LA SABOTEUSE:

An Ecological Theory of Sexual Dimorphism in Animals

Joseph N. Abraham

Department of Biology, University of Mississippi, University MS 38677 and Health Information Management, University of Southwestern Louisiana, Lafayette LA 70504.[1]

Received 14-VII-1995

ABSTRACT

Both male ornamentation and male combat result in increased male mortality. Because population sizes are limited by a carrying capacity, increased age-specific adult male mortality will result in decreased age-specific adult female mortality, as well as decreased juvenile mortality. As intersexual competition is one form of intraspecific competition, through choosing to mate with ornamented and/or combative males, females in polygamous systems reduce intraspecific competition. Because average male fitness must exactly equal average female fitness, male fitness will paradoxically rise with increasing male mortality. This theory also offers new perspectives on peripheral problems to sexual theory, such as mate location, resource guarding, leks, harems, and others.

In 1871, Charles Darwin published *The Descent of Man* and *Selection in Relation to Sex*. Ironically, the originally inflammatory portions of that work, the origins of humanity, have come to be well accepted and even viewed as obvious. It is the less offensive portion of the book, the question about the morphologic divergence of sexes in many species, which has sparked a fascinating debate that has lived on for over one hundred twenty years.

Darwin himself seemed surprisingly uninterested in the "why" of elaborate sexual dimorphism. He argued that female choice could produce male elaborations which run counter to natural selection, but he seemed satisfied with "preference" and "æsthetics" to explain the system. He stated, "No doubt the perceptive power of man and the lower animals are so constituted that brilliant colours and certain forms, as well as harmonious and rhythmical sounds, give pleasure and are called beautiful; but why this should be so, we know no more than why certain bodily sensations are agreeable and others disagreeable", (Darwin, 1871, i. p.256).

---

[1] Correspondence should be addressed to: 515 Roosevelt St., Lafayette LA 70503, USA.

Acta Biotheoretica **46**: 23–35, 1998.

We now believe that emotions such as "preference", and sensations which are "agreeable" or "disagreeable", are proximate causes (Tinbergen, 1963); "beauty" should be a selected preference, and the "attraction" it invokes should be a utilitarian strategy. Some organisms find particular food items extremely offensive; others find those same items extremely desirable. Likewise, beauty as it relates to sexual partners and offspring is equally labile. Beauty, then, would appear to be arbitrary; it is a product of physiology and fitness. Darwin was not wrong. Female "preference" does indeed appear to promote elaborations in males. But it seems that he was incomplete. He did not show a utility, or at least a mechanism which escapes utility, to explain the ultimate meaning of such a preference by the females.

Several important evolutionary biologists have offered different theories as to the reasons for sexual dimorphism in animals, and the debate continues. An excellent brief review of the field is presented by Maynard Smith (1991). Recent additions to the discussion are the theories of fluctuating asymmetry (Møller, 1990) and sensory exploitation (Ryan & Rand 1990, 1993). Suggested here is an additional proposal, based on competition and carrying capacity.

There are some universally agreed points in this area of research:

1) Darwin (1871) noted that in many animal species, males differ greatly from the females.

2) Sexually dimorphic species are overwhelmingly polygamous, wherein the males generally contribute little or no material benefits to the next generation. (Darwin, 1871; Huxley, 1938; Fisher, 1958).

3) In those polygamous systems, a few males copulate with the majority of the females (Bateman, 1948: Kruijt & Hogan, 1967; LeBoeuf, 1972, 1974; Mackenzie *et al.*, 1995). Many males do not copulate at all, and therefore contribute nothing to the fitness of themselves, to their relatives, nor to the available females.

4) Darwin (1871) also noted that in sexually dimorphic species, one of two systems generally occur. Either males enter into physical combat with one another, with the victor "winning" the right to mate with the female(s); or, males elaborate visually attractive exaggerations, which the females seem to prefer in mates.

5) Finally, Darwin (1871) recognized that in either of these situations, the males' traits seemed to run counter to natural selection. The males' size, weapons, behaviors, or ornaments, were obstacles to survival. This has been well documented in many different animals (Haskins *et al.*, 1961; Selander, 1965, 1972; LeBoeuf, 1972, 1974; Endler, 1978, 1980, 1982, 1983; Froehlich *et al.*, 1981; Lloyd & Wing, 1983).

Why the peacock's feathers? Why should females prefer males with characters which make it hard for the males to survive? Perhaps the answer to that question is the question itself: to make it hard for them to survive. Females may be "deliberately" sabotaging males, to increase adult male mortality, and thereby decrease intraspecific competition.

One of the insights which led Darwin (1859) to his theory of natural selection was the principle of limited populations, which Malthus (1798) previously had applied to humans. This concept led Darwin to realize that the struggle for life is not only *inter*specific, but also *intra*specific; and that an important clue to understanding organic evolution lay in examining competition among conspecifics.

Another important insight here was offered by Trivers (1972), that females are generally the "limiting resource". Krebs and Davies (1992) state: "A male can increase its reproductive success by finding and fertilizing many different females, but a female can only increase her success by turning food into . . . offspring at a faster rate." If some way could be found to increase the "limiting resource" (females), then the end product --fitness-- would likewise increase.

