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ON A PREY-PREDATOR NONZERO-SUM GAME AND THE EVOLUTION OF GREGARIOUS BEHAVIOR OF EVASIVE PREY

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I. CONCEALMENT, EVASION, AND THE STRUCTURE OF THE SELFISH HERD

Gregarious behavior of a potential prey has long attracted the attention of naturalists. Explanations commonly relate to courting and mating, location and gathering of food, active mutual help against predation, and passive protection through evasion. Each presumably corresponds to a different set of proximate and ultimate causes (see Wilson [1975] and many references therein). This article concentrates on the last case in the list. Several of those who have considered the problem have found gregarious behavior of prey populations to be rather parodoxical, especially for prey that seem unable to offer any aggressive protection for themselves against predators even when in a large herd (e.g., Hesse et al. 1937; Fisher 1954; Lorenz 1966). It seems that gregarious behavior in some cases can facilitate predation to an almost suicidal degree (Breder 1959). Wynne-Edwards (1962, 1964) considered gregarious behavior as necessary for control of population size, advantageous to the population as a whole, and therefore worth the toll exacted by predators. The crucial question becomes, How can forces of natural selection within the prey population possibly tolerate the evolution of such individually deleterious behavior, even if this behavior is advantageous to the entire population?

The first attempts to explain examples of gregarious behavior on the basis of advantage to the individual were made by Williams (1964, 1966) and, later, by Hamilton (1971). As these authors pointed out, constant predation of peripheral individuals in an already established herd can provide a selective force to intensify gregarious behavior once such behavior has been adopted in a prey population. More important for the understanding of the evolution of gregarious behavior is the observation (Hamilton 1971) that, if a predator picks its prey at random from the first-located group, then the predation probability of any individual in a large herd may be smaller than that of a single individual of the same species. For example, if the predator takes just one individual from the first-located group of prey, and if the location probability of any group of prey is less than proportional to the size of the group, then gregarious behavior from the first stages of its establishment in a population is likely to decrease the individual's relative probability of predation and will thus be selected for.

Analytically, Hamilton's arguments relate to a zero-sum game of N players (let N equal all individuals of the prey population). This means that the total sum of prices

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relevant to the game of natural selection, namely, survival and relative contribution to the next generation, is fixed. (Indeed, this assumption, typical of almost all models of natural selection, is the extreme opposite of the assumption of a group price made by Wynne-Edwards [1962].) We will see, however, that a crucial prerequisite for the zero-sum model of Hamilton is that the role of the predator be restricted to that of a probabilistic nature force rather than to that of an active, rational player. Actually, unlike its prey, the "ideal predator" studied by Hamilton (e.g., his imaginary water snake) is not free to choose among alternative strategies or to react to changes in the strategy of the prey.

This passive role may well fit the observed behavior of predators of aphids, snails, eggs of nesting birds, and, sometimes, fish (e.g., see Breder 1959; Bullis 1960). In all these examples, the main activity of the predator concerns location rather than an active pursuit of the prey. However, the situation is completely different for birds of prey or for big predators of ungulates in the open plain. More generally, it seems that if prey is abundant, if cover is sparse, and if hunting is energy consuming the predator is not likely to attack the first-located group of prey but, rather, to choose a strategy that will minimize the energy consumed in hunting a single prey (see, e.g., Wilson 1975, p. 142). In such cases, it is a common interest of both the predator and the high-quality prey individuals to minimize mistakes on the part of the predator. The structure of the conflict then changes into that of a nonzero-sum game of $N + 1$ individuals (let $N + 1$ equal the predator [or pack of predators] and the individuals of the prey population). Moreover, in all such situations, where at least one stage of the game is characterized by an active pursuit and evasion, different individuals of the prey population may have different chances to escape, and in many cases they are also likely to have some way to assess these chances. Thus, unlike zero-sum games, corresponding to populations of a concealing prey, nonzero-sum games of a predator and an evasive prey are likely to be nonsymmetric also in respect to individuals of the prey population.

Although the zero-sum model studied by Hamilton appears to fit mainly situations of a passively concealing prey, gregarious behavior is by no means restricted to such situations. On the contrary, it appears to be even more common among ungulates, birds, and fish of open spaces (Williams 1964, 1966; Hesse et al. 1937; Hamilton 1971). This empirical finding stands in agreement with the prediction of the nonzero-sum game of predator and evasive prey analyzed in the next sections.

More specifically, it is shown that in the extreme case, in which no cover is available, evasion is the only means to escape predation, and each individual of the prey population is provided with complete information about his own speed relative to that of his companions, the game always results in the following. (1) All individuals of the prey population except, maybe, for the slowest one form a single herd. (2) The predator always prefers a single prey, if available. (3) The slowest prey is to be caught by the predator independently of whether it joins the main herd or not. For, if it joins the herd, it will be caught by a pursuit, and if not, it will be preferred by the predator as a single prey.

