J. Math. Biol. 45, 1–21 (2002)
Digital Object Identifier (DOI):
10.1007/s002850200138

**Mathematical Biology**

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# A long-term genetic model for the evolution of sexual preference: the theories of Fisher and Zahavi re-examined

Received: 7 March 2001 / Revised version: 15 November 2001 /

**Abstract.** Long-term co-evolution of male's sexual extravagance and female's preference for it is studied. Fisher's "Sexy Son" principle is checked against Zahavi's Handicap Principle. It is shown that although both principles are equally likely to explain this sort of co-evolution in the short run, only the second one allows for a long-term evolutionarily stable females' preference for costly male's extravagance. It is shown, however, that Fisher's argument, although not sufficient on its own to explain long-term persistence of females' choice, may tacitly appear as an indispensable component for the application of Zahavi's theory to the important case of dense polygenous populations.

## 1. Introduction

This work suggests a quantitative study of the co-evolution of male's sexual extravagance and female's preference for it in large polygenous populations. For biological discussion of this study, the reader is referred to Eshel et al. (2000). Following Lande (1981), Kirkpatrick (1985, 1987), Pomiankowski (1987), Grafen (1990), Maynard-Smith (1991), Otto (1991), Iwasa et al. (1991), Pomiankowski et al. (1991), Iwasa and Pomiankowski (1995), Pomiankowski and Iwasa (1998), we compare and analyze the two leading theories about the evolution of sexual conflict, namely Fisher's "Sexy Son" principle (Fisher 1915, see also 1930 pp 135–162) versus Zahavi's Handicap Principle (Zahavi 1987, 1991). Differently from previous works, we assume a long-term genetic model in which any mutation, affecting either male's or female's strategy, can sooner or later be introduced into the population (e.g. see Eshel 1995, Eshel et al 1999 and references there). We assume, for simplicity, that male's and female's behavior are affected each by a different single locus.

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*Key words or phrases:* Sexual selection – Handicap principle – Runaway process – Long-term evolution

Following the arguments of both Fisher and Zahavi, we assume that each female has to choose a mate from a random number of encountered male's, the choosing-rule Γ being based only on one observed quantitative trait of the candidate, whose trait value shall be denoted by $x$. This trait can therefore evolve as a means of sexual advertisement. We assume, however, that advertisement, at least above some fixed optimum $x_0$, is costly in terms of viability. Most crucially we assume that male's and female's strategies are both at least partially heritable and are, therefore, subject to natural selection. Natural selection on the male's locus operates to increase male's reproductive success. Dealing with polygenous populations in which male's only pass their DNA to offspring, it is assumed, however, that the choice of mate does not affect the direct reproductive success of a female (e.g. Fisher 1930. See also Eshel et al. 2000 and references there. For a different assumption, however, see Grafen 1990). Instead, natural selection on female's preference is assumed to favor the choice of fittest possible mate, thereby assuring good genes to be passed to offspring.

While the evolution of males' extravagance, when favored by females, is by no means surprising, a more delicate question concerns the maintenance of female's preference for such a trait, which reduces the male's viability. Different answers, given to this question by R. A. Fisher and by A. Zahavi will be quantitatively studied in this work. As we see in the next two paragraphs, they should require two different sets of extra assumptions.

According to Fisher's "*Sexy Son Argument*" (Fisher 1915, 1930), the female's preference for high values of the $x$-trait might have initiated as historical accident when directly advantageous, namely when males' $x$-values were, on the average, lower than $x_0$. Once this female's preference becomes established in the population, sexual selection can indeed promote further increase of male's advertising above the viability-optimal value of $x_0$. At this stage, however, the fixation of the female's preference for male's high (now exaggerated) $x$-values might still remain stable because in such a case the male offspring of any otherwise-choosing mutant female, although of higher viability, would be likely to remain without a mate. As predicted by Fisher, a so-called "*Runaway Process*" can start then, at which females' preference for male's extravagance would lead to the evolution of an ever higher exaggeration, thus to a more intense competition among males. As maintained by Fisher, this can provide females with further incentive to choose highly advertising males and, as suggested, the process should continue up to the level at which natural and sexual selection would balance each other.

The *Handicap Principle* of Zahavi, on the other hand (Zahavi 1987, 1991), suggests a frequency-independent advantage of females' preference to extravagant males, based on two plausible extra assumptions. First, that male's advertisement, even though costly to all, is more costly to those males which are intrinsically less viable to start with, namely, in the terminology of Zahavi, low quality males. Second, that males can adjust their level of advertisement to their quality. On this basis it was claimed by Zahavi that by optimizing their level of advertisement each to its own quality (clearly in a way that the investment in advertisement would increase with the male's quality), males inevitably provide trustful signals about their quality, available to females. A crucial question to be checked in this case is whether, at equilibrium, the cost of advertisement imposed on the son of the choosing females is always overbalanced by its expectedly higher quality.

We see that Fisher's "sexy son" argument can indeed lead to a runaway process in which females' preference for males' extravagance would persist while males' extravagance increases up to a certain exaggerated level. Yet, contrary to the prediction of Fisher, and in agreement with the quantitative models of Iwasa et al. (1991), and of Pomiankowski et al. (1991), we see that such a process cannot possibly lead to a long-run maintenance of females' preference for males' extravagance. Contrary to Iwasa and Pomiankowski (1995), it is shown, instead, that long-term dynamics should always bring the population to a stable equilibrium at which females prefer non-advertising males.

We see that the situation is different if, as suggested by Zahavi, the cost of advertisement is different for males of different quality, in which case it is shown that a single evolutionarily stable strategy exists, in which females prefer advertising males. In this, the findings of our long-term-evolution model stand partly in agreement with those of the quantitative genetic models of Pomiankowski (1987), Grafen (1990) and Iwasa et al. (1991). They stand in disagreement with those of Kirkpatrick (1986). Quite interestingly, though, it appears that the offspring of a highly advertising male at equilibrium, even though of a higher quality than that of a poorly advertising male, is not necessarily more viable, given its high tendency to advertise. Yet sexual success (in this case combined with high quality) ensures a higher-than-average total reproductive success of such an offspring. On the basis of this findings it is maintained in Sect. 4 that although Fisher's "sexy son" argument alone cannot explain the persistence of males' extravagance, this argument proves a tacit but indispensable component in the application of Zahavi's handicap principle to the quantitative theory of sexual selection.

## 2. Long-term analysis of Fisher's argument

Following the argument of Fisher we assume that the viability $\eta(x)$ of a male with trait value $x$ is determined by a function $\eta$, which is supposed to be a unimodal differentiable function, with a maximum at $x = x_o$ and with $\eta(x) \to 0$ as $x \to \infty$. It is further assumed that once a male survives to maturity, the number of females it encounters is independent of its x-trait. The total reproductive success $\chi$ of such a male, conditioned on its survival to maturity, is therefore proportional to, and for simplicity will be measured by, its probability of success in the competition over a single courted female, thus $0 \leq \chi(x) \leq 1$. Unlike the frequency independent viability $\eta$ of a male, its expected reproductive success $\chi$, conditioned on survival, depends not only on its x-trait, but also on both the distribution $F$ of this trait in the male population and that of the preference-rule $\Gamma$ in the female population. Here a female's mate-preference $\Gamma$ is any rule, either deterministic or probabilistic, to choose one x-value out of any finite set of such values. As two special cases we denote by $\Gamma_0$ the female preference for a mate with x-trait closest possible to the viability-optimum $x_o$ and we denote by $\Gamma^+$ the female preference for a mate with highest possible value of this trait. The expected net reproductive success of a male, namely its *fitness*, is given by

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

Note that the fitness $\omega$ of a male, as given in (2.1), is proportional also to the expected number of genes this male passes to the next generation. Assuming genetic heritability of the trait value $x$, we take over the simplest "replicator" assumption, namely that the relative frequency of males with a given trait value $x$ is multiplied, at any given generation, in proportion to the fitness of males of this trait in that generation. Restricting our attention here to panmyctic populations in which males' contribution to females is limited to DNA, it is also assumed that natural selection operates in favor of any female-preference that guarantees higher fitness of chosen mates, hence of male offspring (for further details see Eshel et al. 2000).