This is the crux of this paper, that by sabotaging males, females reduce intraspecific competition, and correspondingly increase the "limiting resource". Before discussing this further, it should be noted that this theory immediately offers two very important benefits. First, it reunites male elaborations and male combat. Since both traits result in increased male mortality, they are equal in relieving females and juveniles of intraspecific competition, a point to which I will return later.

But the larger appeal of this theory is a more parsimonious evolutionary theory; this solution folds sexual selection back into fundamental framework of natural selection. Intraspecific competition is the keystone of evolutionary reasoning, and intraspecific competition is the centrum of this paper. As noted in statement 5) above, Darwin proposed sexual selection in response to male characters which seemed to defy natural selection. By showing that those male characters do not defy natural selection, this paper refutes Darwin while supporting him, *i.e.*, I argue that his original theory of evolution is sufficient in itself, and his secondary theory of sexual selection may have been unnecessary. This paper seeks to fully restore Darwinian selection to its original pristine, minimalist strength. This is no small point: Darwinian selection was the philosopher's stone which transmuted our discipline into a science, and sexual selection has proven a controversial, problematic exception to Darwinian selection.

This theory of female "sabotage" is not entirely new. Seger and Trivers (1986) showed that under certain conditions, females could benefit by hampering males. This paper differs from theirs in three important ways. First, they saw increased mortality of sons as a possible obstacle to success of female sabotage. I will show that the sons' fitness paradoxically rises with increasing male mortality. Second, they suggested only a few limited applications for their model. This paper hypothesizes that most of what has been called "sexual selection" can be explained under a model of female sabotage. Third, their model was a complex, multi-variable system analyzing the spread of such a strategy, the mathematics of which is largely inaccessible to most biologists. What follows is a much simpler game theory approach, where only resource distribution is considered, and where the conclusion is in terms of ultimate pay-off, *i.e.* fitness.

Consider the figure. In a polygamous system, males are expending most of their resources in nothing more than mating. Actually, this diagram is probably generous in its estimate of male nurturing; in many polygamous systems, male contribution to nurturing amounts to no more than a complement of DNA, suggesting an energetic input of zero.

A mathematical argument can be constructed of this system.

Let: p = male percentage of population biomass
q = female percentage of population biomass
M = male resources dedicated to mating effort
m = female resources dedicated to mating effort
N = male resources dedicated to nurturing effort
n = female resources dedicated to nurturing effort
K = carrying capacity, i.e., the total resources available to the population
$\omega = pN + qn$ = offspring investment, one aspect of fitness.

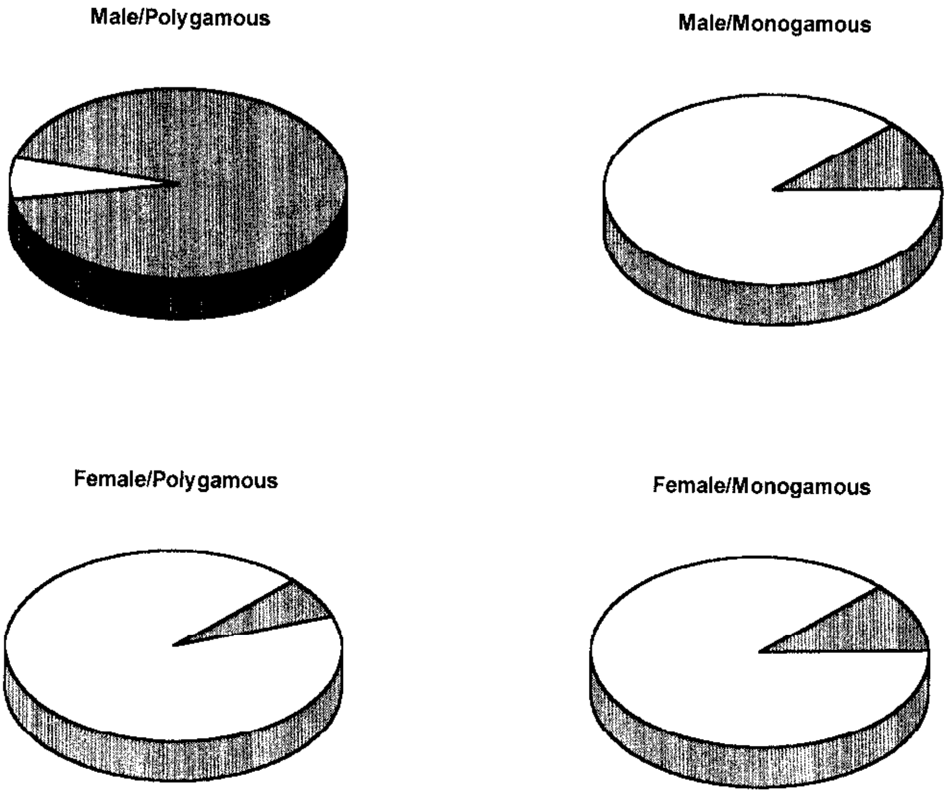

Fig.1. Resources allocated to nurturing and mating. Light areas reflect nurturing effort, dark areas signify mating effort. After Krebs and Davies (1992); adapted from Alexander and Borgia (1979).

