Sexual Selection Unhandicapped by the Fisher Process

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A population genetic model of sexual selection is constructed in which, at equilibrium, males signal their quality by developing costly ornaments, and females pay costs to use the ornaments in mate choice. It is shown that the form of the equilibrium is uninfluenced by the Fisher process, that is, by self-reinforcement of female preferences. This is a working model of the handicap principle applied to sexual selection, and places Zahavi's handicap principle on the same logical footing as the Fisher process, in that each can support sexual selection without the presence of the other. A way of measuring the relative importance of the two processes is suggested that can be applied to both theories and facts. A style of modelling that allows simple genetics and complicated biology to be combined is recommended.

1. Introduction

Many current mathematical models of sexual selection have at their centre Fisher's (1915) idea of the self-reinforcement of female preferences (Lande, 1981; Kirkpatrick, 1982; and many later works). From a genetical point of view Fisher's process is manifested in these models as linkage disequilibrium between loci controlling female preference and loci controlling the preferred male trait. The existence of these formal genetic models has led to the popularity of the view that the Fisher process is central to the operation of sexual selection.

In this paper I present genetic models of sexual selection in which Fisher's process and linkage disequilibrium play no role. These models produce at their genetic equilibria all the appearances of sexual selection: males possess costly ornaments, females choose between males on the basis of those ornaments, and pay costs in order to do so. This shows that the phenomena for which Darwin (1871) coined the term "sexual selection" can occur without the Fisher process.

The models are genetic models of signalling. Males vary in quality, and signal that variation by choice of ornament. Females interpret the signals, and treat males according to their quality. The models provide a formal exposition of Zahavi's (1975, 1977, 1987) handicap principle, and demonstrate its logical coherence in the context of sexual selection. They show that the handicap principle alone, unaided and uninfluenced by the self-reinforcement of preferences discovered by Fisher (1915), can account for extravagance of sexual ornaments and all the appearances

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of sexual selection. The companion paper (this phrase will refer to Grafen, 1990) developed game theory models of the handicap principle in a more general context.

The operation of the handicap principle in sexual selection has been a matter of some disagreement, with Kirkpatrick (1986) declaring in his intemperate title that "The handicap mechanism of sexual selection does not work", and Pomiankowski (1987) replying more moderately that "The handicap principle does work—sometimes". Even where it has been claimed to work (Pomiankowski, 1987; see also a review and synthesis by Pomiankowski, 1988), the handicap mechanism has been seen as a modifier of the Fisher process, altering zones of attraction of equilibria and rates of change. It has not been recognized as a stand-alone force in sexual selection. The models to be presented in this paper will have no Fisher process, and show sexual selection flourishing by the handicap principle alone. The reason for the difference of conclusion and emphasis from previous work is the use of modelling techniques more appropriate to the strategic nature of the handicap principle. The differences are not specifically related to sexual selection, and previous interpretations of the handicap principle are accordingly dealt with in section 9 of the companion paper.

Fisher's self-reinforcement of preferences and Zahavi's handicap principle therefore have the same logical standing, as processes which can in theory underlie sexual selection, and can do so without the presence of the other. One can ask, of a mathematical model or of an example of sexual selection in nature, how much is due to Fisher, and how much to Zahavi? I will propose the "Fisher index" as rough way of answering this question.

Section 2 presents the population genetic model of sexual selection, along with results whose proofs are reserved for the appendices. Section 3 gives a conspectus of the appendices for those with modest mathematical ambition. The general model has three arbitrary functions, and section 4 makes particular choices for those functions and presents some graphical results that illustrate the workings of the model. Section 5 introduces the "Fisher index", and explains my own view on the relative importance of the two processes. Section 6 draws conclusions.

2. A Population Genetic Model of Sexual Selection

This section introduces an adapted version of the game theory model of the companion paper. The idea is that males should vary continuously in quality, which must matter to females. Females should have some continuous way of expressing preference between males, that has a cost related continuously to strength of preference, and that impinges continuously on the fitness of males. The emphasis on continuity, which is shared with the game theory models, will ensure that artificial boundaries do not obscure the close interactions of the advertizing and preference systems. The first difference from the game theory model is that the model should be explicit about how females use information about male quality, rather than relying on the conceptual construct of inferred quality. The second difference is that the model should be genetic. The game theory model was important as a stencil

not only for construction of this more complex model, but also for finding some simple proofs in this more complex setting.

Next I describe the model that fulfils all these requirements, before discussing the results of the model. In order to have all the required continuity, and a simple genetics, we need to build all the complexity into the effects of alleles at a single locus. Consider an infinite sexual haploid population with discrete generations with one autosomal locus. There are four stages within one generation. In the first stage, males are randomly assigned a quality independently of their genotype, with a cumulative frequency distribution $G(q)$. The important facts about quality are that females have a higher fecundity if they mate with a male of higher q, in a way to be specified in a moment; and that females cannot directly observe q. The fact that q is environmentally determined makes the model analytically tractable, but does not affect the essential workings of the advertizing-preference system. Julee Greenough and I are currently working on a model by computer simulation in which quality is determined genetically.

The second stage is that each male receives an advertizing level. The contents of the one locus specify a function relating quality to advertizing. So a male's advertizing level is determined by the function specified by his allele, applied to the quality he received in the first stage. Advertizing rules will be denoted $A(q)$, $A^*(q)$, $A_1(q)$ and so on. One class of possible rules are unconditional, such as do not advertize at all no matter what quality you are. Other rules can make advertizing an increasing function of quality, while yet others can make it a decreasing function of quality. All (integrable) functions are allowed.

The third stage is one of pre-breeding mortality for males. A male survives this phase with a chance, denoted $\alpha(q, a)$, that depends on his quality and his advertizing level. Higher quality increases survival, while more advertizing decreases survival. Further the survival disadvantage of increasing advertizing is greater for lower quality males. Formally,

$$\text{if } a_1 < a_2 \text{ and } q_1 < q_2, \text{ then } \frac{\alpha(q_2, a_2)}{\alpha(q_1, a_1)} < \frac{\alpha(q_2, a_2)}{\alpha(q_2, a_1)}. \tag{1}$$

The benefits of advertizing will be the same for all males in this model. It is because the costs are decreasing with quality that it will turn out that the balance point between gains and losses for high quality males involves more advertizing than the balance point for low quality males. This condition on α is crucial to the operation of the model.

The fourth stage is of breeding itself. There is a breeding season of finite length, say from time 0 to time T. Females start unmated, and encounter surviving males at random with respect to genotype and quality, in a homogeneous Poisson process. When a female meets a male, she applies a rule based on the time in the breeding season and the male's advertizing level to decide whether to mate with him or not. Female rules will be denoted $D(a, t)$, $D^*(a, t)$, $D_1(a, t)$ and so on. Specifically, a strategy assigns a probability $D(a, t)$ of acceptance of a male advertizing at level a encountered at time t. If she does mate, she leaves the pool of unmated females,

and does not mate again. If she does not mate, she continues to encounter males in the same way as before. The rule she applies is specified by her allele.

Note that the same locus therefore specifies the male advertizing rule, when in a male body, and the female preference rule, when in a female body. Other kinds of genetic model will be discussed later.

The fecundity of a mated female is the product of two factors. The first, denoted $m(t)$, depends on the time in the season at which she mates, and the second depends on the quality of her mate, denoted $z(q)$ for a male of quality q. The idea is that the seasonal function is zero at the beginning and end of the season, when conditions are not very good, and better in between, when conditions are better. Formally, we assume that the seasonal function is zero at the beginning of the season, is continuous, and declines over some interval at the end. A higher quality male gives a greater fecundity. It may seem unrealistic to assume that males can mate many times, and yet they can have a non-genetic effect on fitness. While the combination is largely assumed for reasons of convenience, it can be achieved if the quality of a male reflects the fertility of his sperm, and females are constrained to mate once by, for example, a mating plug.

If the rate of meeting males is high, it will be advantageous for females to wait until just before the most advantageous time for mating until accepting any males, so that they will meet and mate with a male while the seasonal function is high. With a low rate of meeting males, females may be forced to accept males from earlier, in order to avoid the chance of being unmated at the end of season, or of having to breed at a disadvantageous time late in the season. Choosing not to mate with a class of males is costly to the female, because it reduces her ability to mate at the best time. The choosier she is, the wider a range of mating times she must accept, or the greater the chance of remaining unmated at the end of the season she must accept.

The four stages, together with the specification of the rules corresponding to the alleles, define a complete recursion over genotype frequencies. We can calculate the frequency of each type of mating, defined by the genotypes of male and female, the quality of the male, and the time of the mating. This defines the fecundity of the female, and the genotypes of the offspring, and it defines the numbers of each genotype contributed by that type of mating to the progeny generation. Summing up over types of mating yields the genotypic array of the progeny generation. Details of this one locus genetic model may be found in Appendix 1.

The exact details of the four stage model just described are not important. What matters for the full operation of the handicap principle is the "continuity in everything" explained earlier. The four stage model is the simplest explicit model of the operation of advertizing and female preference that I could think of, which satisfied all the continuity requirements.

With the exact recursion derived from our genetic model, there are many routes that could be taken. The most useful is to seek an uninvasible allele S^*, from the set of all possible advertizing rules and all possible preference rules. S^* would have to specify a pair of strategies such that, once they were common, no allele specifying any alternative pair of strategies could invade. Some alternative pairs will specify

the same strategy for one sex while changing the other. It turns out in Appendix 1 that functions ϕ_M and ϕ_F can be defined that may conveniently be called fitnesses. Suppose almost all members of a population are playing A^*, D^*. An alternative allele specifying the same female strategy but a variant male strategy A has the fitness $\phi_M(A; A^*, D^*)$. An alternative allele specifying the same male strategy but a variant female strategy D has the fitness $\phi_F(D; A^*, D^*)$. These are usefully called fitnesses because the condition for S^* to be uninvasible, derived in Appendix 1, is that

$$\phi_M(A^*; A^*, D^*) \geq \phi_M(A; A^*, D^*) \quad \text{for all } A \neq A^*$$
$$\phi_F(D^*; A^*, D^*) \geq \phi_F(D; A^*, D^*) \quad \text{for all } D \neq D^*.$$

In words, no alternative male strategy A has a higher fitness than A^* in a population playing A^*, D^*; and no alternative female strategy D has a higher fitness than D^* in a population playing A^*, D^*. This is an ESS-like expression of the condition for uninvasibility.

The question arises whether any such pairs (A^*, D^*) exist. Under the assumptions we have made, and one or two more technical assumptions made explicit in the appendices, it is shown in Appendix 4 that there are in effect exactly two pairs. The first is the non-signalling equilibrium, in which males choose to advertize at the lowest possible level, and females treat all advertizing levels the same. The second is the signalling equilibrium, in which advertizing level is a continuous and strictly increasing function of quality, and females pay costs to express graded preferences for different qualities of male, preferring higher to lower quality. This main result is summed up in the Theorem of Appendix 4. The route of argument is explained less technically in section 3.

The signalling equilibrium with one uninvasible allele exhibits all the features of sexual selection. A male ornament (i.e. with no "real" function, no non-signalling function) that is costly, is developed as a result of female preference. Further, the female preference is adaptive because by exercising that preference females obtain higher quality mates and therefore higher fecundity. Females pay a cost for their choice, and obtain real benefits.

The equilibrium has two other notable features. First, there is no element of Fisherian self-reinforcing preferences contributing to the form of the equilibrium. By looking for an uninvasible allele in a model without local structure, we have defined away the possibility that the Fisher process is operating in determining the equilibrium. Despite these definings away we have fully operational sexual selection. Second, it shows Zahavi's handicap principle at work. The ornament functions as a signal only because it is costly—the cost is not incidental. It is reasonable to say of a high quality male that he is preferred by females because his ornament is costly. The ornament lowers (one compartment of) his fitness, and the over-compensating increase in the other component relies on the females' response to his advertizing level. Signalling is honest. Honesty can be interpreted in the model as follows. Females observe a male's advertizing level, but in their choice of whether to mate with a male, it is only the male's quality that is relevant. Because choice of advertizing reveals quality, females can deal with males according to their quality. Now a mutant

male that advertizes more, introduced into the equilibrium population, will be treated by females as if he were of higher quality than he is—and this is dishonest signalling. But it is not advantageous, as we can tell from the definition of equilibrium as comprising uninvasible alleles. So dishonesty is disadvantageous, and at the equilibrium, signalling is honest. This sense of honesty is made more explicit in Appendix 5, where a formal link is made with the game theory models of the companion paper.

One further property is worth mentioning. In the companion paper, one of the features that was found to be capable of creating unlimited exaggeration of the male ornament was the presence of males with very deleterious effects on female fitness. It is interesting to find the same phenomenon confirmed analytically in the full model of Appendix 4. Thus if the worst males reduce the fitness of their mates close enough to zero, then advertizing can be exaggerated to any level. This suggests that the need to avoid males who would provide very low fecundity may be an important force in bringing about high costs of advertizing in equilibrium.

3. A Guide to the Proofs

The main result of section 2 is that the genetic model has exactly two equilibria: one with no signalling, and one with signalling. The proofs of these are given in the appendices, but they are rather technical. This section aims to give the gist of the proofs.

Appendices 1 to 3 present three different genetic models, and the importance of this will be discussed in section 5. For the moment, it suffices to explain that an investigation of non-invasible alleles in all three models leads to the same maximizations, those presented in section 2.

The game theory model of Appendix 4 therefore begins with one maximization for males, and one for females. Writing stars for the optimal strategies, A for male and D for female strategies, and ϕ_M and ϕ_F for the male and female maximands, the maximizations look like this:

$$\phi_M(A^*; A^*, D^*) \geq \phi_M(A; A^*, D^*) \quad \text{for } A \neq A^*$$

$$\phi_F(D^*; A^*, D^*) \geq \phi_F(D; A^*, D^*) \quad \text{for } D \neq D^*.$$

A^* is therefore a most successful male strategy for a rare mutant when all other males play A^* and females play D^*. D^* is a most successful female strategy for a rare mutant in the same circumstance.

It turns out that ϕ_M is just the expected number of offspring of a male playing A in a population playing (A^*, D^*), and that ϕ_F is just the expected number of offspring of a female playing D in a population playing (A^*, D^*). This means that even though this is a model of sexual selection, the equilibrium condition is that each individual maximizes its expected number of offspring. So an ESS model, in which this would have been the natural assumption, would have been perfectly satisfactory. One reason this happens is that we are looking for uninvasible alleles in the genetic model. Any equilibrium therefore has genetic uniformity.

The fact that number of offspring is maximized shows that the Fisher process is not at work, because the Fisher process involves choosing a mate so as to increase the fitness of one's sons. The fitness of females' sons is irrelevant to whether a rare mutant spreads or not against the equilibria in the model of section 2.

At the end of Appendix 1, functional forms are found for the maximands ϕ_M and ϕ_F. The maximizations then define the equilibria—and we now turn our attention to the questions: are there any equilibria? how many are there? what are they like? The fundamental result is stated as the Theorem in Appendix 4 and it says there are, in effect, exactly two equilibria. One, the non-signalling equilibrium, has males advertizing at the lowest level, and females treating all advertizing levels the same. The second, the signalling equilibrium, has a male strategy that specifies no advertizing for the lowest quality of male, and then increasing advertizing for better males. Every quality advertizes at a different level, so females can distinguish between qualities of males by basing their mating decisions on advertizing levels. Females choose whether to mate with a male in a way that is appropriate to the male's quality, as revealed by his advertizing. Appropriate means so as to maximize female fecundity.

