

FEMALE INCITATION OF MALE COMPETITION:
A MECHANISM IN SEXUAL SELECTION

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The role of the female in determining which male will sire her offspring was treated by Darwin (1871) in his theory of sexual selection. Fisher (1930) and Huxley (1938) saw two principles involved in sexual selection. Huxley termed behavioral interactions between males and females epigamic selection and behavioral interactions between members of the same sex (usually males) intrasexual selection. Female choice, which occurs when a female selects only one or a few among many male suitors, is an example of epigamic selection, and fighting among males to monopolize females, with the result being that some males breed more than others, is an example of intrasexual selection. The distinction between the two types of selection is often difficult to make. For example, if a female increases her fitness by choosing among male sexual partners she will outcompete females that do not choose. Darwin thought that both epigamic and intrasexual aspects of his theory helped to explain the evolution of striking differences between the sexes.

Females that discriminate between potential mates should be favored by selection because one-half of the genetic complement of their offspring comes from the father, and in some species, he also helps to rear the young. In other words, a female's reproductive success is tied up with her offspring whose fitness is in part determined by an unrelated male. Because reproductive success is not simply a matter of the number of offspring that an organism leaves but also a matter of the "quality or probable success of these offspring" (Fisher 1930, p. 143), the male that is chosen to be the other parent should be the most fit male available, i.e., the one whose genes will make the greatest contribution to the next generation relative to other available genes. In species where males invest little in the offspring beyond their sex cells, females should choose males on the basis of genotype alone. Where males engage in parental care, female choice should also involve the male's willingness and ability to be a good parent (Orians 1969; Trivers 1972). In several birds there is strong evidence that females choose males on territories which are rich in food (Hinde 1956; Verner 1964; Zimmerman 1966; Verner and Engelson 1970). Williams (1975), however, disagrees with the idea that female discrimination should favor the genetically fittest male because, in his opinion, this would require an unrealistically high heritability of fitness.

Female choice has received less attention and is a more controversial subject than male-male competition (Ghiselin 1974). Perhaps the study of female choice has been neglected because it implied to Darwin "powers of discrimination and taste," attributes which are difficult to study. On the other hand, competition among males is more physical and obvious, and thus appears easier and more significant to investigate. Some say female choice is not as important an evolutionary force as Darwin thought (e.g., Wallace 1889; Huxley 1938; Lack 1968) but others disagree (e.g., Fisher 1930; Orians 1969). The fact is that pure epigamic selection is hard to document in the field (Wilson 1975). According to Trivers (1972), most studies have shown merely that females choose sexual partners that are sexually mature, of the right species, and of the right sex. It has proven more difficult to document subtle discriminations among many appropriate males. Even in lek-forming grouse, the ruff and other polybrachygynous birds (Selander 1972; Wiley 1973), and a few ungulates (Beuchner and Schloeth 1965; Leuthold 1966), where female choice has been demonstrated, little is known about the basis on which females choose.

In the broadest sense, female choice operates whenever a female influences what male will sire her offspring regardless of the means by which she brings this about. Investigators have tended to emphasize positive responses of the female as an indication of choice, i.e., moving toward the male or soliciting him. But moving away from a suitor or rejecting him can also be instrumental in determining with whom a female will mate. For example, copulatory mounts protested by a periostrous female may not simply be due to unreceptivity, as is often claimed, but may be contingent on the identity of the suitor. A bitch in heat may reject one male and a few seconds later accept a different male (Beach and Le Boeuf 1967; Le Boeuf 1967*b*). Similarly, moving away from courting males has often been interpreted as unreceptive behavior or as a female's attempt to avoid a sexually overeager male (Summers-Smith 1963). But this behavior may also allow the female to test the vigor, tenacity, and speed of the several males which pursue her, attributes which are probably correlated with fitness. Selection should favor that behavior of a female which results in a sexual union with optimal genetic consequences for her.

We describe one way in which a female can maximize the probability of mating with the "best male" without discriminating among males or choosing the best territory. She may incite males to compete for her and then mate with the winner. In many species, this may be the most direct strategy for insuring copulation with a mature male who has conquered his rivals and who, by mating with other females, has demonstrated his reproductive success. Trivers (1972) and Selander (1972) discuss the advantages to a female of mating with such a male.

Specifically, we describe how female elephant seals, *Mirounga angustirostris*, respond to copulatory attempts with loud vocalizations and vigorous escape movements. This behavior alerts nearby males who attempt to prevent the copulations of others. Competition ensues among males of varying social ranks with the result that mating is most likely to occur with the highest-ranking

adult male. We discuss how a similar mechanism might operate in other species where several males compete simultaneously for a sexually receptive female.

The social organization and breeding behavior of elephant seals has been described in detail elsewhere (Bartholomew 1952; Le Boeuf and Peterson 1969; Le Boeuf 1972, 1974; Le Boeuf et al. 1972), so only those aspects of behavior relevant to the present paper will be reviewed here.

