^* - cs_i)$ is taken to correspond to their probability of surviving to some maximum age as an adult, as in the basic signalling model. The rest of the model, including the treatment observer fitness is unchanged.

In order to observe which was the preferred signal was preferred, the initial conditions were set up as follows:

- Random observer and signalling parameters (uniform in $[0, 1]$).
- All observers prefer each signal equally ($\alpha = 0.5$).
- Population of 200 individuals and a 50:50 sex ratio.

5.1.2 Results and Discussion

Simulated runs of this model follow one of two patterns. In one scenario (see figure 5.1) there is no altruism and conventional signalling evolves just as in the original signalling model. In the other, altruism is selected for and conventional signalling is extinguished (see figure 5.2).

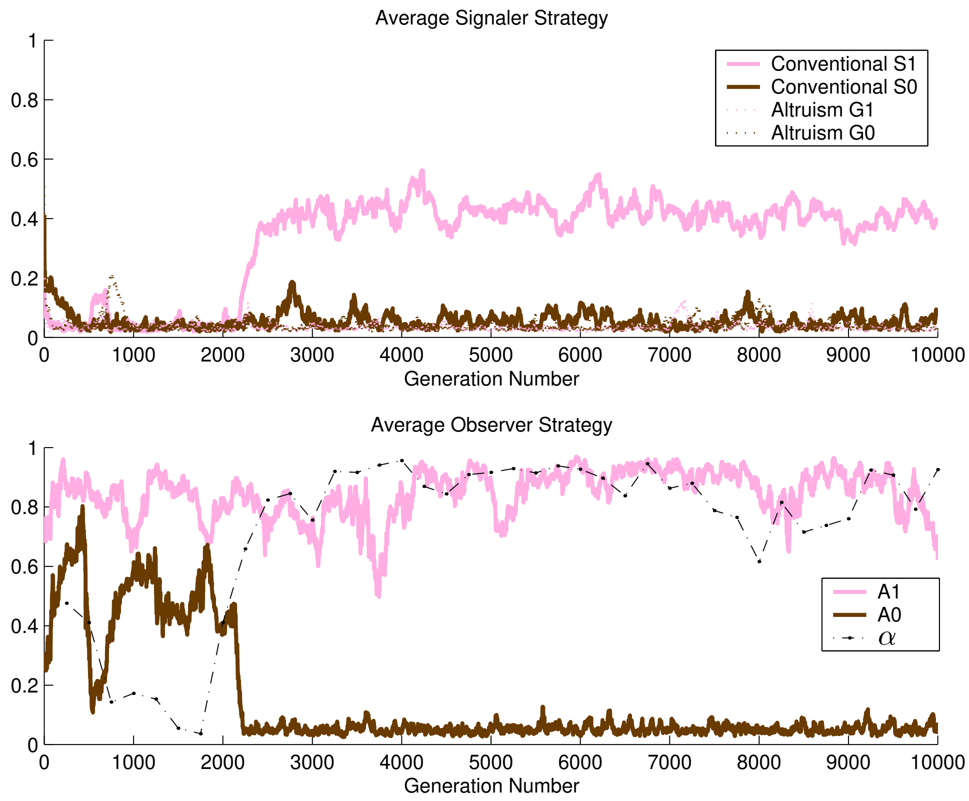

Figure 5.1: Conventional signalling established. Note how the mean value of α evolves towards a value of 1. While initially preferring altruists, observers switch their preference to conventional signallers.

To elaborate, the quality of the choices an observer makes influences the establishment of a preference for one type of signal or another. The quality of this choice depends on how accurately an observer can assess the underlying quality of a particular mate via its signal. In this model, selective indifference between the two signals is to be expected as both are able to provide equally reliable indications of quality.

