Sexual Signalling in an Artificial Population: When Does the Handicap Principle Work?

Jason Noble

Center for Adaptive Behavior and Cognition
Max Planck Institute for Human Development
Lentzeallee 94, D-14195 Berlin, Germany

Abstract. Males may use sexual displays to signal their quality to females; the handicap principle provides a mechanism that could enforce honesty in such cases. Iwasa et al. [1] model the signalling of inherited male quality, and distinguish between three variants of the handicap principle: pure epistasis, conditional, and revealing. They argue that only the second and third will work. An evolutionary simulation is presented in which all three variants function under certain conditions; the assumptions made by Iwasa et al. are questioned.

1 Sexual Signalling and the Handicap Principle

Sexual selection is a distinct subset of natural selection. The idea is that evolution is an exam with two papers: in order to reproduce, an animal must not only survive to adulthood, but, in a sexual species, it must gain mating opportunities with members of the opposite sex. One of Darwin's insights was that selection for sexual attractiveness and selection for survival could exert opposing evolutionary pressures. If, for some reason, females came to prefer males with elaborate and costly ornaments, such as the peacock's tail, then sexual selection would push towards yet more costly ornaments, because males with longer tails experience greater mating success. At the same time, natural selection would push for less costly ones, because males with longer tails are more vulnerable to predation and less likely to survive to adulthood.

An early explanation for extreme male ornament traits and female preferences was that an initial, random bias led to linkage between trait and preference genes and that a runaway cycle of exaggeration then took place [2]. Another possibility, more recently explored, is that male ornaments function as "indicator mechanisms", i.e., that they are used by males to signal their quality as mating partners to females [3]. This paper describes an evolutionary simulation, based on a population-genetic model by Iwasa et al. [1], that explores the conditions under which this kind of sexual signalling could evolve.

The suggestion that male ornaments are signals of mate-quality leads to a problem in understanding how honest signalling could be maintained. Why should low-quality males ever honestly signal their condition, when by doing so they will make themselves unlikely to be chosen as mates? Why wouldn't all

males produce the maximum advertisement, regardless of their true quality—all claiming, in effect, to be the most desirable. Zahavi's handicap principle provides a possible mechanism by which a sexual signalling system could be kept honest.

Zahavi [4] suggested that honesty could only be maintained in a communication system if the signals were costly in some way. He proposed the counter-intuitive idea that signallers sacrifice some of their fitness (i.e., impose a handicap on themselves) in order to produce signals that will be believed by receivers. In the sexual signalling case, perhaps males are signalling their quality (e.g., vigour, viability or territory size) to females, and are being rewarded with a mating episode if they "convince" a female that they are of high quality. Let us suppose that the male signal is tail length. Zahavi realized that if growing a longer tail was cheap, i.e., if it had little deleterious effect on male fitness, then the signalling system would be vulnerable to bluffing: *all* males would come to have long tails, and the female preference for longer-tailed males would no longer be selected for. But if growing a long tail was costly in fitness terms, the communication system would not be corrupted by bluffers: lower quality males would not be able to afford the necessary resources for growing a long tail. Tail length becomes an honest indicator of male quality because "cheating" is prohibitively expensive. Zahavi reasoned that only those communication systems in which the signal happened to be costly would escape collapse due to bluffing. Therefore, the stable systems found in nature are maintained by this mechanism.

When the handicap principle was first introduced, it was generally not accepted by theoretical biologists. Population-genetic models [5, 6] seemed to show that it could not be evolutionarily stable. However, the potential effectiveness of the handicap principle has been validated by several mathematical models in recent years; foremost among these is a model by Grafen [7]. This model establishes that the handicap principle can work, but specifies an important proviso: the unit cost of producing the signal must be greater for a low quality signaller than for a high quality signaller. In other words, the fitness cost of extending one's tail by an extra centimetre must be higher for unhealthy or weak males than for healthy strong ones.

The handicap principle was maligned and misunderstood because Grafen's proviso about differential unit costs was not clear from Zahavi's original formulation, and because several distinct interpretations of the principle are possible. Iwasa et al. [1] attempted to cut through the confusion. They detailed three variant interpretations of the handicap principle, listed below, and suggested that different findings concerning the evolutionary stability of handicapped signalling could be explained by the fact that some authors were modelling one version and others another.