Assume that $M + N = m + n = 1$. If,

$$K = pK(M + N) + qK(m + n),$$

then it follows,

$$1 - pM - qm = \omega.$$

But since often $N = 0$, then $M = 1$ and the equation simplifies to,

$$q(1 - m) = \omega. \qquad (1)$$

Several topics are addressed in this model. First, offspring investment should increase with q, female biomass. If the carrying capacity is limiting, the only way to increase female biomass is to decrease male biomass. Under this model, as age-specific male mortality increases, more resources become available for the females and their offspring; age-specific female mortality and juvenile mortality will therefore decrease.

Intersexual competition is a subset of intraspecific competition. Normally one thinks of males and females as reproductive collaborators, but as soon as their strategies diverge -- as soon as polygamy "invades" (Emlen & Oring, 1977) -- then males and females become competitors for resources. The above equation states that as long as females are contributing more resources to the next generation than males are, then theoretically the fewer the males, the more offspring can be produced.

Such a model does not violate Fisherian investment (Fisher, 1958) which says that parental resources should be equally distributed between the sexes. Darwin (1871) at great length pointed out that females and juveniles tend to resemble one another, and that production of weapons and elaborations occur only at maturation, *after* parental investment. Therefore, increased male mortality which results from adult secondary sexual characters is in line with investment theory.

Some workers have suggested that this model requires group selection (John Maynard Smith, Mark Kirkpatrick, *pers. comms.*) and therefore cannot work. Group selection requires that unrelated conspecifics benefit from a trait more than the individuals expressing the trait (Williams, 1966). At first consideration, all local females would benefit from decreased competition, while sabotaging females would presumably suffer a loss of fitness through increased mortality of their sons. As noted above, this was one of Seger and Trivers (1986) concerns.

But neither the sabotaging females nor their sons are losing fitness in this system. To the contrary: in a system beginning at Fisherian sex ratios (Fisher, 1958), average male fitness must *exactly* equal average female fitness. If fewer sons survive, and therefore more daughters do, the daughters will produce more offspring, and increase the mother's fitness. But since each of the offspring must have one mother and one father, given assortative mating, increase in the number of offspring demands that the sons' *average* fitness increase, despite the increased mortality.

Consider that matings approximately equal fitness. If the number of matings increase, then the average fitness of both females *and* males have likewise increased. Given that total matings can only increase when the number of females -- again, the limiting resource -- also increases, then male numbers are immaterial. This point cannot be overstated. Average survivorship does not equal average fitness, and fitness is only a question of which strategy produces the greatest number of offspring. No matter how catastrophic the mortality of the sons, given assortative mating, if enough sons remain to carry out the required matings, the *average* fitness of the sons absolutely must increase with the average fitness of the daughters. For this reason, in a polygamous system male fitness paradoxically increases with increasing male mortality. And because of this, females do not lose fitness through their sons.

One might point out monomorphic conspecifics in such a system are equally benefited by the death of the dimorphic males. This is true, but they will never benefit more than the females in a dimorphic system: given that increased sons' mortality is not an obstacle, the benefits of sabotage are never visited upon nearby non-participants more than upon the *saboteuse*. There is no penalty to the dimorphs, except in relation to populations which contain an even larger percentage of sabotaging females.

Consider that in a population of mixed dimorphs and monomorphs, offspring will be produced at a faster rate -- correlative with the percentage of dimorphs in the population -- than in any population of pure monomorphs.

For that reason, the mixed population will enjoy increased relative fitness, and their offspring will emigrate and spread. But the benefit of increased offspring production is linked only with dimorphism. As the offspring emigrate, when monomorphs leave the vicinity of dimorphs, the monomorphs' fitness will again return to previous levels. Some fitness benefit, however, is always visited upon the dimorphs themselves.

Given random emigration of the dimorphs, "clumping" will eventually occur (if herd behavior, contiguous population spread, or preferential association of dimorphs do not cluster them first). Such clumping will produce populations which contain higher percentages of dimorphs than the natal population. The larger the percentage of dimorphs in a population, the greater the overall advantage and benefit for all individuals in the population, monomorphic and dimorphic.

But for any population which contains monomorphs, a population with fewer monomorphs will always be able to "invade"-- *i.e.,* populations which contain more dimorphs will always enjoy increased fitness over neighboring population containing fewer dimorphs. Eventually, pure populations of dimorphs will appear, and they will enjoy higher fitness than any mixed population.

Once a dimorphic population of *saboteuses* have established an area of geographic continuity (or again, physical continuity, as with a herd), the benefits of increased male mortality will be visited more upon the interior of that group, than on peripheral non-sabotaging neighbors. The interior of the geographic area will produce offspring at a faster rate, and will tend to expand.

It should be noted that this theory of female sabotage does not immediately exclude other theories of sexual dimorphism, and could conceivably work in tandem with one or more of them. But whether this theory alone generates the level of sexual dimorphism we see in animals, or whether another theory is primarily responsible, once dimorphism is established, females and juveniles derive a material benefit from increased male mortality.