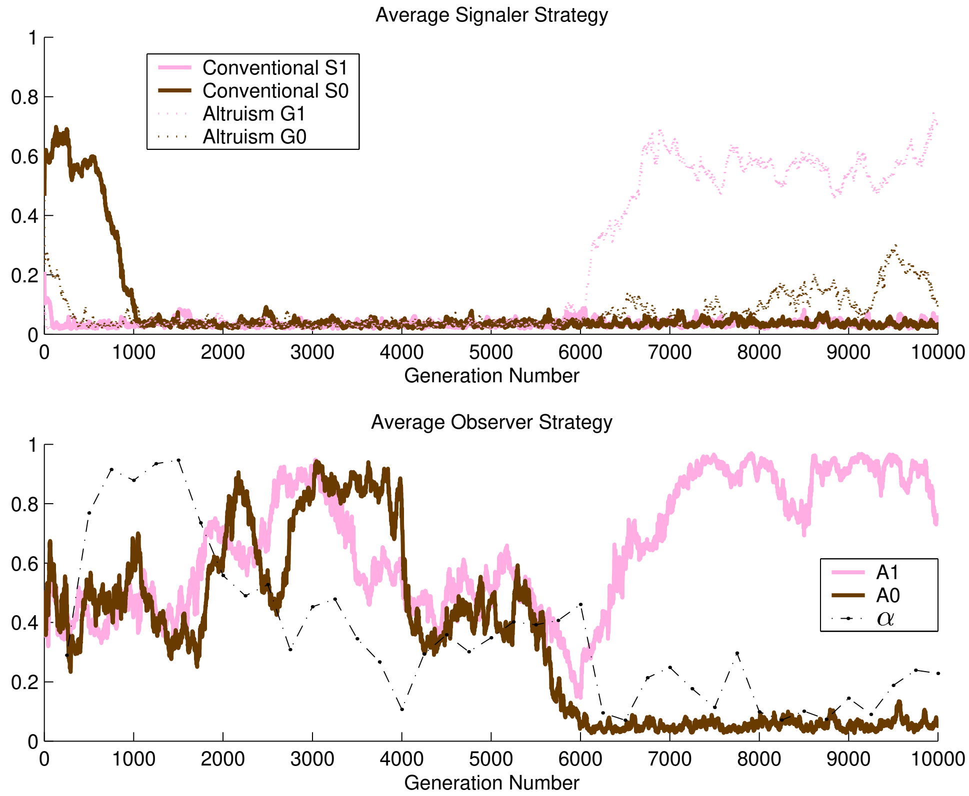

Figure 5.2: In contrast to figure 5.1, altruistic signalling prevails.

That the conventional signal can be reliable was shown in chapter 3. In this model, the altruistic signal can contain just as much information, too. Whlie their absolute signal level can increase, their ability to signal relative to one another does not change, as each signaller receives an equal benefit from the altruism of others. Therefore their signals are still a reliable indicator of underlying quality. Additionally, signalling occurs only once, so the altruism received cannot be used to enhance their own signal.

An additional insight gained from the model was the hypothesis that a signal, once established, could be maintained by a process of Fisherian selection. Once a majority of the population prefers it, a signal has become fashionable. This means that both signaller and observer are now putting themselves at a disadvantage if they go against the trend. The maverick signaller that does so will not be allocating its reserves to the most rewarding use as there won't be as many observers looking for it. If it signals at all, it will be at a low level. The alternative observer will therefore have a harder time extracting reliable information from those signallers that make use of it and there will be selective pressure against the unfashionable signal.

Figure 5.3 shows evidence for this example of Fisherian sexual selection in action. The data was gathered from the evolved preferences of 1000 individuals spread over 30 populations, after 15000 generations. It shows that the majority of the individuals pay nearly exclusive attention to either one signal or the other. The bimodal distribution adds weight to the idea that, once a signal becomes sufficiently fashionable, it will be maintained on the basis of its popularity. Whether this still the case even if one signal is able to provide better information about the qualities of interest requires further research.