1.1 Pure Epistasis Handicap

In this variant, a particular set of genes determine a male's tail length, and the longer his tail, the less likely he is to survive to reproductive age. However, his survival is also determined by his quality: higher-quality males are more likely to survive, and for any given level of quality, a male is more likely to survive

if he has a *shorter* tail. Therefore the males that are most likely to die before reaching reproductive age are those of low quality with long tails. Observing the adult population, one would find a correlation between the genes for quality and tail length. In technical terms, epistatic selection has resulted in linkage disequilibrium; in plainer language, long tails are linked to high quality, because all the long-tailed low-quality males died young. In consequence, a female's preference for mating with long-tailed adult males will mean that she is more likely to achieve her goal of mating with a high-quality male.

1.2 Conditional Handicap

A long tail still reduces a male's chances of survival to reproductive age, and again survival is primarily determined by quality. However, the expression of the gene for tail length is modified by quality: males of lower quality will not realize their full, genetically specified tail length but will grow a proportionately shorter tail. It is assumed that only the highest quality males have the resources to fully realize the tail length encoded in their genes. Because the expression of the tail-length gene is quality-dependent, observable tail length is correlated with quality even before mortality has taken its toll. A female preference for long tails will therefore translate into a preference for high-quality males.

1.3 Revealing handicap

The expressed tail length of males is determined directly by a gene, as with the pure epistasis handicap. Survival to reproductive age depends on quality modified by tail length, as before. However, when the males reach reproductive age and are competing to be selected by females, only high-quality males succeed in maintaining their tails at their original, genetically specified length. Males of lower quality are less well able to withstand the rigours of their environment, and their tails are shortened due to, for example, attacks by predators or parasites [8]. Low quality males *reveal* their status by tending to have shorter tails as adults. Females preferring to mate with long-tailed males will thus mate with higher quality males on average.

2 Modelling Sexual Signalling of Genetic Quality

Almost all of the models that have recently demonstrated the plausibility of the handicap principle [7, 9, 10] have made a major simplifying assumption: namely, that the underlying male quality of interest to females is environmentally determined. This could mean, for example, that males are advertising their level of nutrition, or the quality of the territory they possess. This assumption misses the interesting subset of cases in which males are believed to be informing females of their *genetic* quality. For example, when sage grouse *Centrocercus urophasianus* mate the males contribute only their sperm, leaving all other aspects of the project of raising offspring to females. Nevertheless, the females choose their

mate carefully on the basis of his ornaments, display behaviour, and central position in the mating arena [11, 12]. If the males are advertising anything in this case, it must be their inherited genetic quality.

It is not clear that an honest signalling equilibrium will exist for signals of genetically determined quality. A central problem is that there might not be any residual variation in male quality, and thus nothing to signal about. If the males were honestly advertising their quality, and females were choosing to mate with high-quality males, then after a few generations the males will all be clustered around the optimum quality level. As Maynard Smith [13] has argued, there should be no heritable variation remaining in fitness-related traits at equilibrium. And yet female sage grouse pay the costs of choice (e.g., time costs and predation risk) in order to choose the best male, when the male will contribute only his genes. This is known as the paradox of the lek: why aren't modern sage grouse males all maximally viable, and thus equally attractive to females? The most likely answer is that mutation on fitness-related traits is negatively biased. That is, a single mutation event affecting the genes controlling a fitness-related trait is more likely than not to decrease the value of that trait. There is some empirical evidence for this: at least one component of fitness is mildly heritable in *Drosophila* [14]; this could only occur if mutational load kept fitness-related traits below their optimum value. A similar conclusion was reached in a review of evidence from many avian species [15].

Iwasa et al. [1] constructed a population-genetic model of the evolution of costly male advertisements and female preferences; they incorporated just such a negative mutation bias on the viability trait. Iwasa et al.'s model purports to show that honest signalling of genetically determined male quality can be evolutionarily stable. It is one of the very few models to deal with genetically determined quality, and provides the basis for the simulation described in this paper.