Consider that many models for "runaway" have suggested that females can push males to increased mortality on mere whim, *i.e.* "preference" (O'Donald, 1962, 1977; Lande, 1980, 1981; Lande & Arnold, 1985; Kirkpatrick, 1982; Heisler, 1985; Seger, 1985; Pomiankowski *et al.*, 1991; Pomiankowski & Iwasa, 1993). "Preference" is apparently an entity without properties, as evidenced by the fact that none of these authors has ever supplied the variable "trait" -- ostensibly a vector (longer, broader, brighter) -- with any dimensions whatsoever. If runaway can predict the increase of an entirely undefined variable, and in so doing produce a maternal increase in sons' mortality, without any stronger impetus than "preference", then how much stronger must those theories be when a clear material advantage can be shown?

Nevertheless, whatever theoretical objections one may offer, they are moot. We do not use theory to test the facts: females in dimorphic systems have already saddled males with traits which result in increased male mortality. And if increased male mortality does not leaves more resources for females and offspring, then all of Darwinian evolution is in jeopardy. When theoreticians suggest that a situation cannot exist, and it already does, then we have an important caution about investing too much confidence in untested theory.

Therefore, in a polygamous system female preference for costly male traits produces sabotage, regardless of whatever mechanism is hypothesized to be driving the system. However, it must be noted -- and this is no small point -- that this is the only theory of sexual dimorphism to date in which any advantage to female preference can be directly measured.

Let us return to male combat. As noted above, Darwin (1871) suggested that there were two mechanisms involved in sexual dimorphism: female "preference" for some males types; and male competition for "possession" of females. Poulton (1890) defined the first of these as "epigamic", after which Huxley (1938) discussed them as "intersexual" and "intrasexual" selection. This tradition continues as a tension between "female choice" (intersexual selection) and "male competition" (intrasexual selection), and a debate over who "controls" mating (Trivers, 1972; Parker, 1979, 1983; Andersson, 1982; Halliday, 1983; Hammerstein & Parker, 1987; Bradbury & Davies, 1987; Ryan & Rand, 1990; Maynard Smith, 1991; Droney, 1992). We have generally assumed that the winner of an arbitrary contest also "wins" the female. But no less an authority than Darwin (1871, ii. p.269) himself points out, "The female could in most cases escape, if wooed by a male that did not please or excite her; and when pursued, as so incessantly occurs, by several males, she would often have the opportunity, whilst they were fighting together, of escaping with, or at least of temporarily pairing with, some one male."

It is therefore not apparent why victory of one animal over a second animal provides *de facto* access to a third animal: despite the widespread acceptance of the theory, no one has ever explained how this might work. However, fighting of males, particularly with weapons, often leads to heavy male mortality (Gorsuch, 1934; McHugh, 1958; Bannikov *et al.*, 1967; Schaller, 1972; Geist, 1966, 1971, 1974; Sorenson, 1974; Sussman & Richard, 1974; Wilkinson & Shank, 1976; Clutton-Brock *et al.*, 1979; Silverman & Dunbar, 1980). The theory of "intrasexual" competition portrays females as hapless victims, when it is clear that they are equally capable of every ruthlessness which have been traditionally assigned to males.

In addition, if victory over other males led irrevocably to possession of females, then we might ask why the strategy of male combat has not invaded the arena of male elaborations: a "less stimulating" but more pugilistic male should quickly appear, who would fight with the object of the female's fancy, and thereby acquire mating rights by superior force. Therefore we might ask which is more reasonable, do males exploit females by fighting with other males (and if so, how?), or do females exploit males by exclusively mating with males who fight and win?

Male elaborations and combat produce another benefit for females. An important cause of animal mortality is predation, and predators are also held at a carrying capacity. Male elaborations/traits often result in increased predation (Endler, 1978, 1980, 1982, 1983; Haas, 1976; Ryan, 1985; Breden & Stoner, 1987). If ornaments and battle wounds more readily attract predators, create obstacles to swift escape, and/or physiologically weaken males so that they are more easily captured, then predation load will shift away from females, and onto males. If so, through their preference for costly male traits, females are getting more "bang for their buck": they are being relieved of both interspecific and intraspecific competition.

Likewise, this model of sexual dimorphism addresses the "bright male" situation. Hamilton and Zuk (1982) suggested that male elaborations can serve as indicators of health. That being so, we should expect that the larger the elaboration, the further away an accurate health assessment can be made. If ornamentation loudly broadcasts "health" or the lack thereof, as has been postulated for "stotting" or "spronking" in gazelles (Estes & Goddard, 1967; Walther, 1969; Zahavi in Dawkins, 1976), then large male ornaments will aid predators in assessing prey health and in identifying the easier prey (Endler, 1978, 1980, 1982, 1983;, Haas 1976; Breden & Stoner, 1987).

Another point offered by equation (1) is that offspring investment decreases as m, female mating investment, increases. This suggests an explanation as to the relative roles of males and females in mate location (Trivers, 1972; Parker, 1978; Alexander & Borgia, 1979; Hammerstein & Parker, 1987; Kirkpatrick, 1987; Real, 1990). When there is a cost or risk to attracting a mate, *e.g.*, acoustics or bioluminescence, it is generally the males who take the risk (Parker, 1978; Arak, 1983; Lloyd & Wing, 1983; Ryan, 1985). When the greater cost or risk is not in attracting a mate, but in locating one -- as in pheromonal systems -- then the males tend to take that risk (Beer *et al.*, 1958; deVos *et al.*, 1967; Wood, 1970; Kaissling, 1971; Myers & Krebs, 1971; Parker, 1978). Females should assume whichever is the less costly role in mate location.