A formation of a herd of an evasive prey may, then, be interpreted as a stable coalition of all players (including the predator and excluding the slowest prey) against the slowest prey.

Some natural examples in which the survival of prey completely depends on its speed are studied in Section III. I also attempt to explain biological patterns, other than gregariousness, which are typical to these examples on the basis of the suggested model. I specifically concentrate on systems of prey-predator communication typical of the nonzero-sum structure (cf. Zahavi 1975). Finally, in the last section I study a more general model, in which both evasion and concealment in various degrees are possible for the prey. As it appears, gregarious behavior then seems most likely to develop just in situations close to the two extremes, namely, that of a purely evasive and that of a purely concealing prey. Thus, we may quite generally talk about two basic types of selfish herds of prey, each being characterized by distinct morphological and behavioral patterns.

II. BASIC PRINCIPLES AND SHORT SUMMARY OF THE MATHEMATICAL ANALYSIS OF THE PREY-PREDATOR NONZERO-SUM GAME

The first objective of this section is to illustrate more specifically the exact biological assumptions of the simplest model of a game between a pursuing predator and more than one potential prey. A more important objective, maybe, is to specify both the mathematical and the biological meaning of what we refer to as a solution (or solutions) of the game. There is more than one evolutionary-meaningful criterion for such a solution (cf. Maynard Smith 1974).

All mathematical proofs are omitted. The interested reader is referred to a technical report by the author (Eshel 1975).

I start by representing a noncooperative game of $N + 1$ individuals, say, N prey individuals and a single predator. It is convenient to label the first N individuals, namely, the prey population, from 1 to N so that if $1 \leq i < j \leq N$ we say that the individual j is faster than the individual i. The individuals of the prey population are assumed to be informed about their relative speeds (this assumption will later be relaxed). The predator, on the other hand, can assess relative speeds of the prey only by actual pursuit. The N individuals of the prey population can arrange themselves in various groups. The predator is to choose one group of prey and pursue it. The result of the game is predation of the slowest member in the pursued group. We naturally assume that each prey attempts to survive, whereas the predator tries to save energy by picking the slowest available prey. The payment function may thus be chosen to be -1 for the victim, 1 for any surviving prey, and a decreasing function of the speed index of the victim for the predator.

The individuals of the prey population may arrange themselves in various groups. A strategy of any individual of this population determines whether it is satisfied with a given arrangement and, if not, where it prefers to move (each individual is free to leave and join any group). A strategy of the predator is any preference among the available groups of prey. Traditionally, the strategies of the various players are said to be in a Nash equilibrium or determining a Nash solution (see, e.g., Luce and Raiffa 1957) if no single player can gain by exclusively changing his own strategy. Note that, in any population, if intrinsic behavioral tendencies do not satisfy the criterion of a Nash solution then, by definition, some individuals would gain by changing their tendencies. In such a population natural selection is, therefore, likely to favor the tendency of individuals to make such changes, provided, indeed, that the gain function relates to survival or fertility. The criterion of Nash thus appears to be a necessary (though not always a sufficient) condition for any evolutionary stability of behavioral tendencies in a population.

Whenever $N \geq 3$ (Eshel 1975), there is always more than one Nash solution obtained in pure strategies (i.e., by deterministic behavior of prey and predator). Accordingly, there are several arrangements of the prey population and more than one possible preference of the predator, each coevolving with an appropriate arrangement of the prey population. However, all Nash solutions guarantee predation of the slowest prey. In all of them it is only the slowest prey that may (or may not) stay out of any group, and in all cases it is the rational strategy of the predator to prefer an isolated prey, if available. Under slightly stronger and apparently more satisfactory conditions (Eshel 1975) all Nash solutions, except for two, are unstable. These two solutions are characterized by a single herd, consisting of all individuals of the prey population except, maybe, for the slowest. The slowest prey may or may not join this herd. These are called the gregarious solutions.

In order to understand the stronger stability property of these two solutions, when compared to all other Nash solutions of the game, note, more specifically, that for any game the (weak) stability of a Nash solution is required only in respect to one-step exclusive changes of strategies by single individuals. However, if successive changes of strategies are allowed (as is the case in our game), deviation of an individual from a Nash strategy may become advantageous in the sense that it forces other individuals (i.e., makes it directly advantageous for them) to change their strategies in a way favorable to the original player. In this sense, the Nash solution may be unstable in respect to a more than one-step change of strategies. It is possible, on the other hand, that deviation of an individual player from his Nash strategy will either inflict on him a direct loss, or else force another individual to change his strategy in a way harmful to the original player. In this case, we say that the original change of strategy is punishable.

