

## On Fisher–Zahavi’s handicapped sexy son

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### ABSTRACT

This study looked at the long-term dynamics of male investment in secondary sexual traits and female attraction to such traits in dense polygenous populations. It was assumed that mate-choice in such a population does not affect the direct reproductive success of females, but does affect the distribution of genes among their offspring and hence the offspring’s success. Fisher’s ‘sexy son’ argument is compared to Zahavi’s Handicap Principle.

*Keywords:* Handicap Principle, long-term evolution, runaway process, sexual selection, ‘sexy son’ argument.

### INTRODUCTION

Sexual selection and natural selection were suggested by Darwin (1859) to be the two major causes of biological evolution. Darwin’s interest in sexual selection focused on the evolution of secondary sexual traits, which, to be distinguished from primary sexual traits, are not directly involved in the process of reproduction, yet their maintenance appears to be quite costly in terms of individual resources. As maintained by Darwin, the cost of such traits should reach a balance with their advantage in attracting mates of the opposite sex. However, the evolution of a sexually attractive trait in one sex inevitably depends on the simultaneous evolution of an appropriate mate-preference in favour of it in the other sex. Thus, having explained the evolution of the exaggeratedly long tail of peacocks on the basis of female preference, a question not touched by Darwin was how a preference for such an apparently deleterious feature could have possibly evolved among peahens to start with. This question, however, became the focus of later studies of sexual selection, started by R.A. Fisher (1915; see also Fisher, 1930: 135–162) and followed by numerous quantitative studies in the last two decades (e.g. Lande, 1981; Kirkpatrick, 1982, 1985, 1986, 1987; Heisler, 1985; Pomiankowski, 1987a,b; Grafen, 1990; Maynard-Smith, 1991; Otto, 1991; Iwasa *et al.*, 1991; Pomiankowski *et al.*, 1991; Iwasa and Pomiankowski, 1995; Pomiankowski and Iwasa, 1998).

Following Lande (1981), most quantitative studies of sexual selection have employed the classic quantitative genetic model, with or without major genes. Female mate-preference was generally characterized by the relative chance of a male of specific character being chosen as

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a mate. The advantage of female genes for 'choosiness' in these models can be summarized in terms of the covariance matrix they establish with appropriately advantageous male genes. Under such assumptions, Lande (1981) showed how secondary traits that seriously impair the survival of their carrier can become fixed, with total extinction of the population as a possible theoretical result.

This prediction stands in contrast with previous analyses, based on the inevitable restriction of female choice to a limited group of males available during the mating season (Eshel, 1979). This limitation should impose an even stronger restriction on female ability to choose, and hence on the vigour of sexual selection as the population, especially that of adult males, becomes sparse, an inevitable result of the advance of sexual selection itself. This factor is indeed missing in existing quantitative models, assuming a fixed relative chance of a male of specific character being chosen as a mate.

Here, we study a quantitative model in which each female has to choose from a random group of surviving males available in her vicinity. We assume that less attractive males are occasionally chosen not by mistake, but simply because they happen to be the best mate available to the choosing female. We further employ a long-term evolution model of stabilizing selection and rare mutations (e.g. Eshel, 1996; Eshel *et al.*, 1998) in which, as we see, natural selection is more sensitive to non-linear effects. Following previous work, we concentrate on dense polygenous populations. Our point of departure will be the following observations, promoted by Fisher as a basis to his theory of sexual selection:

- The male contribution to offspring is negligible in polygenous populations. Hence, such populations are generally characterized by a lack of mate-preference on the part of males and, consequently, by the absence of secondary sexual traits on the part of females.
- Consequently, females in polygenous populations (unless very sparse) can always ensure being fertilized by one or, if necessary, by several males, thus optimizing their progeny size according to expected natural resources, regardless of mate-choice (for a different approach, see Pomiankowski, 1987b; Grafen, 1990).
- An appropriate choice of a mate, instead, can guarantee better genes passed on to the offspring of the choosey female and, consequently, a higher reproductive success of these offspring.
- In choosing a mate, however, no direct information about its genes is available to the female. Instead, females are selected to sexually prefer phenotypic traits in correlation with fitness.
- Consequently, males are selected not only for high fitness but also for passing the female judgement on high fitness, either by exaggeration or fake.
- At the same time, natural selection is expected to favour such female behaviour that enables 'calling the male bluff'. The female need for prolonged courtship and preliminary games may well serve this evolutionary function.

This led Fisher to a question which is of great concern in the modern study of sexual selection: Why do females in many natural populations still prefer secondary male traits that apparently pose a handicap to their survival?

In the next two sections, we study quantitatively the alternative answers to this question provided by the two current theories of sexual selection, namely that of Fisher himself and that of Zahavi (1975, 1977). Following Grafen (1990), although under different assumptions, we look for the possible existence and uniqueness of a long-term stable

equilibrium of the male–female game in which both males and females are selected to increase the expected number of their own genes, passed to future generations. We shall see that Fisher’s ‘sexy son’ argument can indeed lead to a runaway process in which female preference for male extravagance would persist, while male extravagance increases up to a certain exaggerated level. Yet, contrary to the prediction of Fisher, and in agreement with that of Iwasa *et al.* (1991) and Pomiankowski *et al.* (1991), we see that such a process cannot possibly remain in evolutionarily stable equilibrium at this level. It is shown, moreover, that long-term dynamics should always bring the population to a stable equilibrium at which females prefer non-advertising males. This finding is at odds with those of Iwasa and Pomiankowski (1995; see also Pomiankowski and Iwasa, 1988), who predicted, under the assumption of a quantitative genetic model with major genes, the possible maintenance of a permanent cycling.