Many authors have addressed the tension between "natural selection" and "sexual selection", and the limits they impose on male characters (Fisher, 1915; Arnold & Wade, 1984; Breden & Stoner, 1987; Endler, 1980, 1982, 1983). The above equation offers an alternate hypothesis for the upper and lower limits on male characters: maximization of female biomass, and minimization of female mating costs. This model suggests that male elaborations and fighting should increase male mortality just to the point that males cease to become readily available for mating, *i.e.*, the point at which m becomes too large.

This model also offers a different perspective to some other aspects of mating behavior. Many authors have studied systems in which one male reportedly "controls" a group of females (Hrdy, 1977; Clutton-Brock *et al.*, 1977; LeBoeuf, 1972, 1974; Dunbar, 1984). Despite the apparent similarities between human and animal harems, it is not at all clear the methods by which one or a few males physically restrain and dominate a female biomass many times their own. The concept that males can "dominate" females would seem to stem from the Victorian mores of Darwin and his contemporaries. Again, females are not hapless victims, and they are capable of every ruthlessness. If females who live in harems only allow one male into their territory, and he excludes all other males, then there will be an increase in material benefits for females and their young, when compared to a system with equal numbers of adult sexes. If that one male is also primarily responsible for physically protecting the harem from competitors and predators, then females are also relieved of that cost.

Similarly, resource defense polygyny has often been seen as male exploitation of females (Verner & Willson, 1966; Orians, 1969; Emlen & Oring, 1977; Borgia, 1979). But if one male denies all other males access to vital resources, he is in fact aiding the females in concentrating those resources into offspring investment. Females who prefer to mate with males who exclude other males from limited but vital resources will experience increased fitness.

Leks are a prominent polygamous behaviour, and are very expensive metabolically for males, sometimes exhaustingly so (Ryan, 1985; Gibson, 1990; Hausfater *et al.*, 1990; Höglund *et al.*, 1992). And yet, some lekking species are dimorphic, while others are monomorphic. Female sabotage offers a different explanation for lekking, particularly in monomorphic species. In a brief period sheer exhaustion from lek displays can insure as much male mortality as taxing elaborations may require months to do. By protracting the rendezvous between the sexes over several days, and preferring to mate with males who repeatedly perform athletic activities, females can push males to extreme fatigue and a loss of metabolic reserves. Males who perform for only a limited period during lekking may be spared some of the mortality, but they should also experience proportionately fewer matings (Mackenzie *et al.*, 1995). And since position within the lek is important (Gibson, 1990, Droney, 1992) males who do not stay the duration will lose access to prime display areas.

It is interesting that lekking, and the exhaustion it exacts, are not explained by any of the other theories of sexual dimorphism. Runaway (Fisher, 1915, 1958), sensory exploitation (Ryan & Rand, 1990, 1993), and fluctuating asymmetry (Møller 1990b) do not explain nor predict such behavior. Handicap (Zahavi, 1975, 1977), and bright male (Hamilton & Zuk, 1982) predict it, but only if females wait until the end of a lekking period before choosing a mate; the females who arrive early should not be able to make a reliable evaluation of mate quality.

One final problem that this theory addresses, and one which provides an interesting "test case" for the various theories of sexual dimorphism, is the frequent appearance of non-mimetic males in Batesian mimic butterflies (Turner, 1978). The hypotheses of runaway, bright male, fluctuating asymmetry, and sensory exploitation all predict that males should be brightly colored, as do revealing handicap (Hamilton & Zuk, 1982; Iwasa *et al.*, 1991; Maynard Smith, 1991) and conditional handicap (Zahavi, 1977, West-Eberhard, 1979; Andersson, 1986; Iwasa *et al.*, 1991; Maynard Smith, 1991). Only pure epistasis (Zahavi, 1975, Maynard Smith, 1985, 1991) predicts that males should be dull (or perhaps that males should be brightly colored in a different pattern) thereby proving that they can survive without subterfuge; but pure epistasis is the portion of the handicap principle which the theoretical models do not support (Maynard Smith, 1976, 1978, 1985; Heisler, 1985; Davis & O'Donald, 1976, Kirkpatrick, 1986).

The sabotage hypothesis predicts that Batesian mimic males should be dull. If predators avoid butterflies with certain bright coloration, and there is an advantage to maximizing the ratio of mimics to models, then female mimics should seek to minimize the numbers of mimetic males, and thereby preserve the females' advantage. If females can force males to be either bright mimetics or dull non-mimetics, the females should prefer disadvantaged non-mimetics, and thereby reduce the females' predation load.

Finally, just as Darwin (1859) used artificial selection to illustrate natural selection, so artificial population maximization (specifically, game management) can be used to illustrate female sabotage as a method of natural population maximization: preferential hunting and fishing of males is a long-established cornerstone of wildlife preservation and renewal.

