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The American Naturalist, Vol. 106, No. 951. (Sep. - Oct., 1972), pp. 574-580.

Vol. 106, No. 951 The American Naturalist September–October 1972

MALE DIMORPHISM AS A CONSEQUENCE OF SEXUAL SELECTION

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Dimorphism among males is known for a small number of insect species. Bateson and Brindley (1892) describe striking bimodalities in the length-frequency distributions of the forceps of the common earwig (*Forficula auricularia*) and of the cephalic horns of a beetle, *Xylotrupes gideon.* These bimodalities are restricted to males which possess larger forceps or cephalic horns. Huxley (1932) considered and rejected the possibility that these bimodalities are the result of allometric growth when his finer analysis of the data revealed that males of certain size classes could possess forceps or cephalic horns falling in the range of either of the two modes. Two other examples of male dimorphism are known in beetles, though the phenomenon has not been documented quantitatively. Scott (1926) notes two classes of males of a ciid beetle, *Xylographus seychellensis,* on the basis of the development of mandibular processes; Bates (1879) found a similar situation with respect to the mandible length in the cerambycid beetle, *Stenodontes molarium.*

Male dimorphism has been noted in at least two species of halictine bees of the subgenus *Chilalictus* of *Lasioglossum* (Wilson 1971). One form is typical, while the other has reduced wings but a gigantic head and mandibles, and appears to be well equipped for combat. Houston (1970) proposes that the latter form may serve as a soldier caste, but Wilson (1971) is very skeptical of the suggestion and regards this male dimorphism as a serious puzzle. Finally, Darling (1937) notes the occurrence of sexually mature antlerless red deer males (*Cervus elaphus*). Such males, termed ''hummels,'' persist in the population in spite of efforts of game wardens to eliminate this trait from the population.

ALTERNATIVE STRATEGIES

Antlerless and antlered male deer or typical and soldier-like male halictine bees may represent two alternative ways of mating with as many females as possible. The former strategy may utilize resources saved by relinquishing weapons of combat in improving some other ability such as agility, while the latter may rely on superiority in male combat. Thus, Darling (1937) mentions that antlerless male deer appear to be in better physical condition.

Assume that such alternative solutions do exist and are genetically based. I now inquire into the conditions under which such a dimorphism may persist in a population. As a general rule assume that one or the other type would be superior under any given set of environmental conditions. Perpetuation of a dimorphism in a population may then depend on the two alternatives being favored over each other at different times or over different parts of the range of the species, or on heterosis or mutation pressure, etc. The possibility of the two alternatives possessing completely equal selective advantage and thereby persisting is considered negligible and is ignored. My goal is to show that a mechanism may exist which would continually act toward an equalization of selective advantages of the two alternatives, and therefore lead to a persistent dimorphism.

COST-BENEFIT ANALYSIS

The extent of an investment in the production and maintenance of a device such as antlers or cephalic horns depends on the balance between the benefit derived from a given amount of investment and its cost. The investment may be measured in terms of the energetic cost of production and maintenance of antlers, the benefit in terms of the increased mating success, and the cost in terms of the decline in survival due to the additional burden on the economy of the animal. Here I concern myself only with males, and for simplicity, I assume nonoverlapping generations. Then, the fitness of an investment strategy is given by the product of the probability of survival to maturity and the number of offspring produced. The probability of survival may be assumed to decline monotonically with an increase in the investment in a competitive device. At the same time, the mating success of the male may be assumed to increase with an increase in investment, at least over a part of the range of possible investment. Such a decline in survival and increase in mating success with increased investment is depicted in figure 1. The behavior of mating success as a function of investment has several interesting features. Even in the total absence of investment, a small

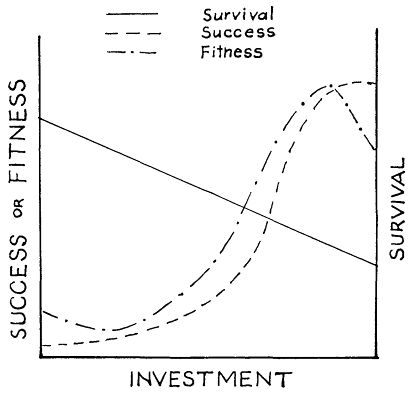

FIG. 1.—Survival, mating success, and fitness as a function of investment in a device for male competition, such as antlers. The optimal level of investment is that at which fitness is maximized.

chance of mating success exists. The curve may then rise to an asymptote representing the maximal mating success possible for a male at a value of investment exceeded by very few males in the population. I return to this dependence of mating success on the distribution of investment in the population below. Fitness as a function of investment is specified by the product of survival and mating success. It is bimodal for the case represented in figure 1. Natural selection favors investment at the level at which this fitness is maximized.