During the breeding season males fight and threaten each other to establish rank in a social hierarchy which determines access to females who clump together in one or more harems. A male displaces another by threat or overt attack. The subordinate avoids an encounter by retreating from a male that dominates him. Males prevent subordinates from approaching females and interrupt their copulatory attempts. The higher a male's social rank, the closer his physical proximity to females and the more frequently he interrupts the mounts of others; conversely, he is interrupted by others less frequently. Only the highest-ranking male, or alpha male, can mount females repeatedly without being displaced by a competitor. The correlation between social rank and reproductive success, as indicated by copulatory frequency, is high and positive (Le Boeuf 1974).

All males attempt to enter the harem and mate with females while at the same time attempting to keep other males out of it. The number of males in a harem is a function of its size. Only the alpha bull resides in a harem composed of less than 40 females. As the number of females in a harem increases, additional males gain entrance. For example, 10–15 males may be found in a harem of 300 females, and others may enter when the opportunity arises. When the harem is large, the alpha bull can no longer patrol the entire harem, so he compromises by dominating only one sector of it. The beta and gamma males, and so forth, occupy and defend increasingly smaller subsections of the harem. Low-ranking males are relegated to the periphery of the harem or beyond.

Females give birth to a single pup approximately 6 days after arrival on the rookery. The pup is nursed daily for about 28 days then weaned when the female returns to sea. Females copulate during the last few days of nursing before they depart. During estrus, defined here as the period between the first day and last day of copulation (the day of departure), a female may copulate several times with one or more males.

Males do not court or investigate the perineal region of the female prior to mounting. They mount from one side without any preliminaries and seemingly attempt to overpower the female who is less than half their size. Males use the great bulk and weight of their forequarters, a foreflipper clasp, and a neck bite to restrain the female. They mount females regardless of their stage in the estrous cycle: pregnant females, females giving birth, postparturient females, and estrous females. Only the frequency, not the form of these mating attempts, varies with the female's estrous cycle. A mount ends in one of three ways: (1) the male ceases to attempt copulation and the female is allowed to move away, (2) the mounter is moved from the female by the aggressive action of a more dominant male, or (3) intromission (copulation) occurs.

Females respond to male mounts by active protest or passive acceptance. We use the word "protest" simply as a term of convenience to describe the corpus of behavioral components which makes it difficult for the male to obtain penile intromission. A female protests by issuing a virtually continuous train of vocal threats (Bartholomew and Collias 1962) and by whipping her hind-quarters vigorously from side to side. She may also direct sand-flipping movements of her foreflippers back and upward toward the male, nip his neck, or struggle to get away. Alternatively, the female may remain passive throughout the mount or she may facilitate intromission by spreading her hindflippers. Females do not court the male or solicit copulation. The conditions under which a female protests or acquiesces when mounted and the consequences of this behavior form the substance of this paper.

METHODS

The elephant seal colony at Año Nuevo Island, California (Le Boeuf et al. 1972, 1974), was observed during the 1975 breeding season. All observations were made from an elevated blind overlooking a sandy point occupied by a large harem of breeding females. At peak season, around January 26, approximately 550 females and 60 males resided on this beach, and an additional 40 males visited the area intermittently during the season.

Forty females, marked individually with paint or a bleaching agent (Le Boeuf and Peterson 1969), were observed during the daylight hours in the periods January 3–6, January 27–February 3, and February 11–21. All sexual interactions involving these females were recorded.

Twenty-three marked females did not copulate during the study period, so observations of their behavior cover only the period prior to the onset of estrus. Seventeen marked females were observed while in estrus; 14 were observed before and throughout estrus; three were observed only subsequent to the onset of estrus. Females were in estrus for 3–5 days.

When marked females were inactive, sexual interactions involving unmarked females in various stages of the estrous cycle were recorded. The estrous condition of unmarked females could be determined with certainty only if they were pregnant (nonestrous) or seen copulating (estrous).

All 180 males in the colony had names bleached on both sides of their bodies. Dominance relationships among males were known as well as the exact age of 20 males, which included the majority of the top-ranking individuals. When age was unknown it was estimated, a procedure which is accurate to within 1 yr (Le Boeuf 1974).

For analytical purposes, males were classified into one of four categories based on age, size, development of secondary sex characteristics and social rank.

1. Subadult male 3 (SA3): 6–7 yr of age, about 3.6 m long, neck shield beginning to develop, and nose just beginning to dangle. A male who underwent puberty in the previous year.

2. Subadult male 4 (SA4): 7–8 yr of age, about 3.9 m long, incompletely

developed neck shield and nose. Well past puberty, but not quite fully grown.

3. Adult male: fully grown male, 8–14+ yr of age, 4.2–4.8 m long with fully developed neck shield and a dangling proboscis, approximately 0.3 m long.