Denote by $p_k$ the probability that, courting a female, a random male would find itself in presence of $k$ other contenders ($k = 0, 1, 2, \dots, \sum\limits_k p_k = 1, p_0 < 1$). We assume that this probability is independent of either the males' feature or past events, and that competitors are independently drawn from the population of adult males.

A natural and apparently common evolutionarily stable equilibrium is given by the pair of strategies $\langle \Gamma_o, x_o \rangle$, in which natural selection simultaneously maintains the viability-optimum $x_o$ of the male's x-trait and the preference of this trait by females in the population. In this section we are interested, however, in the existence and possible development of an alternatively stable equilibrium $\langle \Gamma^+, F \rangle$ in which $F$ determines a distribution of males' trait value $x$ which is evolutionarily stable under the females' choosing rule $\Gamma^+$, and $\Gamma^+$ is evolutionarily stable, given the distribution of the males' trait value $x$. Following Fisher, we start our analysis by assuming a historical event that may have lead to a temporal fixation of the females' mate-preference $\Gamma^+$ in the population. We then study the population-dynamics of the males' x-trait thereby induced and its asymptotic behavior. Given this population-dynamics, we check, in turn, the stability of the mate-preference $\Gamma^+$ during the process and in long-term equilibrium, if it exists.

**Lemma 2.1.** *Assuming fixation of the females' mate-preference* $\Gamma^+$*, no long-term stable distribution* $F$ *of the trait value* $x$ *exists, which contains a positive probabilistic weight at a given value* $x^*$*. More specifically, any distribution* $F$ *of the trait value* $x$*, which contains such a probabilistic atom, is unstable against the increase of the frequency of (either mutant or resident) x-values sufficiently close to this atom and above it.*

*Proof.* Given $\Gamma^+$ and $F$, $\chi$ becomes a function of $x$ alone. Moreover, in such a case any small shift of the male's trait-value from $x^*$ to a higher value $x$ should guarantee sexual priority of the male of the trait value $x$ over any competitors with the trait-value $x^*$, if encountered. But if $F$ has a positive probabilistic weight at $x^*$, the probability of such an encounter is positive, hence $\chi$ must have a jump at this point and, since $\eta$ is continuous, so must have $\omega = \eta\chi$, with advantage to trait-values sufficiently close to $x^*$ and above it. □

Assume, on the other hand, that $F$ does not have a positive probabilistic weight at any given value $x$. In such a case a x-male, courting a female in competition with

$k$ other males, would be chosen for a mate if and only if the trait-value of all its competitors would be strictly lower than $x$, which occurs in probability $(F(x))^k$. The general probability of an x-male to be chosen by a courted female is therefore given by:

$$\chi(x) = \sum_k p_k (F(x))^k = \phi(F(x)), \tag{2.2}$$

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 (2.1) thus becomes:

$$\omega(x) = \omega_F(x) = \eta(x)\chi(x) = \eta(x)\phi(F(x)) \tag{2.3}$$

**Lemma 2.2.** *Assume females' mate-preference* $\Gamma^+$, *then for any value* $x_1 \geq x_0$ *for which* $\eta(x_1) > 0$, *there exists a value* $\delta = \delta(x_1) > 0$ *such that starting from any initial distribution* $F$ *of the male's x-trait with support* $\mathrm{Supp}F = [x_1, x_2]$ *where* $x_1 + \delta > x_2 > x_1$, *the distribution* $F^{(n)}$ *of the males' x-trait in the population of the n-th generation tends to fixation on* $x_2$ *as n tends to infinity.*

*Proof of Lemma 2.2.* Let us choose any value $\xi$, $x_1 < \xi < x_2$, on which the distribution $F$ does not have a positive probabilistic weight, and let $F(\xi) = p$, $0 < p < 1$. Let X, $Y$ and $Z$ be values of the x-trait, randomly chosen independently, X from the entire population, Y from below and Z from above $\xi$ respectively. By simple combinatorial arguments one readily gets $p\{Y > X|Y < \xi\} = \frac{p}{2}$ and $p\{Z > X|Z > \xi\} = \frac{1+p}{2}$ regardless of the distribution $F$. Hence $E\{\chi(Y)|Y < \xi\} = \phi\left(\frac{p}{2}\right)$ and $E\{\chi(Z)|Z > \xi\} = \phi\left(\frac{1+p}{2}\right)$. But for all $x_1 \leq y < \xi$, $\eta(y) \leq \eta(x_1)$, hence $E\{\omega(Y)|Y < \xi\} \leq \eta(x_1)\phi\left(\frac{p}{2}\right)$, and in the same way $E\{\omega(Z)|Z > \xi\} \geq \eta(x_2)\phi\left(\frac{1+p}{2}\right)$. It follows that $\frac{E\{\omega(Z)|Z>\xi\}}{E\{\omega(Y)|Y<\xi\}} \geq K\frac{\eta(x_2)}{\eta(x_1)}$ where $K = Min_{0\leq p\leq 1}\frac{\phi(\frac{1+p}{2})}{\phi(\frac{p}{2})}$. From the monotony and continuity of the generating function $\phi$ it follows that $K > 1$ and from the continuity of $\eta$ it follows that a value $\delta > 0$ exists, such that if $x_2 < x_1 + \delta$, then $K\frac{\eta(x_2)}{\eta(x_1)} > 1$ hence $\frac{E\{\omega(Z)|Z>\xi\}}{E\{\omega(Y)|Y<\xi\}} > 1$ regardless of the value $p$ and hence of the distribution $F$, given only $\mathrm{Supp}F \subseteq [x_1, x_2]$. From the replicator assumption that the relative frequency of males with a given trait value $x$ is multiplied, at any given generation, in proportion to the fitness of males of this trait in that generation, it follows that the proportion of males with a trait-value lower than $\xi$ decreases from one generation to the next in a geometric rate. This being true for any $\xi$ below the supreme of $\mathrm{Supp}F$, on which the distribution $F$ does not have a positive probabilistic weight, completes the proof. □

As a special case of Lemma 2.2 we get:

**Lemma 2.3.** *Assume females' mate-preference* $\Gamma^+$. *Then for any trait-value* $x_1 \geq x_0$ *for which* $\eta(x_1) > 0$ *there is a positive value* $\delta = \delta(x_1) > 0$ *such that* *if the males' population is fixed on the point-distribution* $x_1$*, then a new mutation* $x$ *with* $|x_1 - x| < \delta$ *will be successfully established in the population if and only if* $x > x_1$*. Moreover, in such a case the new mutation will eventually become fixed in the population.*

As a result of the last two lemmas we get:

**Proposition 2.1 (Fisher's Runaway Process with small-effect mutations).** *Assume that the event of mutation is sufficiently rare in the population. Assume that at some time during the course of evolution, females' mate-preference* $\Gamma^+$ *has been fixed in the population. Assume further that at that time the x-values in the male population were bounded from above by some value* $x^* > x_0$ *for which* $\eta(x^*) > 0$*. For any such* $x^*$*, there exists a value* $\delta = \delta(x^*) > 0$ *such that if both the effect of a single mutation and the initial differences in x-values among males in the population were bounded by* $\delta$*, then long-term evolution must lead to Fisher's Runaway Process, at least as long as the* x-values *in the male population does not precede the value* $x^*$*, during which time females' mate-preference* $\Gamma^+$ *should remain stable.*

Here, with long-term evolution we mean the dynamics in which the combination of natural selection and rare random mutation events operates to repeatedly shift the population from the vicinity of one genetic equilibrium to another, each being stable for a different set of alleles, temporarily present in the population (See Eshel 1991, 1995, Eshel et al. 1999).