To conclude, Fisher (1958, p155) asserted, "To judge, however, of the relative efficacy of the different possible situations in which sexual preference may confer a reproductive advantage, detailed ecological knowledge is required." His comment is certainly supported by this paper. Just as Fisher used the advances in genetic theory of his day to propose an explanation of sexual dimorphism, so this paper is an attempt to use the ecological theory of our day to propose a different explanation of that same dimorphism.

ACKNOWLEDGEMENTS

This paper is being submitted in partial fulfillment of the Doctor of Philosophy in Biology, University of Mississippi, Oxford. Special thanks to Gary Miller, Robert Jaeger, Andrew Pomiankowski, and two referees who provided valuable comments.

REFERENCES

Alexander, R.D. and G. Borgia (1979). On the origin and basis of the male-female phenomenon. In: M. Blum and N. Blum, eds., Sexual Selection and Reproductive Competition in Insects, pp. 417-440. New York, Academic Press.

Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. Nature 299: 818-820.

Andersson, M. (1986). Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. Evolution 40: 804-816.

Arak, A. (1983). Sexual selection by male-male competition in natterjack toad choruses. Nature 306: 181-210.

Arnold, S.J. and M.J. Wade (1984). On the measurement of natural and sexual selection: applications. Evolution 38: 720-734.

Bannikov, A.G., L.V. Zhirnov, L.S. Lebedeva and A.A. Fandeev (1967). Biology of the Saiga. Jerusalem, Israel Program for Scientific Translations. (Translated from the Russian: 1961. Biologiya Saigaka. Izdatel'stvo Sel'skokhozyaistvennoi Literatury, Zhurnalov i Plakatov, Moscow.)

Bateman, A.J. (1948). Intra-sexual selection in *Drosophila*. Heredity 2: 349-368.

Beer, J.R., L.D. Frenzel and C.F. MacLeod (1958). Sex ratios of some Minnesota rodents. American Midland Naturalist 59: 518-524.

Borgia, G. (1979). Sexual selection and the evolution of mating systems. In: M. Blum and N. Blum, eds., Sexual Selection and Reproductive Competition in Insects, pp. 19-80. New York, Academic Press.

Bradbury, J.W. and N.B. Davies (1987). Relative roles of intra- and intersexual selection. In: J.W. Bradbury and M.B. Andersson, eds., Sexual Selection: Testing the Alternatives, pp. 143-163. Chichester, John Wiley & Sons.

Breden, F. and G. Stoner (1987). Male predation risk determines female preference in the Trinidad guppy. Nature 329: 831-833.

Clutton-Brock, T.H., P.H. Harvey and B. Rudder (1977). Sexual dimorphism, socionomic sex ratio and body weight in primates. Nature 269: 797-800.

Clutton-Brock, T.H., S.D. Albon, R.M. Gibson and F.E. Guinness (1979). The logical stag: adaptive aspects of fighting in Red Deer (*Cervus elaphus* L.). Animal Behavior 27: 211-225.

Darwin, C. (1859). On the Origin of Species by Means of Natural Selection. London, John Murray.

Darwin, C. (1871). The Descent of Man and Selection in Relation to Sex. 2nd ed., rev. (1898). New York, D. Appleton and Co.

Davis, G.W.F. and P. O'Donald (1976). Sexual selection for a handicap: A critical analysis of Zahavi's model. Journal of Theoretical Biology 57: 345.

Dawkins, R. (1976). The Selfish Gene. Oxford, Oxford University Press.

deVos, A., P. Brokx and V. Geist (1967). A review of social behavior of the North American cervids during the reproductive period. The American Midland Naturalist 77: 390-417.

Droney, D.C. (1992). Sexual selection in a lekking Hawaiian *Drosophila*: the roles of male competition and female choice in male mating success. Animal Behaviour 44: 1007-1020.

Dunbar, R.I.M. (1984). Reproductive Decisions: An Economic Analysis of Gelada Baboon Social Strategies. Princeton, Princeton University Press.

Emlen, J.T. and L.W. Oring (1977). Ecology, sexual selection and the evolution of mating systems. Science 197: 215-223.

Endler, J.A. (1978). A predator's view of animal color patterns. Evolutionary Biology 11: 319-364.

Endler, J.A. (1980). Natural selection on color patterns in *Poecilia reticulata*. Evolution 34: 76-91.

Endler, J.A. (1982). Convergent and divergent effects of natural selection on color patterns in two fish faunas. Evolution 36: 178-188.

Endler, J.A. (1983). Natural and sexual selection on color patterns in poeciliid fishes. Environmental Biology of Fishes 9: 173-190.

Estes, R.D. and J. Goddard (1967). Prey selection and hunting behavior of the African wild dog. Journal of Wildlife Management 31: 52-70.

Fisher, R.A. (1915). The evolution of sexual preference. Eugenics Review 7: 184-192.

Fisher, R.A. (1958). The Genetical Theory of Natural Selection, 2d revised edition. New York, Dover Publications.

Froehlich, J.W., R.W. Thorington, Jr. and J.S. Otis (1981). The demography of Howler Monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. International Journal of Primatology 2: 207-236.