4. Alpha male: one of five adult males that dominated a subsection of the crowded harem on the point beach in 1975. Although a dominance relationship existed among these males, it was rarely expressed because of the large harem size. Each male had more females than he could mate with in his own subsection so he spent most of his time there and attempted to keep subordinates out.

In addition to individual dominance relationships within each age category, there existed age- and size-related dominance between categories; all adults dominated males in the SA4 category and the latter dominated all males in the SA3 category. It is important to note that all males present, regardless of their age, attempted to mate with females. Although 5-yr-old, pubertal males are capable of copulating, they were usually prevented from doing so by older, larger males.

Each time a female was mounted the following was recorded: the date, time, duration, and location of the episode; the identity, age category, and social rank of the male; and the identity of the female. Most important, the behavioral response of the female and interactions between the mounting male and males nearby which followed were noted. We distinguished three categories of female response:

1. Total protest: the female issues threat vocalizations, whips her hind-quarters from side to side, or tries to escape. This response continues throughout the duration of the mount and is only terminated if the male dismounts or in the rare event that he achieves insertion.

2. Partial or initial protest: same as above except that the female protests initially but stops doing so before the male dismounts or achieves insertion. The duration of the protest phase was noted.

3. No protest: the female emits none of the behavioral components of total protest except that she may try to move away. Usually, she accepts the mount passively. In some cases, she may spread her hindflippers in such a manner as to facilitate insertion. A female may also call her pup (a radically different call than the threat vocalization), flip sand, or nip at the male's neck.

Where germane, we cite preliminary observations of female reproductive strategies made in 1974 as well as annual observations of elephant seal behavior made by Le Boeuf since 1968.

RESULTS

Estrous as well as nonestrous females protest the majority of mounts attempted by males. A total of 1,478 mounts were observed, of which 79.0% were protested for the entire duration of each episode, 13.7% were partially protested, and 7.3% were not protested at all. All mounts ($N = 189$) directed to marked, known nonestrous females were totally protested. Of 271 mounts to marked females known to be in estrus, 62.7% were totally protested, 24.4%

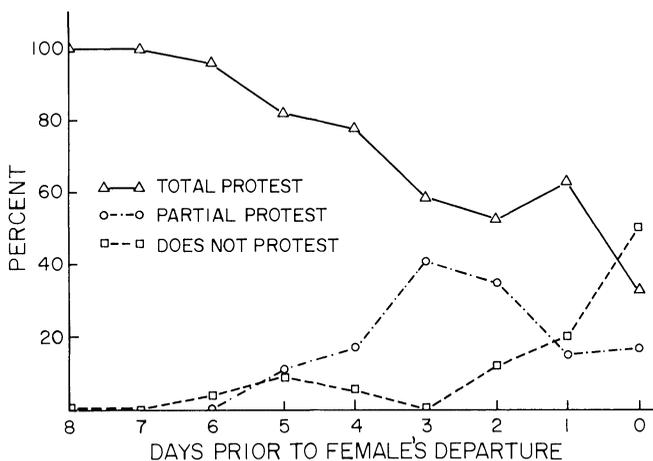


FIG. 1.—Percentage of mounts which 14 marked females protested totally, protested only initially, or did not protest at all. All females copulated for 3–5 days prior to departure.

were partially protested, and 12.9% were not protested. Thus, protesting throughout the duration of a mount is not necessarily a sign of nonestrus, while no protest or partial protest is a reliable indication that the female is in estrus.

In early estrus, females protest virtually all mounts. As estrus proceeds, females stop protesting toward the end of a mount of long duration. No-protest responses begin increasing in frequency and are the most common response on the last day of estrus. Changes in the receptivity of 14 females observed before and throughout estrus are illustrated in figure 1. A trend away from protesting totally begins about 5–6 days prior to departure, i.e., when the earliest females begin coming into estrus. Some females began protesting only at the start of a mount, and a few of them did not protest at all. In 73 mounts directed to females subsequent to their first copulation on the first day of estrus, 67.1% were totally protested, 26.0% were partially protested, and 6.8% were not protested. Females accepted mounts more readily as estrus proceeded so that by the last day, the day of departure, passive acceptance was the most common response.

Males mounting estrous females are more likely to be driven off by nearby males when the female protests than when she does not. Only 25% of 108 mounts that were unprotested by estrous females were interrupted. In contrast, more than double this amount were interrupted when the estrous female totally protested ($97/158 = 61.4\%$). Initially protested mounts were interrupted with about the same frequency as unprotested mounts ($43/202 = 21.3\%$).