However, the situation changes if, as suggested by Zahavi, the cost of advertisement is different for males of different quality. In such a case, even though we do not assume that the quality of a mate affects the direct fertility of a female, it is shown that a single evolutionarily stable strategy then exists, in which females prefer advertising males. In this case, the findings of our long-term evolution model partially agree with those of the quantitative model of Pomiankowski (1987a), Grafen (1990) and Iwasa *et al.* (1991); they disagree with those of Kirkpatrick (1986). Interestingly, it appears that the offspring of highly advertising males at equilibrium, even though of higher quality than those of poorly advertising males, are not necessarily more viable, given their strong tendency to advertise. Yet sexual success (in this case combined with high quality) ensures the higher-than-average total reproductive success of such offspring.

On the basis of these findings, we maintain that, although Fisher’s ‘sexy son’ argument alone cannot explain the persistence of male extravagance, this argument proves a tacit but indispensable component in the application of Zahavi’s Handicap Principle to the quantitative theory of sexual selection.

### FISHER’S ‘SEXY SON’ ARGUMENT RE-EXAMINED

A point of departure in Fisher’s ‘sexy son’ argument is that a female’s mate choice in a polygenous population can only affect the success of her offspring. Thus, anything else being fixed, females are selected to increase the expected reproductive success, say general fitness, of their male offspring. Yet the fitness  $\omega$  of a male, say its total reproductive success, depends not only on its viability  $\eta$ , but also on its expected reproductive success  $\chi$ , given it survives to maturity. Thus

$$\omega = \eta\chi \tag{2.1}$$

Although the viability  $\eta$  of a male may depend on its own traits only, its expected reproductive success  $\chi$  as an adult male inevitably also depends on the distribution of the females’ mate-preference as well as on the traits of competing males in the actual population. Thus, suppose that at a certain time in the evolution of a species, a female preference for a long tail has emerged. This might have been initiated by a positive correlation between tail length and male viability at that time. Yet such a female preference would then be likely to render favourable a certain exaggeration in the length of male tails even above the functional optimum, while most females still mistakenly prefer an exaggeratedly long tail. But is it necessary that natural selection would then favour a minority of ‘smart’ mutant females

which, calling the bluff of the exaggeratedly long tail, would prefer tails closer to the functional optimum? This, as maintained by Fisher, may not be the case if the female preference for long tails is already established in the population. Then, the male offspring of a minority female, inheriting genes for a shorter-than-average tail, would indeed have a better chance of surviving to maturity, but then may have difficulty in finding a mate. Natural selection, in such a case, would operate to stabilize both male tail length and female preference for long tails.

Next, Fisher speaks of what he nicknamed a ‘runaway process’, in which situations like that described above would repeat and perpetuate themselves: Once female preference for an exaggerated male trait is established in the population, further exaggerations on the part of the males become selectively advantageous. Then, as long as a further exaggeration is selected on the basis of general female preference, it becomes selectively advantageous for any female to follow the rule of the majority. It was further hypothesized by Fisher that an equilibrium should be reached at some point at which the forces of natural and sexual selection should balance each other.

For the quantitative analysis of Fisher’s argument, we denote by  $p_k$  the probability that a random male courting a random female would find itself in the presence of  $k$  other contenders, where

$$k = 0, 1, 2, \dots, \sum_k p_k = 1, p_0 < 1$$

We assume that this probability is independent of either the male features or past events, and that competitors are independently drawn from the population of adult males. Note, however, that the probability  $p_k$  of encountering exactly  $k$  competitors is most likely to depend on the density of the adult male population, which, in turn, depends on the proportion of males surviving to adulthood. This proportion, depending on the distribution of the male’s  $x$ -trait among juveniles, may change from generation to generation, tending to zero if the runaway process occurs and proceeds far enough (Eshel, 1979). Following Fisher, we assume that female mate-preference is based on a single, conspicuous, quantitative trait of the male, say its  $x$ -trait. Equivalently, female mate-preference is any decision rule  $\Gamma$  for the choice of a single value  $x_i$  out of any finite set  $\{x_1, x_2, \dots, x_{k+1}\}$  of available values of the  $x$ -trait. Female preference for high values of the  $x$ -trait will be denoted by  $\Gamma^+$ . A typical male strategy in any distribution  $F(x)$  of the  $x$ -trait.

We assume that both the male  $x$ -trait and the female mate-preference are genetically inherited, and thus subjects for selection, each in different loci. Following the argument of Fisher, we assume that the viability of a male is a unimodal differentiable function  $\eta(x)$  of its  $x$ -trait, with a maximum at  $x = x_0$  with  $\eta(x) \rightarrow 0$  as  $x \rightarrow \infty$ . Assuming that the expected number of females encountered by a male, given it reaches maturity, is independent of its  $x$ -trait, the reproductive success  $\chi(x)$  of such a male can be measured by its probability of success in competing over a single courted female. We assume, for simplicity, that natural selection operates to increase the frequency of a male’s  $x$ -trait in proportion to the fitness  $\omega(x) = \eta(x)\chi(x)$  of males with this trait. Concerning female reproductive success, we further adopt Fisher’s assumption that the choice of mate does not affect the expected number of the female’s offspring, thus female mate-preference is selected according to its effect on the expected reproductive success of the female’s male offspring.