COEVOLUTION

A hypothetical set of mating success and survival curves is shown in figure 1. A peculiarity of the kind of investment under consideration is that the benefit curve simply cannot be specified without knowledge of the extent of investment by other competing males in the population. As Darwin (1871) puts it, ''Unarmed . . . males would succeed equally well . . . in leaving behind a numerous progeny, but for the presence of better endowed males.'' The mating success of a male does not depend so much on his absolute investment, but on his investment relative to other males. While the investment is as yet small, there will always be an advantage to investing a little bit more than other males. If the extent of investment is assumed to be specified by a set of genes, then the selective advantage of a set is not fixed at all; further, it does not depend simply on its own frequency, but depends on the frequency and identity of all other genes specifying investment present in the population. Therefore, the genetic makeup of the population must continually evolve. This is analogous to the process of coevolution between the lodge pole pine and its red squirrel predator (Smith 1970). A hardening of the bracts of the pine cone generates selective pressures leading to the evolution of stronger jaw musculature by the squirrel which in turn favors a further evolution of the hardening of the bracts.

This problem may be analyzed graphically by simultaneously considering the curves of mating success and the frequency distribution of the extent of investment under consideration in the male population. Figure 2 shows the relation between the curve of mating success and the frequency distribution of investment for two different populations, *a* and *b*. For a given population, the success curve rises to an asymptote at a level of investment close to the right-hand extreme of its frequency distribution. This implies that maximally successful males are those investing more than most others.

The system is a dynamic one, since the mating success of different strategies of investment depends on their frequency distribution in the population, and, moreover, the distribution of mating success with investment generates selection pressures which mold the frequency distribution of the investment. I begin my analysis by considering a population with the frequency distribution of investment x_2 (fig. 3). This population is assumed to be composed largely of animals with very little investment in a device for male competition. Hence, the curve of mating success rises to an asymptote at a relatively low value of investment, as shown by the solid line in x_1. Survival

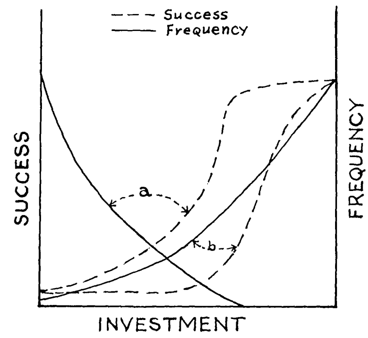

FIG. 2.—Benefit accrued in terms of mating success as a function of investment and the frequency distribution of investment within a population, for two populations *a* and *b*.

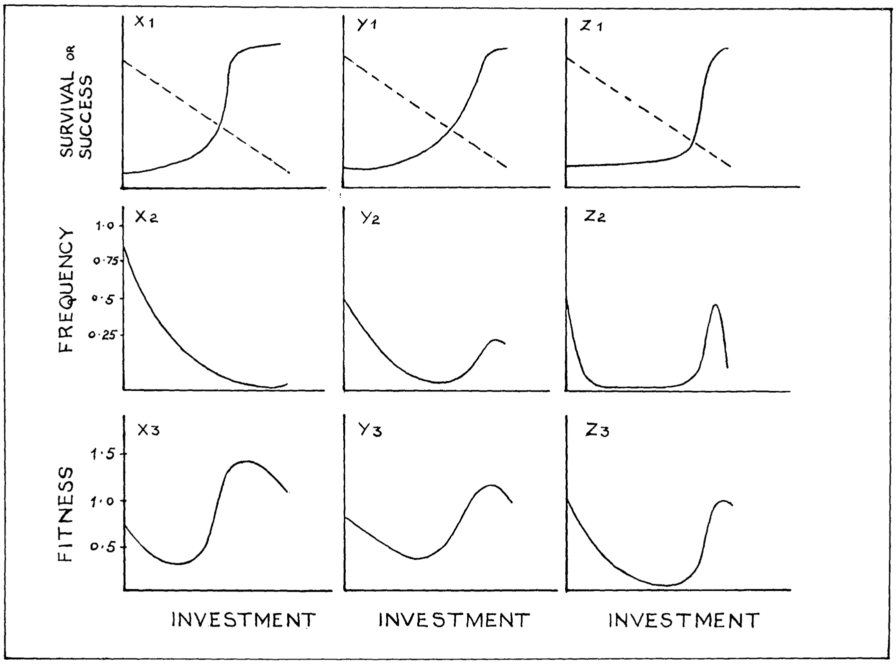

FIG. 3.—Survival, mating success, and fitness as a function of investment in three hypothetical populations x, y, and z, with three different frequency distributions of investment in a device (such as antlers) for male competition.

is a monotonically decreasing function of investment represented by the dashed line in x_1. Since survival is only a function of investment and, unlike mating success, does not depend on the frequency distribution of the investment in the population, it remains unchanged in y_1 and z_1. The distribution of fitness as a function of investment for this population is given by the product of the two curves of x_1 and is represented in x_3. Mating success reaches its high asymptotic value at a relatively low value of investment for which there has not been too great a decline in survival. Fitness therefore reaches its maximum at this value of investment. Hence, directional selection exists for an investment in a competitive device greater than that made by the majority of males; the frequency distribution of investment gradually shifts from a distribution such as x_2 to one like y_2. With an increase in the frequency of animals with greater investment in a competitive device, the curve of mating success shifts to the right as in y_1; only animals with relatively high investment can now achieve maximal mating success. Since these males with a high mating success have a relatively low probability of survival, their fitness is not very much greater than that of males with low investment. Nevertheless, as y_3 shows, males with an investment greater than that of most other males are maximally fit, and the frequency distribution of investment continues to change toward an increase of males with higher investment until it reaches a condition such as z_2. Such a population contains many individuals with high investment, and as a consequence the curve of mating success as a function of investment is shifted even farther to the right, as in z_1, such that only males with a very high investment achieve maximal mating success. Survival of these males may be so low that in spite of their high mating success, their fitness does not exceed that of males which have opted out of the competition altogether. The resulting curve of fitness as a function of investment is depicted in z_3 and shows that the fitness of males with no investment equals the fitness of males with maximal mating success, while the fitness of males with an investment greater than that of the latter is further depressed. Directional selection for investment higher than that of most males in the population thus ceases at this point.