Young, small, and low-ranking males are interrupted most frequently and most quickly. The percentage of mounts by males from different age and social rank categories that were interrupted is shown in table 1. The younger a male and the lower his social rank, the more frequently he was prevented from copulating by other males. This relationship holds true regardless of the female's

TABLE 1
MOUNTS INTERRUPTED BY MALES FOLLOWING VARIOUS TYPES OF
FEMALE RESPONSES TO MOUNTER

AGE OR SOCIAL RANK CATEGORY OF MOUNTING MALE	RESPONSE OF FEMALES		
	Total Protest	Partial Protest	No Protest
Alpha	3/24 = 12	0/58 = 0	1/26 = 4
Adult	54/86 = 63	25/104 = 24	18/66 = 27
SA4	26/31 = 84	10/27 = 37	6/12 = 50
SA3	14/17 = 82	8/13 = 62	2/4 = 50

NOTE.—Proportion and percentage of interrupted mounts relative to total mounts is shown. All females were in estrus.

TABLE 2
MEAN DURATION AND STANDARD DEVIATIONS OF MALE-INTERRUPTED MOUNTS AND
UNINTERRUPTED MOUNTS THAT WERE TOTALLY PROTESTED BY ESTROUS AND
NONESTROUS FEMALES (in Seconds)

Age or Social Rank Category of Mounting Males	Interrupted Mounts (<i>N</i> = 567)	Uninterrupted Mounts (<i>N</i> = 543)
Alpha	37.7 ± 11.6 (<i>N</i> = 3)	50.6 ± 71.0 (<i>N</i> = 109)
Adult	27.2 ± 39.2 (<i>N</i> = 249)	36.1 ± 56.4 (<i>N</i> = 268)
SA4	15.4 ± 21.7 (<i>N</i> = 202)	26.1 ± 40.6 (<i>N</i> = 97)
SA3	17.3 ± 29.4 (<i>N</i> = 116)	24.6 ± 36.6 (<i>N</i> = 69)

response, but the relationship was strongest when the female protested throughout the mount.

Table 2 shows that the duration of mounts protested by females is also a function of the mounting male's age and social rank. Young, low-ranking males were interrupted more quickly ($F = 6.56$, $df = 2$ [alpha male group excluded because of small N], 564, $P < .01$) and, even when they were not moved by a dominant male, they did not persist in their copulatory attempts as long as older, higher-ranking males ($F = 4.57$, $df = 3$, 539, $P < .01$). When young, low-ranking males mounted a female it was apparent from their shifty eyes and nervous behavior that they were constantly monitoring the movements of nearby, larger males and were afraid of being attacked.

Even when mounts are not interrupted by dominant males, estrous females are most apt to respond with total protest if the mounter is an immature male. Data supporting this point are shown in table 3. All of the uninterrupted mounts of SA3 males were totally protested. In contrast, less than a third of the mounts of alpha males were protested totally. Table 3 also indicates that young males were least likely to encounter estrous females that did not protest. One explanation is that young males were unable to obtain access to nonprotesting

TABLE 3
 RESPONSES OF MARKED ESTROUS FEMALES TO MOUNTS BY MALES
 VARYING IN AGE OR SOCIAL RANK

Age or Social Rank of Mounting Male	Mounts Observed (N)	Totally Protested (%)	Partially Protested (%)	Not Protested (%)
Alpha	74	37	43	20
Adult	70	49	34	17
SA4	9	78	22	0
SA3	4	100	0	0

NOTE.—Interrupted mounts are excluded.

females, usually females in the process of departing from the rookery. These females attracted a great deal of attention, and the most mature, high-ranking males on the periphery of the harem kept all of the younger, subordinate males away from them. Indeed, young males had a difficult time mounting any estrous female, as the number of mounts observed indicates. Older, dominant males prevented them from entering the harem, chased them out of it, or interfered with their attempts to mount females. Even when they were successful in eluding the guard of dominant males, the behavior of females made it difficult for them to copulate.

Mature, high-ranking males are most often involved in mounts in which the female's behavior changes from initial protest to passive acceptance. This point is supported by data in table 3. The distribution of partial protests favoring adult males is important because the first copulations of the majority of females occurred during mounts in which the female initially protested but then became passive. During the first copulations of 10 females observed, seven of them protested partially, one protested throughout the mount, and two did not protest.

Figure 2 shows that as estrus proceeded the mean duration of the protest phase of partially protested mounts decreased ($F = 4.29$, $df = 3, 41$, $P < .01$).

What may account for the differential response of females to mounts by males varying in age and social rank? This outcome may be caused by the behavior of the mounting male, the female, or the interaction between them. Since adult males were dominated by fewer individuals than younger males and they were less likely to be interrupted (table 1), they had more time to persevere in attempting copulation (table 2). Their greater size seemed to help them to overpower and exhaust the protesting female. On the other hand, the adult males may not have induced a change in a female's behavior independent of her choice. It is possible that a female distinguished a high-ranking, mature male from others by the duration and vigor of his mounts and simply stopped protesting when mounted by the former. Trivers (1972 p. 167) points out that ". . . in many species females may guarantee reproductive success by mating with those males who are most vigorous in courtship, since this vigor may correlate with an adequate supply of sperm and a willingness to transfer it."