*Proof of Proposition 2.1.* Assume first that females' mate-preference in the population is $\Gamma^+$. From Lemma 2.2 it follows that for any closed interval $[x_0, x^*]$ such that $x^* > x_0$ and $\eta(x^*) > 0$ (hence $\eta(x) > 0$ for all $x_0 \leq x \leq x^*$, $\eta$ being an unimodal function of $x$), there is a value $\delta > 0$ such that as long as differences among males' x-values are smaller than $\delta$, pure natural selection should lead the population to the fixation of the maximal x-value, originally present in the population, provided this maximal value does not exceeds $x^*$. Assume further that mutations for the x-trait are rare and bounded in their quantitative effect by $\delta$, Lemma 2.3 then indicates that, starting from the vicinity of fixation of a single x-value, the only possible long-term shifts from one short-term equilibrium to another are those leading to fixation on a slightly higher level of the x-value. On the other hand, since during the whole process, males with higher x-values are selected for, so should be the females' preference $\Gamma^+$ for such values; Hence the process is bound to ever perpetuate itself. □

A natural question to be asked is, indeed: Should the process stop, as it was maintained by Fisher, at some point in which the forces of natural and sexual selection are balancing each other? As it follows from our analysis, no such a point can possibly exist. Short-term selection would always operate to null small differences in the males' trait value $x$; and with any fixation of this trait on a single value, mutations for its increase, if of a sufficiently small effect, would always be selected for. This, indeed, seems a non-realistically too strong a result. Does it mean that Fisher's runaway process should inevitably continue till the total extinction of the population?

*Remark.* Note that the distribution $\{p_k\}$ of the number of competitors encountered by a single courting male indeed depends on the density of the population. Moreover, when the population becomes close to extinction, most (but not all) courting males would find no competitor at all. In the present article, allowing for long-term co evolution of male and female strategies with all sorts of mutations, a fixed population size was assumed, for simplicity, at least at birth. In a previous paper based on the analysis of changes in genotype frequencies without mutation (Eshel 1979) but allowing for the effect of courtship behavior on the population density of juveniles, it was shown, on the other hand, that in this case either a stable equilibrium or an ecogenetic cycling can be maintained, in which case the establishment of male-extravagance leads to a drop in the population size, then to the advantage of the non-exaggerating male type which, in turn, results with the increase of the population size and so on. For the case of long-term evolution, allowing for all sorts of small effect mutations we see, however, that at least no stable equilibrium can exist. As we know from Lemma 2.3, for any trait-value $x^* > x_0$ for which $\eta(x^*) > 0$, if fixed in the population, a value $\delta > 0$ exists such that mutations of lower effect should be successfully established and fixed in the population if and only if they increase the x-value of their carrier.

We now see that the situation is different when less restricting assumptions than those of Proposition 2.1 are taken over, allowing for all sorts of mutations to occasionally occur.

**Proposition 2.2.** *Under the conditions of Proposition 2.1, but allowing for all sorts of mutations:*
*i) Fisher's Runaway Process should continue in probability one up to the trait value* $x^*$ *in which*

$$\eta(x^*) = p_0\eta(x_0)\Big(\int_0^1 \phi(s)ds\Big)^{-1}, \tag{2.4}$$

*where* $x_0$, *as we recall, is the value at which the unimodal function* $\eta$ *obtains its maximum.*
*ii) Once the trait value* $x^*$ *is surpassed, the process may continue but may, at any moment in time, be reversed by a single large-effect mutation, drastically reducing the value of the x-trait.*

*Remark.* Since $\eta$ is a continuously decreasing function for $x > x_0$ and since $\int_0^1 \phi(s)ds > \phi(0) = p_0$, equation (2.4) has always a unique solution.

*Proof of Proposition 2.2.* It is easy to see that if the males' population is fixed on a single value $x$, then the probability of a resident x-male to be chosen by a random female is $\sum_{k=0}^{\infty} \frac{p_k}{k+1}$ which, as one can readily verify, equals $\int_0^1 \phi(s)ds$. The fitness of a resident x-male in a population fixed on $x$ is, therefore:

$$\omega(x) = \eta(x) \int_0^1 \phi(s)ds. \tag{2.5}$$

A sexually inferior mutant $y < x$, in such a case, will be chosen by a courting female only in the absence of any other male competitor, hence $\chi(y) = p_0$ and $\omega(y) = p_0\eta(y)$. Having $\eta(y) \leq \eta(x_0)$, it therefore follows from (2.5) that if $x < x^*$, $x^*$ being the solution of (2.4), no mutation $y < x$ can be selectively advantageous. Having, on the other hand, $\int_0^1 \phi(s)ds > p_0$, it follows from (2.5) that if $x > x^*$, then a mutation $y < x$, sufficiently close to $x_o$, will be selectively advantageous. Yet, at the same time we know from Corollary 2.3 that any mutation $y > x$, if of a sufficiently small effect, will also be selected for. □

Indeed, 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 would come to an end as natural selection would then favor females with preference just for 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 behavior of the general long-term evolution of the male's trait value would then be hard to follow. Instead we now ask about a possible limit distribution $F$ of this trait value, in long-term equilibrium, given the females' mate-preference $\Gamma^+$. For any such a distribution, if it exists, there must be a constant $c > 0$ such that

i) For any $x \in \mathrm{Supp}F$, $\omega_F(x) = c$.
ii) For any $x \notin \mathrm{Supp}F$, $\omega_F(x) \leq c$.

The first condition is necessary and sufficient for the requirement that short-term selection will not change the shape of $F$. The second condition is necessary for the immunity of $F$ to an invasion by a new mutation. A version of condition (ii) with a sharp inequality is a sufficient condition for such immunity.

From Lemma 2.1 (together with the fact that $F$ is monotone increasing) we already know that a distribution function $F$ in long-term equilibrium, if it exists, must be continuous as a function of $x$. From the equilibrium-conditions (i) we know, further, that for any $x$ in the interior of $\mathrm{Supp}F$, $\omega(x) = \eta(x)\phi(F(x)) = c$. $\eta$ is a positive differentiable function of $x$, hence $\phi(F(x))$ is a differentiable function of $x$. From this and the fact that $\phi$ has a derivative bounded from below by a positive value, it follows that $F$is differentiable for any $x$ in the interior of $\mathrm{Supp}F$, with a density function $f = F'$. It is indeed differentiable for any $x \notin \mathrm{Supp}F$ with $f(x) = F'(x) = 0$, hence $F$ is a proper probability distribution, differentiable almost anywhere. It therefore follows from (2.3) that

$$\omega'(x) = \eta'(x)\phi(F(x)) + f(x)\eta(x)\phi'(F(x)) \tag{2.6}$$

almost anywhere. As an immediate result we get:

**Lemma 2.4.** *i) For any value* $x > x_0$, $\omega'(x) \leq 0$.
*ii) For any value* $x > x_0$ *with* $x \notin \mathrm{Supp}F$, $\omega'(x) < 0$.