Following Fisher, we begin our analysis of the model by assuming temporal fixation of the female mate-preference  $\Gamma^+$  and study the population dynamics of the male  $x$ -trait

thereby induced. Given this population dynamics, we check the stability of the mate-preference  $\Gamma^+$ . We are interested in the asymptotic behaviour of the combined dynamics and, more specifically, in the existence of a stable equilibrium  $\langle \Gamma, F(x) \rangle$  in which  $\Gamma^+$  and  $F(x)$  are mutually stable against each other. It is not difficult to see that the male strategy  $F(x)$  should be continuous in this case (I. Eshel and I. Volovik, unpublished).

Assuming a continuous population male strategy  $F(x)$ ,  $x$ -male, courting a female in competition with  $k$  other males, would be chosen as a mate if, and only if, the trait-value of all its competitors was strictly lower than  $x$ , which occurs with probability  $(F(x))^k$ . The general probability of  $x$ -male being chosen by a courted female is therefore given by:

$$\chi(x) = \sum_k p_k (F(x))^k = \phi(F(x)) \quad (2.2)$$

where  $\phi(s) = \sum_k p_k (s)^k$  is the generating function of the number of competitors encountered by a random male in the population. Equality (1) thus becomes:

$$\omega(x) = \omega_f(x) = \eta(x)\chi(x) = \eta(x)\phi(F(x)) \quad (2.3)$$

With this structure of male fitness, it is not difficult to show (I. Eshel and I. Volovik, unpublished) that if, at some evolutionary stage, female mate-preference  $\Gamma^+$  is fixed in the population and if the distribution  $F(x)$  at this stage is limited to a sufficiently narrow interval, then natural selection should operate towards fixation of the highest  $x$ -trait value on this interval. Indeed, the sexual advantage of males with the highest  $x$ -trait value would then be independent of the distribution of this trait in the population. The cost in terms of viability for having such a trait, on the other hand, tends to zero with the absolute value of the difference. Hence, as long as the differences in the  $x$ -value in the population are small to start with, natural selection should operate to keep them even smaller, eliminating the lower values of this trait from the population. In the same way, if the population is close to fixation on any  $x$ -value  $x_1$  for which an  $x_1$ -male can still survive, there should be a selective advantage to any mutation for the increase of the  $x$ -trait by a small enough value (depending on  $x_1$ ). No small-effect mutation for a decrease in the  $x$ -value can succeed.

We thus see that, as long as the female mate-preference  $\Gamma^+$  is fixed in the population, and as long as differences in the  $x$ -trait are small, natural selection on the  $x$ -trait keeps these differences small with a permanent selective advantage to higher values of the  $x$ -trait. But, on the other hand, we know that as long as the selective advantage of higher values of the  $x$ -trait is maintained, natural selection on female mate-preference should operate to stabilize the fixation of  $\Gamma^+$ . As an immediate result, one readily has:

**Corollary 2.1.** Fisher’s runaway process with small-effect mutations.

Assume an evolutionary stage at which female mate-preference  $\Gamma^+$  is fixed in the population. Assume that differences in  $x$ -values among males at that stage are small. Suppose further that mutations of the  $x$ -trait are rare and bounded in their quantitative effect by a sufficiently small value. Then, long-term evolution must lead to Fisher’s runaway process.

Here, by long-term evolution we mean the dynamic process in which the combination of rare random mutations and selection operate to shift the population from the vicinity of a stable equilibrium in one genotypic space to another (see Eshel, 1991, 1996; Eshel *et al.*, 1997, 1998). Eshel and Volovik (unpublished) provide a complete proof of the proposition, given the density-dependent structure of sexual selection as defined by (2.2).

Indeed, a natural question is: Should the process stop, as was maintained by Fisher, at some point in which the forces of natural and sexual selection balance each other? As follows from our analysis, no such point can possibly exist. Short-term selection should always operate to nullify small differences in the male  $x$ -trait and with any fixation of this trait on a single value, mutations for its increase, if of a small enough effect, should always be selected. This, however, seems an unrealistically strong result. Does it mean that Fisher's runaway process should inevitably continue until the complete extinction of the population?

The situation is different, however, when less restricting assumptions than those of Proposition 2.1 are made, allowing for all sorts of mutations to occur. Then, it is not difficult to show:

**Corollary 2.2.** Fisher's runaway process with large-effect mutations.

If all sorts of mutations of the  $x$ -trait are allowed with some positive intensity, then:

- (i) Fisher's runaway process should still continue with probability 1 up to a certain value  $x = x^* > x_0$ .
- (ii) Once the value  $x = x^*$  is surpassed, the process may continue but may, at any moment, be reversed by a single large-effect mutation.
- (iii) As time passes, the long-term process should sooner or later be reversed with probability 1.