Definition

A set of Nash solutions is said to be strictly stable if any deviation from this set by an individual change of strategy is punishable. As a special case, if a strictly stable set consists of exactly one solution, we say that this solution is strictly stable. I now show that the set of gregarious solutions is strictly stable. Since the set is independent of the strategy of the slowest prey, no change in the strategy of this player can result in a deviation from the set. A change in the strategy of another prey may result in a deviation from the set only if this individual abandons the main herd. After abandoning the main herd, this individual may either stay alone or join the slowest prey. In the first case, the abandoning individual is directly punished by possible predation. In the second case (which is possible only if the slowest prey remains outside the main herd), it becomes advantageous for the slowest prey to expose its new companion to predation by abandoning him and joining the main herd (here we assume again $N > 2$). In either case, the deviation is punishable. Finally, the only possible deviation of the predator from the set is by abandoning its preference of a single prey, an obviously punishable change of strategy. The set is, therefore, shown to be strictly stable. It may further be shown that the gregarious solutions comprise the only strictly stable set of solutions. Finally, note that the gregarious solutions are independent of the order of all individuals except for the slowest one.

Corollary

In our model the only information needed by the prey in order to establish gregarious behavior of the prey population is the identity of the slowest individual (or, in a little more complicated situation as studied in Section IV, the identity of the few slowest individuals) in this population. It is shown here that if it is hereditary in origin and not the result of a complicated calculation of strategies made by the individual, the tendency to gregariousness will be selected for when associated with high- and medium-rank individuals whose contribution to the genetic pool is relatively high, and it will not be negatively selected even in the case of the lower-rank individual. Hence, gregarious behavior will be selected in populations.

III. ON THE NONZERO-SUM STRUCTURE OF AN EVASIVE HERD AND NATURAL BEHAVIOR OF SOME PREY AND PREDATORS

Both Hamilton's (1971) zero-sum model for the concealing herd and the nonzero-sum model for the evasive herd predict the same gregarious behavior of potential prey. It appears therefore that no direct observation of gregariousness in nature can decide between the two models. However, other behavioral or even morphological patterns of both prey and predator are likely to distinguish between the two typical structures of the selfish herd.

The observed phenomenon of predators of either birds or ungulates preferring single prey (Tinbergen 1951; Wynne-Edwards 1962) is employed by Hamilton in helping to explain the advantage to the individual gained by gregarious behavior of the potential prey. Yet without consideration of the expected differences in quality between the single and the gregarious prey, this fact in itself remains inexplicable. Without such an expected difference, it is likely that the chance of finding a lame or weak individual would increase with the sample of prey in the herd.

That optimal arrangement of the prey individuals is also optimal for the predator, at least in some cases, is indicated by various means of prey-predator communication. Among these, warning signals given by hungry predators are perhaps the most significant since, by alerting the prey, these signals seem to decrease the probability of predation. Typical prehunting behavior of wild dogs (e.g., see Van-Lawick-Goodall and Van-Lawick-Goodall 1970) and wolves (Mech 1970) or the roar of big cats (Schaller 1972) are a few examples. The fact that occasionally a stampeded prey is more easily caught by the predator can serve only as a partial explanation for the development of the warning behavior of the predator. Indeed, coevolution of a signal and a response should indicate some common interest of the producer and the recipient of the signal, i.e., a nonzero-sum structure of their game (cf. Zahavi 1975). In the game studied here, the common interest of the predator and most of its prey is to establish such a pattern of pursuit and evasion that will assure the predation of the slowest prey. In the case of a medium-sized predator it is also a common interest of both prey and predator to avoid direct confrontation, in which the prey may have very little chance but the predator may still be injured. Note that, in order to guarantee a substantial probability of predation, contradicting demands imposed on the behavior or even morphology of the predator require that the information conveyed to the prey will be restricted to the appropriate time and distance. This is specifically true for short-running predators.

Some patterns, characteristic of predators of evasive prey, seem to be best explained on the basis of an optimal compromise between the contradicting demands of a good camouflage and a recognizable marker, each taking over at an appropriate distance. Perhaps most common is the typical spotted pattern of many medium-size mammalian predators. That this pattern, contrary to common belief, has not been selected for on the mere basis of its being an ideal camouflage is indicated by the fact that it rarely, if ever, occurs in herbivores. It is true though, that some colored photographs of leopards and other spotted cats in their natural environment, when observed from an appropriate distance, produce an almost perfect effect of assimilation of the animal in its background. This effect is quite reversed when the animal is observed from a short enough distance so that one can recognize its unmistakable symmetric, black on bright yellow pattern which resembles no natural background whatsoever. A different pattern with quite similar characteristics is typical to various birds of prey.