The argument proceeds in a series of lemmas. Lemma 1 finds the optimal female response to any male strategy A, using a dynamic programme. With this characterization of the female response, in Lemma 2 we prove that in any optimal pair (A, D), A must be either constantly zero, or else continuous and strictly increasing. Lemma 3 picks up the first possibility and shows there is indeed an optimal pair (A, D) with A constantly zero. This establishes the existence of the non-signalling equilibrium of the theorem.

Our next aim is to follow up the second possibility of Lemma 2, and to show that there is a unique function A that achieves it. This takes many steps. First, we set out a system of equations $SE(1:10)$ that must hold at an equilibrium in which A is strictly increasing. To show that there exists a solution, we aim to apply a fixed point theorem in function space, to be specific, in L^1, the space of integrable functions. As technical preliminaries, we define a subset C of L^1, and prove in Lemma 4 that C is non-empty, closed, bounded, convex and compact. From now on, we consider only functions A that belong to C. Now $SE(1:9)$ takes one function A as "input", and produce another function A^* as "output". $SE(10)$ simply states that the input and output are equal. In Lemma 5, we prove that input of $SE(1:9)$ uniquely defines the output, and that if the input is in C, then so is the output. This defines a function f from C to C. Note that the argument and result of this function are themselves functions. Lemma 6 proves that this function is continuous and compact, which is another technical preliminary for application of the fixed point theorem. In Lemma 7, we apply Schauder's Fixed Point Theorem (Deimling, 1985), using the technical results of Lemma 4 and Lemma 6, to show that the whole system of equations $SE(1:10)$ has at least one solution. In addition, Lemma 7 establishes that any solution has $A(q_{min}) = 0$, and has A continuous and strictly increasing. The remaining lemmas show the relationship between this solution to $SE(1:10)$ and the maximizations. Lemma 8 shows that any solution to $SE(1:10)$ is a solution to the maximizations. Lemma 9 proves that there is at most one continuous and strictly

increasing function A that can satisfy the maximizations along with its optimal female response. Together, Lemmas 7 to 9 prove that there exists exactly one equilibrium with a strictly increasing A. This fulfils our aim of "making good" the second possibility in Lemma 2.

Both possibilities of Lemma 2 have therefore been shown to produce their own unique equilibrium. This is the main content of the Theorem of Appendix 4. The theorem also states some facts that are evident from $SE(1:10)$ about the signalling equilibrium. These are that three quantities are strictly increasing in male quality, namely the mating success of a male [i.e. $K(q)$], the product of the viability and the mating success of a male [i.e. $\alpha(q, A(q))K(q)$], and the net fitness of male [i.e. $\alpha(q, A(q))K(q)z(q)$]. The importance of the intermediate result is that net fitness is expected to increase because $z(q)$ increases; the intermediate result is net fitness apart from the factor $z(q)$.

Appendix 5 shows how the ESS model of the companion paper can be used as a "model of the model". This is a justification for using ESS models even when they gloss over many details. The ESS model is not a substitute for the full model, but it tells no lies about it, and many truths.

I now turn to a few remarks about the style of modelling used in the Appendices. The style may seem unnecessarily rigorous. The first defence is that the conclusion of the paper, that sexual selection can flourish in the absence of Fisherian self-reinforcement of preferences, is contrary to widely held beliefs. It is therefore important to show quite definitively that the equilibria really do exist, and in as general a setting as possible. The second defence is that this is a complicated type of model that is not common in biology. As a consequence, it was not clear before constructing the full argument, what was actually going to turn out to be true. A third defence, of the length of the exposition, is that if, as I hope, non-Fisherian models of sexual selection become common, it will be useful to have a range of techniques of proof available in a worked example.

Much of the complexity is introduced by the use of the fixed point theorem. It may seem to some readers, as it seemed once to me, that equations $SE(1:10)$ could be reformulated as differential equations, and then existence and uniqueness proved from that angle. This would cost a few extra assumptions, but the main objection is that it doesn't actually work. The equations are readily transformed into differential equations over time, from the beginning to the end of the season. The problem is that some boundary conditions need to be specified at the beginning, and some at the end of the season. Thus neither existence not uniqueness can be proved by standard results about differential equations (for example those in Sokolnikoff & Redheffer, 1966).

I should now mention two complicating factors in the analysis. First, I must say why there are only *in effect* exactly two equilibria. The set of possible strategies for males are integrable functions, and these include some very strange functions. For example,

$$A(q) = 1 \quad q = q_{min}$$
$$0 \quad q > q_{min},$$

defines an integrable function which equals zero almost everywhere (the area under the curve is the same as if the function equalled zero everywhere). *In effect* means that with each "real" solution (A^*, D^*) there is a class of solutions for whose members A equals A^* almost everywhere, and for all a, $D(a, t)$ equals $D^*(a, t)$ for almost all t. Puzzled readers should ignore this complication, as I have done in this section. Unfortunately it is not possible to ignore it in the appendices.

The second complicating factor is that I demand of an equilibrium not only that A^*, D^* satisfy the maximizations, but also that they satisfy "local flat extrapolation". This condition is explained and motivated in Appendix 1 of the companion paper, and expressed technically in Appendix 4 of this paper. Local flat extrapolation concerns how females behave when they meet an advertizing level that is not played by any male at equilibrium. This behaviour is not tested at equilibrium, and so is apparently not subject to selection. Yet it can be very important for whether a mutant that does play such an advertizing level will spread. Local flat extrapolation requires that females extrapolate from the closest played level, at least for unplayed levels very close to played levels.

As a final remark, the genetics in the model turns out to be trivial compared to the biology. This comes about by deliberate intent. I focussed on uninvasible alleles, so that at equilibrium, there basically was no genetics. I allowed a single allele to specify a whole function, or even two whole functions, that specified conditional behaviour. The advantage of these starting points is that a rich complexity of behaviour, including variation in behaviour, could be present at a genetically trivial equilibrium. This means that the ESS approach can be applied even in a fully genetically rigorous world. The biological problem becomes specifying strategy sets, in this case very natural ones, and how they interact to affect mating frequencies and offspring numbers. Finding uninvasible strategies from very large (infinite dimensional!) strategy sets is not so hard when the genetics is very simple.

Representing variation in behaviour, and complex behaviour, with single alleles seems to me a worthwhile modelling strategy. Representing them with genetic variability tangles together genetic complications and complications from, say, the mating system. Tangling these complications together in our model in the same way as they are tangled together in the world has obvious advantages. But when, as always, we are ignorant of the genetics of interesting traits, our models are likely to supply more understanding if we keep these complications separate. My modelling strategy is therefore to define such a broad class of allelic effects that any biological outcome can be supported by a genetically monomorphic equilibrium, and to look for uninvasible monomorphic equilibria. This is the spirit of the ESS approach, and I believe that the ESS revolution has some way to go before its consummation. The appendices of this paper show that ESS theory can be sensibly applied to sexual selection, by showing explicitly that genetics make no difference.

The general view is summed up in a needless admission by its chief protagonist (Maynard Smith, 1982: 132) that game theory is insufficient to study sexual selection. Parker (1983) ignored this advice, and constructed game theory models of advertizing, and of mate choice based on quality. Although this paper therefore contains all the ingredients of the handicap principle, they were treated separately and not

combined. There was no signalling of quality. Hammersetin & Parker (1987) have also applied game theory to sexual selection. I look forward to further successes of the strategic approach to evolution.

4. An Example

The results of the model of section 2 were obtained for arbitrary functions z, G, m and α. The rate of encounter of males by females, μ, is also arbitrary. This makes the results very strong, but perhaps also rather remote and hard to visualize. By making choices for the functions z, G, m, and α, and for the constant μ, the uninvasible strategies have been calculated for a particular case. The choices for the functions were:

$$z(q) = q$$

$$G(q) = \text{med}\{0, q - q_{\min}, 1\}, \quad \text{where "med" means the median value of the set}$$

$$m(t) = [4(t - 1/2)^4 - 2(t - 1/2)^2 + 1/4], \qquad 0 \le t \le 1$$

$$\alpha(q, a) = \exp[q - q_{\min} - 1 - a(q_{\min} + 1 + k - q)],$$

leaving only the parameters k, $q_{\min}$ and μ undetermined. These choices mean measuring quality by its effect on female fecundity, assuming a uniform distribution of quality over the interval $[q_{\min}, 1 + q_{\min}]$, and having the time of the season effect on female fecundity shown in Fig. 1. The survivorship function α satisfies the requirements of (1). The computations were based on a discretized version of the system of equations $SE(1:10)$ in the Appendix, all represented in the time domain. The closeness of approximation was confirmed by checking that increasing the number of steps did not alter the solutions very much.

There remain the three parameters μ, k and $q_{\min}$ to specify. Figure 2 shows what the solutions look like for $\mu = 20$, $k = 0.2$, and $q = q_{\min} = 0.3$. Part (a) shows male advertizing as a function of male quality, and part (b) shows for each time in the season, the threshold level of advertizing above which a male is acceptable to females.
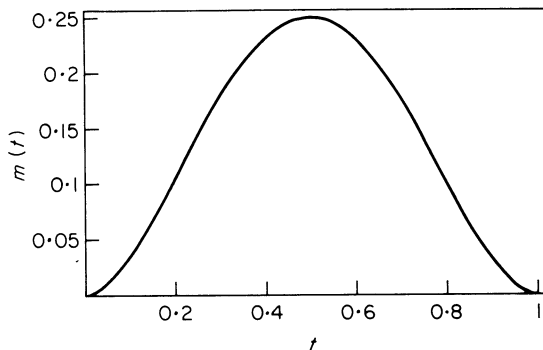

FIG. 1. This figure shows the time of the season factor, $m(t)$, in determining female fecundity used in the example described in the text.
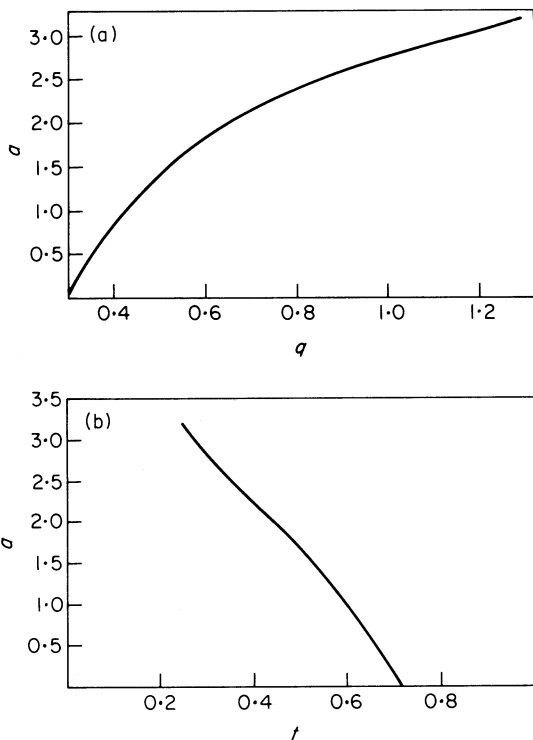
FIG. 2(a). This figure shows advertizing (a) as a function of male quality (q) at the signalling equilibrium in the example described in the text. (b) This shows the female strategy at the signalling equilibrium in the example described in the text. Before $t = 0\cdot25$, no male is accepted. Between $t = 0\cdot25$ and $t = 0\cdot175$, a male is accepted providing he is advertizing at more than the threshold level (a) shown in the figure. After $t = 0\cdot715$, all males are accepted.

There are two points which contradict tempting conjectures about the operation of sexual selection. The first tempting conjecture is that males of higher quality, although advertizing more and so reducing their net viability, do not advertize so much that their net viability falls below that of lower quality males. According to this conjecture, net viability of males should be monotonically related to quality at equilibrium. Figure 3 shows this is not true, just as it is not true in the example of the companion paper.

The second tempting conjecture is that females should be better off with a signalling system, because it allows them to choose higher quality males. Sexual selection would then likely benefit the species. This turns out not to be true in this example. The mean fitness of females in the advertizing equilibrium is $0\cdot183672$. The fitness of a rare non-discriminating female when males and all other females are playing the advertizing equilibrium is $0\cdot170284$. This difference of over 7% means a female would be prepared to sacrifice a further 7% of her fitness to be choosy rather than be completely undiscriminating. But the mean fitness of females at the non-signalling equilibrium is $0\cdot211223$. The overall survival of males is reduced by their advertizing
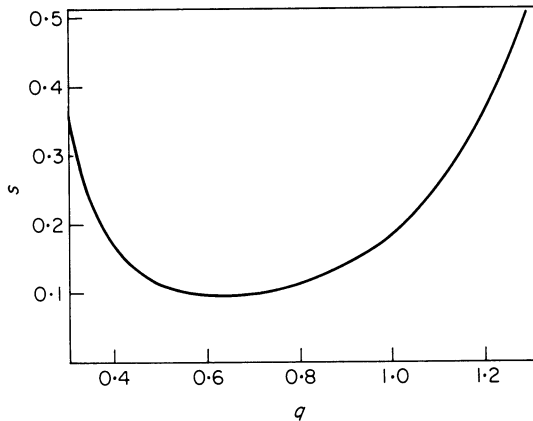
FIG. 3. This figure shows the net viability (s) of males as a function of their quality (q). If males varied in quality alone, the curve would decrease. If males varied in advertizing alone, the curve would increase. The combined effect is that low and high quality males survive better than intermediate males. The fitness of intermediate males is still higher than that of poor quality males, as their mating success more than compensates.

to such an extent that females are less able to mate at the best time in the season, and this reduction in their fitness more than compensates for the increase obtained through mating with higher quality males.

The properties of sexual selection could be explored by varying the three parameters k, q_{min} and μ, and observing the effects on the equilibrium. I do not mention this to tantalize readers with results not presented here. My point is that speculations about the effects of meeting rates, variation in quality and the costs of advertizing, can be investigated in a formal model. This supplies a formal framework for a range of commonsense biological thinking about sexual selection.

5. The Fisher Index

In this section I discuss the relations between the Fisher process, linkage disequilibrium and the handicap principle, and go on to introduce the "Fisher index" as a way of measuring the effect of the Fisher process.

The Fisher process arises when there is independent genetic variability in the female preferences and the male trait that is the object of female choice. The operation of the preferences brings about a genetic correlation between the two characters that is potentially destabilizing. Linkage disequilibrium will be the manifestation of this genetic correlation if the characters are controlled by separate loci.

The fact that the genetic model described in section 3 is single locus and haploid does not prevent the Fisher process from operating. What does prevent it is the combination of seeking an uninvasible allele, the assumption of no local structure, and the equivalence of all offspring. An equilibrium with a single uninvasible allele

has no genetic variability, and hence there can be no correlation between female preference and male trait at the equilibrium itself. To test if the allele is uninvasible, a mutant allele is introduced at very low frequency. Without local structure, this allele never meets itself, and so the interaction between its effect on female preference and its effect on male trait never occurs. The success of a mutant allele depends just on its interaction with the common allele. The genetic correlation between preference and trait is too weak to have any effect.

The reader may be concerned that we have virtually *defined* away the effect of the Fisher process, and indeed we have. But if the Fisher process really were an essential part of sexual selection, we should have at the same time defined away the possibility of sexual selection. Yet sexual selection manifestly flourishes in the model of section 2. So the defining away of the Fisher process is perfectly reasonable.

The irrelevance of the Fisher process is explored in two additional genetic systems besides the single locus model of section 2, formally modelled in Appendix 1. One is a two locus model, analysed in Appendix 2, with one locus controlling preference and one locus controlling the trait. Another is presented in Appendix 3, and is a modification of the two locus model, in which the effects of linkage disequilibrium are nullified by adding an extra (unrealistic) step into the model. In each generation just after zygote formation, the zygotes are replaced by a new set with exactly the same gene frequencies but linkage disequilibrium set to zero. Both genetic systems have exactly the same uninvasible equilibria as the single locus model of section 2. This shows that linkage disequilibrium plays no role in the determination of the equilibrium even when two loci are involved. The widespread belief that linkage disequilibrium is an essential part of sexual selection explains the apparent overkill of having three genetic models to hammer home the point.