*Proof of Lemma 2.4.* From both the equilibrium-conditions (i) and (ii) it follows that for $x \in \mathrm{Supp}F$, $\omega'(x) = 0$. From (2.6) it follows that for any $x \notin \mathrm{Supp}F$, as $f(x) = 0$, $\omega'(x)$ is equal in sign to $\eta'(x)$ which for $x > x_0$ is negative. □

**Lemma 2.5.** *Given the females' mate-preference* $\Gamma^+$, *the distributions* $F$ *in long-term stable equilibrium are exactly the solutions, if they exist, of the equation*

$$\eta(x)\,\phi(F(x)) = p_0\eta(x_0) \tag{2.7}$$

*on* $\mathrm{Supp}F = [x_0, a]$, *where* $a$ *is the solution of the equation*

$$\eta(a) = p_0\eta(x_0) \tag{2.8}$$

*Proof of Lemma 2.5.* Assume first that $F$ is in long-term equilibrium. If $x < x_0$ then both $\eta(x) < \eta(x_0)$ and $\phi(F(x)) < \phi(F(x_0))$, hence $x \notin \mathrm{Supp}F$. It follows that $F(x_0) = 0$ and, thus, $\omega_F(x_0) = \eta(x_0)\phi(0) = p_0\eta(x_0)$.

On the other hand, if $x > a$, where $a$ is the solution of equality (2.8), then $\omega_F(x) \le \eta(x) < \eta(a) = p_0\eta(x_0) = \omega_F(x_0)$ which, again, implies $x \notin \mathrm{Supp}F$. We, thus, infer that $\mathrm{Supp}F \subseteq [x_0, a]$, and we get $\omega_F(a) = \eta(a)\phi(1) = \eta(a) = p_0\eta(x_0) = \omega_F(x_0)$.

Finally assume $a \ge x > y \ge x_0$, and suppose $x \in \mathrm{Supp}F$. In this case we know that $\omega_F(x) = \omega_F(x_0)$. If, on the other hand, $y \notin \mathrm{Supp}F$, then it follows from part (ii) of Lemma 2.4 that $\omega'_F(y) < 0$. From this it follows that for some value $z$, $x > z \ge x_0$, $\omega'_F(z) > 0$ which contradicts Lemma 2.4. It therefore follows that $\mathrm{Supp}F = [x_o, e]$, where $x_0 < e \le a$. But then we know that $\omega_F(e) = \omega_F(x_0) = \eta(a)$ while, on the other hand, $\omega_F(e) = \eta(e)\phi(1) = \eta(e)$, hence $e = a$ and $\mathrm{Supp}F = [x_o, a]$. We further know that for any $x \in \mathrm{Supp}F$, $\eta(x)\,\phi(F(x)) = \omega_F(x) = \omega_F(x_0) = p_0\eta(x_0)$, hence $F$ is a solution of (2.7).

Assume, on the other hand, that $F$ is a solution of (2.7) on $\mathrm{Supp}F = [x_o, a]$. In such a case we have already seen that

a) For any $x \in [x_0, a]$, $\omega(x) = \omega(x_0) = p_0\eta(x_0)$.

b) For any $x \notin [x_0, a]$, $\le \omega(x) < p_0\eta(x_0)$.

This implies that $F$ is in long-term equilibrium. □

**Example. The case of the Poisson encounters.** Without loss of generality, let us assume $x_0 = 0$ and let us measure the 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 $p_k = e^{-\lambda}\frac{\lambda^k}{k!}$, where $\lambda$ is a measure of the population-density. Equation (2.7) thus becomes $e^{-x}e^{[F(x)-1]\lambda} = e^{-\lambda}$, with $\mathrm{Supp}F = [0, \lambda]$. This yields $F(x) = \frac{x}{\lambda}$ for all $x \in [0, \lambda]$. $F(x)$ is, therefore, a uniform distribution with density $\frac{1}{\lambda}$ over the interval $[0, \lambda]$.

A natural question to be asked is why one does not seem to 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* $\langle \Gamma^+, F \rangle$ *can exist.*

*Proof of Proposition 2.3.* A necessary condition for $\langle \Gamma^+, F \rangle$ to be long-term stable is that, given the females' mate preference $\Gamma^+$, $F$ will be in equilibrium. From Lemma 2.5 we know that this holds if and only if $F$ satisfies the equality (2.7). Assume that a proportion $\varepsilon > 0$ of the females correspond to a mutant type $\Gamma^0$, ignoring the males' trait x, thus mating at random. The rest of the females are resident $\Gamma^+$. An adult x-male would then have a probability $1 - \varepsilon$ to encounter a $\Gamma^+$-female and a probability $\varepsilon > 0$ to encounter a $\Gamma^0$-female. Conditioned on the first possibility, we already know that the probability of the x-male to successfully mate is $\phi(F(x))$. Conditioned on the second possibility, any male, regardless of its x-trait, has the same, positive, probability of success, say $A > 0$. The general success-probability of an adult x-male in such a case is, therefore, $(1-\varepsilon)\phi(F(x)) + \varepsilon A$, and its fitness is, thus, given by

$$\omega_F(x) = \eta(x)\left[(1-\varepsilon)\phi(F(x)) + \varepsilon A\right] \tag{2.9}$$

Suppose now that $F$ is in equilibrium for the females' mate-preference $\Gamma^+$. We know from Lemma 2.5 that it must satisfy equality (2.7), namely $\eta(x)\,\phi(F(x)) = p_0\eta(x_0)$. Substituting in (2.9) we, thus, get

$$\omega_F(x) = (1-\varepsilon)p_0\eta(x_0) + \varepsilon A\eta(x) \tag{2.10}$$

Hence $\omega_F$, like $\eta$, is a decreasing function of $x$ for all $x > x_0$. This means that with the invasion of the equilibrium $\langle \Gamma^+, F \rangle$ by any small proportion of the females' mutation $\Gamma^0$, natural selection should operate against males with high values of the x-trait, and hence, against the resident strategy $\Gamma^+$ of preferring such males. The pair $\langle \Gamma^+, F \rangle$ is, therefore, long-term unstable. □

From Proposition 2.1 we know, though, that, in agreement with Fisher, until a certain level of males' extravagance is reached, the sexy-son effect alone can initiate a runaway process, which, in turn, stabilizes the females' preference $\Gamma^+$. Above this level, our analysis is not indicative about the exact long-term dynamics. As it follows from Proposition 2.2, this dynamics depends on the random order of the mutations and it is, therefore, 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, with females' strategy $\Gamma^+$, hence the sexy-son argument alone is insufficient to account for what appears to be a permanent maintenance of males' extravagant secondary sexual traits. Note, on the other hand, that the natural equilibrium given by the pair of strategies $\langle \Gamma_o, x_o \rangle$, with fixation of the viability-optimum $x_o$ of the male's x-trait, is always evolutionarily stable under the assumption of Fisher's model.

## 3. Long-term analysis of Zahavi's Handicap Principle

Following Zahavi we now assume that the viability of a male is a function $\eta = \eta(q, x)$ of both its investment $x$ in advertisement and some genetically inherited feature $q$, referred to as *quality*, $\eta$ being continuous and differentiable to the second degree, with

$$\frac{\partial}{\partial q}\eta(q, x) > 0. \tag{3.1}$$

For any fixed value of the quality $q$ it is assumed that $\eta$ is a unimodal function of $x$, obtaining its maximum at a point $x_0^q$ and tending to zero as $x \to \infty$. A crucial prerequisite for Zahavi's argument is that the cost of advertisement should, in some way, be more painful to individuals of low quality than to those of high quality. This was interpreted by Grafen (1990) as

$$\frac{\partial^2}{\partial q \partial x}\eta(q, x) > 0. \tag{3.2}$$

Assumption (3.2), however, may prove unrealistically (and as we shall see, unnecessarily) strong as it implies that for all $q > q_0$, $\frac{\partial}{\partial x}[\eta(q, x) - \eta(q_0, x)] > 0$. This means that for any trait-value $x^*$, $\lim_{x\to\infty}\eta(q, x) \geq \lim_{x\to\infty}\eta(q, x) - \lim_{x\to\infty}\eta(q_0, x) > \eta(q, x^*) - \eta(q_0, x^*) > 0$, contradicting the most natural assumption, given above, that for any value of $q$, $\lim_{x\to\infty}\eta(q, x) = 0$. The unacceptability of condition (3.2) to realistic situations is intuitively clear since a male of the lowest quality cannot possibly loose, in absolute value, more than all its viability, which may be very small to start with. Hence, condition (3.2) tacitly requires that a male of high quality cannot possibly loose more than a small portion of its viability even if it grows, say, a tail, thousand kilometers long. In this section we shall demonstrate a more realistic requirement that is shown to be both a necessary and sufficient condition for the evolution of males' exaggerated investment in advertisement.