Indeed, the sexual disadvantage of a new, sexually inferior mutant  $y < x$  is independent of the absolute distance of  $y$  from  $x$ . The advantage of  $y$  over  $x$ , on the other hand, is an unbounded function of this distance. Hence, as the  $x$ -trait of the male population surpasses some critical value  $x = x^*$ , large-effect mutations to reduce the male's  $x$ -value, when they occur, should become advantageous. Yet we know that mutations for small increases in the  $x$ -value must also remain. For the exact value of the threshold value  $x^*$ , the reader is referred to Eshel and Volovik (unpublished).

Next, once a new mutation for large-scale reduction of the exaggerated  $x$ -trait becomes established in the population, it is possible that the runaway process could come to an end, since natural selection would then favour females with a preference for only low values of the  $x$ -trait. Another possibility (actually one of many) is that a polymorphism between the two male types would become established in the population, with the possibility that other mutations will follow. The asymptotic behaviour of the general long-term evolution of the male trait  $x$  would then be hard to follow. Instead, we now ask about a possible limit distribution  $F(x)$  of the trait male  $x$ -trait in long-term equilibrium, given the female mate-preference  $\Gamma^+$ .

Indeed, given such a distribution, the total reproductive success  $\omega(x)$  of  $x$ -male should be constant on the support of  $F(x)$  with lower or equal values outside it. Employing (2.3), one can thus readily get

$$\omega'(x) = \eta'(x)\phi(F(x)) + f(x)\eta(x)\phi'(F(x)) \quad (2.4)$$

where  $f(x) = F'(x)$  is the appropriate probability density. From this one can easily deduce

$$\eta(x)\phi(F(x)) = p_0\eta(x_0) \quad (2.5)$$

on  $SuppF = [x_0, a]$ , where  $a$  is the solution of the equation

$$\eta(a) = p_0\eta(x_0) \tag{2.6}$$

**Example.** The case of Poisson encounters.

Without loss of generality, let us assume that  $x_0 = 0$  and let us measure trait  $x$  by its logarithmic cost in terms of viability; thus  $\eta(x) = e^{-x}$ . Let females encounter courting males at random, so that the number of competitors encountered by a single courting male has a Poisson distribution  $p_k^\Omega = e^{-\lambda}(\lambda^k/k!)$ . In such a case, equation (2.5) becomes  $e^{-x}e^{[F(x)-1]\lambda} = e^{-\lambda}$ , with  $SuppF = [0, \lambda]$ . This yields  $F(x) = x/\lambda$  for all  $x \in [0, \lambda]$ .  $F(x)$  is, therefore, a uniform distribution with density  $1/\lambda$  over the interval  $[0, \lambda]$ , where  $\lambda$  is the (unique) solution of the equation  $\lambda = (c/\lambda) \int e^{-x} dx = (c/\lambda)(1 - e^{-\lambda})$  or, equivalently,  $\lambda^2 = c(1 - e^{-\lambda})$ .

A natural question to ask is why one does not observe similar distributions of secondary sexual traits in nature. The theoretical answer to this question may follow from the next proposition, which is the main result of this section.

**Proposition 2.3.** Under the assumption of the model, no long-term stable equilibrium  $\langle \Gamma^+, F(x) \rangle$  can exist.

**Proof of Proposition 2.3.** A necessary condition for  $\langle \Gamma^+, F(x) \rangle$  to be long-term stable is that, given females’ mate preference  $\Gamma^+$ ,  $F(x)$  will be in equilibrium. In such a case, however, we know that given the female mate-preference  $\Gamma^+$ , the male reproductive success  $\omega(x)$  should be constant on the support of  $F(x)$ . It is, therefore, not difficult to show that, once a mutant female mate-preference  $\Gamma$  for low  $x$ -values is introduced into the population, even with low frequency, natural selection over the support of  $F(x)$  would favour low values of the  $x$ -trait, and hence would also favour the female mate-preference  $\Gamma$ . Note that the same argument should remain valid for the female mutant strategy  $\Gamma$  of preferring non-advertising males.

This result is in agreement with those of previous studies (e.g. Pomiankowski *et al.*, 1991). From Corollary 2.2 we know, however, that as with Fisher, until a certain level of male extravagance is reached, the sexy-son effect alone can initiate a runaway process, which, in turn, stabilizes the female mate-preference  $\Gamma^+$ . Above this level, our analysis is not indicative of the exact long-term dynamics, which, depending on the random order of the mutations, are by definition stochastic. Proposition 2.3 asserts, however, that contrary to Fisher’s hypothesis, such a process cannot possibly lead to a long-term stable equilibrium, nor can it allow for any sort of permanent cycling, since a mutant preference for non-advertising males (though not only this male-mutant) can always enter the population. Hence the sexy-son argument alone is insufficient to account for what appears to be the permanent maintenance of males’ extravagant secondary sexual traits.

### ZAHAVI’S HANDICAP PRINCIPLE

The reservation that Zahavi has with Fisher’s model stems from the observation that extravagant male traits commonly serve the dual purpose of deterring potential competitors of the same sex as well as attracting mates of the opposite sex. Fisher’s theory, short of accounting for the first of the two roles is, as argued by Zahavi, not likely to provide a plausible explanation for the entire phenomenon. According to Zahavi’s Handicap

Principle, either physiological or behavioural male extravagant exhibition serves as a reliable test for what the author refers to as the 'quality' of the exhibiting male. Therefore, cost should not be regarded as a mere accidental by-product of escalated male competition, but rather as an essential component of a reliable signal.