To explain the perhaps surprising irrelevance of the Fisher process in the model of section 2, it is convenient to introduce a rough measure called the Fisher index. This is obtained by partitioning the variance in male advertizing level into two components. The first component is the dependence of advertizing level on male quality, the trait in which females have an interest. The second component is the dependence of advertizing level on the rules males use to relate quality to advertizing. The Fisher index is the fraction of total variance in advertizing due to this second rule, component. Figure 4 illustrates two extreme cases. Part (a) shows one low-advertizing rule with weak dependence on quality and one high-advertizing rule also with a low dependence on quality. Here most of the variance in advertizing is the result of differences between males in the rules they apply, and so the Fisher index is high. Part (b) shows two very similar rules, one slightly higher than the other, both with a strong dependence on quality. Here most of the variance in advertizing results from variance in male quality, and only a little is contributed by differences in male rules. The Fisher index is therefore low.

Models may be placed at points on the continuum between a Fisher index of zero and one of a hundred. Most sexual selection models have had a high Fisher index, including those of Lande & Kirkpatrick, and Maynard Smith. In this case advertizing level is an unreliable guide to male quality. The high Fisher index is reflected by the important part played by the Fisher process self-reinforcement of
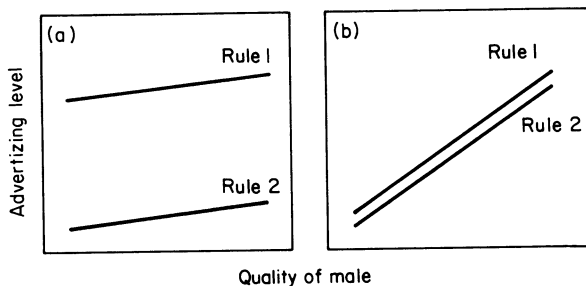
FIG. 4. This figure illustrates a case of a high Fisher index (a) and a case of a low Fisher index (b). In (a), the variation in advertizing is mainly due to variation in the advertizing rules of the males. It follows that advertizing is a poor guide to quality and females are unlikely to rely on it much in mate choice. In (b), the variation in advertizing is due mainly to quality, and so advertizing is a good guide to quality. Females are accordingly more likely to use advertizing in mate choice.

preferences in these models. My model has a Fisher index of zero, because the criterion of uninvasibility is applied when candidate alleles are fixed, and this ensures a zero Fisher index. In this case, advertizing is a reliable indicator of quality. The low Fisher index is reflected in the irrelevance of the Fisher process to the equilibrium.

Male traits in nature may also be placed on this same continuum. If the Fisher index is generally high for sexually selected traits, then we would expect the Fisher process to be important in causing exaggeration of traits; while if it is generally low, then the handicap theory of Zahavi is likely to be more important. In my view, then, the empirical values of the Fisher index should be of great interest to students of sexual selection. The main difficulty in measuring it is knowing what the underlying quality is in which females are interested. This would make a measurement of the Fisher index even more interesting, because it would require us to understand something about sexual selection in nature.

Dr Olof Leimar has pointed out to me that in the case where quality is environmental, the heritability of the male is a measure of the Fisher index. When quality is genetic, it would be necessary to compute the heritability of the residuals from the regression of male trait on male quality.

We may consider from a theoretical point of view which forces contribute to determining the Fisher index, which is itself determined by the variance in advertizing induced on the one hand by variance in quality, and on the other by variance in the rules relating quality to advertizing. Variation in quality may be environmental, or it may be genetic and based on one of the currently fashionable models for retaining additive genetic variability in fitness. Variation in the rules is likely to be maintained by mutation-selection balance, as it is, for example, in Lande's (1981) model.

My own guess is that the real biological factors causing variation in mate quality are likely to be much more important than the imperfections of the genetic system in attaining the optimal rules. For example, it seems likely to me that peahens are choosing males for real advantages, and that variation between males in the train-

producing rules contributes little to variation to train length. Of course guesswork is cheap.

I conclude that, theoretically, the Fisher process is not a necessary part of models of sexual selection. Empirically, it is an open question whether the Fisher process should be invoked to account for the extravagance of sexually selected characters. The "Fisher index" is a useful indicator of the importance of the Fisher process in models and data.

6. Concluding Remarks

The creative processes of Fisher and Zahavi may be compared. Fisher had very deep and original ideas, which showed a high degree of internal consistency and beauty. Zahavi seems to work from facts about animals, and slowly to develop an understanding of how those facts are inter-related. Fisher solved the sex ratio problem, and later work on that problem is an embellishment of his solution. On the other hand, his theory of dominance has turned out to be simply wrong (Charlesworth, 1979). Zahavi's method explains how in slowly developing for himself the idea of a strategic choice handicap, he juggled facts between the categories of assumed constraints and implied results leading, I believe, to the condition-dependent handicap and the revealing handicap, as well as to the strategic choice handicap. As an account of sexual selection, I believe that Zahavi's upward struggle from fact will triumph. Fisher's ingenious idea is too clever by half.

The main biological conclusions of this paper are the same as those of Zahavi's original papers on the handicap principle. The extravagance of sexually selected characters is conventionally viewed as a side-effect of the Fisher–Lande process (Fisher, 1915; Lande, 1981), in which the costliness to males is merely irrelevant. According to the handicap principle, the cost is an essential element in the persuasive power of the sexually selected characters and an inescapable feature of persuasive signalling systems.

According to the handicap principle as outlined here, there is nothing to stop sexual selection occurring under monogamy, as Andersson (1986) showed for the condition-dependent handicap. It may also occur in both sexes simultaneously provided each sex has an unobservable quality affecting its suitability as a mate.

According to the handicap principle, then, there is rhyme and reason in the incidence and form of sexual selection. By studying what organisms want to know about their mates, and how signals impose costs, we could in principle explain the diversity of sexual selection. This is in contrast to the Fisher–Lande process, in which the form of the signal is more or less arbitrary and whether a species has undergone a bout of runaway selection is more or less a matter of chance. To believe in the Fisher–Lande process as an explanation of sexual selection without abundant proof is methodologically wicked, and I know of no relevant evidence at all. Such a belief inhibits the search for patterns which might disprove it. The main implication of the handicap principle for present purposes is that sexually selected ornaments have meanings which are worth discovering, and forms which can be explained; and that the key to both is their cost.

Professor J. A. Mirrlees taught me all I know about the mathematics of maximization, and more. He also directed me to the superb text on functional analysis by Deimling (1985). Sean Nee heroically worked through an earlier and less clear version of the Appendices, much to the benefit of the current version. He and Andrew Pomiankowski have consistently, and ultimately successfully, prevailed upon me to moderate the unreasonableness of my attacks on previous models of sexual selection. Julee Greenough and Laurence Hurst made helpful comments on previous versions. Amotz Zahavi explained to me 10 years ago that the handicap principle could be modelled successfully, but only with mathematical methods not yet developed. This has turned out to be closer to the truth than I believed at the time. I now accept that he was basically right, and I was quite wrong. On the same occasion he said that if only I knew Hebrew, he could explain the handicap principle to me in a way I would understand. This alternative should be borne in mind by readers who find minor difficulties in understanding this paper or its companion.

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APPENDIX 1

A Single Locus Genetic Model

The gene frequency recursions are to be given for the genetic model defined in section 2, and the conditions for an allele specifying the functions (A, D) to be uninvasible are expressed as maximizations.

Suppose there are two male strategies, A_1 and A_2, and two female strategies D_1 and D_2, present in the population, with the common allele determining A_1D_1, and a rare mutant determining A_2D_2. We will calculate whether the mutant can spread. Let the frequencies at formation of zygotes of the two haploid genotypes (A_1D_1) and (A_2D_2) be denoted π_1 and π_2. Sex is assumed to be determined independently of the strategies and so the frequencies are equal in the two sexes at the time of zygote formation. We will study the recursion of π_1 and π_2.

Let f^i_j be the number of offspring produced by matings between i-type males and j-type females. We can write these in terms of the F^i_j, which can be interpreted as the success of i-males and j-females at producing offspring compared to their frequencies in the population, as follows:

$$f^i_j = \pi_i\pi_jF^i_j.$$

This is convenient because the F^i_j will turn out to be non-zero to 0th order in π_2, and the stability condition will turn out to be expressed in terms of the F^i_j evaluated at $\pi_2 = 0$.

Matings between i-type males and j-type females are between genotypes i and j, and the offspring produced are half of type i and half of type j. Hence

$$C\pi'_1 = f^1_1 + \tfrac{1}{2}(f^1_2 + f^2_1)$$

$$C\pi'_2 = f^2_2 + \tfrac{1}{2}(f^1_2 + f^2_1),$$

where C is determined by $\pi'_1 + \pi'_2 = 1$. Substituting F's for fs, evaluating C and substituting for it, and linearizing around $\pi_2 = 0$, we obtain

$$\pi'_2 = \frac{F^1_2 + F^2_1}{2F^1_1}\pi_2.$$

The stability of the system can be studied by considering the π_2 subsystem because the two variables satisfy the linear constraint $\pi_1 + \pi_2 = 1$. The eigenvalue of this "system" is just the factor

$$\frac{F^1_2 + F^2_1}{2F^1_1}.$$

The common allele will be invaded if this is greater than one, and will not be invaded if this is less than 1. To ensure that no possible rare allele can invade, it must be the case that $F^1_2 \leq F^1_1$ and $F^2_1 \leq F^1_1$ for any possible alternative strategies A_2 and D_2. This conclusion supplies maximization conditions for the uninvasibility of the rules A_1 and D_1 that will be familiar to students of ESS theory. F^1_2 has a simple interpretation as the number of offspring produced by a rare D_2 individual in a population playing A_1D_1, and F^2_1 is the same for a rare A_2 individual. The maximizations therefore state that for A_1 and D_1 to be uninvasible, there must be no alternative strategy, for males or females, that when rare produces more offspring than A_1 and D_1 do for the individuals playing them.

If we let $\phi_M(A; A^*, D^*)$ represent the number of offspring produced by a male playing A in a population playing (A^*, D^*), and $\phi_F(D; A^*, D^*)$ represent the

number of offspring produced by a female playing D in a population playing (A^*, D^*), then we can express necessary conditions for uninvasibility of an allele specifying (A^*, D^*) formally as

$$\phi_M(A; A^*, D^*) \le \phi_M(A^*; A^*, D^*) \quad \text{for all } A \ne A^*$$

$$\phi_F(D; A^*, D^*) \le \phi_F(D^*; A^*, D^*) \quad \text{for all } D \ne D^*.$$

With strict inequalities, these conditions would be sufficient for uninvasibility. This is important because it shows how well the maximizations represent uninvasibility, even though it will turn out that these sufficient conditions can never be met owing to the existence of strategies (A, D) that differ from (A^*, D^*) in trivial ways. The exact genetic recursion has therefore led us formally to a game, with maximands ϕ_M and ϕ_F. The existence, enumeration and characterization of solutions to these maximizations is the topic of Appendix 4.

These maximizations show the strong connection between ESS models and population genetic models of the strategic handicap. Had we made an ESS model, its ESS strategies would have been the same as the uninvasible strategies of the population genetics model. Offspring number is the natural maximand to choose in an ESS model, even of sexual selection, provided that offspring are all of equal value at equilibrium. When offspring are not of equal value, for example, in sex ratio models, the maximand is a weighted sum of the numbers of the different kinds of offspring.

Functional forms can be found for the maximands as follows. The general form for a female strategy is a function $D(a, t)$ which is the probability with which a female accepts a male advertizing at level a encountered at time t. It will turn out that for the optimal policy this probability is usually zero or one. We will use $D_j(a, t)$ for the strategy function of a j-type female.

To ensure compatibility of notation with later appendices, which have more complex genetic models, let Π^i be the fraction of males that are i-types, and let Π_j be the fraction of females that are j-types. In the single locus genetic model just developed, they are given simply by $\Pi^i = \pi_i$ and $\Pi_j = \pi_j$.

Females begin unmated at time $t = 0$. The hazard rate (see e.g. Kalbfleisch & Prentice, 1980 for a general introduction to survivorship theory) of a j-type female leaving the unmated class at time t is given by the rate of meeting acceptable males, which is

$$\mu \int_q \sum_k [\Pi^k \alpha(q, A_k(q)) D_j(A_k(q), t)] \, dG(q).$$

Let $U_j(t)$ be the chance of a j-type female being unmated at time t. Then by standard survivorship theory U is given by integrating the hazard as follows:

$$U_j(t) = \exp \left\{ -\mu \int_q \sum_k [\Pi^k \alpha(q, A_k(q)) D_j(A_k(q), t)] \, dG(q) \right\}.$$

The rate at which unmated j-type females meet i-type males of quality q at time t is

$$\mu \Pi^i \alpha[q, A_i(q)] U_j(t) \, dG(q),$$

and so the total number of offspring produced by j-type females and i-type males is

$$\Pi_j \int_q \mu \Pi^i \alpha[q, A_i(q)] z(q) \left(\int_t U_j(t) m(t) D_j[A_i(q), t] \, dt \right) dG(q),$$

where $z(q)$ and $m(t)$ are determinants of female fecundity relating to male quality and time in the season. They are discussed in section 2. Hence

$$F_j^i = \int_q \mu \alpha[q, A_i(q)] z(q) \left(\int_t U_j(t) m(t) D_j[A_k(q), t] \, dt \right) dG(q).$$

Evaluated at $\Pi^2 = \Pi_2 = 0$, these are the required maximands. Let $U(t; A, D)$ be defined by

$$U(t; A, D) = \exp \left\{ - \int_q \alpha[q, A(q)] \int_{\tau=0}^t \mu D[A(q), \tau] \, d\tau \, dG(q) \right\}.$$

Then $U_1(t) = U(t; A_1, D_1)$ and $U_2(t) = U(t; A_1, D_2)$. Hence the linearized F_2^1 and F_1^2 can be finally expressed as;

$$F_2^1 = \int_q \mu \alpha[q, A_1(q)] z(q) \left(\int_t U(t; A_1, D_2) m(t) D_2[A_1(q), t] \, dt \right) dG(q)$$

$$F_1^2 = \int_q \mu \alpha[q, A_2(q)] z(q) \left(\int_t U(t; A_1, D_1) m(t) D_1[A_2(q), t] \, dt \right) dG(q).$$

APPENDIX 2

A Two Locus Genetic Model

In this Appendix, we repeat the exercise of Appendix 1, except that we suppose that male and female strategies are determined at separate unlinked loci. Our purpose is to find a pair of strategies (A^*, D^*) such that a pair of alleles specifying these functions at their respective loci would be uninvasible by alleles specifying any other strategies.

Suppose there are two male types, A_1 and A_2, and two female types D_1 and D_2, segregating in the population. Let the frequencies at formation of zygotes of the four haploid genotypes $A_1 D_1$, $A_1 D_2$, $A_2 D_1$ and $A_2 D_2$ be denoted π_{11}, π_{12}, π_{21}, π_{22}. Sex is assumed to be determined independently of the A and D loci so the frequencies are equal in the two sexes at the time of zygote formation. We will study the recursion not of the π_{ij} but of $(\delta, \varepsilon, \kappa)$ defined by

$$\delta = \pi_{21} + \pi_{22}$$

$$\varepsilon = \pi_{12} + \pi_{22}$$

$$\kappa = \pi_{22},$$

which represent the fraction of A_2, the fraction of D_2 and the fraction of A_2D_2 respectively.

Let $\Pi^i = \pi_{i1} + \pi_{i2}$, the fraction of males that are i-type.