Another crucial prerequisite for Zahavi's argument is that, despite purifying selection for high quality, a substantial heritable variance in heritable males' quality is permanently maintained in the population, e.g. due to mutation-selection balance in many loci. We therefore assume that some distribution $G$ of the male's quality $q$ is permanently maintained in the population, $G$ being a continuous distribution with positive density over some interval $[q_0, q^*]$.

As in the previous section it is assumed that, *given the male's quality* $q$, natural selection on the male's $x$-trait operates to increase the male's fitness as given by (2.1). Restricting our attention to polygenous populations in which the male's role is limited to fertilization, it is assumed, on the other hand, that the fertility of a female is independent of either the quality of its mate or the investment of this mate in advertisement. It is assumed, though, that both quality and tendency to advertise are at least partly heritable, hence natural selection operates in favor of female's mate-choice that increases the average male offspring's fitness. Females, however, are not able to directly measure either the fitness or the quality $q$ of a male, but they are provided with full information about its secondary trait $x$. Thus, as in the previous section, a female's strategy $\Gamma$ is any rule of mate-preference based on the male's trait $x$, $\Gamma^+$ being the female's preference of high values of this trait.

Contrary to the assumption of the previous section, we now assume that males are able to adjust their secondary trait $x$ to their quality. A male's pure strategy is, thus, a measurable mapping $x(q)$ of qualities $q \in [q_0, q^*]$ into trait-values. A general (mixed) male's strategy is a mixture of such mappings, determining an induced mapping $\{F_q(x)\}_{q_0 \leq q \leq q^*}$ of male-qualities into distributions of trait-values. Since in this work we resort only to those properties of mixed strategies that are given by their induced mappings $\{F_q(x)\}_{q_0 \leq q \leq q^*}$, we identify mixed strategies with their induced mappings. We employ an induced mapping, all the same, to characterize a population strategy, in which case we know also the distribution $G$ of the male's quality $q$. Thus, given the population strategy $\{F_q(x)\}_{q_0 \leq q \leq q^*}$, the distribution of the trait-value $x$ among all males in the population is given by

$$F(x) = \int F_q(x) dG(q). \tag{3.3}$$

As in the previous section, we start by assuming fixation of the females' mate-preference $\Gamma^+$ and ask about all possible males' strategies $\{F_q(x)\}_{q_0 \leq q \leq q^*}$ that are long-term stable against $\Gamma^+$. Then we ask about the mutual evolutionary stability of the pair $\left(\Gamma^+, \{F_q(x)\}_q\right)$, guaranteeing permanent maintenance of females' preference for males' extravagance.

If, given $\Gamma^+$, the males' strategy $\{F_q(x)\}_q$ is at equilibrium, then, using arguments similar to those given in the previous section, one can easily verify that the distribution $F$, defined by (3.3), cannot possibly have a positive probabilistic weight concentrated on a single point $x$. Being interested in males' strategies which, given $\Gamma^+$, are evolutionarily stable (and are, thus, indeed at equilibrium), we therefore restrict our attention to the case in which $F$ is a continuous distribution of the male's secondary trait with density $F' = f$, $f$ being continuous except, maybe, for a set of isolated points. In such a case (still given the females' mate-preference $\Gamma^+$), the fitness of a $(q, x)$-male is given, in exactly the same way as in the previous section, by:

$$\omega(q, x) = \omega_F(q, x) = \eta(q, x)\, \phi(F(x)) \tag{3.4}$$

where $\phi(F(x))$ represents the expected reproductive success of an adult male. A male's strategy $\{F_q(x)\}_q$ is in equilibrium (given $\Gamma^+$) if for all $q \in [q_0, q^*]$, there is a constant $c_q$ such that:

i) For all $x \in \mathrm{Supp} F_q$, $\omega_F(q, x) = c_q$.
ii) For all $x \notin \mathrm{Supp} F_q$, $\omega_F(q, x) < c_q$.

A necessary condition for the equilibrium property of $\{F_q(x)\}_q$ is that, in addition to (i), requirement (ii) holds at least as a weak inequality. The first condition is indeed necessary and sufficient for preventing short-term natural selection from re-shaping $F_q$. The second condition is responsible for long-term stability of this distribution against invading mutant strategies. From (i) and (ii) together it follows that for any value $x \in \mathrm{Supp} F_q$,

$$\frac{\partial^-}{\partial x}\omega(q,x) \geq 0 \geq \frac{\partial^+}{\partial x}\omega(q,x), \tag{3.5}$$

where $\frac{\partial^-}{\partial x}$ and $\frac{\partial^+}{\partial x}$ stand for the left and right derivatives respectively. At a point $x \in \mathrm{Supp}F_q$ in which the density function $f(x)$ is continuous, this becomes

$$\frac{\partial}{\partial x}\omega(q,x) = 0. \tag{3.6}$$

**Lemma 3.1.** *Suppose that, given* $\Gamma^+$, *the male's strategy* $\{F_q(x)\}_q$ *is at equilibrium, then for all* $q \in [q_0, q^*]$, $\mathrm{Supp}F_q \subseteq [x_0^q, \infty)$.

*Proof.* Suppose $x \in \mathrm{Supp}F_q$. Assume for simplicity that at this point $f(x)$ is continuous, then it follows from (3.4) and (3.6) that

$$\frac{\partial}{\partial x}\omega(q,x) = \frac{\partial}{\partial x}\eta(q,x)\phi(F(x)) + \eta(q,x)f(x)\phi'(F(x)) = 0 \tag{3.7}$$

This implies $\frac{\partial}{\partial x}\eta(q,x) = -\eta(q,x)f(x)\phi'(F(x))/\phi(F(x)) \leq 0$ with sharp inequality whenever $f(x)$ is strictly positive. Recalling that $\eta = \eta(q,x)$ is a unimodal function of $x$ with a maximum at $x_0^q$, it follows from the last inequality that $x \geq x_0^q$ with sharp inequality whenever $f(x) > 0$. With some technical elaboration, employing (3.5), this simple argument can be readily generalized to discontinuity-points of $f$.