Although the theory of costly signalling was well developed within the framework of economical marketing, a crucial difficulty in its application to the evolution of mate preference concerns the heritability of the signal itself. Indeed, keeping in mind any genetic basis for natural selection, it appears that the Handicap Principle can only be evolutionarily relevant if, besides the quality of the male, its handicapping signal is at least partly heritable as well (for a different opinion, see Grafen, 1990). On this basis, Maynard-Smith (1991) argued that, even if surviving with a handicap yields some statistical indication of other advantageous traits of the survivor, a choice of a handicapped mate is not likely to be advantageous if the handicap itself is heritable. A similar conclusion was reached by Kirkpatrick (1986), based on the dynamic analysis of a quantitative genetic model in which a three-dimensional normal distribution of quality, handicap and female preference is determined for each generation by a vector of means and a covariance matrix. Different results were obtained by Pomiankowski (1987a), Grafen (1990) and Iwasa *et al.* (1991).

The analyses of Kirkpatrick (who opposed the handicap principle), and of Pomiankowski and Iwasa *et al.* (who defended it), were based on a quantitative genetic model in which positive covariance between handicap and quality results from the deleterious epistatic effect of the combination of handicap and low quality. A tacit working assumption was that there are genes for quality and others for handicaps, which operate independently of each other (although with an epistatic effect on the viability of their carriers). It appears that the negative result of Kirkpatrick (1986) depended heavily on this structural assumption. A crucial although tacit assumption in the theory of Zahavi, however (see also Grafen, 1990), is the possibility of an individual phenotypically adjusting its handicap to its quality, a phenomenon well-validated by natural observations. A genetically selected tendency for a handicap should thus be more appropriately characterized by a mapping – not necessarily linear – from quality to handicap. As we will see, the results of the analysis are radically changed with this assumption.

The positive results of Pomiankowski (1987a), Grafen (1990) and Iwasa *et al.* (1991), on the other hand, appear to depend on the consideration that female 'choosiness' should entail some cost (see also Pomiankowski, 1987b) but that mating with a male of high quality may increase the direct fertility of a female. This is not at all an obvious assumption when considering dense polygenous populations in which males only contribute sperm and females can (and do) ensure pregnancy by multiple mating. In this section we assume, instead, that the fertility of a female is independent of her choice of mate (or mates) and that the male quality  $q$  is at least heritable. Males are selected to maximize their own fitness, which, in turn, depends on the population's female preference. Females, while choosing a mate, are selected to maximize the fitness of their male offspring. Females, however, are not able to directly measure either the fitness or the quality  $q$  of a male, but have full information about its secondary trait  $x$ . Thus, as in the previous section, the female strategy  $\Gamma$  is any rule of mate-preference based on the trait  $x$ . Another necessary assumption is that, despite purifying selection forces in favour of high quality, a substantial heritable variance in male quality should be permanently maintained in the population, for example due to mutation-selection balance in many loci (e.g. Kondrashov, 1984). We thus assume that a



fixed, continuous distribution  $G(q)$  of male quality on some interval  $[q_0, q^*]$  is permanently maintained in the population.

As in the previous section, the symbol  $\Gamma^+$  will denote the female preference for high values of  $x$ . Following Grafen, we assume that the viability of a male is a function  $\eta(q, x)$  of both its quality  $q$  and its trait  $x$ , with  $\eta(q, x)$  being monotone-increasing, continuous and differentiable to the second order. For any value of  $x$ ,  $\eta(q, x)$  is assumed to be an increasing function of the quality  $q$ . For any value of  $q$ , it is assumed to be a unimodal function of  $x$ , obtaining its maximum at point  $x_0^q$  and tending to zero as  $x \rightarrow \infty$ .

A crucial assumption of our model is that males are able to adjust their secondary trait to their quality. A male’s pure strategy is thus a measurable mapping  $x(q)$  of qualities on  $x$ -traits. Any mixture of such strategies in the population, say a population strategy, is a mapping of male qualities  $q$  into distribution  $F_q(x)$ . Given such a mapping, the distribution of the  $x$ -trait among all males in the population is given by

$$F(x) = \int F_q(x) dG(q) \tag{3.1}$$

As in the previous section, we start by assuming fixation of the female mate-preference  $\Gamma^+$  and question all possible male strategies that are long-term stable against  $\Gamma^+$ . Then we question the mutual evolutionary stability of the pair  $\langle \Gamma^+, \{F_q(x)\}_q \rangle$ , guaranteeing permanent maintenance of female preference for male extravagance.