Geist, V. (1966). The evolution of horn-like organs. Behaviour 27: 175-214.

Geist, V. (1971). Mountain Sheep. Chicago, University of Chicago Press.

Geist, V. (1974). On fighting strategies in animal combat. Nature 250: 354.

Gibson, R.M. (1990). Relationships between blood parasites, mating success and phenotypic cues in male sage grouse *Centrocercus urophasianus*. American Zoologist 30: 271-278.

Gorsuch, D.M. (1934). Life history of the Gambel quail in Arizona. University of Arizona Bulletin 5 (Biological Scientific Bulletin No. 2).

Haas, R. (1976). Sexual selection in *Nothobranchius guentheri* (Pisces: Cyprinodontidae). Evolution 30: 614-622.

Halliday, T.R. (1983). The study of mate choice. In: P. Bateson, ed., Mate Choice, pp. 3-32. Cambridge, Cambridge University Press.

Hamilton, W.D. and M. Zuk (1982). Heritable true fitness and bright birds: a role for parasites? Science 218: 384-387.

Hammerstein, P. and G.A. Parker (1987). Sexual selection: games between the sexes. In: J.W. Bradbury and M.B. Andersson, eds., Sexual Selection: Testing the Alternatives, pp. 119-142. Chichester, John Wiley & Sons.

Haskins, C.P., E.F. Haskins, J.J.A. McLaughlin and R.E. Hewitt (1961). Polymorphisms and population structure in *Lebistes reticulatus*, an ecological study. In: W.F. Blair, ed., Vertebrate Speciation, pp. 329-395. Austin, Univ. Texas Press.

Hausfater, G., H.C. Gerhardt and G.M. Klump (1990). Parasites and mate choice in gray treefrogs, *Hyla versicolor*. American Zoologist 30: 299-311.

Heisler, I.L. (1985). Quantitative genetic models of female choice based upon "arbitrary" male characters. Heredity 55: 187-198.

Höglund, J., J.A. Kålås and P. Fiske (1992). The costs of secondary sexual characters in the lekking great snipe (*Gallinago media*). Behavioral Ecology and Sociobiology 30: 309-315.

Hrdy, S.B. (1977). The Langurs of Abu: Female and Male Strategies of Reproduction. Cambridge, Harvard University Press.

Huxley, J.S. (1938). Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. American Naturalist 72: 416-433.

Iwasa, Y., A. Pomiankowski and S. Nee (1991). The evolution of costly mate preferences. II. The "handicap" principle. Evolution 45: 1431-1442.

Kaissling, K.E. (1971). Insect olfaction. In: L. Beidler, ed., Handbook of Sensory Physiology, Vol. 4. Chemical Senses. New York, Springer-Verlag.

Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. Evolution 36: 1-12.

Kirkpatrick, M. (1986). The handicap mechanism of sexual selection does not work. American Naturalist 127: 222-240.

Kirkpatrick, M. (1987). The evolutionary forces acting on female mating preferences in polygynous animals. In: J.W. Bradbury and M.B. Andersson, eds., Sexual Selection: Testing the Alternatives, pp. 119-142. Chichester, John Wiley & Sons.

Kodric-Brown, A. and J.H. Brown (1984). Truth in advertising: the kinds of traits favored by sexual selection. American Naturalist 124: 309-23.

Krebs, J.R. and N.B. Davies (1992). An Introduction to Behavioral Ecology. London, Blackwell Scientific.

Kruijt, J.P. and J.A. Hogan (1967). Social behavior on the lek in Black Grouse, *Lyrurus tetrix tetrix* (L.) Ardea 55: 203-240.

Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34: 292-305.

Lande, R. (1981). Models of speciation by sexual selection of polygenic traits. Proceedings of the National Academy of Sciences USA 78: 3721-3725.

Lande, R. and S.J. Arnold (1985). Evolution of mating preference and sexual dimorphism. Journal of Theoretical Biology 117: 651-664.

LeBoeuf, B.J. (1972). Sexual behaviour in the Northern Elephant Seal *Mirounga angustirostris*. Behaviour 41: 1-26.

LeBoeuf, B.J. (1974). Male-male competition and reproductive success in elephant seals. American Zoologist 14: 163-176.

Lloyd, J.E. and S.R. Wing (1983). Nocturnal ærial predation of fireflies by light-seeking fireflies. Science 222: 634-635.

Mackenzie, A., J.D. Reynolds and V.J. Brown (1995). Variation in male mating success on leks. The American Naturalist 145: 633-652.

Malthus, T. (1798). Essay on the Principle of Population as it Affects the Future Improvement of Society, with Remarks on the Speculations of Mr. Godwin, M. Condorcet, and Other Writers.

Maynard Smith, J. (1976). Sexual selection and the handicap principle. Journal of Theoretical Biology 57: 239-242.

Maynard Smith, J. (1978). The handicap principle a comment. Journal of Theoretical Biology 70: 251-252.

Maynard Smith, J. (1985). (Mini Review) Sexual selection, handicaps and true fitness. Journal of Theoretical Biology 115: 1-8.

Maynard Smith, J. (1991). Theories of sexual selection. Trends in Ecology and Evolution 6: 146-151.