While studying the evasive behavior of many herbivorous herds, one should take into account the commonly overlooked factor that quite inevitably an evasive herd is actually led by those individuals which have the least chance to be preyed on. Taking this into consideration, the complicated pattern of maneuvers exhibited by a flock of starlings in the presence of a sparrow hawk may be interpreted as an attempt of the leading birds to outmaneuver the weaklings rather than an attempt of the entire (social) group of prey to outmaneuver the predator. Actually, it is not at all clear whether spreading out, each bird seeking its own cover (a strategy which is often successfully employed by slower birds) is not preferable in decreasing the general probability of predation. The fact that evading in flocks enables the predator to recognize and prey on the weaklings even increases the general predation probability. However, this fact does not increase the predation probability of the leaders or of most of their followers, and aggregation of these individuals into a flock leaves no alternative to the weaklings.

When fast adjustment to the majority is advantageous, a good strategy for all individuals of the prey population may be to follow a single or a few high-rank individuals. Such a strategy is well recorded in evasive populations with an established pecking order, such as jackdaws and other flocks of birds, as well as monkeys (Lorenz 1966). Indeed, such a strategy endows high-rank individuals with a substantial advantage in terms of survival probability. Even if the top-rank individuals are not the fastest in the prey population, they may keep their initial leading positions by making it hard for other individuals to follow them and even harder to pass them. Thus a more complicated pattern of evasion, acceptable to most of the followers and forced on the few weaklings, may be favorable for the few leaders.

IV. ON STRUCTURES OF A PREY-PREDATOR GAME COMBINING BOTH CONCEALMENT AND EVASION OF THE PREY

Although many natural situations of gregarious behavior of a potential prey seem to be rather satisfactorily explained either by the model of purely evasive prey or by that of a passively concealing prey, it should be noted that these models, if not taken as first approximations, represent two extremes in a range of possible prey-predator relations. For further application of these models it is, therefore, essential to check the stability of their results in respect to small perturbations in the parameters assumed for their development (see Karlin and McGregor 1974). Moreover, it is of interest to study, though less extensively, a more general continuum of prey-predator relations characterized by two basic factors: (1) the concealment ability of the prey, and (2) the a priori escape probability of the slowest individual in a group of prey.

The first factor is determined by both availability of cover and scarcity of prey and predator. The second factor is determined by both uncertainty about the identity of the slowest prey individual and nondeterministic factors in the hunting process itself. As we will see later, these two factors cannot each be characterized by a single quantitative parameter, and generally they are not unrelated. Passive dependence on cover may render differences among individuals in the prey population irrelevant to their escape probability when located by the predator. Dependence on speed, on the other hand, minimizes uncertainty both in relative speeds of the prey and in random factors in the hunting process. Note that even then the model, assuming ability of the predator to stick to one prey, does not analyze the most general situation of a prey-predator game.

Even for the most general model it is obviously true that if staying alone is favorable for a given prey, it is more so for any slower prey which can gain less by joining any given group of prey. Hence, in our model we get:

Corollary 1.—In any prey-predator game with differences in escape probabilities among individuals of the prey population, it is advantageous for the predator to prefer a single prey, if located. (This is indeed incorrect for predatory fish which can eat many fish at a time or which have a better chance to catch even one prey out of many.)

Corollary 2.—If the concealment probability of a single prey is less than the escape probability of the slowest prey in the main herd (i.e., a herd consisting of all N individuals of the prey population), then an arrangement of all the prey in one herd is always strictly stable in the sense of a Nash solution.

Obviously, in this case, an individual in the prey population will always lose by abandoning the main herd. Also, the predator cannot gain by changing its strategy of preferring a single prey once located. Moreover, if through a change of strategy by the predator it becomes advantageous for any individual to abandon the main herd, it becomes even more so for the slowest prey. The slowest prey may at least assure its given escape probability by staying with the herd (assuming it is only the predator who has changed its strategy). Therefore the slowest prey, by abandoning the herd, can increase its escape probability and the predator, then, always loses.