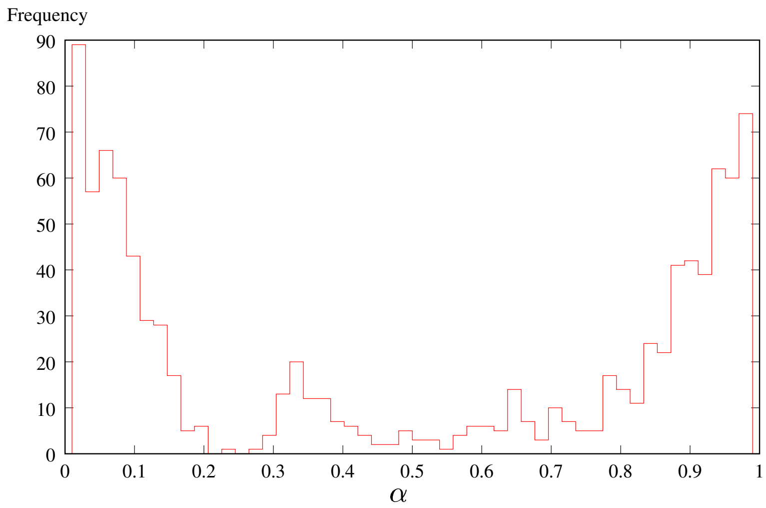

Figure 5.3: Histogram of evolved signal preferences after 15,000 generations. The system tends to one or the other extreme.

5.2 Altruism Over Time

The previous section hinted at the problems of modelling altruistic behaviour if it can occur more than once over the lifetime of the individual. Time complicates the situation as, over its lifetime, a social organism would have the opportunity to take part in many altruistic transactions. There is no reason to assume that these should be exclusively one way. A signaller could use the benefits received from another to bolster its current level of "altruism".

For observers, this possibility would appear to differentiate altruistic and conventional signalling. Suppose the altruistic act under consideration is the gifting of food, as is the case for Zahavi's babblers. By accepting the gift, a bird would in turn be able to signal altruistically to a degree unrepresentative of its underlying quality. Its signal is thus uncoupled from the underlying qualities of interest to the observers due to the help it had received. Dishonesty can creep in.

The less bearing this signal has on this underlying quality, the less an observer will gain by paying attention to it. There is therefore less information contained in the altruistic signal when the altruist is accepting gifts. An observer ignoring the help received and choosing purely on the basis of how altruistic a signaller was would be making poorer decisions than one relying on a more conventional signal. As observers are driving the behaviour by selecting the individuals to ally with, the altruistic signal would be expected to disappear from the population, possibly to be replaced by an alternative.

An altruist involved in multiple altruistic transactions can therefore stand on the shoulders of its peers and, in doing so, reduce the reliability of its signal. Of course, this situation can be remedied if the observer takes into account the difference between what the altruist gives out and what it receives. A bird which is observed to give 20 units of altruism and receive 10 can be established as of lower quality than one which gives the same without recompense.

In addition, the observer adopting this strategy in a social group will not be fooled by the altruists helping each other out "behind its back". Because the altruism is for the observer's benefit, an altruist which helps out without been seen to do so is incurring a net cost. Therefore, an observer can be assured that what it is seeing is not a charade.

Still, the fact that enough time needs to be spent in order to establish each signaller's altruistic balance sheet suggests that those observers using altruism as their signal will be selected against in non-social animals. Without the constant social contact to lower the cost of assessment, an observer may as well find some other way to discover a signaller's qualities of interest. However, the story does not end here.

5.3 Altruism Rejected

Zahavi's babblers actively try to prevent others from being nice to them. Due to interference from the alpha male, for example, the third-ranked male sometimes performs guard duty more often than the second-ranking one. The alpha male will continually prevent the second-ranked bird from guarding by replacing it at its post with a gift of food.

Interestingly enough, the alpha male is also the most altruistic. He spends more time guarding than the others, and is in the most exposed position when the birds mob a potential threat. At the same time, he receives the least amount of help. Indeed, in the babbler society, offering food to a superior is seen as a challenge to authority. Higher ranking birds have been known to force the challenger to eat the food it has offered and a lower order bird will respectfully wait for a higher ranking bird to finish guarding before replacing it.

This behaviour would appear to be sexually selected. The males are competing for mates: it is the females who choose and not vice-versa. The top-ranked male is usually chosen in preference to the others. Thus, there are sexually selective pressures for the males to behave the way they do.