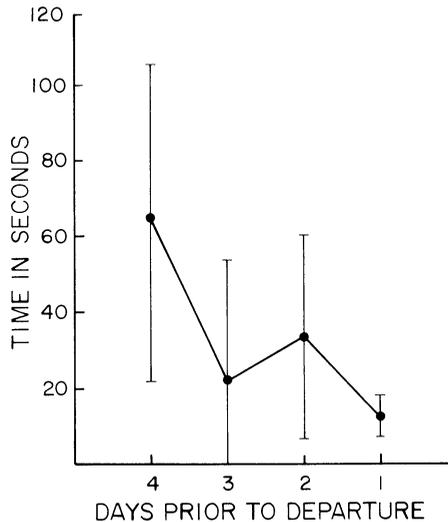


FIG. 2.—Mean duration (± 1 SD) of the protest phase of partially protested mounts.

Females that protest mounts at the beginning of estrus increase the probability that their first copulation will be with the highest-ranking male in the vicinity. Figure 1 showed that the frequency of total protests was greatest at the beginning of a female's estrous period. Table 1 showed that the protesting behavior of females alerts nearby males who threaten the subordinate mounter and prevent copulation. Thus, indirectly, the female's behavior reduces the probability of mating by younger males. The result is that the first copulations of 11 of 14 females were with the closest alpha male (we do not know who copulated at night but we assume from previous observations [Le Boeuf 1972] that daytime activity reflects accurately what goes on at night). Two females copulated for the first time with the beta male, and the remaining female copulated with a mature male with a social rank of 10, relative to all males on the beach.

A similar result was observed in 1970. There were 256 females in the harem at peak season and one male dominated the entire harem; the first copulations of 10 marked females were noted. Four females copulated first with the alpha bull, three with number 2, one with number 3, one with number 4, and one with an adult male ranked eighth in the social hierarchy. Thus, the four top-ranking bulls were responsible for 90% of the first copulations in this sample.

Females continued to copulate most frequently with high-ranking males up until the final day of estrus. Marked females copulated a total of 28 times between their first and last day of estrus. Fourteen copulations were with an alpha male, 11 were with adult males with social ranks between 2 and 10, two were with adults ranked lower than 10, and one was with a SA4 male. The same point is reinforced by considering which males mated most frequently. During the period February 11–21, the five alpha males copulated 27, 20, 17, 15, and

15 times, respectively. Only two other males, both fully grown and ranked just below the alphas, copulated as frequently as the least successful alpha males, 17 and 16 times, respectively. In general, the mating frequency of males declines with decreasing social rank (Le Boeuf 1974).

A previous study in the same area (Le Boeuf 1974) showed that the probability of a female mating with a high-ranking male depends in part on the number of females in the harem. As the number of females in the harem increased, more males copulated, including young, low-ranking, previously non-breeding males. The latter were most successful when males dominant to them were fighting, mating, or sleeping. From the female point of view, an increasing harem size means that the odds of mating with a mature, high-ranking male decrease.

Females near the end of estrus rarely protest mounts and readily accept copulation with peripheral males. The behavior of females changed drastically on their last day of estrus (fig. 1). During the last hour or two on land, they were extremely receptive to all males. This was especially noticeable in their response to peripheral males as they moved out beyond the periphery of the harem on their way to the water. We interpret this change in behavior as a female's means of insuring fertilization.

Two aspects of male competition might lower a female's chances of becoming fertilized, an outcome that she will be selected to avoid. First, mounts and copulations in progress are interrupted frequently (see also Le Boeuf and Peterson 1969; Le Boeuf 1974), which brings up the possibility that all of the copulations of some females are incomplete. Second, the few males that monopolize breeding throughout the 6-wk-long season copulate repeatedly, both day and night, a state of affairs that might lower their fertility by causing a reduction in volume, concentration, and total number of spermatozoa. Under these circumstances, it is possible that some females are not fertilized despite having copulated several times. One might expect selection to favor females that gain insurance of pregnancy by copulating on the last day of estrus with a male who has not mated frequently in the past. However, such a union cannot occur in the harem because it is ruled by high-ranking males, all of whom copulate frequently. Accordingly, females should mate somewhere outside their sphere of influence.

Most females mate with a male on the harem's periphery as they leave the rookery on their return to sea. We observed 20 females leaving the harem during the 1975 study period; four of them were marked and had been observed copulating in the harem for 3–5 days prior to their departure. We assume that all other females had also been in estrus for several days prior to departure, based on numerous observations of departing females in previous years. Seventeen of the 20 females copulated near the water's edge or in the shallow water offshore.

Most females copulated with the highest-ranking adult male present among the 10–12 males on the periphery of the harem. These males adopted the strategy of pursuing departing females. The male that copulated was usually a

low-ranking male relative to males in the harem and one who copulated infrequently, less than 10 times during the entire breeding season. Other peripheral males were also low-ranking adults or subadults. Copulations outside the harem were seldom interrupted. Only one out of every 10 mounts directed to departing females was protested. Only rarely did an alpha male in the harem follow a female as she departed, and this was only for a short distance and usually near the season's end when only a few females remained in the harem. Whereas alpha males were usually the first male with whom a female copulated, in only three out of 20 cases was he the last.