Generally, a solution of the game may not be determined by two quantitative parameters as it is under the special condition of corollary 2. Actually, concealment probabilities of various groups of prey, as well as the escape probability of the slowest individual in a given group of prey, may depend on the setup of the groups in question. Even if the entire set of parameters determining the above probabilities is known, a Nash solution of the game, either pure or mixed, may not necessarily exist (for irrelevance of the general Nash theorem to our model see Section II). Consider, e.g., a simple structure in which predation of the slowest prey in a located group is certain, and assume further a positive probability for a single prey to be concealed. In such a case, it is always preferable for the second slowest prey to join the slowest one. Hence, no arrangement can possibly be stable under these given assumptions. In the remaining part of this section I concentrate on a more restricted model in which only one herd can possibly exist in a given area. In this case, each individual of the prey population can only choose between two alternatives at the most: it can either join the main herd if it exists, or stay alone and try to conceal itself. Let p $(0 \leq p \leq 1)$ be the concealment probability of a single prey, and let s be the escape probability of the slowest individual in the herd, if attacked by the predator $(0 \leq s \leq 1)$. We finally assume that location of the main herd, if such exists, is certain. From corollary 1 we therefore infer that the main herd, if it exists, is attacked if and only if no single prey is located by the predator. More specifically, we assume that single individuals of the prey population manage to hide independently of each other. Therefore, if there are k such individuals $(k \leq N - 2)$, then the probability that the predator will still attack the main herd is p^k. Thus, the predation probability of the slowest prey in the main herd is $(1 - s)p^k$. If this individual chooses to leave the herd, the chance that the predator will locate and prey on a single prey will be $1 - p^{k+1}$. The predation probability of each single prey will then be $(1 - p^{k+1})/(k + 1)$. Thus we have:

Corollary 3.—If all the $k - 1$ slowest individuals stay alone outside the main herd, it is also advantageous for the kth slowest individual to stay alone if and only if

$$\frac{1 - p^k}{k} < p^{k-1}(1 - s) \tag{1}$$

—equivalently, if and only if

$$p^{k-1}[1 + (1 + s)k] > 1. \tag{2}$$

Note that, when

$$k < \frac{1}{-\ln p} - \frac{p}{1 - s}, \tag{3}$$

the left side of (2) increases with k. This means that with inequality (3), if it is advantageous for the first $k - 1$ individuals to leave the herd, it becomes even more so for the kth individual. Note that if p is close to one (i.e., if a good cover is available for the prey) the right side of (3) may be as large as we wish. If it is larger than N, then inequality (2) may be true for large but not for small k. In this interesting case the entire herd, once established, is stable against desertions of less than a critical number of individuals at one time. However, once that critical number of individuals has abandoned the herd, it becomes advantageous for each of them to stay outside the herd. It then becomes favorable for each of the remaining individuals to abandon the herd once all the slower individuals have done so. In this case, the prey population can stay in two stable structures, namely, that of a single herd or that of a complete dispersal into solitary individuals. Note that in case of a complete dispersal the predation probabilities of each individual prey, including the fastest, are essentially the same. Dispersal of the herd is therefore quite unfavorable for the leaders of the herd, the few fastest individuals, which by determining the route of escape can partially influence the rules of the game. One way of influencing the game rules (see previous section) is by repeatedly and randomly changing the route of escape. In this manner, the leaders introduce a hazardous factor to the game, thereby increasing the escape probability (s) of the slowest prey. The left side of (3) then decreases, and it becomes less advantageous for each individual, once he remains the slowest in the herd, to abandon it. Introducing a random factor to the game by increasing the survival probability of the slowest prey may stabilize the structure of the herd for the advantage of its leaders. In some cases, it may even be advantageous for the leader to endanger himself slightly in order to protect the weaklings and make it favorable for them to stay with the herd.

Another situation of interest may occur when the right side of (3) assumes a medium value and (2) then holds only for medium values of k. In this case, if a crucial number of individuals abandon the main herd, it again becomes advantageous for more individuals to abandon it. Yet, a kernel of the fastest individuals will still stick together.

For any given k, the left side of (2) is monotone increasing with p and decreasing with s; therefore we get:

Corollary 4.—As the concealment probability of a single prey increases, it becomes favorable for more individuals of the prey population to abandon the herd.

Corollary 5.—As the escape probability of the slowest individual in a pursued group increases, it becomes favorable for more individuals to stay with the herd.

Corollary 4 does not preclude evolution of gregarious behavior in conditions of a good cover. In some natural situations, just the opposite may be true. These are the situations, analyzed by Hamilton (1971), in which the prey completely depends on cover. In the terminology of the present model this means that s may be so close to one that, even when p is quite large, the condition (2) is never satisfied. As a special case, if $p < s$, both being close to one, then the right side of (3) is negative, which means that the left side of (2) decreases with k. But even for $k = 1$ the left side of (2) is then $1 + p - s < 1$, and this means global stability of the gregarious solution.

On the other hand, for an evasive prey, s is likely to be close to zero. It then immediately follows from (2) that as the amount of cover increases it becomes favorable to more individuals to abandon the herd. This finding will fit into the observations of Williams (1964, 1966), Hesse et al. (1937), and others (stated also by Hamilton) that gregarious behavior of evasive species like fish, birds, and ungulates is typical to open spaces and is rare in areas rich in cover.