Using arguments similar to those in the previous section, one can easily verify that the distribution  $F(x)$ , defined by (3.1), when in equilibrium with  $\Gamma^+$ , is continuous with density  $F'(x) = f(x)$ ,  $f(x)$  being continuous except maybe for a set of isolated points. Then (still given the female mate-preference  $\Gamma^+$ ), the fitness of a  $(q, x)$ -male is given in exactly the same way as in the previous section by:

$$\omega(q, x) = \eta(q, x)\phi(F(x)) \tag{3.2}$$

where  $\phi(F(x))$  represents the expected reproductive success of an adult male. With this structure of male fitness and for any distribution  $\{p_k\}$  of the number of male competitors, one can prove the following:

- (i) A necessary condition for the existence of an evolutionarily stable pair  $\langle \Gamma^+, \{F_q(x)\}_q \rangle$  of male  $x$ -trait and female preference for high values of this trait is that, for all relevant  $q$  and  $x$ ,

$$\frac{\partial^2}{\partial q \partial x} \ln \eta(q, x) \geq 0 \tag{3.3}$$

- (ii) A sufficient condition for the existence of such a stable pair is that (3.3) holds as a strict inequality. Moreover, in this case there is a unique stable pair of this sort.
- (iii) Given the strict version of (3.3) and the female mate-preference  $\Gamma^+$ , the unique stable male strategy is pure, given by a mapping  $x(q)$  of the quality  $q$  over the secondary trait  $x$ .
- (iv)  $x(q)$  is a continuous, monotone-increasing function with  $x(q_0) = x_0^{q_0}$ , while for all  $q > q_0$ ,  $x(q) > x_0^q$ .
- (v) For all  $q$  and  $x = x(q)$ ,  $(\partial/\partial x)\omega(q, x) = 0$ .

Finally, and most importantly:

- (vi) The expected male reproductive success  $\omega(q, x(q))$  as given by (3.2) is a monotone-increasing function of the quality  $q$  and, therefore, of the observed secondary trait  $x(q)$ ; thus, the pair  $(\Gamma^+, x(q))$  is evolutionarily stable.

The development of (i)–(v) is beyond the mathematical scope of this paper and is therefore given elsewhere (I. Eshel and I. Volovik, unpublished).

Condition (3.3) requires that the relative cost of advertisement should be a decreasing function of the quality  $q$ . In agreement with the verbal argument of Zahavi, results (i) and (ii) state that this condition is necessary and (as a strict inequality) sufficient for the stable maintenance of the female mate-preference  $\Gamma^+$ . Recalling  $\partial\eta/\partial q > 0$  and (as concerning  $x > x_0^q$ )  $\partial\eta/\partial x < 0$ , it can readily be shown that the strict version of condition (3.3) is weaker than the condition

$$\frac{\partial^2}{\partial q \partial x} \eta(q, x) > 0 \quad (3.4)$$

given by Grafen (1990), although under a different assumption, it is sufficient for the maintenance of  $\Gamma^+$ , requiring instead a decrease in the absolute cost of advertisement.

Result (iv) states that at equilibrium a female can be guaranteed a high quality of mate just by choosing the one with the highest secondary trait  $x$ . Having assumed that female reproductive success is proportional to mate quality, this finding was used by Grafen to demonstrate the stability of the female mate-preference  $\Gamma^+$  against the stable male strategy. Having assumed, on the other hand, that the only advantage accrued to a female by an appropriate choice of mate is due to the ‘good genes’ passed on to the offspring, the most essential result guaranteeing the maintenance of the male’s handicap in the population is, indeed, given by (vi).

Finally, result (v) enables us to calculate the male optimal strategy  $x(q)$  in any specific case.

**Example.** The case of Poisson encounters of males and females.

Assume random encounters of males and females. Then, we already know that the number of males encountered by a courted female, and the number of competitors encountered by a random courting male, both have the same Poisson distribution with parameter  $\lambda$ . The parameter  $\lambda$ , in this case, can be interpreted as the density of the adult male population. Now further assume that this density is determined by ecological factors (e.g. by the carrying capacity of the population) regardless of the distribution of the relative juvenile-viability  $\eta(q, x)$ , hence  $\lambda$  is independent of  $F(x)$ . In such a case, let us recall,

$$\phi(s) = e^{\lambda(s-1)} \quad (3.5)$$

As in the previous section, let us measure the parameter  $x$  in units of logarithmic cost, this time the cost of the lowest-quality male, thus  $\eta(q_0, x) = e^{-x}$ . For any value  $q > q_0$ , we assume

$$\eta(q, x) = c(q) e^{-xr(q)} \quad (3.6)$$

where  $c(q)$  is a positive-increasing and  $r(q)$  is a positive-decreasing function of  $q$ , with  $c(q_0) = r(q_0) = 1$ . Given  $\Gamma^+$ , one then readily obtains  $(\partial/\partial x) \ln \omega(q, x) = \lambda f(x) - r(q)$ . Thus, at a point  $x = x(q)$  at which  $(\partial/\partial x) \omega(q, x) = 0$ , we get

$$\lambda f(x) = r(q) \tag{3.7}$$

But, for any monotone-increasing mapping  $x(q)$ ,  $F(x(q)) = G(q)$ . Hence  $f(x(q)) = g(q)/x'(q)$  and, therefore,

$$x'(q) = \lambda \frac{g(q)}{r(q)} \tag{3.8}$$

With the appropriate restrictions, (3.8) yields:

$$x(q) = \lambda \int_{q_0}^q \frac{dG(y)}{r(y)} \tag{3.9}$$

which is, indeed, an increasing function of  $q$  but also proportional to the population density  $\lambda$ .

**THE STRONG AND THE WEAK VERSIONS OF THE HANDICAP PRINCIPLE:  
TOWARDS A UNIFIED THEORY OF SEXUAL SELECTION**

The purpose of this section is not to suggest a new, unified theory of sexual selection, but to demonstrate the interdependence of the two current theories investigated above.

