The Courtship Handicap—Phenotypic Effect

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A simple model showing the possibility of direct selective advantage to
those females which choose handicapped males as their mates.

1. Introduction

By proposing his *handicap principle*, Zahavi (1975, 1977) claims that for
a communication system to be reliable and less exposed to the possibility
of cheating, it should contain a reliability component, which takes the form
of a handicap. In other words, in order that a message will have some
valuable meaning, it should constitute a burden or a cost to the advertiser.

One of Zahavi's main applications of the handicap principle is to the
theory of sexual selection. Zahavi suggests that many sexually attracting
markers and behavioral patterns are really handicaps, which actually lower
the fitness of their carriers. Because of their discriminatory effects on
different quality types of the selected sex, these handicaps are of use to
the selecting sex, since they test the quality of the mate.

In their critical papers, Maynard Smith (1976, 1978a) and Davis &
O'Donald (1976), using simple quantitative models, concluded that the
handicap is very unlikely to be selected for in any natural population. Eshel
(1978), on the other hand, points to natural situations which enable the
evolution of the handicap, and he emphasizes the importance of linkage
between the marker and "quality" to that evolution.

It is not the intention of this work to deal with the more controversial
part of Zahavi's theory of sexual selection. We restrict ourselves here to
certain situations in which both the evolution of the handicap in males,
and the evolution of the tendency in the females to prefer the handicapped
males, are more likely to occur. The situations considered here are those
cases in which the effect of natural selection on the various "quality" types
in the population is particularly expressed during the period *after* the
females have chosen their mates. More specifically, we are dealing with

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monogamous populations with parental care. Here, the male's "quality" sought by the females is his ability to contribute to the fertility of the pair and to the viability of the offspring. Following Zahavi, it is assumed that this sort of "quality" is correlated with traits which enable the individual to cope, quite successfully, with precarious situations happening before mating. The objective of this article is to show that in certain circumstances, if such situations are not likely to occur before mating, it may be advantageous for the male to deliberately put himself into them, thus proving his quality even at the expense of some reduction in his viability, and that it is advantageous for the female to choose such a handicapped male. This is demonstrated by the following, very simplified model.

2. The Model

We consider a monogamous population, with parental care. For the sake of mathematical convenience, we assume that this population is haploid.

A will denote the high quality and a the low quality types, and that trait is expressed in both males and females. A second trait, the marker, is expressed in males only, which can be either conspicuous (having the handicap) or cryptic (without that marker).

The relative fecundities of A and a are 1 and $1 - s$ $(0 < s \le 1)$, respectively. The handicap affects the survival chances, prior to the pair formation, of the conspicuous males, and these chances, relative to those of the cryptic males, are $1 - t$ for the handicapped A male and $1 - v$ for the handicapped a male. We assume $t < v$, which means that the handicap is more disadvantageous for the low quality than for the high quality males. We also assume that the fecundity of a pair is the product of the fecundities of its components.

We will compare now the expected reproductive success of a female that chooses a handicapped male as her mate (a *choosing* female) with that of a female that chooses her mate at random (a *non-choosing* female). Since we assume both quality and the handicap to be inherited traits, we have to consider not only the expected size of next-generation progeny, but also the composition of that progeny as to the various possible types. Descendants of a high quality male are more likely to be of the high quality type themselves, as well as choosing a handicapped male as a mate results in handicapped descendants, and these factors should be considered. Thus we compare the expected size of the third generation (i.e. the expected number of young grand-descendants) of the various females. (See, for example, Fisher's (1958) argument concerning the evolution of the sex ratio.)

We denote by p and $q = 1 - p$ the relative frequencies, prior to selection, of A and a, respectively. Assuming the marker to be very rare, the expected numbers of mature descendants of a non-choosing female are

Type of female	Expected number of descendants	
	A type	a type
A	$p + \frac{1}{2}q(1-s)$	$\frac{1}{2}q(1-s)$
a	$\frac{1}{2}p(1-s)$	$[\frac{1}{2}p + q(1-s)](1-s)$

Hence, for a random non-choosing female, the expected third-generation size is

$$W_1 = p\{p + \tfrac{1}{2}q(1-s) + \tfrac{1}{2}q(1-s)^2\} + q\{\tfrac{1}{2}p(1-s) + [\tfrac{1}{2}p + q(1-s)](1-s)^2\}$$
$$= p^2 + pq(1-s) + pq(1-s)^2 + q^2(1-s)^3.$$

For a choosing female, the expected numbers of mature descendants are

Type of female	Expected number of descendants	
	A type	a type
A	$[\tilde{p} + \tfrac{1}{2}\tilde{q}(1-s)](1-\theta t)$	$\tfrac{1}{2}\tilde{q}(1-s)(1-\theta v)$
a	$\tfrac{1}{2}\tilde{p}(1-s)(1-\theta t)$	$[\tfrac{1}{2}\tilde{p} + \tilde{q}(1-s)](1-s)(1-\theta v)$

where $\tilde{p}$ and $\tilde{q} = 1 - \tilde{p}$ are the frequencies of A and a among the conspicuous males just before pair formation. Assuming no linkage disequilibrium between the "quality" and the marker (an assumption which is less favorable to the evolution of the handicap), we have

$$\tilde{p} = \frac{p(1-t)}{p(1-t) + q(1-v)}.$$

(Indeed, even with free recombination, a positive linkage disequilibrium will be established within one generation). The number θ stands for the proportion of the handicapped descendants among the progeny. If we assume a $1:1$ sex ratio among the young, then $\theta = \frac{1}{2}$ if the female also carries the (here, inactive) marker genes, and $\theta = \frac{1}{4}$ if she is not of the handicapped genotype.