Iwasa et al. reasoned that if females were prepared to pay a cost for their preference, then there must be information worth having in the expressed values of the advertisement trait, and it was therefore an honest indicator of quality. Iwasa et al. derived three conditions for the existence of such a costly-preference equilibrium. The first was that mutation on the viability trait had to be negatively-biased. Otherwise, male viability levels would be clustered around the optimum, and the females would be in a position where random mating was just as likely to result in a high-viability partner as was a costly preference. The second condition was that the genetic correlation between preference and viability had to be greater than the product of the correlations between advertisement and preference and between advertisement and viability. Another way of putting this is that there must be a link between preference and viability that does not come about solely because of their joint relationship with the male advertisement trait. Finally, Grafen's proviso, that the unit costs of signalling must be greater for lower-quality signallers, must also hold.

Iwasa et al.'s second equilibrium condition implies that whereas the conditional and revealing handicaps will work, the pure epistasis handicap will not.

In the conditional and revealing handicaps, the viability trait directly affects the expression of the male's advertisement—viability modifies the expression of the genes for growing an ornament of a particular size, or, in the case of the revealing handicap, low viability means that a large ornament cannot be successfully maintained as an adult. Valuable information for females concerning male viability has thus been built into the expressed male trait. However, in the pure epistasis handicap, the realized size of the male advertisement is only linked to viability indirectly, via differential survival. This means, in turn, that there is no special link between the genes for preference and for viability.

In order to keep their analysis tractable, Iwasa et al. made a number of simplifying assumptions. Most critical was the assumption that the genetic covariances between male advertisement, female preference, and the viability trait could all be treated as positive constants. In the real world, genetic covariances are of course not constant but change as the population evolves over time; even if we suppose that the covariances might start out positive, it is not clear that they would remain so. And it is more likely that the covariances in a plausible initial population would be close to zero. The problem highlights a weakness of the population-genetic approach: despite the name, there is in fact no population, which means that such important variables as genetic variances and covariances must be input into the model as parameters, rather than being measurements that are made with respect to an evolving lineage. The question as to whether Iwasa et al.'s conclusions would hold without assuming constant positive covariances [3] presents an excellent opportunity for an evolutionary simulation.

3 Description of the Model

The work reported here is an implementation of Iwasa et al.'s [1] model as an individual-based evolutionary simulation. The population consists of sexual individuals breeding in discrete, non-overlapping generations. Individual organisms have both a genotype and a phenotype; the genotype consists of real-valued genetic parameters. Each organism carries a gene for the male advertisement or ornament trait (t_{gen}), the female preference trait (p_{gen}), and the general viability trait (v_{gen}). An individual's phenotype consists of two real values: either t_{phen} or p_{phen}, depending on sex, and v_{phen}. Genotypic and phenotypic parameters are always real numbers between zero and one inclusive.

3.1 Development stage

At birth, each individual's sex is chosen at random, and its phenotypic trait values are determined. Normally, each trait is read off the genome, then a random gaussian error term is added ($\mu = 0$, $\sigma = 0.005$), and the resulting value stands as the expressed trait. The phenotypic male advertisement is normally read off the genotypic value of t_{gen}. However, in the conditional and revealing handicaps the male's viability also influences the expressed ornament size—the phenotypic

viability is therefore calculated first. For the conditional handicap, the advertisement size that would otherwise be expressed is reduced by an amount proportional to v_{phen}. In other words, $t_{phen} = t_{gen} \times v_{phen}$. Only males with the maximum possible viability actually produce an advertisement that is as big as their genotype specifies.

3.2 Survival stage

Some individuals survive to adult reproductive age, and some die young.[1] An individual's basic probability of survival is equal to its phenotypic viability: less viable animals are less likely to survive. However, both male advertisements and female preferences are costly, and the cost of these characteristics is manifested as a reduction in an individual's probability of survival, according to the degree of the trait's phenotypic expression.

Grafen's proviso, in which the unit costs of advertisement are lower for higher-quality signallers, is enforced at this stage. The basic probability of survival (v_{phen}) is first converted to an odds ratio, and then scaled by $(1 - t_{phen})^{C_{adv}}$, where C_{adv} represents the cost of advertising. If $C_{adv} = 0$ then there is no cost at all to males for growing ornaments; if $t_{phen} = 0$ then a male will pay no costs regardless of how high C_{adv} might be. The scaled odds ratio is then converted back to a probability value. The result of all this manipulation is the following expression for the probability of survival:

$$p_{survival} = \frac{v_{phen}(1 - t_{phen})^{C_{adv}}}{v_{phen}(1 - t_{phen})^{C_{adv}} - v_{phen} + 1} \quad . \tag{1}$$

The scaling factor implements Grafen's proviso, because individuals with high phenotypic viability will be best able to bear the costs of advertisement.