Let $\Pi_j = \pi_{1j} + \pi_{2j}$, the fraction of females that are j-type.

Let $\sigma_{ij} = \pi_{ij}/\Pi^i$, the fraction of i-type males that are of genotype ij.

Let $\tau_{ij} = \pi_{ij}/\Pi_j$, the fraction of j-type females that are of genotype ij.

As before, let f^i_j be the number of offspring produced by matings between i-type males and j-type females. Again, we can write these in terms of F^i_j as follows:

$$f^i_j = \Pi^i \Pi_j F^i_j.$$

F^i_j will turn out to be non-zero to 0th order in δ, ε, κ, and the relevant eigenvalues will turn out to be expressed in terms of the F^i_j evaluated at $\delta = \varepsilon = \kappa = 0$.

Matings between i-type males and j-type females can be of four types genetically. The type of an individual fixes the strategy determined for its own sex by its genotype, but not the strategy determined for the other sex. The frequencies with which $i \times j$ matings are of genotypes $im \times nj$ is $\sigma_{im}\tau_{nj}$. An $im \times nj$ mating in the two locus system produces with equal probabilities offspring of genotypes im, ij, nm, nj. The frequencies of these genotypes produce the π_{ij} of the next generation, which can be used to compute $(\delta, \varepsilon, \kappa, x)$ for the next generation too. x denotes $1 - \delta - \varepsilon + \kappa$, the frequency of the A_1D_1 genotype. Using primes to denote the values in the next generation, and C for the mean fitness, a few pages of tedious but straightforward algebra lead to the recursion:

$$4C\begin{pmatrix}\delta\\\varepsilon\\\kappa\\x\end{pmatrix}' = \left(\begin{matrix}2(1-\delta)(\delta-\kappa) & 2\kappa(1-\delta)\\2(1-\varepsilon)(\varepsilon-\kappa) & 2\varepsilon(1+\varepsilon-\delta-\kappa)\\(\varepsilon-\kappa)(\delta-\kappa) & \kappa(1-\delta+\varepsilon-\kappa)\\(2-\varepsilon-2\delta+\kappa)(2-2\varepsilon-\delta+\kappa) & (1-\varepsilon-\delta+\kappa)(2\varepsilon-\kappa)\end{matrix}\right.$$
$$\left.\begin{matrix}2\delta(1-\varepsilon+\delta-\kappa) & 2\delta(\varepsilon+\kappa)\\2\kappa(1-\varepsilon) & 2\varepsilon(\delta+\kappa)\\\kappa(1-\varepsilon+\delta-\kappa) & (\delta+\kappa)(\varepsilon+\kappa)\\(1-\varepsilon-\delta+\kappa)(2\delta-\kappa) & (\delta-\kappa)(\varepsilon-\kappa)\end{matrix}\right)\begin{pmatrix}F^1_1\\F^1_2\\F^2_1\\F^2_2\end{pmatrix}, \quad (A2.1)$$

which is well defined because C can be evaluated using $x + \delta + \varepsilon - \kappa = x' + \delta' + \varepsilon' - \kappa' = 1$. When C is solved and the system is linearized in δ, ε, κ around $\delta = \varepsilon = \kappa = 0$ the equation yields:

$$4F^1_1\begin{pmatrix}\delta\\\varepsilon\\\kappa\end{pmatrix}' = \begin{pmatrix}2(\delta-\kappa) & 2\kappa & 2\delta & 0\\2(\varepsilon-\kappa) & 2\varepsilon & 2\kappa & 0\\0 & \kappa & \kappa & 0\end{pmatrix}\begin{pmatrix}F^1_1\\F^1_2\\F^2_1\\F^2_2\end{pmatrix}$$

$$= \begin{pmatrix}2(F^1_1+F^2_1) & 0 & 2(F^1_2-F^1_1)\\0 & 2(F^1_1+F^1_2) & 2(F^2_1-F^1_1)\\0 & 0 & F^1_2+F^2_1\end{pmatrix}\begin{pmatrix}\delta\\\varepsilon\\\kappa\end{pmatrix}.$$

The stability of the system can be investigated by considering this $(\delta, \varepsilon, \kappa)$ subsystem, as the four variables satisfy the linear constraint $x + \delta + \varepsilon - \kappa = 1$. Because of the positioning of zeros in the transition matrix, the eigenvalues λ_1, λ_2 and λ_3 are simply given by the diagonal elements of the matrix divided by F_1^1. If any eigenvalue is greater than one, then some allele or alleles can invade the fixed point $(0, 0, 0)$. A necessary condition for uninvasibility is therefore that for any alternative strategies A_2, D_2, we have

$$F_2^1 \le F_1^1 \quad \text{and} \quad F_1^2 \le F_1^1,$$

as before. Again strict inequalities would make a sufficient condition. The two locus model has exactly the same conditions for uninvasibility as the one locus system. The eigenvectors of the first two eigenvalues are $(1, 0, 0)$ and $(0, 1, 0)$, representing the frequency of A_2 and D_2, respectively. This shows that whether each strategy spreads is determined by its own success, and is not affected by the presence of the other strategy.

APPENDIX 3

The Strange Genetics

The "strange genetics" is a modification of the two locus model of Appendix 2 that enforces linkage disequilibrium in every generation at zygote formation. The transition eqn (A2.1) needs to be modified, omitting the equation for κ', and substituting in the right hand side for κ using $\kappa = \delta\varepsilon$. The modified transition equation is

$$4C \begin{pmatrix} \delta \\ \varepsilon \\ x \end{pmatrix}' = \begin{pmatrix} 2(1-\delta)(\delta-\delta\varepsilon) & 2\delta\varepsilon(1-\delta) \\ 2(1-\varepsilon)(\varepsilon-\delta\varepsilon) & 2\varepsilon(1+\varepsilon-\delta-\delta\varepsilon) \\ (2-\varepsilon-2\delta+\delta\varepsilon)(2-2\varepsilon-\delta+\delta\varepsilon) & (1-\varepsilon-\delta+\delta\varepsilon)(2\varepsilon-\delta\varepsilon) \end{pmatrix}$$

$$\begin{pmatrix} 2\delta(1-\varepsilon+\delta-\delta\varepsilon) & 2\delta(\varepsilon+\delta\varepsilon) \\ 2\delta\varepsilon(1-\varepsilon) & 2\varepsilon(\delta+\delta\varepsilon) \\ (1-\varepsilon-\delta+\delta\varepsilon)(2\delta-\delta\varepsilon) & (\delta-\delta\varepsilon)(\varepsilon-\delta\varepsilon) \end{pmatrix} \begin{pmatrix} F_1^1 \\ F_2^1 \\ F_1^2 \\ F_2^2 \end{pmatrix},$$

in which the constant C is evaluated using $1 = x + \delta + \varepsilon - \delta\varepsilon$. When linearized in δ and ε around $\delta = \varepsilon = 0$ the reduced equation for δ and ε alone is

$$\begin{pmatrix} \delta \\ \varepsilon \end{pmatrix}' = \begin{pmatrix} \dfrac{F_1^1 + F_1^2}{2F_1^1} & 0 \\ 0 & \dfrac{F_1^1 + F_2^1}{2F_1^1} \end{pmatrix} \begin{pmatrix} \delta \\ \varepsilon \end{pmatrix}.$$

The eigenvalues are just the diagonal elements, leading to exactly the same conditions as in Appendices 1 and 2 for the spread of the alleles A_2 and D_2. It follows that eliminating linkage disequilibrium from the model of Appendix 2 has no effect on which strategies must be specified to ensure uninvasibility.

APPENDIX 4

Solving the Maximizations

The genetic models of Appendices 1, 2 and 3 provide us with the following jointly necessary conditions for A^* and D^* to be strategy functions specified by an uninvasible allele or alleles:

$$\phi_M(A; A^*, D^*) \le \phi_M(A^*; A^*, D^*) \quad \text{for all } A \ne A^* \tag{A4.1a}$$

$$\phi_F(D; A^*, D^*) \le \phi_F(D^*; A^*, D^*) \quad \text{for all } D \ne D^*. \tag{A4.1b}$$

Male strategies A must satisfy $A(q) \ge 0$, as zero is the minimum advertizing level. Female strategies must satisfy $0 \le D(a, t) \le 1$, as D is a probability of acceptance of a male. As shown in Appendix 1, the model described in section 2 provides the following functional forms for ϕ_M and ϕ_F, for rare invaders A and D in a population playing A^* and D^*:

$$\phi_M(A; A^*, D^*) = \int_q \mu\alpha[q, A(q)]z(q)$$
$$\times \left(\int_t U(t; D^*, A^*)m(t)D^*[A(q), t]\, dt \right) dG(q) \tag{A4.2a}$$

$$\phi_F(D; A^*, D^*) = \int_q \mu\alpha[q, A^*(q)]z(q)$$
$$\times \left(\int_t U(t; D, A^*)m(t)D[A^*(q), t]\, dt \right) dG(q), \tag{A4.2b}$$

where,

$$U(t; A, D) = \exp\left\{ -\int_q \alpha[q, A(q)] \int_{\tau=0}^{t} \mu D[A(q), \tau]\, d\tau\, dG(q) \right\}.$$

In this Appendix it will be proved under certain assumptions that there exist exactly two solutions to this joint maximization that satisfy the local flat extrapolation condition given in Appendix 1 of the companion paper. This condition may be formally expressed as:

Local flat extrapolation criterion. Given a male and female strategy (A, D). Let $S_A = \{a | A(q) = a \text{ for some } q\}$. Then (A, D) is said to satisfy the local flat extrapolation criterion if for every $a \in \partial S_A$ and t, there exists a constant $\bar{D}$ such that;
  (i) there is sequence $N^k, k = 1, 2, \ldots$, of neighbourhoods of a such that $N^m \subset N^k$ for $k < m, \int_{N^k} da' \to 0$ as $k \to \infty$, and

$$\frac{\int_{N^k \cap S_A} D(a', t)\, da'}{\int_{N^k \cap S_A} da'} \to \bar{D},$$

  (ii) there exists a neighbourhood N of a such that $D(a', t) = \bar{D}$ for $a' \in N, a' \notin S_A$. If $a \in S_A$, and $A(q)$ is continuous at all points q' such that $a = A(q')$, then this is equivalent to the simpler condition that there exists a neighbourhood N of a such that $D(a', t) = D(a, t)$ for $a' \in N, a' \notin S_A$.

Less formally, local flat extrapolation means that the female decision rule treats unplayed advertizing levels the same as the closest level that is played by A, provided that closest level is close enough.

As there are a multitude of definitions and lemmas, the theorem will be stated shortly for accessibility. We must first define $SE(1:10)$, a system of equations mentioned in the statement of the theorem. The functions not defined by the system will all be defined formally later, as will the sets Q of male qualities. T of times in the season, and R the real line.

Definition of SE(1), SE(2) *etc.* Let SE denote the following system of equations for $A: Q \rightarrow R$, $v: T \rightarrow R$, $Y: T \rightarrow R$, $u: T \rightarrow R$, $K: Q \rightarrow R$, $A^*: Q \rightarrow R$, $SE(i)$ denote the ith equation, and $SE(i:j)$ denote the i through jth equations. Let α^1 denote the logarithmic derivative of α with respect to its first argument.

$$v(T) = 0 \qquad\qquad SE(1)$$

$$v'(T) = 0 \qquad\qquad SE(2)$$

$$v'(t) = -\mu \Big\{ m(t) \int_{z(q)>v(t)/m(t)}^{q_{max}} z(q)\alpha[q, A(q)] \, dG(q)$$

$$- v(t) \int_{z(q)>v(t)/m(t)}^{q_{max}} \alpha[q, A(q)] \, dG(q) \Big\} \qquad 0 < t < T \qquad SE(3)$$

$$Y(T) = 0 \qquad\qquad SE(4)$$

$$Y(t) = \frac{v(t)}{m(t)} \qquad 0 < t < T \qquad SE(5)$$

$$u(t) = \exp \Big\{ -\mu \int_{\tau=0}^{t} \int_{z(q)>Y(\tau)} \alpha[q, A(q)] \, dG(q) \, d\tau \Big\} \qquad SE(6)$$

$$K(q) = \int_{z(q)>Y(\tau)} u(\tau)m(\tau) \, d\tau \qquad SE(7)$$

$$A^*(q_{min}) = 0 \qquad\qquad SE(8)$$

$$\int_{q_{min}}^{q} \alpha^1[q', A^*(q')] - \alpha^1[q', A^*(q)] \, dq' = -\ln \frac{K(q)}{K(q_{min})} \qquad SE(9)$$

$$A(q) = A^*(q) \qquad \forall q. \qquad SE(10)$$

This system of equations is designed to represent the equilibrium conditions at a "splitting equilibrium" (i.e. each quality of male advertizes at a different level, so that a female can treat each quality differently by treating each advertizing level differently) with a strictly increasing advertizing function A. $v(t)$ is the future fecundity of a female, unmated at time t, that plays the optimal response to A. $Y(t)$ represents the female strategy, and is a threshold value of z. If $z(q) > Y(t)$, then a female playing the optimal response to A will accept males of quality q at time t, but reject them if the inequality is reversed. $u(t)$ is the probability that a female playing Y is unmated at time t. $K(q)$ is the expected number of offspring of a male advertizing at level $A(q)$, divided by $z(q)$. A^* is a strategy that will equal A if A

is the optimal response of a rare male in a population playing (A, D). If $A = A^*$, then A, D is uninvasible.

Theorem: Let a function A^* be called a "full solution" if there exists a D^* for which (i) (A^*, D^*) satisfies local flat extrapolation (ii) $\phi_M(A; A^*, D^*) \leq \phi_M(A^*; A^*, D^*)$ for all A and (iii) $\phi_F(D; A^*, D^*) \leq \phi_F(D^*; A^*, D^*)$ for all D. Then;

    (1) there exist two full solutions. The *non-signalling equilibrium*, say A_{non}, has $A_{non}(q) = 0$. The *signalling equilibrium*, say A_{sig}, is uniquely defined by the property of satisfying $SE(1:10)$ for A, and has the following properties:

      (i) $A_{sig}(q_{min}) = 0$, and $A_{sig}(q)$ is continuous and strictly increasing

      (ii) $K(q)$ and $\alpha[q, A_{sig}(q)]K(q)$ and $\alpha[q, A_{sig}(q)]z(q)K(q)$ all strictly increase in q;

    (2) any other full solution A^* satisfies either $A^*(q) = A_{non}(q)$ for almost all q, or $A^*(q) = A_{sig}(q)$ for almost all q.

The proof of this result is unfortunately long and complicated. First the assumptions and notation must be laid out formally, and then nine lemmas need to be proved before the proof of the theorem can be given. The strategy of the whole argument is described in section 3 of the text of the paper.

Definition of **R, I**. These have their usual meanings of the real line and the unit interval $[0, 1]$ of the real line, respectively.

Definition of μ. Let $\mu \in \mathbf{R}$, $\mu > 0$. μ represents the rate at which females encounter males.

Definition of **Q**, q_{min}, q_{max}. Let q_{min}, $q_{max} \in \mathbf{R}$, $q_{max} > q_{min} > 0$, and let $\mathbf{Q} \subset \mathbf{R}$ be $[q_{min}, q_{max}]$. **Q** represents the range of male qualities present in the population.

Definition of **T**, T. Let $T \in \mathbf{R}$, $T > 0$, and $\mathbf{T} \subset \mathbf{R}$ be $[0, T]$. **T** represents the times in the breeding season.

Definition of m. Let $m: \mathbf{T} \rightarrow \mathbf{R}$, be continuous with $M > m(t) > 0$ for $0 < t < T$, $m(0) = 0$, for some M and such that

$$\min \{t \mid m(t) \text{ is non-increasing on } [t, T]\} < T.$$

Let there exist no strictly positive constants k_1, k_2 such that $m(t) = k_1 \exp(-k_2 t)$ over any interval of **T** with positive length. This restriction is necessary because of a clash with the local flat extrapolation criterion, as will be explained in a remark at the end of this appendix.