	Altruism Received	Altruism Given	Difference
Babbler One	20	30	10
Babbler Two	0	10	10

Figure 5.4: Why should a female prefer babbler number two?

The question is: why should rejecting altruism be seen as desirable if an observer can determine a bird's quality by reference to the difference between what it gives and what it receives? For example, suppose an observer has to make a choice from the information in figure 5.4. The net difference in altruism is the same for both individuals and thus the underlying quality of each can be assessed as equivalent. The observers which are driving the process should be expected to be indifferent between the two.

Consequently we should not expect the signallers go to any special effort to reject the help of others. Rejecting help is costly. The benefits from accepting gifted food must be foregone. In the case of territorial defense, a signaller must actively reject the benefit and incur a cost by replacing the altruist currently on duty.

5.3.1 A Solution: Variance

Marcus Frean suggested that this behaviour may be explained if the observers find it more difficult to gauge the difference if the magnitudes involved are large. The hypothesis is that an observer's uncertainty increases the greater the absolute magnitudes involved. That the difference between 100 and 110 units of altruistic behaviour is less discernible than between 20 and 30 would appear plausible, but has not been followed up.

If true, then an observer choosing the male which received the least amount of help would be more sure of its choice. Such an observer would be at an advantage in the same way that one which payed attention to signals of quality would make better decisions than one that chose at random. Such observers would be expected to proliferate within the population, and with them a sexually selective pressure for those signallers which actively rejected altruistic favours.

5.3.2 A Solution: Differential Benefits

The behaviour could also be explained if a high-quality signaller benefited less from a given amount of altruism than his lower quality brother. A plausible example would be that of a babbler skillful at foraging. The food received from another would be worth less to it in terms of time and energy than it would to a less able bird.

This implies that equation 5.2 incorporates a function of q modifying the amount of benefit derived from the altruism received. A signaller's quality can then be described by:

$$q_i^* = q_i - g_i + \overline{g} \times f(q_i) \tag{5.7}$$

Two possibilities for f are shown in figure 5.5.

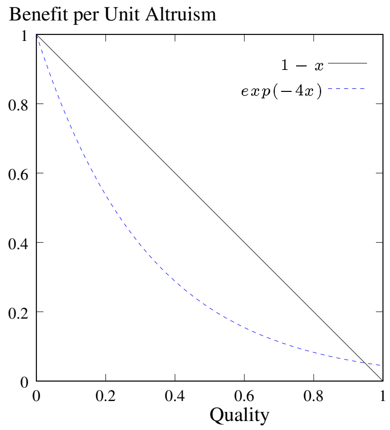

Figure 5.5: Two examples of a function conveying differential benefit on signallers of different qualities. Both curves descend, encapsulating the idea that gifts are more valuable to lower quality individuals.

If this assumption holds, it turns out that a signaller which accepts altruistic gifts decreases the amount of information its signal provides about its underlying quality. The basic idea is that his signal has lost its value as it could have been made by a lower quality bird. In accepting altruistic gifts, he is increasing the uncertainty over whether or not he is just an ordinary Joe. In special cases, an observer will be unable to deduce anything about the signaller's underlying quality by accounting for the help received and level of signalling displayed.

This is demonstrated in figure 5.6. Both show the signal level that an altruist of a given quality can achieve having received a given amount of altruism. Remember that the observer is interested in determining the hidden quality via the signal level and amount of assistance observed. Notice also that the slope in the x-direction determines the ease with which the quality of an altruist can be determined. In the worst case of gift $= 1$, it is not possible to infer the underlying quality of the signaller!