**Proposition 3.1.** *A necessary condition for the Evolutionary Stability of the pair* $\left\langle \Gamma^+, \{F_q(x)\}_q \right\rangle$ *(for both short and long-term evolution) is that for any value* $q \in [q_0, q^*]$ *and for all* $x \in \mathrm{Supp}F_q$,

$$\frac{\partial^2}{\partial q \partial x}\ln \eta(q,x) \geq 0. \tag{3.8}$$

*Proof of Proposition 3.1.* Suppose first that, given $\Gamma^+$, $\{F_q(x)\}_q$ is Evolutionarily Stable and, thus, indeed, in equilibrium. In this case (3.7) holds for all $x \in \mathrm{Supp}F_q$. This yields

$$f(x)\phi'(F(x)) = -\frac{1}{\eta(q,x)}\frac{\partial}{\partial x}\eta(q,x)\phi(F(x)). \tag{3.9}$$

It also follows from (3.7) that for all $x$ and $q$,

$$\frac{\partial^2\omega(q,x)}{\partial q \partial x} = \frac{\partial^2}{\partial q \partial x}\eta(q,x)\phi(F(x)) + \frac{\partial}{\partial q}\eta(q,x)f(x)\phi'(F(x)) \tag{3.10}$$

Inserting (3.9) into (3.10) we, thus, get, for all $x \in \mathrm{Supp}F_q$

$$\frac{\partial^2 \omega(q,x)}{\partial q \partial x} = \frac{\partial^2}{\partial q \partial x}\eta(q,x)\phi(F(x)) - \frac{1}{\eta(q,x)}\frac{\partial}{\partial q}\eta(q,x)\frac{\partial}{\partial x}\eta(q,x)\phi(F(x))$$
$$= \eta(q,x)\phi(F(x))\frac{\partial^2}{\partial q \partial x}\ln\eta(q,x). \tag{3.11}$$

Out of continuity arguments it is sufficient to prove (3.8) for all values of $q$ in the open interval $(q_0, q^*]$. Thus, suppose that for some value $q^{\sim} \in (q_0, q^*]$ and for some $x^{\sim} \in \mathrm{Supp}F_{q^{\sim}}$, the condition (3.8) is not satisfied, thus at $(q^{\sim}, x^{\sim})$, $\frac{\partial^2}{\partial q \partial x}\ln\eta(q,x) < 0$. From (3.11) it would, then, follow, that at this point $\frac{\partial^2\omega(q,x)}{\partial q \partial x} < 0$ while indeed $\frac{\partial}{\partial x}\omega(q,x) = 0$. This means that for some value $q_{\sim} < q^{\sim}$ sufficiently close to $q^{\sim}$, and for $x = x^{\sim}$, we get $\frac{\partial\omega(q,x)}{\partial x} > 0$. But we know also that as $x \to \infty$, $\eta(q,x) \to 0$ and, therefore, $\omega(q,x) \to 0$, hence $\omega(q,x)$ must get its maximum at some point $x_{\sim} > x^{\sim}$. This means that the females' strategy $\Gamma^+$ would prescribe the preference of a $(q_{\sim}, x_{\sim})$-male over the $(q^{\sim}, x^{\sim})$-male, whose quality was chosen to be higher. Moreover, having $x^{\sim} \in \mathrm{Supp}F_{q^{\sim}}$, we know that, given $\Gamma^+$, $\omega(q^{\sim}, x^{\sim}) \geq \omega(q^{\sim}, x)$ for any value of $x$ (otherwise it would be disadvantageous for a male of quality $q^{\sim}$ to choose the trait-value $x = x^{\sim}$); hence, as a special case, $\omega(q^{\sim}, x^{\sim}) \geq \omega(q^{\sim}, x_{\sim})$. But from $q_{\sim} < q^{\sim}$ and (3.1) we indeed know that $\omega(q^{\sim}, x_{\sim}) > \omega(q_{\sim}, x_{\sim})$, hence $\omega(q^{\sim}, x^{\sim}) > \omega(q_{\sim}, x_{\sim})$.

We thus end up with the conclusion that if (3.8) does not hold, then the females' strategy $\Gamma^+$ should prescribe the preference of a male $(q_{\sim}, x_{\sim})$ with a relatively lower fitness over a male $(q^{\sim}, x^{\sim})$ with a relatively higher fitness (given $\Gamma^+$). Hence, given $\{F_q(x)\}_q$, $\Gamma^+$ cannot possibly be the best mate-preference for a female and therefore the pair $\left\langle \Gamma^+, \{F_q(x)\}_q \right\rangle$ cannot be evolutionarily stable. □

Note that both condition (3.8) and condition (3.2), previously suggested by Grafen, seem to stand in agreement with the verbal argument of Zahavi, that a trustful signal for quality requires a cost of investment which decreases with quality. Condition (3.8), however, requires that the *relative* cost of advertisement should be decreasing with $q$. Instead, condition (3.2) requires a decrease in the *absolute* cost of advertisement, an unrealistic requirement as it was shown above. Recalling $\frac{\partial\eta}{\partial q} > 0$ and (as concerning $x > x_0^q$) $\frac{\partial\eta}{\partial x} < 0$, we have $\eta\frac{\partial^2\ln\eta}{\partial q\partial x} = \frac{\partial^2\eta}{\partial q\partial x} - \frac{1}{\eta}\frac{\partial\eta}{\partial q}\frac{\partial\eta}{\partial x} > \frac{\partial^2\eta}{\partial q\partial x}$, hence condition (3.8) is indeed weaker than condition (3.2). The main result of this section is, thus, given in the following proposition.

**Proposition 3.2.** *Assume females' mate-preference* $\Gamma^+$, *and assume that for any pair of values* $q$ *and* $x$, *the viability-function* $\eta(q,x)$ *satisfies a sharp version of the condition (3.8), say:*

$$\frac{\partial^2}{\partial q \partial x}\ln\eta(q,x) > 0, \tag{3.12}$$

*then:*

*i) Any males' equilibrium-strategy is given by a continuous, monotone increasing one-to-one mapping* $x(q)$ *of the male's quality* $q$ *into the males secondary trait* $x$, *with* $x(q_0) = x_0^{q_0}$.

*ii) The fitness* $\omega(q, x(q))$ *of a male of quality* $q$ *is then an increasing function of its quality* $q$ *and hence of its observed secondary trait* $x(q)$. *This, in turn, makes females' mate-preference* $\Gamma^+$ *evolutionarily stable.*

In order to prove Proposition 3.2, we first prove the following Lemmas:

**Lemma 3.2.** *Assume condition (3.12) (for any* $x$ *and* $q$*) and suppose that, given* $\Gamma^+$, $\left\{F_q(x)\right\}_q$ *is an equilibrium-strategy, then*

*i)* $\left\{F_q(x)\right\}_q$ *is separating, prescribing different secondary traits* $x$ *to different male-qualities* $q$.

*ii) If* $q_1 < q_2$, $q_1, q_2 \in \left[q_0, q^*\right]$, *then for any secondary trait-value* $x_1 \in \mathrm{Supp}F_{q_1}$, *there is a secondary trait-value* $x_2 \in \mathrm{Supp}F_{q_2}$ *such that* $x_2 > x_1$*; for any secondary trait-value* $x_2 \in \mathrm{Supp}F_{q_2}$, *there is a secondary trait-value* $x_1 \in \mathrm{Supp}F_{q_1}$ *such that* $x_2 > x_1$.

*Proof of Lemma 3.2.* i) Inequality (3.12) implies that for any value of $x$, $\frac{\partial}{\partial x}\omega(q, x)$ is a strictly increasing function of $q$, hence, given $x$, the condition (3.6) for $x \in \mathrm{Supp}F_q$, namely $\frac{\partial}{\partial x}\omega(q, x) = 0$, cannot hold simultaneously for two different values of $q$.

ii) If $q_2 > q_1, x_1 \in \mathrm{Supp}F_{q_1}$, we already know that $\left.\frac{\partial\omega(q_2,x)}{\partial x}\right|_{x=x_1} > 0$. Recalling that for all $q$, $\omega(q, x) \to 0$ as $x \to \infty$, it follows that $\omega(q_2, x)$ gets its maximum at some point $x_2 > x_1, x_2 \in \mathrm{Supp}F_{q_2}$. In the same way, if $x_2 \in \mathrm{Supp}F_{q_2}$, $\left.\frac{\partial\omega(q_1,x)}{\partial x}\right|_{x=x_2} < 0$. But $\omega(q_1, x)$ is indeed an increasing function of $x$ for $x < x_0^{q_1}$, hence $\omega(q_1, x)$ obtains a maximum at some point $x_1 < x_2, x_1 \in \mathrm{Supp}F_{q_1}$. □

**Lemma 3.3.** *Assume condition (3.12) and suppose that, given* $\Gamma^+$, $\left\{F_q(x)\right\}_q$ *is an equilibrium-strategy, then* $\mathrm{Supp}F$ *must be an interval, say* $\mathrm{Supp}F = \left[x_0, x^*\right]$.