Definition of z(q). Let $z: \mathbf{Q} \rightarrow \mathbf{R}$ be a continuous and strictly increasing function with $z(q_{min}) > 0$. z is a factor in the product determining female fecundity, and represents the effect of male quality.

Definition of t'. Let $k_1 = \int \alpha(q, 0) \, dG(q)$ and $k_2 = \int z(q)\alpha(q, 0) \, dG(q)$. Then let t' equal

$$\max \left\{ \min \{t \mid m(t) \text{ is non-increasing on } [t, T]\}, \quad T + \frac{1}{k_1} \ln \left[1 - \frac{k_1}{k_2} z(q_{min}) \right] \right\},$$

t' will be shown to be a time so late that females are bound to be accepting any male at that stage. That $t' < T$ is ensured because the first element in the set is less than T by definition of m, and the second is less than T because the argument of "ln" is less than one. Notice that we here rely on $z(q_{min}) > 0$. The argument of "ln" cannot be less than zero, because k_2/k_1 is the average z of all surviving males, which cannot be less than the minimum value of z.

Definition of K_{min}, K_{max}. Let $K_{min} = \int_{t'}^T \exp\{-\mu\tau\}m(\tau)\,d\tau$, and $K_{max} = \int_T m(\tau)\,d\tau$. It is clear that $K_{max} > K_{min} > 0$. These will be shown to be a lower bound to $K(q_{min})$ and an upper bound to $K(q_{max})$.

Definition of α. Let $\alpha : \mathbf{Q} \times [0, \infty) \to \mathbf{I}$ satisfy (i) $\alpha(q, \cdot)$ and $\alpha(\cdot, a)$ are absolutely continuous (see, e.g. Weir, 1973: 67) for all q, a, (ii) $\alpha(q_{max}, 0) = 1$ (iii) $q_1 < q_2$ implies $\alpha(q_1, a) < \alpha(q_2, a)$ (iv) $a_1 < a_2$ implies $\alpha(q, a_1) > \alpha(q, a_2)$, (v)

$$q_1 < q_2 \quad \text{and} \quad a_1 < a_2 \quad \text{imply} \quad \frac{\alpha(q_1, a_2)}{\alpha(q_1, a_1)} < \frac{\alpha(q_2, a_2)}{\alpha(q_2, a_1)},$$

and (vi) $\text{Lim}_{a \to \infty} \alpha(q_{max}, a) < K_{min}/K_{max}$. $\alpha(q, a)$ represents the pre-breeding survival of a male of quality q with advertizing level a, relative to a male of quality q_{max} advertizing at 0. Note that (iv) implies $\alpha > 0$.

Definition of α^1, α^2. As α is absolutely continuous, there exist integrable functions α^1 and α^2 representing the partial derivatives with respect to the first and second arguments of the logarithm of α. Condition (v) of the definition of α implies the important facts that $\alpha^1(q, a)$ is strictly increasing in a for almost all q, and that $\alpha^2(q, a)$ is strictly increasing in q for almost all a.

Definition of B. Let B be defined by $\alpha(q_{max}, B) = K_{min}/K_{max}$. B exists by the assumptions on α. B will be shown to be an upper bound to the advertizing levels played by males.

Definition of G. Let $G : \mathbf{R} \to \mathbf{I}$ be continuous, and strictly increasing on $\mathbf{Q}$, with $G(q_{min}) = 0$, $G(q_{max}) = 1$. G represents the probability distribution function of male quality.

Definition of L^1. Let L^1 as usual (see, e.g. Weir, 1973) be the space of integrable functions. We will mainly be concerned with $L^1(\mathbf{Q})$, the set of integral functions from $\mathbf{Q}$ to $\mathbf{R}$, considered as a linear space with norm

$$|A| = \int_Q |A(q)|\,dG(q).$$

$L^1(\mathbf{Q})$ is a real Banach space (Weir, 1973: 166, 221). We will use briefly the space $L^1(\mathbf{T})$, as a linear space with norm

$$|Q|_T = \int_T |Q(\tau)|\,d\tau.$$

Definition of C. Let $C \subset L^1(\mathbf{Q})$, be $\{A | A$ non-decreasing a.e., $0 \le A(q) \le B$ a.e.$\}$

Definition of $Z(a)$, $G_a(q)$, $H(q; y)$ *and* $\psi(t; D)$. Given a male strategy A, a female strategy D, and $a \in A(\mathbf{Q})$. Let $G_a(q)$ be defined by

$$\mathrm{d}G_a(q) \propto \mathrm{d}G(q) \quad A(q) = a$$
$$0 \qquad \text{otherwise}$$

$$G_a(q_{\min}) = 0$$
$$G_a(q_{\max}) = 1.$$

Let $Z(a)$ be defined by

$$Z(a) = \frac{\int_q \alpha[q, A(q)] z(q) \, \mathrm{d}G_a(q)}{\int_q \alpha[q, A(q)] \, \mathrm{d}G_a(q)},$$

and $H(q; y)$ by

$$\mathrm{d}H(q; y) = \mathrm{d}G(q) \quad Z[A(q)] \ge y$$
$$0 \qquad \text{otherwise}$$

$$H(q_{\min}, y) = 0 \qquad \text{for all } y.$$

Let $\psi(t; D)$ be defined by

$$\psi(t; D) = \frac{1}{U(t; A, D)} \int_{\tau \ge t} \int_q \mu \alpha[q, A(q)] z(q) U(\tau, A, D) m(\tau)$$
$$\times D[A(q), \tau] \, \mathrm{d}G(q) \, \mathrm{d}\tau.$$

$G_a(q)$ is the probability distribution of males that play a. $Z(a)$ is the average of $z(q)$ for males that play a. $H(q; y)$ is the incomplete probability distribution of quality among those males whose advertizing level is played by males with an average $z(q)$ of greater than or equal to y. $\psi(t; D)$ is the expected future fecundity of a female playing D conditional on being unmated at time t.

Lemma 1: Given a male strategy A. Let $D^*(a, t)$ satisfy

$$\phi_F(D^*; A, D^*) \ge \phi_F(D; A, D^*) \quad \text{for all } D.$$

Then $\psi(t; D^*)$ equals $\psi^*(t)$, a continuous and non-increasing function defined by;

$$\psi^*(t) = -\mu \left(\psi^*(t) \int_q \alpha[q, A^*(q)] \, \mathrm{d}H\left(q; \frac{\psi^*(t)}{m(t)}\right) \right.$$
$$\left. - m(t) \int_q \alpha[q, A^*(q)] z(q) \, \mathrm{d}H\left(q; \frac{\psi^*(t)}{m(t)}\right) \right) \qquad 0 < t < T$$
$$\psi^*(T) = 0.$$

$D^*(a, t)$ satisfies (for almost all a, t)

$$D^*(a, t) = 1 \quad Z(a) m(t) > \psi^*(t)$$
$$0 \quad Z(a) m(t) < \psi^*(t).$$

Proof: By definition, $\psi(0; D) = \phi_F(D; A, D')$, the female maximand, but note that ϕ_F does not in fact depend on D'. We will differentiate $\psi(0; D)$ with respect to $D(a, s)$, and so obtain the marginal effect on the maximand of increasing D at (a, s). Using

$$\frac{\partial \ln U(t; A, D)}{\partial D(a, s)} = \frac{1}{U(t; A, D)} \frac{\partial U(t; A, D)}{\partial D(a, s)} \propto -\mu \int_q \alpha[q, A(q)] \, dG_a(q) \quad t > s$$

$$0 \qquad \text{otherwise}$$

and $U(0; A, D) = 1$, we obtain after some manipulation that

$$\frac{\partial \psi(0; D)}{\partial D(a, s)} \propto \mu U(s; A, D) \int_q \alpha[q, A(q)] \, dG_a(q)[Z(a)m(s) - \psi(s; D)].$$

The factors except the last must be positive, and this bracketed difference has a simple interpretation. The left hand term is the expected fecundity of a female mating with a male advertizing at level a at time s. The right hand term is the expected future reproductive success conditional on being unmated at time s. A female has maximized her expected fecundity if $D(a, s) = 1$ where the derivative is positive, and $D(a, s) = 0$ where the derivative is negative. That is, she should accept a male if the fecundity she would gain immediately [namely $Z(a)m(s)$] is greater than her expected fecundity if she does not [namely $\psi(s; D)$], and reject him if it is the other way round. If D^* is an optimal strategy, therefore, it must satisfy almost everywhere

$$D^*(a, t) = 1 \quad Z(a)m(t) > \psi(t; D^*)$$

$$0 \quad Z(a)m(t) < \psi(t; D^*).$$

The optimal policy has now been characterized sufficiently to allow a dynamic program to be written that establishes it exactly. Suppose $\psi^*(t)$ is $\psi(t; D^*)$ for some optimal D^*. The idea is that knowing $\psi^*(t)$ for $t > s$, the optimal policy at s is known. We can therefore work backwards from $t = T$, as $\psi^*(T)$ is known to be zero from its definition, working out $D^*(\cdot, t)$ and $\psi^*(t)$ simultaneously. The trick is to transform integrals using our incomplete characterization of D^* in terms of ψ^*. D^* is removed from integrands, but the region of integration is altered to include all those points where D^* is known to be 1, and to exclude those points where D^* is known to be 0. It turns out that whether regions where D^* is unspecified are included or not does not affect the final differential equation. This is natural, as D^* is unspecified only where in some sense it does not matter what value it takes. The derivative of $\psi(t; D)$ with respect to t,

$$\psi'(t; D) = -\frac{U'(t; A, D)}{U(t; A, D)} \psi(t; D)$$

$$-\frac{1}{U(t; A, D)} \int_q \mu\alpha[q, A(q)]z(q)U(t; A, D)m(t)D[A(q), t] \, dG(q),$$

can, on the assumption of the optimality of D, thus be transformed into

$$-\psi(t; D) \int_q \alpha[q, A(q)]\mu \, dH\left[q; \frac{\psi(t; D)}{m(t)}\right]$$

$$-\int_q \mu\alpha[q, A(q)]z(q)m(t) \, dH\left[q; \frac{\psi(t; D)}{m(t)}\right].$$

This, with the replacement of $\psi(t; D)$ by $\psi^*(t)$, is one of the defining equations for ψ^* in the statement of the lemma.

I now show that the equations defining ψ^* in the statement of the lemma define a unique solution. Bounding functions can be obtained by solving altered versions of the equation. A lower bound is found by setting $\psi^*(t) = 0$ in the r.h.s. of the differential equation, and this altered equation has a solution because the r.h.s. is then bounded. An upper bound is found by setting $\psi^*(t)/m(t)$ in the argument of H to below q_{min} in the left hand integral and setting the right hand integral to zero. This equation is of the form $\psi^* = k\psi^{*\prime}$, and has a solution. The bounding solutions provide bounds to $\psi^{*\prime}$ as well as ψ^*, so a unique solution ψ^* exists and is continuous.

I remark that the elements of the differential equation have simple interpretations in the form

$$\psi^{*\prime}(t) = -\mu \int_q \alpha[q, A^*(q)] \, dH\left(q; \frac{\psi^*(t)}{m(t)}\right)$$

$$\times \left(\psi^*(t) - m(t) \frac{\int_q \alpha[q, A^*(q)]z(q) \, dH\left(q; \frac{\psi^*(t)}{m(t)}\right)}{\int_q \alpha[q, A^*(q)] \, dH\left(q; \frac{\psi^*(t)}{m(t)}\right)}\right).$$

The decline in expected future fecundity is proportional to the first factor, which is the rate at which acceptable males arrive at time t. The first term in the bracket represents the possibility that no acceptable male is found at time t. The loss is $\psi^*(t)$ because that is the expected future fecundity at t, and so is the rate at which fecundity is lost by not finding a male. The second term represents the possibility that a male is found. $m(t)$ is the time in the season factor for fecundity, and the ratio of integrals is the average quality of males that are acceptable at time t.

It remains to prove that $\psi^*(t)$ is non-increasing. Suppose that $\psi^*(t)$ increases from t_1 to t_2. A female unmated at t_1 could accept no males between t_1 and t_2, and let us call the optimal policy with this exception $\bar{D}$ [i.e. $\bar{D}(a, t) = D^*(a, t)$ except that $\bar{D}(a, t) = 0$ for all a and $t_1 \leq t < t_2$], and this ensures that $\psi(t_1; \bar{D}) = \psi^*(t_2)$. But D^* is the optimal policy, so $\psi^*(t_1) \geq \psi(t_1; \bar{D}) = \psi^*(t_2)$ contradicting the supposition. Hence $\psi^*(t)$ is non-increasing. This completes the proof of Lemma 1.

Lemma 2: Suppose (A, D) satisfies the local flat extrapolation criterion and the maximizations (A4.1). Then either $A(q)$ differs only on a set of measure zero from a function $\tilde{A}$ such that $\tilde{A}(q) = 0$ for all q; or A differs only on a set of measure zero from a strictly increasing and continuous function $\tilde{A}$ with $\tilde{A}(q_{min}) = 0$.

Proof: Let $L(a)$ be defined by

$$L(a) = \int_t U(t; A, D) m(t) D(a, t) \, dt.$$

$L(a)$ represents the mating success of a male playing a in a population playing A, D. If $A(q)$ is an optimal strategy, then inspection of the functional forms of the maximand ϕ_M in (A4.2) shows that for almost all q,

$$\alpha(q, a) L(a)$$

must be maximized by $a = A(q)$. Suppose A is not a non-decreasing function of q. Then there must exist q_1, q_2 such that $q_1 < q_2$, and such that an optimal a for q_1, say a_1, is strictly greater than an optimal a for q_2, say a_2. This implies that

$$\alpha(q_1, a_1) L(a_1) \geq \alpha(q_1, a_2) L(a_2) \quad \text{and} \quad \alpha(q_2, a_2) L(a_2) \geq \alpha(q_2, a_1) L(a_1).$$

$L(a)$ must be positive for some a (otherwise females playing D are accepting no males, which is contrary to the hypothesis of the lemma that D is optimal). Hence $L(a_1) > 0$, as a_1 is optimal for some q, and we also have that $\alpha > 0$. From the previous inequalities we therefore have

$$\frac{\alpha(q_1, a_1)}{\alpha(q_1, a_2)} \geq \frac{L(a_2)}{L(a_1)} \geq \frac{\alpha(q_2, a_1)}{\alpha(q_2, a_2)}.$$

But the inequality between the ratio of α's contradicts a defining assumption of α. Hence A is non-decreasing almost everywhere.