Henceforward we assume that the choosing female is of the handicapped type ($\theta = \frac{1}{2}$), a case less favorable to the evolution of that trait. With this assumption, the expected size of the third generation of a random, choosing female is

$$
\begin{aligned}
W_2 = {} & p\{[\tilde{p} + \tfrac{1}{2}\tilde{q}(1-s)](1-\tfrac{1}{2}t) + \tfrac{1}{2}\tilde{q}(1-s)^2(1-\tfrac{1}{2}v)\} \\
& + q\{\tfrac{1}{2}\tilde{p}(1-s)(1-\tfrac{1}{2}t) + [\tfrac{1}{2}\tilde{p} + \tilde{q}(1-s)](1-s)^2(1-\tfrac{1}{2}v)\} \\
= {} & (1-\tfrac{1}{2}t)[p\tilde{p} + \tfrac{1}{2}(1-s)(p\tilde{q} + \tilde{p}q)] \\
& + (1-\tfrac{1}{2}v)[\tfrac{1}{2}(p\tilde{q} + \tilde{p}q) + q\tilde{q}(1-s)](1-s)^2.
\end{aligned}
$$

We investigate the conditions for W_2 to be larger than W_1.

3. Results

Computational investigation of the case in which the choosing females also carry the handicap (which is unexpressed, yet inheritable, if carried by a female) yielded the following result: For every s, t and v in the domain $0 < s \leq 1$ and $0 \leq t < v \leq 1$, there exist two functions, $\phi(s, t, v)$ and $\psi(s, t, v)$, such that if $\phi < \psi$, then for every q, $\phi < q < \psi$, $W_2 > W_1$ (i.e. the females choosing the handicapped males have a selective advantage over the non-choosing females). We shall call the interval (ϕ, ψ) (whenever it exists) the *favoring interval* (favoring the choosing females).

(1) ϕ is an increasing function of t and decreasing in s and v, whereas ψ is a decreasing function of t and increasing in s and v.

(2) The favoring interval can exist for every t and for every v $(t < v)$.

(3) The favoring interval does not exist for every s. (It exists for all $s \geq 0.1315$.) In other words, even if $t = 0$ (i.e. the handicap constitutes a burden to the a type only), but s is very small, the favoring interval does not always exist.

(4) Even in the case of a completely sterile a type ($s = 1$), the favoring interval does not always exist. It exists, then, if, and only if, $v > t + \frac{1}{2}t(1-t)$.

(5) The favoring interval, whenever it exists, does not spread up to include values in the neighborhood of $q = 1$. That is to say, unless $s = 1$ or $v = 1$, ψ is always smaller than 1. Thus, if the relative frequency of the low quality type is large (larger than ψ), choosing by the marker is disadvantageous for the random female. This is because she has a large probability of being an a type herself, and thus her descendants are very likely to be a's. If she chooses by the marker, her mostly a progeny is subject to a great reduction in size because of the inherited handicap.

Table 1 gives examples of favoring intervals for the case in which the choosing females also have the (unexpressed) handicap, as well as for the case in which they are not of the handicapped genotype.

TABLE 1

Examples of favoring intervals

| | | | The favoring interval | |
| | | | if the choosing female is of the handicapped genotype ($\theta = \frac{1}{2}$) | if the choosing female is not of the handicapped genotype ($\theta = \frac{1}{4}$) |
s	t	v		
0·20	0·05	0·85	does not exist	(0·0794, 0·8502)
0·20	0·05	0·90	(0·3762, 0·4783)	(0·0725, 0·8975)
0·20	0·05	0·95	(0·2553, 0·7354)	(0·0667, 0·9471)
0·30	0·05	0·54	does not exist	(0·0793, 0·7957)
0·30	0·05	0·57	(0·2647, 0·4757)	(0·0739, 0·8093)
0·30	0·05	0·60	(0·2282, 0·5280)	(0·0691, 0·8226)
0·50	0·10	0·70	(0·1413, 0·8863)	(0·0645, 0·9506)
0·50	0·15	0·70	(0·2230, 0·8643)	(0·1001, 0·9443)
0·50	0·20	0·70	(0·3188, 0·8315)	(0·1391, 0·9363)
0·60	0·59	0·90	(0·6270, 0·8782)	(0·2814, 0·9694)
0·60	0·60	0·90	(0·6523, 0·8652)	(0·2888, 0·9681)
0·60	0·61	0·90	(0·6826, 0·8474)	(0·2965, 0·9666)
0·70	0·05	0·09	does not exist	(0·4380, 0·8483)
0·70	0·05	0·11	does not exist	(0·2708, 0·9094)
0·70	0·05	0·13	(0·4668, 0·7886)	(0·1982, 0·9295)
0·80	0·05	0·09	does not exist	(0·3638, 0·9373)
0·80	0·05	0·11	(0·5234, 0·8678)	(0·2353, 0·9604)
0·80	0·05	0·13	(0·3696, 0·9170)	(0·1745, 0·9688)

4. Conclusions

This simple model shows the possibility, at least at the appearance of the handicap, of a direct selective advantage to those females which choose the handicapped males as their mates. In these situations, the relative frequency in the population of the choosing females, and with it the frequency of the marker, will increase. A crucial factor for the evolution of the handicap is the existence of a quality variation within the population, a variation we believe to be maintained by may factors in any natural population (see Taylor & Williams, 1982; also Maynard Smith, 1978b).

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