*Proof of Lemma 3.3.* Suppose $x_1 < x_2, x_1 \in \mathrm{Supp}F, x_2 \notin \mathrm{Supp}F$. It is enough to show that for all $x > x_2, x \notin \mathrm{Supp}F$. Suppose, on the contrary, $x \in \mathrm{Supp}F$ exists such that $x > x_2$, then there must be a value $x_3 > x_2$ such that $x_3 \in \mathrm{Supp}F$, but $x \notin \mathrm{Supp}F$ for all $x_2 \leq x < x_3$. From $x_3 \in \mathrm{Supp}F$ it follows that $x_3 \in \mathrm{Supp}F_{q_3}$ for some $q_3 \in \mathrm{Supp}G$. From the fact that $x \notin \mathrm{Supp}F$ for all $x_2 \leq x < x_3$ it follows that $f(x) = 0$ on some left-vicinity of $x_3$. From Lemma 3.1 it, therefore, follows that $x_3 = x_0^{q_3}$.

In the same way: from $x_1 \in \mathrm{Supp}F$ it follows that $x_1 \in \mathrm{Supp}F_{q_1}$ for some $q_1 \in \left[q_0, q^*\right]$. From Lemma 3.1 it then follows that $x_0^{q_1} \leq x_1 < x_3 = x_0^{q_3}$. But condition (3.12) immediately implies that the value $x = x_0^q$ at which $\eta(q, x)$ achieves its maximum is an increasing function of $q$, hence $q_1 < q_3$. We thus infer that for any positive value $\varepsilon > 0$ there exists a value $q \in \left[q_0, q^*\right]$ with $q_3 - \varepsilon < q < q_3$. From the continuity of $x_0^q$ it therefore follows that a value $q \in \left[q_0, q^*\right]$ exists such that $q < q_3$ and $x_2 < x_0^q < x_0^{q_3} = x_3$. But since $q < q_3$ we know from Lemma 3.2 that a value $x \in \mathrm{Supp}F_q$ exists with $x < x_3$.

Employing, again, Lemma 3.1, we infer that $x_2 < x_0^q \leq x$, hence $x_2 < x < x_3$ where $x \in \mathrm{Supp}F$, in contradiction with the assumption that $x \notin \mathrm{Supp}F$ for all $x_2 \leq x < x_3$. Hence $\mathrm{Supp}F$ must be a connected interval. □

Immediately from Lemmas 3.2 and 3.3 we get:

**Lemma 3.4.** *Given (3.12), condition (3.6) is not only necessary, but also sufficient for* $x \in \mathrm{Supp}F_q$.

*Proof of Lemma 3.4.* Assume condition (3.12) and suppose that, given $\Gamma^+$, $\left\{F_q(x)\right\}_q$ is an equilibrium-strategy. Suppose, moreover, that $\frac{\partial}{\partial x}\omega(q,x) = 0$ for some $q \in \left[q_0, q^*\right]$, then it immediately follows from Lemmas 3.2 and 3.3 that $x \in \mathrm{Supp}F_q$. □

With these results we now return to the proof of the proposition.

*Proof of Proposition 3.2.* i) Any male equilibrium strategy determines a unique distribution $F$ of males' trait values. This, in turn, determines the fitness function $\omega(q,x) = \omega_F(q,x) = \eta(q,x)\,\phi(F(x))$. From Lemma 3.4 it follows that, given $F$, males' equilibrium strategies are determined by the points that satisfy $\frac{\partial}{\partial x}\omega(q,x) = 0$ or, equivalently (since $\omega$ is indeed positive on $\mathrm{Supp}F$),

$$\frac{\partial}{\partial x}\ln\omega(q,x) = 0. \tag{3.13}$$

From formula (3.1) it follows that $\eta$ (since it is positive on $\mathrm{Supp}F$) satisfies $\frac{\partial}{\partial q}\ln\eta(q,x) > 0$. This, together with the definition (3.4) of $\omega$ implies that

$$\frac{\partial}{\partial q}\ln\omega(q,x) > 0. \tag{3.14}$$

This same definition, together with (3.12) implies

$$\frac{\partial^2}{\partial q\,\partial x}\ln\omega(q,x) > 0. \tag{3.15}$$

From (3.14) and the Implicit Function Theorem it follows that the solution of (3.13) on the compact interval $[q_0, q^*]$ can be written as a unique continuous function $x = x(q)$ of $q$. Given $F$, and therefore $\omega$, there can be only one such function, since (3.15) implies that for each given $q$ there is at most a single value $x = x(q)$ for which (3.13) is satisfied. From Lemma 3.2 it follows that the solution must be monotone increasing. Hence, given condition (3.12) and assuming the females' mate-preference $\Gamma^+$, any equilibrium-strategy (and thus, indeed, any evolutionarily stable strategy) of the males is given by a continuous, monotone increasing one-to-one mapping $x(q)$ of the male's quality $q$ on the males secondary trait $x$. The restriction $x(q_0) = x_0^{q_0}$ then follows immediately from Lemma 3.1.

ii) Suppose $q_1 > q_2$, $q_1, q_2 \in \mathrm{Supp}G$. We know that $x(q_1)$ is maximizing $\omega(q_1,x)$, hence $\omega(q_1,x(q_1)) \geq \omega(q_1,x(q_2))$. But for any value of $x$, the fitness $\omega(q,x) = \eta(q,x)\,\phi(F(x))$ is a strictly increasing function of $q$, hence $\omega(q_1,x(q_2)) > \omega(q_2,x(q_2))$ and we get $\omega(q_1,x(q_1)) > \omega(q_2,x(q_2))$. □

## 4. The case of random encounters

As in Sect. 2, let us assume now random encounters among males and females, in which case we already know that the number of competitors encountered by a random courting male has a Poisson distribution with a generating function:

$$\phi(s) = \sum_{k=0}^{\infty} e^{-\lambda}\frac{\lambda^k}{k!}s^k = e^{\lambda(s-1)}, \tag{4.1}$$

where the parameter $\lambda$ stand for the intensity of encounters, interpreted as the population density. As in the previous section assume, for simplicity, $x_0^q = 0$ for all $q \in [q_0, q^*]$ and let us further measure the male's investment $x$ in units of a logarithmic cost for the lowest-quality -male, thus $\eta(q_0, x) = e^{-x}$. For any value $q > q_0$, we most generally assume

$$\eta(q, x) = c(q)e^{-xr(q)}, \tag{4.2}$$

where $c$ and $r$ are positive and differentiable functions of $q$, $c' > 0$ and $r' < 0$, $c(q_0) = r(q_0) = 1$. We further assume that the quality-distribution $G(q)$ is continuous with a positive density $G'(q) = g(q) > 0$ for all $q_0 \leq q \leq q^*$.

From (4.2) it follows that $\frac{\partial^2}{\partial q \partial x} \ln \eta(q, x) = -r'(q) > 0$, regardless of $c(q)$, hence $\eta$ satisfies the condition (3.12). From Proposition 3.2 we thus infer the existence of a mapping $x(q)$ of quality over advertisement such that the pair $\langle \Gamma^+, x(q) \rangle$ is evolutionarily stable, $x(q)$ and $\omega(q, x(q))$ being monotone increasing functions of $q$.