DISCUSSION

This study suggests that female elephant seals may influence the genotype of their offspring to their benefit in a simple and direct way without employing deliberate choice or esthetic criteria. By inciting males to compete for her, a female maximizes the probability of mating with a mature, high-ranking male. We assume that this type of individual is likely to be the most fit male of those that are available for several reasons. Few males survive to age 10 or more, the minimal age necessary to achieve a high social rank and dominate breeding (Le Boeuf 1974). The mortality rate of breeding age males on Año Nuevo Island is estimated to be 45% from one year to the next. The mortality rate of males prior to reaching age 8 is estimated to be 86%–97% of those born (see table 7 in Le Boeuf 1974). Accordingly, the probability of surviving to age 10 is very low. If mortality is partially a function of genotype, then males who have survived to maturity have demonstrated an important aspect of their fitness. Other attributes possessed by high-ranking adults which are probably correlated with fitness are sound physiological condition, reflected by their ability to physically dominate other mature males, and sexual experience (see Selander [1972] and Trivers [1972] for a further discussion of the attributes of males whose fitness has been demonstrated).

The consequences of a female's protesting behavior can be expected to vary with the social context. In small harems containing less than 40 females, the alpha male can prevent all other males from approaching females, and consequently he alone mates with all of them (Le Boeuf 1974). In this situation, the female gets no benefit from inciting male competition; she mates with the highest-ranking male, the only one in the harem, regardless of what she does. Yet it has been our observation that females are as likely to protest mounts in small harems as in large ones. Protesting mounts seem to be "wired in" and not specific to social situations. This may be an adaptation to the social environment most frequently found on rookeries; the majority of females in the population breed in large harems containing up to several hundred females at peak season. It is in large harems that incitation of male competition should be of greatest benefit to females. As harem size increases more males enter the harem, and some of them are low-ranking, young males. In this context, the potential for competition and male variation in fitness will be greatest. A female that does

not incite competition in a large harem runs the risk of being inseminated by a young male who may be no more fit than a noncompetitive "marginal" male (see Bartholomew 1970).

It is conceivable that females could detect high fitness in young males of low rank and mate with them as opposed to other young males. However, we think this is improbable, because copulations with young pubertal males are rarely concentrated in a few individuals. Furthermore, a few copulations at this age does not predict breeding success in adulthood, and, in retrospect, males who achieved high reproductive success in adulthood did not reveal their potential by copulating frequently as subadults (see table 6 in Le Boeuf 1974). Finally, even subadults who are somewhat successful in breeding are subject to the same high annual mortality rate as unsuccessful subadults.

The manner in which females incite males to compete for them must be clarified. One cannot distinguish whether females are simply protesting a copulation or attempting to incite noncopulating males to intervene and chase off a mounting male. From the observer's blind, it looks as if protesting females simply do not want to copulate, and this may be the case. The important thing is not the female's intentions or the observer's interpretation of them, but the *effect* of her behavior on nearby males. A blatant, squawking, wriggling, sand-flipping female with a prospective suitor on top of her struggling to pin her down attracts the attention of all males in the vicinity. Since each male's reproductive success is a function of how many females he can keep inaccessible to other males (Williams 1975), one or more of the rivals interferes with the potential copulation. The female's behavior sets in motion a sequence of male movements. For example, a male dominant to the mounter may issue a vocal threat sufficient to move the mounter from the female. But before the aggressor can reach the female he is threatened and displaced by another male dominant to him. Several aggressive interactions involving other males may ensue, resulting in a considerable change in the spatial relationships of males in the area. Episodes like this usually end when the most dominant male in the area gets close to the female and prevents all other males from mounting her or he mounts her himself. Now the female's protests have no effect, for no male can displace the mounter. He attempts to copulate until he is successful or gives up trying and moves off of his own accord.

If females did not protest copulations, males would still compete for females and interfere with each other's copulations. The mating frequency of males would probably be roughly proportional to their social rank, i.e., most females would be inseminated by mature, high-ranking males. This is the pattern which emerges from females who do not protest when mounted. The effect of a female's protesting behavior is to intensify male-male competition and augment its consequences. Her behavior activates the social hierarchy; it literally wakes up sleeping males and prompts them to live up to their social positions. The result is that it is more difficult for young males to mate, and the breeding monopoly of a few adult males is increased. Female choice in birds which lek has a similar consequence, as Trivers (1972) has pointed out.