An observer will thus make poorer selective choices when basing their decision on an altruist which accepts gifts. Conversely, an observer which pays attention to altruists who

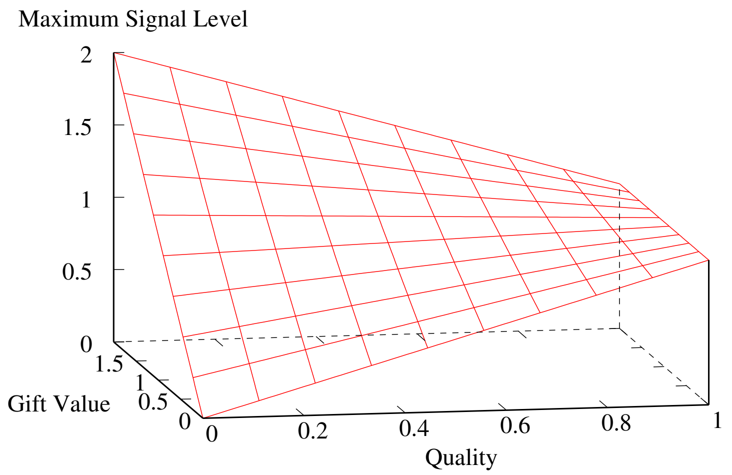

Figure 5.6: The amount of information an altruistic signal contains with a benefit function of $(1-x)$. It implies that high quality signallers will be more certain of looking good if they reject altruistic gifts.

refuse gifts is more likely to have fitter offspring. Thus, there is selective pressure for observers to prefer the latter type of altruist. This, in turn, creates sexually selective pressure for altruists that refuse altruism. For high-quality signallers, refusal makes them look better in the eyes of their beholder. Herein lies our incentive to reject help[1].

There is one more point to clear up. For gift levels above 1, an observer can obtain more information the greater the amount of altruism received by a signaller. This is indicated by the increasingly negative slope in the x-(quality)-direction. Does this imply selective pressure for accepting gifts in some circumstances? It would seem not. In this case, the lowest quality birds must accept a large amount of altruism *and* signal at a high level. However, this indicates to the observers that they are of a lower quality! There is thus an active disincentive for them to signal to their greatest ability and so the observers will remain unenlightened.

5.3.3 A Consequence: Altruism Accepted?

Assessing the altruistic balance sheet of a signaller would appear to be a costly exercise. It requires time and effort on the part of the observer, even within a highly social group. A conventional signal, such as the peacock's tail would seem to be the better choice. Is there anything to recommend the alternative choice of an altruistic signal?

The following idea could provide one such advantage, if differential benefits are assumed. It relies on an argument for taxation. The state-sponsored redistribution of wealth from rich to poor in human societies is often justified on the grounds that the welfare of society is being maximised. It is argued that the loss to the wealthy is smaller than the benefit gained by those who receive it and thus a net increase in utility has been achieved.

The underlying assumption is that humans with different levels of income receive differential benefits from the welfare they receive. This has interesting consequences for the general welfare of a group of biological altruists taken as a whole. If the same assumption holds in an animal population, it could provide an evolutionary advantage for the altruistic signal. Social groups in which altruism was a signal for sexual selection would end up

[1] This leads us to the counter-intuitive conclusion that to accept altruism is to behave altruistically, in the truest sense of the word.

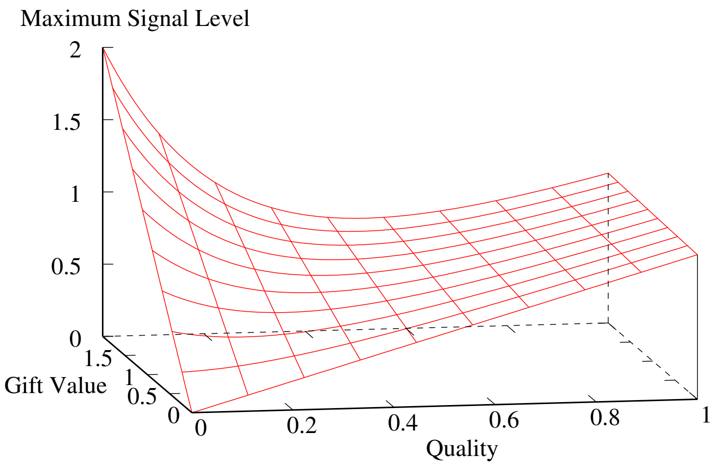

Figure 5.7: Information content with a benefit function of $exp(-4x)$. This further impairs the ability of observers to make good decisions when altruists accept gifts.

redistributing wealth in such a way as to maximise the benefit to the group.