Given $\Gamma^+$, one can employ (3.4) to obtain $\frac{\partial}{\partial x} \ln \omega(q, x) = \lambda f(x) - r(q)$. Thus, at a point $x = x(q)$at which $\frac{\partial}{\partial x}\omega(q, x) = 0$, we get

$$\lambda f(x) = r(q). \tag{4.3}$$

Now, from the monotone increasing of $x(q)$ we get $F(x(q)) = p\{x(Q) \leq x(q)\} = p\{Q \leq q\} = G(q)$, hence, by differentiating, $f(x(q))x'(q) = g(q)$. Inserting into (4.3), we thus get the differential equation

$$x'(q) = \lambda \frac{g(q)}{r(q)}. \tag{4.4}$$

With the restriction $x(q_0) = x_0^{q_0} = 0$, this equation has a unique solution on the interval $q_0 \leq q \leq q^*$:

$$x(q) = \lambda \int_{q_0}^{q} \frac{dG(y)}{r(y)}. \tag{4.5}$$

**Corollary 4.1 (the case of random encounters).** *Given all other parameters of the model, the logarithm of the Evolutionarily Stable viability-cost of male's advertisement, which is an increasing function of the male's quality q, is also proportional to the intensity λ of male-competition.*

Note that at least when concerning the case of random encounters in dense populations, this corollary leads to the inevitable conclusion that, as having been suspected by Maynard Smith (1976), the cost of advertisement of a top male can only be partly compensated by its quality. More specifically it follows from (4.2) and (4.5) that for all $q_0 \leq q \leq q^*$:

$$\frac{d}{dq}\eta(q, x(q)) = \frac{\partial \eta}{\partial q} + x'(q)\frac{\partial \eta}{\partial x} = \left[\frac{c'(q)}{c(q)} - r'(q)x\,(q) - \lambda g(q)\right] c(q)e^{-x(q)r(q)} \tag{4.6}$$

Recalling that $c'(q) > 0$, $r'(q) < 0$, and $g(q) > 0$, it follows that for any value $q_0 \leq q \leq q^*$, there is a value $\lambda_q = \frac{c'(q)-c(q)r'(q)x(q)}{c(q)g(q)} > 0$, such that $\frac{d}{dq}\eta(q, x(q)) > 0$ for $\lambda < \lambda_q$ and $\frac{d}{dq}\eta(q, x(q)) < 0$ for $\lambda > \lambda_q$. Denote $\lambda_1 = Min_{q_0 \leq q \leq q^*}\lambda_q$ and $\lambda_2 = Max_{q_0 \leq q \leq q^*}\lambda_q$, we get:

**Corollary 4.2 (the case of random encounters).** *Given all other parameters of the model, there are two values, $\lambda_1$ and $\lambda_2$, $\lambda_2 \geq \lambda_1 > 0$, such that*

*i) If the population density is sufficiently low, say $\lambda < \lambda_1$, then the male's viability $\eta(q, x(q))$ is an increasing function of its quality (and, hence of its observed evolutionarily stable investment x in advertisement).*

*ii) If the population density is sufficiently high, say $\lambda > \lambda_2$, then the males' viability is a decreasing function of its quality (and, hence of its observed evolutionarily stable investment in advertisement).*

We, thus, see that in the a case of dense populations, although male's extravagant advertisement indeed serves as a trustful proof of quality, the direct advantage of high quality can only partly compensate for the viability cost of advertisement. Proposition 3.2 asserts, on the other hand, that even in this case, as long as the females' mate-preference $\Gamma^+$ prevails in the population, it remains selectively advantageous for any single female to follow the majority-rule, thus to prefer highly advertising males, even though thereby decreasing the expected viability of its offspring. But then, the selective advantage, accrued to a female by choosing such a male can only stem from the perspective of thereby increasing the offspring's sexual success, a success guaranteed only if large enough majority of females in the population indeed follows the mate-preference $\Gamma^+$. Hence, a quantitative examination of Zahavi's argument in this case tacitly leads us back to Fisher's argument of the Sexy Son! For a more thorough discussion of the intricate connections between the two theories of sexual selection and a suggested first step toward their unification see Eshel et al. (2000).

## 5. Summary

A long-term-evolution model of sexual selection in polygenous populations was analyzed, in which females were assumed to choose each a mate from a random group of males. Natural selection on male's genotype was assumed to operate in favor of male's fitness, which was defined as the product of viability and expected reproductive success in maturity, if reached. Assuming, though, independence of progeny size on female's mate choice (see Eshel et al. 2000 for discussion), female's choice was assumed to be selected in favor of offspring's fitness, as affected by father's genes. Naturally assuming that females are unable to directly recognize male's genes, females' mate choice was supposed to be exclusively based on a quantitative secondary trait of the male's phenotype. The model was employed to quantitatively study two principles suggested to explain the evolution and persistence of females' preference for males' extravagance.

In Sect. 2, following Fisher's "Sexy Son" argument, it was assumed that costly male's extravagance could only be favorable because of female's preference for it, and female's preference for male's extravagance, when fixed in the population, could only be favorable because of expected sexual success of extravagant offspring. In agreement with Fisher it was shown that once females' preference for males extravagance is established in the population, a "Runaway Process" is expected to perpetuate itself, thereby stabilizing females' preference for males' extravagance. The process was shown to continue, undisturbed, up to a level in which the cost of advertisement for the most extravagant male drops below the chance of the least favorable male to find a female uncourted by other males. Contrary to the prediction of Fisher it was shown that the population dynamics, in such a case, couldn't possibly lead to a long-term stable equilibrium. The establishment of any equilibrium of the males' extravagant behavior, which is stable in face of females' mate preference for it, was shown to result in the destabilization of females' preference for extravagant males and, hence, the reversion of the process. The only stable end-result of the long-term process was shown to allow no males' exaggeration.

In Sect. 3, following Zahavi's argument of the Handicap Principle, it was shown that the situation is different if males are able to adjust their level of advertisement to their varied qualities. In such a case, a necessary and sufficient condition, say (3.12), was found, under which an evolutionarily stable equilibrium exists in the population, in which females prefer advertising males. In this case it was shown that male's advertisement must be a deterministic, monotone increasing function of individual quality, hence a trustful signal of it. More importantly for the evolution of female's preference, it was shown that despite of the cost of the signal, the total reproductive success of a male remains an increasing function of its quality, hence of the level of advertisement observed by the courted female. In agreement with the verbal argument of Zahavi, condition (3.12) requires that the *relative* cost of investment should be decreasing with quality (Based on a different model, a somehow stronger sufficient condition was suggested by Grafen, 1990, according to which the absolute cost of investment should be decreasing with quality).

In agreement with Grafen (1990) we have assumed that the choice of a less attractive mate, when it occurs, should result from the lack of availability and not from misjudgment on the side of the female (e.g. Kirkpatrick 1987, Iwasa and Pomiankowski 1995, Pomiankowski and Iwasa 1998 and references there). This makes the intensity of sexual selection, and hence the male's optimal investment in advertisement, an increasing function of the population density (see also Eshel 1979). In Sect. 4, concentrating on the case of random encounters between males and females, it was thus shown that while male's viability in sparse population, despite the cost of advertisement, is an increasing function of quality, this is not the case when the population density is sufficiently high. In the latter case it was shown that male's advertisement becomes costly enough as to turn male's viability into a decreasing function of quality. In such case, as it appears from the analysis, females' preference for high male's advertisement could only remain stable in the population due to the tacit effect of offspring sexual success. Fisher's argument of the Sexy Son, although by itself proved insufficient to account for the persistence of males' extravagance, was shown in this case to be an indispensable though tacit component in the evolution and maintenance of this phenomenon according to Zahavi's Handicap Principle.

*Acknowledgements.* For their support and hospitality Ilan Eshel wishes to thank the Department of Mathematics and its Applications, at the University of Napoli, and the Italian CNR. Emilia Sansone wishes to thank the School of Mathematics and the Department of Statistics at Tel Aviv University, where she spend part of the time in which this work was done. Frans Jacobs wishes to thank the National Institutes of Health grant GM56693 for partial support while working on this paper.

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