Selection should favor the most parsimonious mechanism that enables females

to optimize their reproductive success. In elephant seals—where sexual dimorphism is great, the breeding season is short, a rigid social hierarchy exists among males, and females are continually accosted by numerous aggressive suitors—inciting competition seems to be the simplest, least complicated strategy for mating with the best male in the harem. Once a female joins a harem, this is one of the few things she can do to effect a “choice” of males.¹ In species where males fight for territories and the winner gets the most favorably situated one, the one that is richest in food, or the same one each time, the simplest strategy is for the female to select the best territory rather than the male since the greatest benefits will come with the territory. In dragonflies, *Plathemus lydia*, females oviposit at a time and place where the most fit males are available (Campanella and Wolf 1974). Female choice for a particular male based on certain criteria, what is sometimes called the “specific image” type of choice, should be relatively rare, occurring only in social systems where males do not compete for territories or for social rank which is important in mating.

As Darwin (1871) recognized, there are elements of intrasexual competition in both sexes, and the two processes do not operate independently of each other. The outcome of competition within each sex influences the distribution of reproductive success in the other sex. Male elephant seals compete to mate with as many females as possible; they show no signs of choosing among females. If one assumes that the first male to mate with a female is most apt to cause insemination, a good possibility in a mammal that gives birth to a single offspring, then males will be selected to try to mate with a female as early as possible, i.e., to try to rape females. This is the strong impression one gets observing mating in this species. But this strategy of males can work to the advantage of females. Because of the way elephant-seal society is structured, only a mature, high-ranking bull can rape a female, i.e., copulate despite total protest on the part of the female, and it is such a male, who has demonstrated his fitness, that a female is selected to “choose” to sire her offspring. Thus, it would benefit females to optimize the possibility of being raped! How might a female do this? How can a female maximize the probability that the first male to mate with her will be the alpha male? Since there is a limit to how many females an alpha male can inseminate and there is a good possibility that he is overworked (he may copulate as much as 13 times in 6 h with only 5–30-min intervals between matings (Le Boeuf 1972)), it would be advantageous for a female to mate with him early, when he is fresh and before his fertility or sexual interest starts to decline. Thus, we might expect females to compete among themselves to arrive early in the breeding season, to attempt to secure a position near the alpha male and to protest all mounts vigorously up to the point of penile intromission. We know that females who arrive early in the season form

¹ It is conceivable that arriving females exert choice over which harem to join since the fitness of the various alpha males might be expected to vary with the size of the harems defended. Alpha males in large harems might be more fit since they must defend their positions much more frequently and against more competition than alpha males in small harems. We do not know if females choose in this way, but it is known that once a female breeds in a particular harem she tends to return to it to breed in the future (Le Boeuf 1972).

the center of the harem. They are more likely to copulate with the alpha male than females on the periphery, because the alpha male takes up a central position among the females. The more space a harem occupies, the lower the probability that a female on the periphery will mate with the alpha male. Centrally located females are aggressive to females on the edge and keep them from entering the center of the harem, and early arriving females may prevent late arriving females from joining the harem (Christenson 1974). Although it is not clear what permits early-arriving, centrally located females to dominate later-arriving females, we suspect that the former are older and hence, as a group, dominant to the latter. Other factors, having to do with survival of the young, favor females that arrive early in the breeding season (Le Boeuf and Briggs 1977).

Females might be expected to incite male competition in numerous polygynous species. Since males in most polygynous species invest nothing in their offspring except genes, selection should favor females that screen males on the physical manifestation of these genes, i.e., physical superiority over other "sets of genes." This can be done most easily and is most apparent in societies where several males compete to mate with a female, a social hierarchy exists among males, and interference with mating occurs. These conditions exist in several species of fishes, lizards, toads, frogs, snakes, gallinaceous birds, carnivores, ungulates, and primates; we shall give representative illustrations from these animal groups below. As in elephant seals, we expect the behavior of these females to result in an increase in the probability of mating with a fit partner. If the first male to mate with a promiscuous female is most likely to inseminate her (a good possibility but admittedly an unknown), then we would expect females to incite competition most frequently during early estrus and less frequently or not at all toward the end of estrus.

Females may incite male competition by doing anything which alerts males in the area, causes them to compete among themselves to approach and copulate with the female, or causes them to prevent copulations by other males, particularly younger, subordinate males. A similar female strategy may be employed by some monogamous birds during pair bond formation. The signal may involve any sensory modality or combination of modalities.