As maintained by Zahavi (personal communication), once differences in male quality are considered, the very arguments of Fisher, if further developed, should inevitably lead to the Handicap Principle. Thus, if male investment in advertisement is expected to reach a level at which natural and sexual selection are balanced, this balance could not possibly be obtained at the same level for males of different quality. Assuming that each male does his best to bluff the females, males of higher quality, as noted by Zahavi, ‘should always succeed in bluffing more’ – that is, reaching a higher level of balance. But then, this quality-dependent level of balance should inevitably become a reliable signal; hence no bluffing could then be possible. This, as we have seen, was proved to be true under the plausible condition (3.1), which, according to Zahavi’s theory, must therefore be characteristic of secondary sexual traits. We now see, on the other hand, that Fisher’s argument of the ‘sexy son’ may prove to be a crucial, although tacit component in Zahavi’s theory of sexual selection.

As shown in the previous section, if  $x(q)$  is evolutionarily stable against the female mate-preference  $\Gamma^+$ , then, assuming condition (3.1), the fitness  $\omega(q, x(q))$  of a male is an increasing function of its quality  $q$  and hence of  $x(q)$ , the latter being an increasing function of  $q$ . Thus, natural selection must, in turn, favour the female mate-preference  $\Gamma^+$ . Note, however, that the male fitness  $\omega(q, x(q))$  was defined as a product of two components – namely, the viability of the male and its sexual success provided it survives to maturity. Given  $\Gamma^+$ , the latter component is proportional to  $\phi(F(x(q)))$ , which is obviously an increasing function of  $x(q)$  and hence of  $q$ , but may not be so under different female mate-preferences. A crucial question, therefore, is whether under assumption (3.2), the viability  $\eta(q, x(q))$  of a male should necessarily also be an increasing function of its quality  $q$ .

We employ the example of the Poisson encounters to show that the answer to this question may well be negative. Thus, inserting (3.9) in (3.6) we get

$$\ln \eta(q, x(q)) = \ln c(q) - x(q)r(q) = \ln c(q) - \lambda r(q) \int_{q_0}^q \frac{dG(y)}{r(y)} \tag{4.1}$$

As special cases, recalling  $x(q_0) = x_0^{q_0} = 0$ , we get

$$\ln \eta(q^*, x(q^*)) - \ln \eta(q_0, x(q_0)) = \ln c(q^*) - c(q_0) - \lambda r(q^*) E\left(\frac{1}{r(Q)}\right) \quad (4.2)$$

The right-hand side of (4.2) is positive only for sufficiently small values of  $\lambda$  and negative for sufficiently high values of  $\lambda$ , namely for a high density of the adult male population. In the latter case, we see that intense sexual competition should drive top-quality males into a level of investment that inevitably renders them less viable than males of lower quality. Moreover, from (3.6) and (3.9), it follows that for all  $q_0 \leq q \leq q^*$ :

$$\frac{d}{dq} \eta(q, x(q)) = \frac{d\eta}{dq} + x'(q) \frac{d\eta}{dx} = \left[ \frac{c'(q)}{c(q)} - r'(q)x(q) - \lambda g(q) \right] c(q) e^{-x(q)r(q)} \quad (4.3)$$

This expression again tends to be negative when  $\lambda$  is sufficiently large, in which case the viability  $\eta(q, x(q))$  decreases with  $q$ . Then, even though male extravagant advertisement serves as a reliable proof of quality, the direct advantage of high quality can only partly compensate for the cost of advertisement. Proposition (3.3) asserts though, that even in this case, as long as the female mate-preference  $\Gamma^+$  prevails, it remains selectively advantageous for any single female to follow the majority-rule, thus preferring highly advertising males even though thereby decreasing the expected viability of her offspring. But then, the selective advantage, accrued to a female by choosing such a male, can only stem from the perspective of thereby increasing her offspring's sexual success, a success guaranteed only if a large enough majority of females in the population indeed follow the mate-preference  $\Gamma^+$ . Hence, a quantitative examination of Zahavi's argument in this case leads us back to Fisher's argument of the 'sexy son'!

We have seen that Fisher's 'sexy son' argument alone is not sufficient to account for the persistence of female preference for male extravagance. We have also seen that this sort of persistence can always be fully explained by Zahavi's Handicap Principle. In this section, we have shown that, at least in some cases, the 'sexy son' argument of Fisher appears to be an indispensable, though tacit component of Zahavi's Handicap Principle. As emerges from the quantitative model, an important distinction can therefore be made between what we prefer to call the strong and the weak versions of Zahavi's Handicap Principle when applied to sexual selection.

The strong version of the principle is applicable in those cases in which the handicap can be trusted as a signal not only of high quality, but also, despite its cost, of high viability. In such cases, it is selectively advantageous for a female to prefer highly advertising males even if other females are still impartial to the signal.