Such groups would do better than others which relied on a more conventional signal and be selected for at a group-selective level. However, because of the sexually adaptive nature of the altruistic behaviour, these groups avoid the free-rider problem. An altruist is prevented from shirking responsibility because doing so lowers his gene's fitness. Groups in which observers prefer altruistic signals do better. Thus, their genes' selfish interests, it may be possible for both signallers and observers to be coerced into contributing to the well-being of the group.

Conclusions

This report has presented and analysed a simple new evolutionary model of signalling in which honesty can be a reliable outcome. It has also provided a number of new insights into the nature and utility of altruism as a sexually selected signal, and prompted questions which require further research to answer:

- The possibility of a Fisherian lock-in for signals, once established, appears to exist and would be interesting to follow-up.
- The argument for altruistic signalling could presumably apply inter-species. Under what sort of circumstances would it be possible, and does altruism enforced by other species ever occur?
- Without taking into account the effects of received altruism, altruism as a signal would not appear to convey sufficient information. Taking account of the difference between altruism given and altruism received can solve this problem, suggesting that such altruism will only be found in highly social groups.
- Additionally, under the reasonable assumption that signallers receive a differential benefit from received help, an altruistic signal implies that gifts must be rejected if the signal is to contain information about underlying quality.

  It is interesting to note that Zahavi [ZZ97] explains the babbler's altruism as a way to avoid having to make threats of physical aggression. He does not explain the function of rejecting altruism as anything other than the maintenance of the social hierarchy.

  However, his description implies that their behaviour could easily fulfill the requirements of a sexually selective signal. If so, it is possible to explain their rejection of altruism as a necessary mechanism for advertising their quality in the best possible light.
- Finally, given the assumption of differential benefits of gifting, it was speculated that group selection could play a role in favouring the evolution of altruistic behaviour against the selfish interests of both signaller and observer.

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Bibliography

[AH90] R. Alatalo and P. Helle. Alarm calling by individual willow tits, *parus montanus*. *Animal Behaviour*, 40:437–42, 1990.

[Axe84] Robert Axelrod. *The Evolution of Cooperation*. Basic Books, Inc, 1984.

[BC96] S. Bullock and D. Cliff. Modelling biases and biasing models: The role of 'hidden preferences' in the artificial co-evolution of symmetrical signals. Technical report, University of Sussex, 1996.

[BK95] J. Batali and P. Kitcher. Evolutionary dynamics of altruistic behaviour in optional and compulsory versions of the iterated prisioner's dilemma. In *Artificial Life IV*, pages 343–348. MIT Press, Cambridge, MA, 1995.

[BL99] C. Bergstrom and M. Lachmann. When honest signals must be costly. Submitted to the Journal of Theoretical Biology, 1999.

[BL01] C. Bergstrom and M. Lachmann. Alarm calls as costly signals of anti-predator vigilance: The watchful babbler game. *Animal Behaviour*, In Press, 2001.

[Bul97] S. Bullock. An exploration of signalling behaviour by both analytic and simulation means for both discrete and continuous models. In P. Husbands and I. Harvey, editors, *Proceedings of the Fourth European Conference on Artificial Life (ECAL'97)*, pages 454–463. MIT Press, 1997.

[Bul98] S. Bullock. A continuous evolutionary simulation model of the attainability of honest signalling equilibria. In C. Adami, R. K. Belew, H. Kitano, and C. E. Taylor, editors, *Artificial Life VI: Proceedings of the Sixth International Conference on Artificial Life*, pages 339–348. MIT Press, Cambridge, MA, 1998.

[Can99] U. Candolin. Male-male competition facilitates female choice in sticklebacks. *Proceedings of the Royal Society*, 266:785–789, 1999.

[Cro91] Helena Cronin. *The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today*. Cambridge University Press, 1991.

[CS95] R. Clements and D. C. Stephens. Testing models of non-kin cooperation — mutualism and the prisioner's dilemma. *Anim. Behav.*, 1995.

[Daw91] Richard Dawkins. *The Blind Watchmaker*. Penguin Books, 1991.

[Den95] Daniel C. Dennett. *Darwin's Dangerous Idea*. Penguin Books, 1995.