SUMMARY

Following Hamilton (1971), this article attempts to study gregarious behavior of a potential prey on the basis of the selfish drive of each individual in the prey population to minimize its own probability of predation rather than to contribute to the welfare of the entire population. Unlike Hamilton, we concentrate on the asymmetric situation, where active pursuit and evasion endow faster individuals of the prey population with better chances to escape predation. In such situations it is shown that a certain identity of interests between the predator and some of its potential prey can evolve. Conditions

for formation of an evasive herd can be analyzed as a nonzero-sum prey-predator game. Under a wide variety of conditions it can be shown that the optimum behavior for a fast prey is always such as to maximize the predation probability of the slowest prey. Finally, some other biological phenomena, typical to either evasive prey or its predators, are also suggested as following from the nonzero-sum model.

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THE NATIONAL *DROSOPHILA* SPECIES RESOURCE CENTER

The National *Drosophila* Species Resource Center at the University of Texas, Austin, wishes to call attention to the services that it provides. The center is governed by a council appointed by the American Society of Naturalists and is currently supported by a grant from the National Science Foundation. The purpose of the center is to provide cultures of a wide variety of species to researchers, teachers, and students.

The center maintains approximately 350 species representing 8 genera and 34 species groups in the family Drosophilidae. This is the largest collection of living eucaryotic organisms ever assembled whose evolutionary relationships and genetic biology have been extensively studied. Stocks of many species include strains having visible mutants, electromorphs, and chromosomal rearrangements. A list of cultures and details on their maintenance are available from the director. The center intends to expand its holdings of species, especially those with mutants and chromosomal rearrangements, and solicits information concerning them. New cultures will be added at the discretion of the director.

Limited facilities are available for visiting scientists, including the large reference collection of pinned specimens assembled by Professor Emeritus Marshall R. Wheeler as well as a nearly complete reprint file on *Drosophila* systematics. Modern equipment for research in the biochemistry and biology of *Drosophila* is also available to qualified persons through the cooperation of the members of the Genetics Institute and the Department of Zoology.

Cultures are provided at a cost of $5.00 each. However, no reasonable request will be denied because of lack of funds. Address inquiries and requests to Dr. John R. Ellison, Director, Department of Zoology, The University of Texas, Austin, Texas 78712. Telephone (512) 471-5579.

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LETTERS TO THE EDITOR

On the Handicap Principle—A Critical Defence

In a response to a criticism of Zahavi's Handicap principle, a quantitative model which enables the evolution of preference of a handicap is suggested.

In his article "Mate Selection—a selection for a handicap" (1975), Zahavi suggests that many attributes of sexual attraction are rather conspicuous handicaps, designed to guarantee the high quality of their carriers in other respects. He proposes that only a male who is fit in all other respects (namely, in this context, a male *of high quality*) can survive to breed despite the presence of his handicap. And, so long as quality is inheritable in the population, a female can improve the quality of her own offspring by choosing a handicapped male as a mate [for the possible advantage of such a choice in increasing the *fertility* of the choosing female, see Zahavi (1977), Motro (1977)]. Unfortunately, however, if the handicap itself is inherited (which is obviously the interesting case), a female who chooses a handicapped male as a mate (from here on, *a choosing female*) will decrease the fitness of those of her offspring who inherit the handicap. This raises the crucial quantitative question of whether it is possible for average fitness to be higher among the offspring of handicapped males so as to make their choice as mates selectively advantageous.

Employing simple quantitative models, Maynard Smith (1976) and Davis & O'Donald (1976) attempted to show that whenever the handicap is nherited by both sexes, its sexual preference cannot possibly be selected for n natural populations—and it is most unlikely to be selected for, even if he handicap is passed exclusively to male offspring. However, following models quite similar to theirs, but concentrating on a specific range of arameters which seem to be most relevant to the problem, I arrived t different results. Therefore, a short argument about the biological haracterization of the parameters is in order. It appears to be an irrefutable ruth of natural selection (a truth that has been validated again by the omputer tests of Maynard Smith) that the average fitness of offspring born o a random defective individual is generally below the average fitness of the opulation. The exception—namely, the *quality marker handicap*—if it xists at all (and it is the objective of this note to show it can) should, inevitbly, be of a very special sort (which, theoretically, may not mean its rarity n a natural population once it becomes sexually advantageous).