We now show that A must, apart from a set of measure zero, "start at zero". Formally, we will show that if $N^k \subset Q$, $k = 1, 2 \ldots$, is a sequence of neighbourhoods of $q = q_{\min}$ such that $N^{k+1} \subset N^k$, and $\int_{N^k} dG \to 0$ as $k \to \infty$, then

$$\frac{\int_{N^k} A(q) \, dG(q)}{\int_{N^k} dG(q)} \to 0 \quad \text{as } k \to \infty.$$

Let the ratio of integrals be denoted I_k. Then I_k is a decreasing non-negative sequence, because $A(q)$ is non-negative, and is non-decreasing except on a set of measure zero. Hence I_k approaches a limit, say $a' \geq 0$. Suppose $a' > 0$. Then $a' \in \partial A(\mathbf{Q})$, and so by local flat extrapolation there exists a point $a'' < a'$ such that

$$D(a'', t) = \lim_{k \to \infty} \frac{\int_{N^k} D(a, t) \, da}{\int_{N^k} da}.$$

This implies that

$$L(a'') = \lim_{k \to \infty} \frac{\int_{N^k} L(a) \, da}{\int_{N^k} da}.$$

We can therefore choose a value of k such that

$$\frac{\int_{N^k} L(a) \, da}{\int_{N^k} da} < L(a'') \frac{\alpha(q, a'')}{\alpha(q, a')} \quad \text{for all } q,$$

and so,

$$\alpha(q, a) \frac{\int_{N^k} L(a)\, \mathrm{d}a}{\int_{N^k} \mathrm{d}a} < L(a'')\alpha(q, a'') \quad \text{for all } q.$$

It follows that there is a subset $M \subset N^k$ of strictly positive measure in which

$$\alpha(q, a)L(a) < L(a'')\alpha(q, a'') \quad \text{for all } q.$$

But this means there exists a strategy $\bar{A}$ that is strictly better than A, defined by

$$\bar{A}(q) = A(q) \quad A(q) \notin M$$

$$0 \qquad A(q) \in M.$$

This contradicts the optimality for A hypothesized in the statement of the lemma, thus showing that $a' = 0$.

A parallel argument shows that there can be no gaps elsewhere in $A(\mathbf{Q})$. Formally, consider a point a such that $\{a' | a' > a,\ a' = A(q) \text{ for some } q\}$ and $\{a' | a' < a,\ a' = A(q) \text{ for some } q\}$ are sets with strictly positive measure. Then if N_r^k and N_1^k, $k = 1, 2, \ldots$, are right and left neighbourhoods of a, such that $N^{k+1} \subset N^k$ for each sequence separately, and $\int_{N_r^k} \mathrm{d}a \to 0$ and $\int_{N_1^k} \mathrm{d}a \to 0$ as $k \to \infty$, the parallel argument shows that the two sequences

$$\frac{\int_{N_r^k} A(q)\, \mathrm{d}G(q)}{\int_{N_r^k} \mathrm{d}G(q)} \quad \text{and} \quad \frac{\int_{N_1^k} A(q)\, \mathrm{d}G(q)}{\int_{N_1^k} \mathrm{d}G(q)},$$

converge to the same value. The idea is that if there is a gap, then some advertizing level in the gap will be strictly better for a range of qualities than advertizing just above the top of the gap.

We have now established that A is non-decreasing almost everywhere, and that the right and left limiting integral ratios are equal everywhere. This implies that the integral of A is concave up and is continuously differentiable. This shows that there exists a continuous non-decreasing function $\tilde{A}$, namely the derivative of that integral, that differs from A on only a set of measure zero. Further, if (A, D) satisfies the maximizations (A4.1), then so does $(\tilde{A}, D)$.

To complete the proof of the lemma, it remains to show that either $\tilde{A}$ is identically zero or $\tilde{A}$ is strictly increasing. We do this by showing that if there is any interval of positive length over which $\tilde{A}$ is constant, then $\tilde{A}$ is constant over the whole of $\mathbf{Q}$. Suppose $\tilde{A}(q) = a'$ over the interval $[q_0, q_1]$, $q_0 < q_1$, but for no other values of q. The closedness of the interval loses no generality because we have already established that $\tilde{A}(q)$ is continuous. Then we will show that, by the optimality of D, $L(a)$ is discontinuous at a' from above if $q_{min} < q_0$, and from below if $q_1 < q_{max}$.

If $q_{min} < q_0$, then $Z(a'^-)$ is the limit of an average of values of $z(q)$ for q strictly less than q_0. $Z(a)$ is the average of $z(q)$ for values of q between q_0 and q_1. Hence $Z(a^-) < Z(a)$. Lemma 1 says that females playing the optimal response to A, which is also an optimal response to $\tilde{A}$, will accept males advertizing at a' if $Z(a')m(t) > \psi^*(t)$ (for almost all t), and that $\psi^*(t)$ is a continuous function. $m(t)$ is continuous

by assumption. Hence there is an interval of positive length, say $[t_0, t_1]$, over which

$$Z(a')m(t) > \psi^*(t) > Z(a'^-)m(t),$$

for almost all t. Now for a non-decreasing and continuous $\tilde{A}$ and an optimal response D to $\tilde{A}$, $L(a)$ equals:

$$\int_{Z(a)m(t)>\psi^*(t)} U(t; \tilde{A}, D)m(t) \, dt.$$

Hence,

$$L(a') - L(a'^-) = \int_{Z(a')m(t)>\psi^*(t)>Z(a'^-)m(t)} U(t; \tilde{A}, D)m(t) \, dt,$$

which is greater than zero because U and m are both greater than zero, and the interval of integration has positive length. Thus $L(a)$ is discontinuous from the left at a' if $q_{min} < q_0$. A parallel argument shows that $L(a)$ is discontinuous from the right at a' if $q_1 < q_{max}$. Hence $L(a)$ is discontinuous at a' unless $q_0 = q_{min}$ and $q_1 = q_{max}$. We will now show that a discontinuity in $L(a)$ contradicts the simultaneous continuity and optimality of $\tilde{A}$.

According to the optimality of $\tilde{A}(q)$,

$$\alpha[q, \tilde{A}(q)]L[\tilde{A}(q)] \geq \alpha(q, a')L(a') \quad \text{and} \quad \alpha[q_1, \tilde{A}(q)]L[\tilde{A}(q)] \leq \alpha(q_1, a')L(a')$$

and so,

$$\frac{\alpha[q, \tilde{A}(q)]}{\alpha(q, a')} \geq \frac{L(a')}{L[\tilde{A}(q)]} \quad \text{and} \quad \frac{\alpha[q_1, \tilde{A}(q)]}{\alpha(q_1, a')} \leq \frac{L(a')}{L[\tilde{A}(q)]},$$

for almost all $q \in Q$. Then taking limits as q approaches q_0 [which by definition is $\sup \{q' | a' = \tilde{A}(q')\}$] from the left and as q approaches q_1 [by definition $\sup \{q' | a' = \tilde{A}(q')\}$] from the right, on the assumptions that $q_0 > q_{min}$ and $q_1 < q_{max}$, respectively, we obtain

$$\frac{\alpha[q_0^-, \tilde{A}(q_0^-)]}{\alpha(q_0^-, a')} \geq \frac{L(a')}{L[\tilde{A}(q_0^-)]} \quad \text{and} \quad \frac{\alpha(q_1, a')}{\alpha[q_1, \tilde{A}(q_1^+)]} \geq \frac{L[\tilde{A}(q_1^+)]}{L(a')}.$$

Because $\tilde{A}$ is continuous at q_0 and q_1, $\tilde{A}(q_0^-) = \tilde{A}(q_0)$ and $\tilde{A}(q_1^+) = \tilde{A}(q_1)$, respectively, and, as α is continuous, the left hand sides of the inequalities equal one. If $q_0 > q_{min}$, then L is discontinuous from the left at a', and the right hand side of the first inequality is strictly greater than one. If $q_1 < q_{max}$, then L is discontinuous from the right at a', and the right hand side of the second inequality is strictly greater than one. In either case a contradiction would result. Thus we can escape both contradictions only if $q_0 = q_{min}$ and $q_1 = q_{max}$. We have therefore proved that if $\tilde{A}$ is constant in any interval $[q_0, q_1]$ of positive length, then $\tilde{A}$ is constant in the whole of Q.

We have therefore that $A = \tilde{A}$ for almost all q, and that either $\tilde{A}(q) = 0$ for all q, or $\tilde{A}$ is a continuous and strictly increasing function of q with $\tilde{A}(q_{min}) = 0$. This completes the proof of Lemma 2.

Lemma 3: Let $A^*(q) = 0$ for all q, and let $\bar{z} = \int z(q)\alpha(q, 0)\, dG(q)/\int \alpha(q, 0)\, dG(q)$. Then a continuous and non-increasing function $\psi^*: T \to R$ is defined by

$$\psi^{*\prime}(t) = -\mu\left(\psi^*(t)\int_q \alpha(q, 0)\, dG(q) - m(t)\int_q \alpha(q, 0)z(q)\, dG(q)\right) \quad \psi^*(t) < m(t)\bar{z}$$

$$0 \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \psi^*(t) \geq m(t)\bar{z}$$

$$\psi^*(T) = 0.$$

Let $D^*(a, t)$ be defined by

$$D^*(a, t) = 1 \quad \psi^*(t) < m(t)\bar{z}$$

$$0 \quad \psi^*(t) \geq m(t)\bar{z}.$$

Then (A^*, D^*) satisfies local flat extrapolation and the maximizations (A4.1).

Proof: The dynamic program defining ψ^* is just a special case of that in Lemma 1, where $A(q) = 0$. Hence, D^* satisfies the maximizations. It remains to show that A^* satisfies the maximizations and that (A^*, D^*) satisfies local flat extrapolation. As females treat all levels of advertizing in the same way under D^*, there is no advantage to advertizing above zero, and there is a cost. So $A^*(q) = 0$ solves the maximizations strictly. As $D^*(a, t)$ does not vary with a, (A^*, D^*) satisfies local flat extrapolation. This completes the proof of Lemma 3.

Lemma 4: The set $C = \{A|A$ non-decreasing a.e., $0 \leq A(q) \leq B$ a.e.$\} \subset L^1(Q)$ is non-empty, closed, bounded, convex and compact.

Proof: Non-empty. C contains the function

$$A(q) = B\frac{q - q_{min}}{q_{max} - q_{min}}.$$

Closed. Suppose a sequence A^k, $k = 1, 2 \ldots$, all elements of C, converge to a limit A not in C. Then either (i) there is a set $S \subset Q$ of non-zero measure over which $A(q) < 0$ or (ii) there is a set $S \subset Q$ of non-zero measure over which $A(q) > B$ or (iii) there are sets $S_1, S_2 \subset Q$ of non-zero measure such that sup $(S_1) < $ inf (S_2) and,

$$a_1 = \left(\int_{S_1} dG\right)^{-1}\int_{S_1} A(q)\, dG > \left(\int_{S_2} dG\right)^{-1}\int_{S_2} A(q)\, dG = a_2.$$

In the first case, $\int_S |A - \bar{A}|\, dG$ is minimized for $\bar{A} \in C$ by $\bar{A}(q) = 0$, and is by hypothesis strictly positive. The integral over S is part of the integral over Q, which is the norm, and therefore the norm cannot approach zero for any sequence A^k in C. Hence the first case is impossible. A parallel argument choosing $\bar{A}(q) = B$ shows that the second case is impossible. In the remaining third case, let $S = S_1 \cup S_2$. Then $\int_S |A - \bar{A}|\, dG$ is minimized for $\bar{A} \in C$ by $\bar{A}(q) = k$, a constant, for $q \in S$. By the triangular inequality, the contributions to the norm of $A - k$ from S_1 and S_2 are bounded below by $|k - a_1|\int_{S_1} dG$ and $|k - a_2|\int_{S_2} dG$, respectively. The sum of these lower bounds is greater than zero unless $k = a_1 = a_2$ which is contrary to hypothesis.

But if the norm of $A - \bar{A}$ for $\bar{A} \in C$ is bounded below above zero, then no sequence A^k in C can converge to A. This completes the proof that C is closed.

Bounded. Under the defined norm, a function whose values are bounded between 0 and B is itself bounded by the closed ball of radius $B + 1$.

Convex. The inequalities in this section should be understood to hold for almost all q_1, q_2, q_3. If $A_1, A_2 \in C$, and $\lambda \in I$, then let $A_3 \in L^1(\mathbf{Q})$ be a convex combination of them thus:

$$A_3(q) = [\lambda A_1 + (1 - \lambda) A_2](q) = \lambda A_1(q) + (1 - \lambda) A_2(q).$$

The bounding conditions for membership of C are satisfied because;

$$\min\{A_1(q), A_2(q)\} \leq \lambda A_1(q) + (1 - \lambda) A_2(q) \leq \max\{A_1(q), A_2(q)\}.$$

The non-decreasing condition is satisfied because;

$$q_2 > q_1 \quad \Rightarrow \quad A_i(q_2) \geq A_i(q_1) \qquad i = 1, 2$$
$$\Rightarrow \quad \lambda A_1(q_2) + (1 - \lambda) A_2(q_2) \geq \lambda A_1(q_1) + (1 - \lambda) A_2(q_1)$$
$$\Rightarrow \quad A_3(q_2) \geq A_3(q_1).$$

Hence $A_3 \in C$. C is therefore convex.

Compact. This condition requires rather more work. In accordance with Deimling's (1985: 43) definition of a base for a Banach space, it is required to define a sequence $(e_i)\ i = 0, 1, 2 \ldots$ of elements of $L^1(\mathbf{Q})$. The idea is that linear combinations of the first n elements can be found to converge in n to any element of $L^1(\mathbf{Q})$. The sequence to be chosen derives from a sequence (f_i) that approximates the integral $\bar{A}$ of any element A of $L^1(\mathbf{Q})$ by a continuous piecewise linear function, which agrees with $\bar{A}$ at certain values of q. Let f_0 be defined by

$$f_0(q) = 1.$$

Let the sequences n_i, d_i be defined for $i = 1, 2 \ldots$ as the numerators and denominators respectively of the following sequence

$$\frac{1}{1}, \frac{1}{2}, \frac{1}{4}, \frac{3}{4}, \frac{1}{8}, \frac{3}{8}, \frac{5}{8}, \frac{7}{8}, \frac{1}{16} \cdots$$

Let $f_i(q)$ for $i \geq 1$ be defined by

$$f_i(q) = \max\left\{0, 1 - d_i \left| \left(\frac{q - q_{min}}{q_{max} - q_{min}} - \frac{n_i}{d_i}\right) \right| \right\}.$$

Let the coefficients x_i be defined by

$$x_0 = \bar{A}(q_{min})$$
$$x_i = \bar{A}\left(q_{min} + \frac{n_i}{d_i} \frac{q - q_{min}}{q_{max} - q_{min}}\right) - \sum_{j=0}^{i-1} \left[x_i f_i \left(q_{min} + \frac{n_i}{d_i} \frac{q - q_{min}}{q_{max} - q_{min}}\right)\right] \qquad i \geq 1.$$

This sequence proceeds by recursive binary sectioning of the interval $[q_{min}, q_{max}]$. The value at q_{min} is fixed by x_0. The value at q_{max} is fixed by x_1. Succeeding coefficients fix the value of the function at the centre of increasingly finely divided

intervals. The partial sums $\sum_{i=1}^{n} x_i f_i$ are continuous increasing piecewise linear functions agreeing with $\bar{A}$ at the sequence of points q_{min} and the first $n-1$ elements of the sequence

$$\left(q_{min} + \frac{n_i}{d_i} \frac{q - q_{min}}{q_{max} - q_{min}}\right), \qquad i = 1, 2 \ldots.$$

This infinite sequence is dense in the interval $[q_{min}, q_{max}]$, and integrals of members of $L^1(\mathbf{Q})$ are (absolutely) continuous (Weir, 1973: 67). Hence the expansion $\sum_i x_i f_i$ converges pointwise to $\bar{A}$. Let the sequence (e_i) be the derivatives of corresponding elements of (f_i). According to Weir (1973: 66), $\bar{A}$ will have a derivative almost everywhere (because it is increasing), which will equal A almost everywhere. Hence, $\sum_i x_i e_i$ converges pointwise to A almost everywhere, and so converges to A under the norm of $L^1(\mathbf{Q})$. The (e_i) therefore constitutes a base of $L^1(\mathbf{Q})$, according to Deimling (1985: 43). Proposition 7.4 of Deimling (1985) is: "Let X be a Banach space with a base. Then $B \subset X$ is relatively compact iff B is bounded and sup $\{|R_n x| : x \in B\} \to 0$ as $n \to \infty$." $R_n x$ is the remainder function $x - \sum_{i=0}^{n} x_i e_i$.