The survival costs of female preference are assessed in exactly the same way as the costs of the male trait: p_{phen} is simply substituted for t_{phen}, and C_{pref} for C_{adv}, in (1). Theories of handicap signalling generally do not require that female preference should involve anything other than a simple cost that is independent of viability; however, calculating female costs in the same way as male ones allows the costs borne by each sex to be directly compared.

3.3 Mating stage

Surviving males and females are then able to breed: females get to exercise their preferences, and males may experience the benefits of their costly ornaments. A surviving female is randomly chosen, and she is then presented with a "lek" of eight males, also selected at random. With a probability equal to her preference

[1] To prevent extinctions, in the rare event that no males (or no females) survive to adulthood, one male (or one female) is randomly chosen for resurrection.

value $(p_{phen})^2$, she selects the male with the largest expressed advertisement trait to mate with. If she does not choose this male, she chooses randomly from among the eight males. Thus, high-preference females are likely to end up mating with the male with the biggest ornament, while zero-preference females will mate with anyone. The results of an earlier simulation [16] suggest that this method can be effective in producing sexual-selection effects, and that eight is a reasonable lek size. Note that in Iwasa et al.'s model, female preferences were expressed relative to the population mean of the male advertisement trait. Having a model in which individuals really exist allows us to avoid the dubious assumption that females could know the population mean; instead, females choose a mate from among those males they happen to come into contact with.

The mate selection process continues until sufficient offspring have been produced to stock the next generation. Crossover is simple: newborn individuals inherit the mean of their parents' values for each real-valued genetic parameter. The mutation operator is a random gaussian ($\mu = 0$, $\sigma = 0.03$) added to each gene. The all-important negative mutation bias on viability is implemented by subtracting 0.003 from whatever value a newborn individual's genetic viability would otherwise have been. If the mutated value of any trait would be less than zero or greater than one, it is truncated accordingly.

4 Results

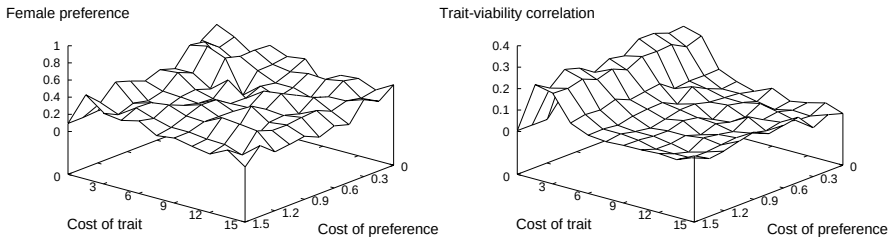
The population consisted of 100 individuals, and evolution proceeded in each run for 5000 generations. Unless otherwise stated, the results summarize a window period over the last 500 generations, and are averaged across 10 repeated runs in each case. The repeated runs in the various conditions were each performed with a different seed for the pseudo-random number generator. The simulations have been conducted over a range of values for the advertising and preference costs C_{adv} and C_{pref}. Earlier work [16] suggests that males will be prepared to bear much higher costs in advertising than females will tolerate in expressing a preference, and the range of cost levels investigated reflects this.

4.1 Pure Epistasis Handicap

Iwasa et al. argue that the key evidence for sexual signalling is the willingness of females to bear a costly preference; Figure 1(a) shows that such preferences do indeed evolve as long as both male and female costs are not excessive. But are females really gaining information about male quality from the advertisement traits they observe? Figure 1(b) shows the correlation, for adult males, between

[2] Phenotypic preference values of less than 0.1 are in fact set equal to zero, i.e., females with sufficiently low preference values mate randomly. This is to avoid a situation in which there is selection pressure for random mating but the mean value of p never quite reaches zero due to recurrent mutation. This would lead in turn to a small female preference being manifested, which might well be enough to push males towards advertising when they would not otherwise have done so.

their expressed advertisement and their underlying quality. It is clear that when the cost of advertising is greater than zero but less than about 5, male ornament size is modestly correlated with viability, and therefore *does* carry information. Signalling of viability does not occur across the full range of cost values, but it certainly appears to be occurring in one region. This contradicts Iwasa et al.'s claim that the honest advertisement of viability cannot be evolutionarily stable given the pure epistasis handicap.