The weak version of the principle is applicable in those cases in which male advertisement, although a reliable signal of quality, becomes too costly in terms of viability to be fully compensated for by quality. As we have shown, even in this case, female preference for high male advertisement remains stable, yet the female advantage of choosing a highly advertising male is then no more independent of male-preference of other females in the population. It is therefore the weak version of Zahavi's Handicap Principle that tacitly involves Fisher's 'sexy son' argument. From this, however, one should not misleadingly infer that the weak version of the Handicap Principle could account for the stability of the female mate-preference  $\Gamma^+$ , but not for the initial stages of its evolution. Indeed, female mate-preference of a given trait, in correlation with quality, is likely to precede the evolution

of male exaggeration and not vice versa. Thus, only after the establishment of  $\Gamma^+$  in the population can the evolution of male exaggeration alter the initially strong version of the Handicap Principle into the weak one.

It is likely, therefore, that the strong version of the Handicap Principle would be typical of all initial stages of the evolution of male advertisement. As we have seen, it appears to remain so in stable equilibrium when concerning sparse populations in which optimal exaggeration is anyhow moderate. The weak version of the Handicap Principle, on the other hand, appears to characterize final, stable situations in dense populations, in which competition has already driven male advertisement towards more costly levels of exaggeration. This has been proved here only for the case of Poisson encounters.

### SUMMARY

A long-term evolution model of sexual selection in polygenic populations has been analysed, in which females were each assumed to choose a mate from a random group of males. Female mate-choice was supposed to be based exclusively on observed phenotypic traits. The fitness of a male was supposed to be the product of its viability and its expected reproductive success, given it reaches maturity. These two might be in conflict, depending on the females’ mate-preference. The expected progeny size of a female, on the other hand, was assumed to be independent of mate choice, being decided only by ecological restraints. However, mate choice was assumed to affect the reproductive success of the female’s offspring through genes obtained from the offspring’s father. The model was employed to study quantitatively two principles suggested to explain the evolution and persistence of female preference for male extravagance.

Following Fisher’s ‘sexy son’ argument, we assumed that, for the sake of the argument, secondary sexual traits are uncorrelated with other male features. The tendency to invest in such a trait, however, was inherited and therefore a subject for natural selection. In agreement with Fisher, it was shown that, historically, once female preference for male extravagance is established in the population, a ‘runaway process’ is expected to perpetuate itself, stabilizing this preference. Still, in agreement with Fisher, the process was shown to continue undisturbed at least up to a level at which the ratio in viability between the population-average and a potential non-advertising mutant male would equal the ratio in sexual success between such a mutant and the population-average. Contrary to Fisher’s prediction, however, it was shown that the population dynamics, in such a case, could not possibly lead to a long-term stable equilibrium. The establishment of any equilibrium of male extravagant behaviour that is stable in the face of female mate-preference for it, was shown to result, in turn, in the destabilization of that female’s mate-preference. It was shown, moreover, that the process should sooner or later reverse itself with the end-result of no male exaggeration.

We showed that the situation is different if there is some heritable variance in male quality in the population, and if each male is able to adjust its level of advertisement to its quality. In such a case, in agreement with the prediction of Zahavi’s Handicap Principle, it was shown that if the relative cost of any investment in male advertisement is a decreasing function of male quality, then optimal male investment in advertisement must be an increasing function of male quality. Hence, advertisement, in this case, becomes a reliable signal of quality. More importantly, for the evolution of such a signal, it was shown that, under the assumption of optimal male signalling, despite signal cost, the total reproductive

success of a male remains an increasing function of its quality and hence of the level of its signal. In this case, unlike under the assumptions of Fisher's model, female preference for highly advertising males is stably maintained in the population.

A distinction was made between a strong version of Zahavi's Handicap Principle, typical of relatively sparse populations, and a weak one, more likely to occur in dense populations with intense male competition. The strong version of the principle was referred to in those cases in which the handicap could be trusted as a signal not only of high quality, but also, despite its cost, of high viability. As we have seen, this is not always the case. The weak version of the principle was thus referred to in those cases in which male advertisement, although a reliable signal of quality, became too costly in terms of viability to be fully compensated for by quality. In both cases, it was shown that female preference for high male advertisement should evolve and remain stable in the population. However, Fisher's argument of the 'sexy son', although on its own insufficient to account for the persistence of male extravagance, was shown to be an indispensable, although tacit component in the evolution and maintenance of this phenomenon according to the weak version of Zahavi's Handicap Principle. A unified theory for the evolution of sexual selection was therefore suggested.

A crucial aspect of sexual selection, not discussed here, is that of the choice of a specific signal (or signals) out of many potentially available ones. A fundamental component in Zahavi's argument, however, is that females are selected to respond exclusively to those signals that can be unmistakably measured and, whenever possible (e.g. in dense polygenous populations), under conditions that clarify the comparison between two available males. In agreement with Grafen (1990), although under a different structural assumption, we have therefore assumed that the choice of a less attractive mate results from a lack of availability and not from misjudgement on the part of the female (see, for example, Lande, 1981; Kirkpatrick, 1986, 1987; Pomiankowski, 1987a; Iwasa *et al.*, 1991; Pomiankowski *et al.*, 1991; Iwasa and Pomiankowski, 1995; Pomiankowski and Iwasa, 1998). Indeed, the assumption that females are never ambiguous even when considering the slightest differences in the secondary male trait, is quite strong and was made in this work only for the sake of mathematical completeness. It would appear to be safe to assume that females can recognize differences small enough as to render their effect on male viability smaller than the advantage of being sexually preferred.

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