[DG91] M. S. Dawkins and T. Guilford. The corruption of honest signalling. *Animal Behaviour*, 41:865–873, 1991.

[DR98] Lee Alan Dugatkin and Hudson Kern Reeve. *Game Theory and Animal Behaviour*. Oxford University Press, 1998.

[Dug97] Lee Alan Dugatkin. *Cooperation Among Animals*. New York: Oxford, 1997.

[ES00] Hebert Gintis Eric Smith, Samuel Bowels. Costly signaling and cooperation. Submitted to the Journal of Theoretical Biology, November 2000.

[Fis30] R. A. Fisher. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford, 1930.

[GG89] James L. Gould and Carol G. Gould. *Sexual Selection*. Scientific American Library, 1989.

[GH94] N. S. Glance and B. A. Huberman. The dynamics of social dilemmas. *Scientific American*, pages 76–81, March 1994.

[GOB99] S. C. Griffith, Ian P. F. Owens, and T. Burke. Female choice and annual reproductive success favour less-ornamented male house sparrows. *Proceeding of the Royal Society*, 266:765–770, 1999.

[God91] H. C. J. Godfray. Signalling of need by offspring to their parents. *Nature*, 352:328–330, 1991.

[Gra90a] Alan Grafen. Biological signals as handicaps. *Journal of Theoretical Biology*, 144:517–546, 1990.

[Gra90b] Alan Grafen. Sexual selection unhandicapped by the fisher process. *Journal of Theoretical Biology*, 144:473–516, 1990.

[Gra99] Alan Grafen. Formal darwinism, the individual-as-maximuzing-agent analogy and bet hedging. *Proceedings of the Royal Society*, 266:799–803, 1999.

[HH92] B. L. Hart and L. Hart. Reciprocal allogrooming in impala. *Animal Behaviour*, 44:615–31, 1992.

[How93] R. Howlett. Beauty on the brain. *Nature*, 361:398–399, February 1993.

[HZ82] W. D. Hamilton and M Zuk. Heritable true fitness and bright birds: a role for parasites? *Science*, 218:384–7, 1982.

[KH99] A. J. Keyser and G. E. Hill. Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proceedings of the Royal Society*, 266:771–777, 1999.

[Kit93] P Kitcher. The evolution of human altruism. *Journal of Philosophy*, October 1993.

[Lan95] Christopher G. Langton, editor. *Artificial Life : An Overview*. MIT Press, 1995.

[Lap01] Joseph Laporte. Must signals handicap? to appear in *the Philosophy of Biology*, 2001.

[MS82] John Maynard Smith. *Evolution and the Theory of Games*. Cambridge University Press, 1982.

[Mun86] C. Munn. Birds that 'cry wolf'. *Nature*, 319:143–5, 1986.

[Nob99a] J. Noble. Cooperation, conflict and the evolution of communication. *Adaptive Behavior. 7(4)*, 7(4), 1999.

[Nob99b] J. Noble. Sexual signalling in an artificial population: When does the handicap principle work? In Floreano D., Mondada F., and Nicoud J., editors, *Proceedings of the Fifth European Conference on Artificial Life*, pages 644–653. Springer-Verlag, 1999.

[Rid94] Matt Ridley. *The Red Queen : Sex and the Evolution of Human Nature*. Penguin Books, 1994.

[Rog98] Gilbert Rogers. Competitive altruism: from reciprocity to the handicap principle. *Proceedings of the Royal Society*, 265:427–431, 1998.

[SG99] Kim Sterelny and Paul E. Griffiths. *Sex and Death : an Introduction to Philosophy of Biology*. University of Chicago Press, 1999.

[SH94] P.J.B Slater and T.R. Halliday, editors. *Behaviour and Evolution*. Cambridge University Press, 1994.

[Wil84] G. S. Wilkinson. Reciprocal food sharing in the vampire bat. *Nature*, 308:181–184, 1984.

[ZZ97] Amotz Zahavi and Avishag Zahavi. *The Handicap Principle: A missing piece of Darwin's puzzle*. Oxford University Press, 1997.