(a) (b)

Fig. 1. Results for the pure epistasis handicap condition, by C_{adv} and C_{pref}. (a) Mean female preference values. (b) Correlation between the expressed male advertisement trait and underlying viability.

4.2 Conditional Handicap

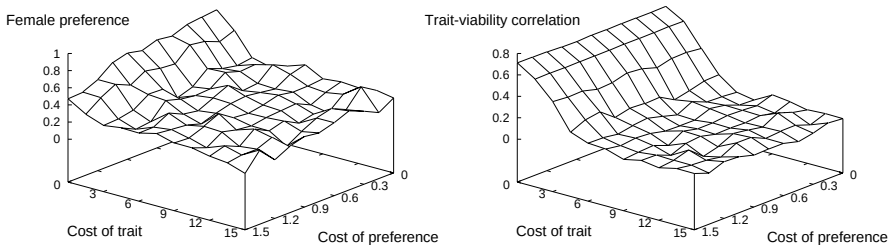
Figure 2(a) shows the mean values for female preference: again, females were sometimes prepared to bear a cost in order to choose ornamented males. It is interesting to observe that, although preference falls off somewhat as its cost increases, high preference values are most likely to evolve when the cost of *advertising* is low. Figure 2(b) shows significant correlations between expressed male advertisement and underlying viability, especially when advertising costs are low. The results therefore support Iwasa et al.'s conclusion that an honest-signalling equilibrium could be stable under the terms of the conditional handicap.

4.3 Revealing handicap

The results for the revealing handicap simulations were very similar to those for the conditional handicap; no additional graphs will be presented.

5 Discussion

Honest signalling of viability occurs in the pure epistasis handicap, despite the fact that Iwasa et al. [1] claimed it could not. In the conditional and revealing



(a) (b)

Fig. 2. Results for the conditional handicap condition, by C_{adv} and C_{pref}. (a) Mean female preference values. (b) Correlation between the expressed male advertisement trait and underlying viability.

handicaps, on the other hand, the results presented here are in accordance with Iwasa et al.'s prediction that honest signalling could be evolutionarily stable. Iwasa et al. intend their paper to clarify some of the controversies around the handicap principle. They argue that their findings explain why some earlier papers have concluded that the handicap principle can work while others have concluded that it cannot: different authors have tried to model different versions of the idea. Iwasa et al.'s intended clarification is an admirable goal; however, the results of the simulations presented here suggest that their conclusions must be taken with a grain of salt. Their assumption that genetic covariances could safely be treated as positive constants does not appear to have been a reasonable one.

The conditional and revealing handicaps deserve closer scrutiny. Consider Figure 2(b), which shows the correlation between expressed advertisement and viability in the conditional handicap case; results for the revealing handicap were similar. The graph shows that the highest correlations were achieved when advertising was cost-free. In the pure epistasis handicap, by contrast, we find that "talk is cheap" in these cases: Figure 1(b) shows that male advertisement was never an indicator of quality when the cost of advertising was zero. Why then, in the conditional and revealing handicap conditions, can females trust the advertisement levels of males who, in theory, can choose any advertisement level they like because there is no cost involved? The answer is that the males *cannot* choose any advertisement level that they might like. The stipulation that the expression of the ornament trait is condition-dependent (i.e., modified by viability) builds in an informational link between advertisement and viability in a rather uninteresting way. It seems disingenuous of Iwasa et al. to hold up the existence of costly female preference and honest advertisements as a deep result when the way in which the male trait is expressed itself enforces honesty. Thus we find that the genetic correlation between the advertisement trait and viability remains low in the conditional handicap case, but the correlation between the

actual expressed advertisements and the underlying viability of adult males is very much higher: the condition-dependent expression of the ornament means that females automatically get useful information about viability. In addition, it is a little odd to claim that "handicap" signalling is occurring when the cost-free signals are the most reliable. Considered closely, Iwasa et al.'s claims for the conditional and revealing handicaps amount to little more than the uncontroversial observation that females will attend to unfakeable information about male quality.

Finally, it should be noted that all of the simulation results depend on Grafen's proviso that the unit costs of advertisement (and in this case preference as well) should be lower for higher-quality individuals. One's faith in the simulation results must depend on one's faith in Grafen's proviso as a real-world condition.

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