This, in fact, is the limit of investment in means of competition. Such a limit may result from an increased cost of competition, and Wilson (1972) provides a discussion of how this cost may become excessively large. In addition to such a simple increase in cost, two factors could diminish the competitive advantage of a higher investment itself. First, the burden of large investment may decrease the male population through a higher death rate, forcing males to postpone maturity beyond the age of sexual maturity for females. Thus, Darling (1937) showed that although the sex ratio for red deer is nearly even at birth, there are almost twice as many sexually mature females as mature males in the adult population. A reduced intensity of competition will naturally reduce the advantage of a competitive superiority. Second, as the combative equipment becomes formidable, an opponent with slightly inferior equipment may still inflict substantial damage. Under these conditions, the superior male may refrain from serious combat, thus failing to gain the full advantage of his superior weapons.

The frequency distribution of investment z_2 may therefore be evolutionarily stable. A distribution with more extreme investment will be brought back toward type z_2 by directional selection for lower investment. A very interesting property of the z_2 type of distribution is the possibility of a bimodality. The mode toward the left represents males which invest little while the mode to the right represents those which invest a great deal in competition. The dynamics of the system sketched above suggest that if a bimodality exists, the phenotypic distribution will continue to shift to the right until the fitness of the males making high investment in competition approximates the fitness of males with little investment in competition. Here, then, is a mechanism for equalizing the heights of the two adaptive peaks and maintaining the polymorphism in the population.

The existence of a mode toward the left of males with very low investment depends on the assumption that such males can manage to achieve a minimal positive reproductive success in spite of their inability to compete with other males. This assumption may not be true in many cases. For example, male secondary sexual characteristics, such as horns on the pronotum of beetles, may serve both as weapons in combat and as species recognition devices. In such cases, a male without a substantial horn may be totally unfit and no possibility of a polymorphism exists.

OTHER IMPLICATIONS

Living organisms are confronted with a variety of environmental challenges to which they respond through evolutionary change. Such a response in turn affects the agency posing the challenge. If it is a physical agency, its response will not necessarily either enhance or depress the effectiveness of the original response. On the other hand, a biological agency itself responds so that the efficacy of the response is either reduced or enhanced in a predictable fashion (Brower 1970; Ehrlich and Raven 1964). Male competition as analyzed here, as well as the case of lodgepole pine and red squirrel (cited above), illustrates the reduction in the effectiveness of the original response.

The model presented above considers an extreme case, namely, competition for a single resource for which there can be no substitute. Few other cases of competition outside of sexual selection approach this condition. A possible case is the competition for light in a tropical rain forest. There are usually substitutes for resources in short supply. As soon as competition for the most desirable resource becomes severe and leads to a wastage of energy which lowers the benefit obtainable from that resource, some competitors should switch to another resource. This is the phenomenon well recognized by evolutionists as character displacement (Brown and Wilson 1956).

Finally, there are other biological interactions where the response of the biological agency shifts the benefit curve not to the right, as in the case of competition, but to the left, that is, toward the direction of a given expenditure of energy bringing in greater, rather than fewer, returns. This should be the case with symbiotic relationships; when a pollinator which receives nectar as a reward from a plant evolves the ability to suck the nectar with greater efficiency, the amount of nectar the flower must produce is reduced. But this sort of mutually beneficial coevolution may not be restricted to symbiotic relationships; it may enter into evolution of antagonistic relationships as well. Many devices seem to reduce undue waste of energy by potential antagonists, such as development of a social hierarchy or of warning coloration by venomous animals.

SUMMARY

A number of insect species and red deer possess two forms of males differing from each other in the extent of development of devices involved in competition for females. Such forms may represent genetically based alternative strategies, one form being inferior in combat but wasting little energy in developing expensive weaponry, the other form being superior in combat but burdened with great energy expenditure to achieve this superiority. The return on investment in weaponry for the latter form depends not on the absolute value of investment, but on the extent of investment relative to the other forms present in the population. Such coevolution leads to an escalation of investment in devices of male competition. This costly arms race comes to an end when those investing in weaponry are just as well off as those which have totally opted out of such investment. Such a mechanism could precisely equalize the selective advantages of the two alternatives. Such coevolution is therefore a possible mechanism for the maintenance of a genetic polymorphism.

ACKNOWLEDGMENTS

I had stimulating discussions with John Lawrence, Robert Trivers, and E. O. Wilson while developing these ideas.

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