On one hand, direct selection against the candidate for a quality marker handicap must not be too high. On the other hand, its correlation with other favourable characteristics (namely, the quality) should be sufficiently high, at least at mating time, to over-compensate for the offspring's deficiency in fitness due to inheriting the handicap. But then it is claimed that a substantial correlation between the handicap and the quality can be maintained only with high selection pressure on the handicap (as well as on the quality loci). And it seems to follow, from the results of Davis & O'Donald and, indirectly, from those of Maynard Smith, that the required selection pressure is always too high to be compensated for by the relatively higher quality of the handicapped. More specifically, Davis & O'Donald have shown that unless for unrealistically high selection pressure (and at least in their model) the average fitness of offspring born to a handicapped male is always lower than the average of the population.

Unfortunately, Davis & O'Donald considered only that part of the handicap-quality correlation that may develop *within one generation.* Tacitly (but quite crucially for their results), they assumed a permanent *linkage equilibrium* at birth—an assumption which, even in their model, becomes false after one generation. Moreover, presumably for the sake of mathematical convenience, they restricted their analysis to a very special situation in which the effect of the handicap is limited to a *linear* exaggeration of the carrier's deficiency in quality. Therefore, what they have shown is that without the cumulative effect of linkage disequilibrium, a linear effect of the handicap on the fitness of its carrier is not sufficient for the evolution of that handicap as a quality-marker.

It appears that a more discriminative effect of the handicap on the fitness of individuals of different quality is needed to enable the development of a substantial quality-handicap correlation, without affecting too drastically the average fitness of the handicapped offspring. Such a discriminative effect may be typical of many known attributes of sexual attraction or social dominance: bright colouration may hardly affect the survival probability of a bird which is fast enough to evade its potential predators, but may be fatal to a slow one. And exaggerated antlers may have only minimal effect on a strong buck, so long as it can actively protect itself against predators, e.g. Mech (1970) and see Wilson (1975) for many other examples.

Since the model of Maynard Smith (unlike that of David & O'Donald) allows for the most general effect of the handicap on the various types, we adopted it initially without modification. We concentrated on the situation in which the effect of a handicap on the fitness of high-quality individuals is minor, but its effect on the fitness of low-quality individuals is fairly drastic. Starting with the case which was less favourable for the handicap

The average fitness of the progeny of a choosing female will therefore be:

$$w_2(p, s, t, h) = \frac{1-p_1p_2}{2}(1-t) + \frac{1-p_1p_2}{2} + \frac{p_1p_2}{2}(1-t)(1-sh) + \frac{p_1p_2}{2}(1-s). \qquad (4)$$

Now, when t is close to 0, and when sh is close to 1, i.e. when the effect of the handicap is negligible for high-quality individuals, but almost fatal to low-quality individuals, this average fitness tends to:

$$w_2(p, s, 0, 1/s) = 1 - \frac{1+s}{2}p_1p_2. \qquad (5)$$

Inserting the values of p_1 and p_2 as expressed in equations (1) and (2), we see that the condition:

$$w_2(p, s, 0, 1/s) > w_1(p, s), \qquad (6)$$

is satisfied if and only if:

$$s > \frac{1}{p(p+2)}, \qquad (7)$$

provided that the right-hand side < 1, i.e. $p > \sqrt{2}-1$. In this case, choosing females will always leave more surviving offspring, and natural selection will favour a preference for handicapped males even before linkage disequilibrium develops. We thus get:

Corollary 1:

If the frequency p of the recessive disadvantageous allele is more than $\sqrt{2}-1$, if the damage inflicted by this allele on its homozygous form is more than $1/p(p+2)$, i.e. if the genetic load is at least $(\sqrt{2}-1)/(\sqrt{2}+1)$, and if the damage caused by a rare handicap is sufficiently low for high-quality individuals and sufficiently high for low-quality individuals, natural selection will favour, from the first appearance of the handicap, the tendency of females to choose handicapped males even if the handicap is expressed in both sexes.

It is expected that if the handicap is expressed in both sexes and if the development of a linkage disequilibrium is taken into consideration (possibly with a flux of mutation to keep variance at the A locus), the range of parameters for which a preference for handicapped males can evolve will increase; and it will increase more with tight linkage. It can be shown that among these factors, tight linkage has the most substantial effect on the evolution of a sexual preference for handicapped males.

principle—the one in which the handicap affects both sexes—we assumed that high quality was determined by a single dominant allele A at one locus, and that the handicap was determined by a single dominant allele B at another, non-linked locus (later, we introduce linkage into the model). Setting $\bar{A}$ for the type of AA and Aa, $\bar{B}$ for BB or Bb, we denote the fitness of the four possible combinations $\bar{A}\bar{B}$, $\bar{A}bb$, $aa\bar{B}$ and $aabb$ by $1-t$, 1, $(1-hs)(1-t)$ and $1-s$ respectively, with $0 < t,\ s < 1$ and $1 < h < 1/s$. The requirement $h > 1$ stands for super-multiplicity of the deleterious effects of aa and $\bar{B}$ [note that in Maynard Smith's original work, the fitness of $aa\bar{B}$ is denoted by $(1-s)(1-ut)$]. Finally, we assumed a source of variance at the locus A (a more realistic model for this may be that of many loci with a mutation pressure at each, e.g. Eshel (1971). However, Maynard Smith's model is preferable for its mathematical simplicity).