McHugh, T. (1958). Social behavior of the American buffalo (*Bison bison bison*). Zoologica 43: 1-42.

Møller, A.P. (1990). Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. Animal Behaviour 40: 1185-1187.

Myers, J. and C. Krebs (1971). Sex ratios in open and closed vole populations: demographic implications. American Naturalist 105: 325-344.

O'Donald, P. (1962). The theory of sexual selection. Heredity 17: 541-552.

O'Donald, P. (1977). Theoretical aspects of sexual selection. Theoretical Population Biology 12: 298-334.

Orians, G. (1969). On the evolution of mating systems in birds and animals. American Naturalist 103: 589-603.

Parker, G.A. (1978). Evolution of competitive mate searching. Annual Review of Entomology 23:173-196.

Parker, G.A (1979) Sexual selection and sexual conflict. In: M. Blum and N. Blum, eds., Sexual Selection and Reproductive Competition in Insects, pp. 123-176. New York, Academic Press. pp123-176.

Parker, G.A. (1983). Mate quality and mating decisions. In: P. Bateson, ed., Mate Choice, pp. 141-166. Cambridge, Cambridge University Press.

Pomiankowski, A. and Y. Iwasa (1993). Evolution of multiple sexual preferences by Fisher's runaway process of sexual selection. Proceedings of the Royal Society, London 253: 173-181.

Pomiankowski, A., Y. Iwasa and S. Nee (1991). The evolution of costly mate preferences. I. Fisher and biased mutation. Evolution 45: 1422-1430.

Poulton, E.B. (1890). The Colours of Animals: their Meaning and Use, especially considered in the case of Insects. London, Kegan Paul, Trench, Trübner, & Co.

Promislow, D.E.L., R. Montgomerie and T.E. Martin (1992). Mortality costs of sexual dimorphism in birds. Proceedings of the Royal Society (London) 250: 143-150.

Real, L. (1990). Search theory and mate choice. I. Models of single-sex discrimination. The American

Naturalist. 136: 376-405.

Ryan, M.J. (1985). The Túngara Frog: A Study of Sexual Selection and Communication. Chicago, University of Chicago Press.

Ryan, M.J. and A.S. Rand (1990). The sensory basis of sexual selection for complex calls in the túngara frog, *Physalæmus pustulosus* (sexual selection for sensory exploitation). Evolution 44: 305-314.

Ryan, M.J. and A.S. Rand (1993). Species recognition and sexual selection as a unitary problem in animal communication. Evolution 47: 647-657.

Schaller, G.B. (1972). The Serengeti Lion. Chicago, University of Chicago Press.

Seger, J. and R. Trivers (1986). Asymmetry in the evolution of female mating preferences. Nature 319: 771-773.

Selander, R.K. (1965). On mating systems and sexual selection. American Naturalist 99: 129-141.

Selander, R.K. (1972). Sexual selection and dimorphism in birds. In: B. Campbell, ed., Sexual Selection and the Descent of Man, pp. 1871-1971. Chicago, Aldine.

Silverman, H.B. and M.J. Dunbar (1980). Aggressive tusk use by the narwhal *Monodon monoceros* L. Nature 284: 57-58.

Sorenson, M.W. (1974). A review of aggressive behavior in the tree shrews. In: R.L. Holloway, ed., Primate Aggression, Territoriality and Xenophobia, pp. 13-30. New York, Academic Press.

Sussman, R.W. and A. Richard (1974). The role of aggression among diurnal prosimians. In: R.L. Holloway, ed., Primate Aggression, Territoriality and Xenophobia, pp. 49-76. New York, Academic Press.

Tinbergen, N. (1963). On aims and methods of ethology. Zeitschrift für Tierpsychology 20: 410-433.

Trivers, R.L. (1972). Parental investment and sexual selection. In: B. Campbell, ed., Sexual Selection and the Descent of Man, pp. 139-179. Chicago, Aldine.

Turner, J.R.G. (1978). Why male butterflies are non-mimetic: natural selection, sexual selection, group selection, modification and sieving. Biological Journal of the Linnean Society 10: 385-432.

Verner, J. and M. Willson (1966). The influence of habitats on mating systems of North American passerine birds. Ecology 47: 143-147.

Walther, F.R. (1969). Flight behaviour and avoidance of predators in Thomsons' gazelle (*Gazella thomsoni* Guenther 1884). Behaviour 34: 184-221.

West-Eberhard, M.J. (1979). Sexual selection, social competition and evolution. Proceedings of the American Philosophical Society 123: 222-234.

Wilkinson, P.F. and C.C. Shank (1976). Rutting-fight mortality among musk oxen on Banks Island, Northwest Territories, Canada. Animal Behavior 24: 756-758.

Williams, G.C. (1966). Adaptation and Natural Selection: A Critique of Some Evolutionary Thought. Princeton, Princeton University Press.

Wood, D.H. (1970). An ecological study of *Antechinus stuartii* (Marsupialia) in a Southeast Queensland rain forest. Australian Journal of Zoology 18: 185-207.

Zahavi, A. (1975). Mate selection -- a selection for a handicap. Journal of Theoretical Biology. 53: 205-214.

Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). Journal of Theoretical Biology 67: 603-605.