For a closed set, relative compactness and compactness are equivalent (Deimling, 1985: 40). If we can only show that sup $\{|R_n A| : A \in C\} \to 0$ as $n \to \infty$, therefore, the compactness of C will have been established. This we proceed to do.

Consider the subsequence (P_k) of $(\sum_{i=0}^{n} x_i e_i)$ indexed by $k \in \{2^j | j = 1, 2 \ldots\}$. Then P_k agrees with $\bar{A}$ at the $k+1$ equally spaced values $q^r = q_{min} + (r/k)(q_{max} - q_{min})$, $r = 0, 1 \ldots, k$. The norm of $R_n A$ equals:

$$\int_{q_{min}}^{q_{max}} |(A - P_n)| \, dG(q),$$

and this equals:

$$\sum_{r=1}^{k} \int_{q^{r-1}}^{q^r} |A - P_n| \, dG(q).$$

Consider values of $A - P_n$ for $q \in [q^{r-1}, q^r]$, for $1 \le r \le k$. As A is increasing and P_n is constant over the interval, $[q^{r-1}, q^r]$ may be divided into two intervals S_1 and S_2 such that $A - P_n \le 0$ over S_1 and $A - P_n \ge 0$ over S_2. Hence

$$\int_{q^{r-1}}^{q^r} |A - P_n| \, dG(q) = -\int_{S_1} A - P_n \, dG + \int_{S_2} A - P_n \, dG,$$

but because the integrals of A and P agree at q^{r-1} and q^r we know that the two integrals on the right hand side sum to zero. Further, as A is increasing, A is bounded on $[q^{r-1}, q^r]$ between its values at q^{r-1} and q^r. P_n must be intermediate between these values or its integral could not equal the integral of A over the interval. Hence

$$\int_{q^{r-1}}^{q^r} |A - P_n| \, dG(q) = 2 \int_{S_2} A - P_n \, dG$$

$$\le 2 \int_{S_2} A(q^r) - A(q^{r-1}) \, dG$$

$$\le 2[A(q^r) - A(q^{r-1})][G(q^r) - G(q^{r-1})]$$

$$\le 2[A(q^r) - A(q^{r-1})] \max \{G(q^r) - G(q^{r-1}) | 1 \le r \le k\},$$

and summing over r yields an upper bound to the whole norm of

$$2[A(q_{max}) - A(q_{min})] \max\{G(q^r) - G(q^{r-1})|1 \leq r \leq k\}$$

$$\leq B \max\{G(q^r) - G(q^{r-1})|1 \leq r \leq k\}.$$

This upper bound holds uniformly for all $A \in C$, and tends to zero because G is continuous and the sequence of points (q^r) becomes dense in $[q_{min}, q_{max}]$ as k goes to infinity. We have therefore found an upper bound to $\sup\{|R_nA|: A \in C\}$ that converges to zero as n tends to infinity, thus completing the proof of the compactness of C. This completes the proof of Lemma 4.

Lemma 5: For any $A \in C$, $SE(1:9)$ defines a unique $A^* \in C$. Further, A^* is strictly increasing.

Proof: $SE(1:3)$ defines v from A, as a special case of the dynamic program of Lemma 1. $SE(4:5)$ defines $Y(t)$ from v. $SE(6)$ defines u from A and Y. $SE(7)$ defines K from Y and u. K is a strictly increasing function, as the integrand is strictly positive, and the regions of integration are strictly nested. Owing to the continuity of $Y(t)$, and the fact that $m(t) \to 0$ as $t \to 0$ implies $Y(t) \to \infty$ as $t \to 0$, regions of integration for lower values of q fall strictly within those for higher values. As the region of integration is defined with a strong inequality, $K(q)$ is continuous from the left. Further, we now establish that $K(q_{min}) \geq K_{min}$ and $K(q_{max}) \leq K_{max}$.
    Now,

$$K(q_{max}) = \int_{z(q_{max}) > Y(\tau)} u(\tau)m(\tau)\,\mathrm{d}\tau$$

$$\leq \int u(\tau)m(\tau)\,\mathrm{d}\tau \leq \int m(\tau)\,\mathrm{d}\tau = K_{max},$$

as $u(t) \leq 1$, establishing K_{max} as an upper bound to $K(q_{max})$. For a lower bound to $K(q_{min})$ we first show that after t', already defined, all females must accept all males. The differential equation $SE(3)$ can be re-written over an interval in which $Y(t) < z(q_{min})$ as

$$Y'(t) = -\mu\left\{\int_{z(q) \geq Y(t)} [z(q) - Y(t)]\alpha[q, A(q)]\,\mathrm{d}G(q)\right\} - Y(t)\frac{m'(t)}{m(t)}.$$

Let $t_m = \min\{t|m(t) \text{ is non-increasing on } [t, T]\}$. Now $t_m < T$ by definition of m. A function $\bar{Y}$ can be defined which over the interval $[t_m, T]$ is an upper bound to $Y(t)$, by finding a lower bound for $Y'(t)$, thus:

$$\bar{Y}'(t) = -\mu\int [z(q) - \bar{Y}(t)]\alpha(q, 0)\,\mathrm{d}G(q).$$

Letting $k_1 = \mu \int \alpha(q, 0) \, dG(q)$ and $k_2 = \mu \int z(q)\alpha(q, 0) \, dG(q)$, this equation has the unique solution

$$\bar{Y}(t) = \frac{k_2}{k_1}[1 - \exp\{k_1(t - T)\}]$$

and takes the value $z(q_{min})$ at the unique time

$$t_{min} = T + \frac{1}{k_1} \ln\left[1 - \frac{k_1}{k_2} z(q_{min})\right].$$

$\bar{Y}$ is a decreasing function, and so for $t > t_{min}$, $\bar{Y}$ lies below $z(q_{min})$. This proves that for $t > \max\{t_{min}, t_m\}$, $Y(t) \leq z(q_{min})$. But by definition $t' = \max\{t_{min}, t_m\}$, and we have shown that after t', optimal females will accept any male. This shows that

$$K(q_{min}) = \int_{z(q_{min}) \geq Y(\tau)} u(\tau)m(\tau) \, d\tau \geq \int_{\tau \geq t'} u(\tau)m(\tau) \, d\tau$$

$$\geq \int_{\tau \geq t'} m(\tau) \exp\{-\mu\tau\} \, d\tau = K_{min},$$

establishing K_{min} as a lower bound to $K(q_{min})$. Summarizing, K is continuous from the left and strictly increasing, $K(q_{min}) \geq K_{min}$ and $K(q_{max}) \leq K_{max}$.

It remains only to show that $SE(8:9)$ defines a unique function $A^* \in C$. Any solution to $SE(8:9)$ inherits various properties of continuity from K. It must be continuous from the left, and have points of discontinuity at exactly those places where K has. At points of continuity and differentiability of $K(q)$, $SE(9)$ can be differentiated to yield

$$A^{*\prime}(q)\alpha^2(q, A^*(q)) = -\frac{d}{dq} \ln \frac{K(q)}{K(q_{min})}, \qquad (A4.3)$$

which defines $A^{*\prime}$ almost everywhere, omitting points where $\alpha^2 = 0$ or $K'(q) = \infty$ or K is discontinuous or not differentiable. Note that therefore $A^{*\prime} > 0$ almost everywhere. At points of discontinuity $SE(9)$ provides

$$\frac{\alpha[q, A(q^+)]}{\alpha[q, A(q^-)]} = \frac{K(q^-)}{K(q^+)},$$

which not only implies that $A(q^+) > A(q^-)$, but also determines $A(q^+)$ in terms of K and $A(q^-)$. A solution is therefore strictly increasing.

$SE(9)$ therefore specifies a derivative almost everywhere, and the exact size of jumps at points of discontinuity. This implies the existence of a solution $\bar{A}(q)$ passing through any point (q, a), $q \in Q$, $a \geq 0$, in some neighbourhood of q. We now prove that the solution passing through $(q_{min}, 0)$ remains bounded for $q \in Q$, and that it is unique. We introduce a function $\tilde{A}(q)$ defined by $\tilde{A}(q_{min}) = 0$ and,

$$\tilde{A}'(q)\alpha^2[q_{max}, \tilde{A}(q)] = -\frac{d}{dq} \ln \frac{K(q)}{K(q_{min})},$$

at points of continuity of K, and by,

$$\frac{\alpha[q, \tilde{A}(q^+)]}{\alpha[q, \tilde{A}(q^-)]} = \frac{K(q^-)}{K(q^+)},$$

at points of discontinuity. A solution exists here as before, but this time we can integrate to obtain

$$\alpha[q, \tilde{A}(q)] = \alpha(q_{min}, 0)\frac{K(q_{min})}{K(q)},$$

which defines the function $\tilde{A}$ near $(q_{min}, 0)$ in view of the monotonicity of $\alpha(q, a)$ in a, which also implies that $\tilde{A}$ is strictly increasing. $\tilde{A}$ remains bounded because, in view of the fact that $K(q)$ is increasing, assumption (iv) about α implies that $\tilde{A}(q_{max}) \leq B$. Now we show that a solution $\bar{A}(q)$ passing through $(q_{min}, 0)$ never exceeds $\tilde{A}$. In a neighbourhood of any value of q where the two functions are equal, the fact that $\alpha^2(q, a)$ is strictly increasing in q almost everywhere (hence $|\alpha^2|$ is decreasing) shows that $\bar{A}'(q) < \tilde{A}'(q)$ almost everywhere. The jumps maintain the direction of the inequality between the two functions. Hence $\bar{A}(q) < \tilde{A}(q)$ for $q > q_{min}$. It follows that any solution $\bar{A}(q)$ passing through $(q_{min}, 0)$ is bounded above for all q, and so the solution exists over the whole of Q. Further, the solution is bounded above by B, and therefore any solution is a member of C.

It remains to prove uniqueness, which is necessary as the expression for the derivative of the solution, (A4.3), may not be bounded. Suppose A_1 and A_2 are two distinct solutions to $SE(8:9)$. Rewrite $SE(9)$ for A_i as

$$\ln \alpha[q, A_i(q)] = \int_{q_{min}}^q \alpha^1[q', A_i(q)]\,dq' - \ln\frac{K(q)}{K(q_{min})}.$$

Then we may assume without loss of generality that for some q, $A_1(q) < A_2(q)$. It is $A_i(q)$ not $A_i(q')$ that appears in the integral, and $\alpha^1(q, a)$ is increasing in a. Hence the right hand side is an increasing function of $A_i(q)$. But the left hand side is a strictly decreasing function of $A_i(q)$. The equation therefore cannot hold for both A_1 and A_2, contradicting the supposition that they are both solutions.

Summarizing, $SE(8:9)$ defines a unique function $A^*(q)$ satisfying $A^*(q_{min}) = 0$, $0 \leq A^*(q) \leq B$, and A^* is non-decreasing. Therefore $A^* \in C$. We have also proved that A^* is strictly increasing. This completes the proof of Lemma 5.

Lemma 6: There exists a mapping $f: C \to C$ defined from $SE(1:9)$ by $f(A) = A^*$. f is continuous and compact.

Proof: The compactness of f means the compactness of $f(C)$. As C itself is compact, by Lemma 4, and Lemma 5 shows that $f: C \to C$, f is indeed compact. It remains to show continuity. Continuity in this sense is in the appropriate function spaces. It follows because each step in the creation of A^* from A is continuous, namely (i) v is a continuous function of A (ii) Y is a continuous function of v (iii) u is a continuous function of A and Y (iv) K is a continuous function of u and finally (v) A^* is a continuous function of K. The proof of only step (iii) will be given, as the others are simpler and very similar in style.

Let $L_A \subset L^1(\mathbf{Q})$ be $\{A|A(q) \geq 0\}$, and let $U: L_A \times L^1(\mathbf{T}) \to L^1(\mathbf{T})$ be the mapping implied by $SE(6)$ that delivers u as a function of A and Y. To show continuity, consider perturbations $A_\gamma \in L^1(\mathbf{Q})$ and $Y_\delta \in L^1(\mathbf{T})$ satisfying

$$|A_\gamma| \leq \gamma, \qquad |Y_\delta|_T \leq \delta.$$

Pointwise exponentiation is a continuous mapping in L^1, so it will suffice to show that $\ln u$ is continuous. Hence we study the perturbation in the logarithm of u induced by the perturbations in A and Y. Define

$$u_\varepsilon = \ln U(A + A_\gamma, Y + Y_\delta) - \ln U(A, Y).$$

Then;

$$u_\varepsilon(t) = \int_{\tau=0}^t \int_{z(q) > Y(\tau) + Y_\delta(\tau)} \alpha[q, A(q) + A_\gamma(q)] \, dG(q) \, d\tau$$

$$- \int_{\tau=0}^t \int_{z(q) > Y(\tau)} \alpha[q, A(q)] \, dG(q) \, d\tau$$

$$= \int_{\tau=0}^t \left[\int\!\!\int_{z(q) > Y(\tau)} \alpha[q, A(q) + A_\gamma(q)] - \alpha[q, A(q)] \, dG(q) \right.$$

$$\left. - \int_{Y(\tau) + Y_\delta(\tau) > z(q) > Y(\tau)} \alpha[q, A(q) + A_\gamma(q)] \, dG(q) \right] d\tau. \qquad (A4.4)$$

The right hand inner integral is bounded by $|G[z^{-1}(Y(\tau) + Y_\delta(\tau))] - G[z^{-1}(Y(\tau))]|$, as values of α lie in I. Because α is continuous, there exists a continuous function $E(q, a, \omega)$ such that $E(q, a, \omega) \to 0$ as $\omega \to 0$, and

$$|\alpha[q, a + E(q, a, \omega)] - \alpha(q, a)| \leq \omega.$$

Divide the left hand inner integral of (A4.4) into:

$$\int_{q \in \{q|E[q,a,A_\gamma(q)] \leq \sqrt{\gamma}, z(q) > Y(\tau)\}} [\alpha(q, A(q) + A_\gamma(q)) - \alpha(q, A(q))] \, dG(q)$$

$$+ \int_{q \in \{q|E[q,a,A_\gamma(q)] > \sqrt{\gamma}, z(q) > Y(\tau)\}} [\alpha(q, A(q) + A_\gamma(q)) - \alpha(q, A(q))] \, dG(q).$$

$$(A4.5)$$

The sets are measurable because A_γ is integrable and E is continuous. The first integral in (A4.5) is bounded above by

$$\int_{q \in \{q|A_\gamma(q) \leq \sqrt{\gamma}, z(q) > Y(\tau)\}} \sqrt{\gamma} \, dG(q)$$

and so by $\sqrt{\gamma}$. The second integral of (A4.5) is bounded above because

$$\int_{q\in\{q|E[q,A,A_\gamma(q)]>\sqrt{\gamma},z(q)>Y(\tau)\}} \left|\left[\alpha(q, A(q)+A_\gamma(q))-\alpha(q, A(q))\right]\right| dG(q)$$

$$\leq \int_{q\in\{q|E[q,a,A_\gamma(q)]>\sqrt{\gamma}\}} 1\,dG(q)$$

$$= \int_Q I_{\{q|E[q,a,A_\gamma(q)]>\sqrt{\gamma}\}}\,dG(q)$$

$$= \frac{1}{\sqrt{\gamma}}\int_Q \sqrt{\gamma}\,I_{\{q|E[q,a,A_\gamma(q)]>\sqrt{\gamma}\}}\,dG(q)$$

$$< \frac{1}{\sqrt{\gamma}}\int_Q A_\gamma(q)I_{\{q|E[q,a,A_\gamma(q)]>\sqrt{\gamma}\}}\,dG(q)$$

$$\leq \frac{1}{\sqrt{\gamma}}\int_Q A_\gamma(q)\,dG(q)$$

$$\leq \frac{\gamma}{\sqrt{\gamma}}$$

$$= \sqrt{\gamma}.$$

We now return to the second inner integral of (A4.4). $G[z^{-1}(y)]$ is a continuous bounded function of y, and so there exists a continuous increasing bounded function $g(d)$ such that $g(d)\to 0$ as $d\to 0$, and $|G[z^{-1}(y+d)]-G[z^{-1}(y)]|<g(d)$ for all y. Let an upper bound to $g(d)$ be $\bar{g}$. Hence the integral is no greater than

$$\int_0^t g[Y_\delta(\tau)]\,d\tau \leq \int_0^T g[Y_\delta(\tau)]\,d\tau.$$

Playing the same trick as before, divide this into;

$$\int_{t\in\{\tau|g[Y_\delta(\tau)]\leq g(\sqrt{\delta})\}} g[Y_\delta(\tau)]\,dt + \int_{t\in\{\tau|g[Y_\delta(\tau)]>g(\sqrt{\delta})\}} \bar{g}\,dt.$$