Like Davis & O'Donald, we started by investigating the possible advantages of choosing handicapped males at the first appearance of the handicap, i.e. we concentrated on the choice of a non-handicapped female when the handicapped male was assumed to be heterozygote. We also assumed linkage equilibrium; then we studied the effect of linkage disequilibrium, especially with tight linkage.

Let p be the frequency of the recessive allele a in the population at the time of birth. With linkage equilibrium, this is also the frequency of this allele among handicapped newborn offspring. Since a surplus of $(1-s)$ of the aa non-handicapped individuals are dying before maturity, the proportion of the allele a among mature non-handicapped individuals is:

$$p_1 = \frac{1-ps}{1-p^2s}\,p. \tag{1}$$

In the same way, the proportion of this allele among mature handicapped individuals is:

$$p_2 = \frac{1-psh}{1-p^2sh}\,p. \tag{2}$$

If the allele B is rare, it may be assumed that virtually no offspring of a non-choosing female will be handicapped, e.g. see Davis & O'Donald, but p_1^2 of her offspring will be of the low quality type aa. Therefore, the average fitness among offspring of a non-choosing female is:

$$w_1(p, s) = 1-p_1^2s. \tag{3}$$

On the other hand, only p_1p_2 of the offspring of a choosing female will be of the low quality type aa. But, with the handicapped male being heterozygote, half of the offspring (either high or low quality) will be handicapped.

In order to study the effect of linkage disequilibrium with tight linkage, we start, again, by assuming no recombination. Let w be a steady rate of mutation from A to a. The frequency of the allele a among non-handicapped individuals will be:

$$p = \sqrt{\frac{w}{s}}.$$

With complete linkage, the frequency of this allele among handicapped individuals (provided that the handicap is expressed in both sexes) will be:

$$\hat{p} = \sqrt{\frac{w}{hs}} = \frac{p}{\sqrt{h}}.$$

The average fitness of offspring born to non-choosing females will be:

$$1 - sp^2.$$

The average fitness of offspring born to choosing females will be:

$$\frac{1-\hat{p}^2}{2} + \frac{1-\hat{p}^2}{2}(1-t) + \frac{\hat{p}^2}{2}(1-s) + \frac{\hat{p}^2}{2}(1-t)(1-hs).$$

For $t = 0$, this becomes:

$$1 - \frac{(h+1)s}{2h}p^2,$$

which for any $h > 1$ is larger than the average fitness $1 - sp^2$ in the population. By arguments of continuity, we readily obtain:

Corollary 2:

For any frequency p of the low-quality allele in the population and for any damage inflicted by the handicap $\bar{B}$ on the low-quality individuals, if the linkage between the handicap and the quality-determining locus is tight enough and if the damage inflicted by the handicap on the high-quality individuals is small enough, there will be a selective advantage to sexual preference for handicapped males.

Results similar to Corollary 1 can also be obtained from the model of David & O'Donald, provided that slight modifications are made in order to allow for a discriminative enough effect of the handicap on individuals of different qualities.

In all cases, it is shown that although a sexual preference for handicapped males can be favoured by natural selection, such a phenomenon is restricted to a very special sort of handicap. Maynard Smith's computer tests demonstrated that for almost any "random" handicap, even if it was limited to one sex, natural selection favoured a sexual preference for non-handicapped males (except for the Fisher effect). But if the exception, even though rare during evolution, became sexually favourable (and we see that it can be so) it may not be that rare in current populations.

Note that in the original model suggested by Maynard Smith, the frequency of the low-quality allele *a* tends to zero and selection for non-choosing females must always take over in the long run. I believe that without any substantial source of variance in the heritable fitness in the population, it is inevitable that the situation in nature and a handicap can not then evolve. However, we followed the assumption of Maynard Smith only through one generation, postulating, further, that a fixed frequency of low quality genes always exists in the population. This may be feasible, for example, in a multi-locus model with a minor flux of mutation at each quality locus.

Unfortunately, such a model, even though easy to conceive, is rather hard to analyse and the 3-locus model should be understood as a convenient simplification. What remains to be considered is the question of which assumption is qualitatively more relevant to natural situation and, to my judgement, the controversy is not yet settled by the suggested models.

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