The left hand side is bounded above by $\int_0^T g(\sqrt{\delta})\,dt = Tg(\sqrt{\delta})$. Now g is strictly increasing, so the right hand side equals

$$\int_{t\in\{\tau|Y_\delta(\tau)>\sqrt{\delta}\}} \bar{g}\,dt \leq \frac{\bar{g}}{\sqrt{\delta}}\int_{t\in\{\tau|Y_\delta(\tau)>\sqrt{\delta}\}} \sqrt{\delta}\,dt$$

$$\leq \frac{\bar{g}}{\sqrt{\delta}}\int_0^T Y_\delta(t)\,dt \leq \frac{\delta\bar{g}}{\sqrt{\delta}} = \bar{g}\sqrt{\delta}.$$

The right hand inner integral of (A4.4) is therefore bounded above by,

$$Tg^{-1}(\sqrt{\delta})+\bar{g}\sqrt{\delta},$$

and so the whole of the integrand in (A4.4) by,

$$2\sqrt{\gamma}+Tg^{-1}(\sqrt{\delta})+\bar{g}\sqrt{\delta}.$$

It follows that the integral (A4.4) is bounded above by

$$\int_0^t 2\sqrt{\gamma} + Tg^{-1}(\sqrt{\delta}) + \bar{g}\sqrt{\delta}\ d\tau \le \int_0^T 2\sqrt{\gamma} + Tg^{-1}(\sqrt{\delta}) + \bar{g}\sqrt{\delta}\ d\tau$$

$$= T[2\sqrt{\gamma} + Tg^{-1}(\sqrt{\delta}) + \bar{g}\sqrt{\delta}].$$

This upper bound to $|u_\varepsilon(t)|$ implies that the norm of u_ε

$$\int_{\tau=0}^T |u_\varepsilon(\tau)|\ d\tau;$$

is bounded above by;

$$= T^2[2\sqrt{\gamma} + Tg^{-1}(\sqrt{\delta}) + \bar{g}\sqrt{\delta}].$$

As $g^{-1}(0) = 0$ and g^{-1} is continuous, it follows that the norm of u_ε can be made as small as desired by making γ and δ small enough. This establishes the continuity of U. Continuity in the other steps can be established in a similar way.
This completes the proof of Lemma 6.

Lemma 7: The system of eqns $SE(1:10)$ has at least one solution, and any solution has $A(q_{min}) = 0$ and A continuous and strictly increasing.

Proof: We will apply Schauder's Fixed Point Theorem to show that the mapping f has a fixed point in C, which therefore satisfies $SE(10)$ and so satisfies the whole of SE.

Lemma 4 shows that C is non-empty, closed, bounded and convex, and Lemma 6 shows that $f: C \to C$ is compact. Thus we can apply;
   Theorem 8.8 of Deimling (Schauder's Fixed Point Theorem). "Let X be a real Banach space, $C \subset X$ non-empty closed bounded and convex, $F: C \to C$ compact. Then F has a fixed point."
   A solution to $SE(1:10)$ therefore exists. Lemma 5 shows that any solution A^* to $SE(1:9)$ has A strictly increasing, and therefore any solution to $SE(1:10)$ is strictly increasing. $SE(8)$ states that $A^*(q_{min}) = 0$, and therefore the solution satisfies this condition.
   It remains to show continuity. Suppose a solution A to $SE(1:10)$ is discontinuous. As A inherits continuity from the left from K, there must be a $q < q_{max}$ such that $A(q) < A(q^+)$. Then by $SE(9)$, this implies that $K(q) < K(q^+)$, and in turn that $Y(t) = z(q) = z_0$, say, over some interval, say $[t_0, t_1]$. Hence $Y'(t) = 0$ in $[t_0, t_1]$, and using $SE(5)$ and $SE(9)$ we obtain

$$0 = -\mu\left\{\int_q^{q_{max}} z(q')\alpha[q', A(q')]\ dG(q') - z_0 \int_q^{q_{max}} \alpha[q', A(q')]\ dG(q')\right\} - z_0\frac{m'(t)}{m(t)},$$

which can be solved for $m(t)$ to obtain

$$m(t) = k_1 \exp\left[-t\frac{\mu}{z_0}\int_q^{q_{max}} [z(q') - z_0]\alpha[q', A(q')]\ dG(q')\right],$$

for some strictly positive constant k_1. The integral is also strictly positive, as $q \neq q_{max}$. Hence a discontinuity in A can arise only if there is an interval of t with positive length in which $m(t) = k_1 \exp\{-k_2 t\}$ for some strictly positive constants k_1, k_2. But this is contrary to a defining assumption of m.

This completes the proof of Lemma 7.

Lemma 8: Suppose A is a solution to $SE(1:10)$. Then there exists a D such that (A, D) satisfies local flat extrapolation and (A, D) solves the maximizations (A4.1). Further for all q, $A(q)$ attains the unique local maximum of

$$\alpha(q, a) \int_t U(t; A, D) m(t) D(a, t) \, dt,$$

for $a \in A(Q)$.

Proof: $SE(8:9)$ yields, in terms of the inverse function A^{-1} of A,

$$K[A^{-1}(a)] \propto \exp\left\{-\int_0^a \alpha^2 [A^{-1}(a), a] \, da\right\}.$$

It follows from the construction of $SE(1:7)$ that the part of the male maximand, ϕ_M of (A4.2a), relating to males of quality q is proportional to $\alpha(q, a) K[A^{-1}(a)]$, and hence to,

$$\alpha(q, a) \exp\left\{-\int_0^a \alpha^2 [A^{-1}(a), a] \, da\right\},$$

whose logarithm is differentiable with respect to a as follows:

$$\alpha^2(q, a) - \alpha^2 [A^{-1}(a), a].$$

This derivative equals zero at $q = A^{-1}(a)$, as it should. But α^2 is strictly increasing in q for almost all a, so the derivative is positive for all larger values of q, and negative for all lower values. This implies that the derivative is positive for $a < A(q)$, and negative for $a > A(q)$, for almost all a. It follows that $A(q)$ is the unique local maximum, as claimed in the lemma, and this implies that $A(q)$ attains a strict global maximum for male fitness for $a \in A(Q)$.

Letting $\bar{a}$ denote min $\{a, A(q_{max})\}$, define D by

$$D(a, t) = 1 \quad v(t) < m(t) z[A^{-1}(\bar{a})]$$

$$0 \quad \text{otherwise.}$$

Notice that $SE(1:3)$ is a special case of the dynamic program of Lemma 1, with v taking the role of ψ, in which it can be assumed that A is strictly increasing. Hence D satisfies the maximization (A4.1b) by Lemma 1. Further, $D(a, t) = D[A(q_{max}), t]$ for $a > A(q_{max})$ and so local flat extrapolation is satisfied too.

This completes the proof of Lemma 8.

Lemma 9: Suppose A_1 and A_2 are continuous and strictly increasing functions, that $A_1(q_{min}) = A_2(q_{min}) = 0$, and that (A_1, D_1) and (A_2, D_2) satisfy the maximizations (A4.1). Then $A_1 = A_2$.

Proof: Define the mating success of a male $L_i(a)$, $i = 1, 2$, by

$$L_i(a) = \int_t U(t; A_i, D_i) m(t) D_i(a, t) \, dt.$$

Then $\alpha(q, a) L_i(a)$ is the part of the male maximand, ϕ_M in (A4.2a), relating to a male of quality q. By hypothesis

$$\alpha[q, A_i(q)] L_i[A_i(q)] \geq \alpha(q, a) L_i(a) \quad \text{for } i = 1, 2, \text{ for all } a.$$

As A_i is continuous and increasing, this implies that the derivative of $\alpha(q, a) L_i(a)$ with respect to a is zero where it is defined. L_i must be continuous and increasing as the optimal response A_i is continuous and increasing. Hence the derivative exists almost everywhere. Taking logs before differentiating, we obtain

$$\frac{L_i'(a)}{L_i(a)} = \alpha^2(q, a),$$

and integrating with respect to a we obtain

$$L_i(a) \propto \exp\left\{ -\int_0^a \alpha^2[A_i^{-1}(a'), a'] \, da' \right\}.$$

Let $n_i(a, t)$ be the derivative with respect to a of $\ln[\alpha(q, a) L_i(a)]$ for $i = 1, 2$, then

$$n_1(q, a) = \alpha^2(q, a) + \alpha^2(A_1^{-1} a, a)$$

$$n_2(q, a) = \alpha^2(q, a) + \alpha^2(A_2^{-1} a, a).$$

Consider some value of q where, without loss of generality, $A_1(q) < A_2(q)$. Because the A_i are strictly increasing and continuous, it follows that $A_1^{-1} A_1(q) > A_2^{-1} A_1(q)$. We also know that $\alpha^2(q, a)$ is increasing in q, so that

$$\alpha^2[A_1^{-1} A_1(q), a] > \alpha^2[A_2^{-1} A_1(q), a].$$

It follows that

$$n_1[q, A_1(q)] < n_2[q, A_1(q)],$$

and by definition $n_1[q, A_1(q)] = 0$. Hence

$$n_2[q, A_1(q)] < 0.$$

The same argument as in the proof of Lemma 8 ensures that $A_i(q)$ is the unique local maximum over $a \in A_i(\mathbf{Q})$ of $\alpha(q, a) L_i(a)$. So if the marginal value of advertizing is negative at $A_1(q)$, then by the unique local maximum property of Lemma 8, the optimal value of a must be less than $A_1(q)$. Hence $A_2(q) < A_1(q)$. This is a contradiction, showing that there can be no q for which $A_1(q) \neq A_2(q)$, and hence $A_1 = A_2$. This completes the proof of Lemma 9.

At last it is possible to present the;

Proof of Theorem: Lemma 3 shows that $A_{\text{non}}(q)$ is a full solution. Lemma 7 and Lemma 8 show that there exists a strictly increasing and continuous function which is a full solution. Let this function be $A_{\text{sig}}(q)$. We have now established the existences

of the theorem. It remains to show that $SE(1:10)$ uniquely determine A_{sig}, and that any other function equals one of these two almost everywhere. Lemma 2 shows that any full solution A either equals zero almost everywhere, in which case it equals A_{non} almost everywhere; or A differs only on a set of measure zero from a strictly increasing and continuous function $\tilde{A}$. But in this second case, Lemma 9 shows that $\tilde{A} = A_{\text{sig}}$ for all q, so that $A(q) = A_{\text{sig}}(q)$ for almost all q. This completes the proof of the theorem.

Remarks on the operation of local flat extrapolation. Use of local flat extrapolation has enabled a very neat result to be obtained, that there are effectively exactly two solutions to the maximizations. Without the criterion, there would have been "partially splitting" equilibria, in which some intervals of males signalled at the same level, and some intervals of males were split with increasing advertizing. I conjecture that any partition of Q into intervals, with arbitrary allocation of each interval to "flat" and "rising" would support a solution to the maximizations. There would be a discontinuity in A around each boundary between flat and rising, and between flat and flat intervals. D would have to be chosen to make the unplayed advertizing levels less good for all males than the played levels.

Local flat extrapolation has led to one restriction on the result, namely the assumption that there should be no interval in which $m(t) = k_1 \exp\{-k_2 t\}$ for strictly positive constants k_1, k_2. The reason is that this can lead to a discontinuity in the middle of a "rising" interval. The full signalling equilibrium exists, with a discontinuity in A, and the only thing wrong with it is that there is nothing to determine the females' response to the unplayed values of a. The restriction is in a sense artificial. When it is not met, in most cases the two equilibria of the theorem will still exist and be effectively unique. When the constants are just right (or wrong!), the fully splitting equilibrium will have discontinuous A, and only the non-signalling equilibrium will exist, and it will be effectively unique.

This comparison of the gains and losses in convenience from using local flat extrapolation is irrelevant to its logical justification. The idea is that the response of females to unplayed advertizing will not in fact be arbitrary. Instead it evolves under the influence of a small amount of perceptual error, so that unplayed advertizing levels close to played levels are actually perceived. In a fuller model, this perceptual error would be incorporated into the model. I conjecture that this would play the same role in eliminating partially splitting equilibria. Moreover, it would "smooth out" infinite slopes to $A(q)$, and so presumably make the restriction on m unnecessary. The logical part played by local flat extrapolation is to mimic the effect of adding this complexity to the model, and so its ultimate justification depends on guesswork.

APPENDIX 5

Modelling the Model

The purpose of this Appendix is to show how results of the ESS model of the companion paper may be applied to the results of this model, thus demonstrating the utility of the ESS model. At the splitting equilibrium, the maximand for males

in the model of Appendix 2 is

$$\alpha(q, a)K(A^{-1}a).$$

$A^{-1}a$ is the quality which a female "presumes" a male to be when she interprets his advertizing. We can write a mapping from the full model to the ESS model as:

$$\alpha(q, a)K(p) \to w(a, p, q).$$

The mapping onto $w(a, p, q)$ shows how to construct a fitness function w in the ESS model to model the population genetic model. The conditions that w must fulfil in the ESS model are easily verified from properties w_1 is negative because α_2 is negative, and w_2 is positive because $K'(p)$ is positive. The equilibrium male strategy according to the ESS model satisfies;

$$P'(a) = -\frac{w_1(a, p, q)}{w_2(a, p, q)},$$

and $A'(t)$ is the inverse of this. This would correctly predict the male equilibrium strategy of the population genetic model, because w_1/w_2 equals

$$\frac{\alpha^2(q, a)}{\dfrac{\mathrm{d}\ln K(p)}{\mathrm{d}p}},$$

and $SE(9)$ can be put in the form

$$A^{*\prime}(q) = -\frac{\dfrac{\mathrm{d}\ln K(q)}{\mathrm{d}q}}{\alpha^2[q, A^*(q)]}.$$

The condition on costs in the ESS model is that

$$\frac{w_1(a, p, q)}{w_2(a, p, q)},$$

is strictly increasing in q, and this translates into

$$\frac{\alpha^2(q, a)}{\dfrac{\mathrm{d}\ln K(p)}{\mathrm{d}p}}$$

being strictly increasing in q. The fact that $\alpha^2(q, a)$ is strictly increasing in q is a necessary assumption for stability in the genetic model as shown in Appendix 4. Thus if the maximand function $\alpha(q, a)K(p)$ were measured at equilibrium, the ESS model would give both the optimal male strategy and the appropriate stability condition. This shows the importance of the arbitrariness of the functions in the ESS modelling in the companion paper, and also that applying the ESS approach to signalling problems including sexual selection is perfectly sensible. The fact that there are extra complications in the full model does not vitiate the application of the ESS model. From an empirical point of view, it is the ESS model that is easier to apply, and it is essential to realize that it is perfectly satisfactory to apply it. We can understand something without understanding everything.