Moving away from a suitor can be an effective visual signal for alerting nearby males. This is an essential component of courtship behavior in some ungulates, rodents, carnivores, and reptiles. Geist (1971) notes that female mountain sheep typically run away when mounted during the first week of the rut, and long chases ensue in which several males pursue the female. The ram follows when the female runs away, and ". . . such a chase will invariably catch the attention of other rams and they will hurry to intercept the female. Competition for the female is increased; the chances that a larger ram than the original one will be drawn to the chase is also increased, and the original ram's chances of siring offspring is reduced (p. 223)." A similar behavior pattern seems to occur in several other species of North American ungulates, e.g., the white tailed deer, *Odocoileus virginianus* (Newsom 1926) and bison, *Bison bison* (Dale Lott, personal communication). In black rats, *Rattus rattus*, females initially reject

males by running away. Ewer (1971) observed that "if more than one male is present, they may all follow the female in a line, one behind the other." Following of the female is often interrupted while a dominant male chases off subordinates. Running away from a suitor is a reliable component of courtship in the estrous bitch and excites all dogs nearby to join in the chase (Le Boeuf 1967a). Noble (1937) reports that many male snakes (notably the brown snake, *Storeria dekayi*, and the garter snake, *Thamnophis sirtalis* and *T. butleri*) are attracted to a moving female. Several males may give chase and jockey with each other for the copulatory position on the female's dorsum. Similar behavior has been observed in the terrestrial crab, *Coenobita pertatus* (Ernst Reese, personal communication).

Females may adopt unusual postures during locomotion to signal receptivity and provoke male competition. Magnuson and Prescott (1966) described the exaggerated, wobbling swimming exhibited by female Pacific bonito (*Sarda chiliensis* Cuvier) when ready to spawn. This display elicits following in a group of males who give lateral threat displays to each other and compete for a position immediately behind the female. Eventually, the female pairs with one male, they swim in a circle, and gametes are released.

Aerial chases in which females are pursued by several males are common elements in the courtship of many birds. Females initiate these chases in pintail ducks, *Anas acuta* (Smith 1968), the winter wren, *Troglodytes troglodytes* (Armstrong 1955), and in the sanderling, *Calidris alba* (Parmelee 1970).

Sounds made by females often trigger competition among males. In sage grouse, *Centrocercus urophasianus*, arriving females fly straight across the lek, and their quacking call stimulates males to strut on their territories (Wiley 1973). Nero (1956) reports that first-year male red-winged blackbirds (*Agelaius phoeniceus*) often attempt to approach a resident female, but typically the female gives a loud, rapid, shrill call, accompanied by fluttering wingtips, to which the resident territorial male responds by flying up immediately and driving off the young male. Vocalizations by chimpanzees, *Pan troglodytes*, often cause dominant males to prevent subordinates from mounting or consorting with them. During copulation, a female emits loud, distinctive calls which attract males from a wide area who subsequently copulate with her (P. R. McGinnis, personal communication).

The behavior of many female insects attracts courting males. For example, the flight tone of the female mosquito, *Aedes aegypti* L., sets off the pursuit activity of males (Roth 1948). In honeybees there may be considerable intra-sexual competition among drones swarming around flying queens (Gary 1963). However, it is not clear whether this is simply attracting a mate, inciting competition, or both. Indeed, it appears that most female insects exert less control over what male inseminates them than one finds in vertebrates. Because of the rapid development of most insects, females cannot cue on maturity, social rank, or sexual experience as an indication of fitness. (Alexander [1975] discusses other criteria which might figure in mate selection by females.) There seems to be more of a priority in insects to mate quickly as opposed to selectively.

In several species of ducks females incite their mates to attack strange drakes

(e.g., Tinbergen 1958). If the stranger wins, the female may desert her mate and court the victor (Johnsgard 1968).

In polyandrous species where females court males to get them to invest in their eggs and rear offspring one would expect the sex role reversal to be complete (see Trivers 1972); males should incite competition among females. In Wilson's phalarope, *Phalaropus tricolor*, Howe (1975) found that as soon as males arrive in the spring short flights, consisting of a male being pursued by several females, take place during pair formation. Males initiate the aerial chase by swooping down over swimming females, causing them to fly up and join the chase. This results in a larger group of pursuing females and a corresponding increase in competition among them.

Behavioral signals are but one means by which females can incite male competition. Hormone-controlled morphological changes during the estrous cycle of some females advertises their receptivity in an undirected way and can produce the same effect. The color and turgidity of the perineal sex skin of many primates communicates the precise estrous condition of the female and determines male access to females. Although female baboons, *Papio ursinus*, may be mounted by young males early in the estrous cycle, at the time of maximal perineal swelling and redness, when ovulation occurs, mature males chase younger males away and they alone copulate (e.g., Hall and DeVore 1965). The advantage of this morphological signal over a behavioral one is that it stays on for a long time. In the baboon it is graded throughout the estrous cycle. Unlike a behavioral signal, it is an inflexible, permanent fixture. The female cannot avoid signaling her estrous condition to all males. The element common to both physical and behavioral signals of this kind is the consequence: the signaling female is most apt to be fertilized by a mature, high-ranking male. It seems that selection has so favored this outcome in many primates that females near ovulation would have a difficult time copulating with a young male even if they wanted to, for older males would prevent it. Similarly, some spawning fishes undergo a change in coloration which attracts males and causes them to compete for the female (e.g., the Blue Acara, *Aequidens pulcher* Steindachner; E. Shaw, personal communication).

It is well known that pheromones released automatically by some female mammals in estrus attract members of the opposite sex and remain effective for several days (e.g., urine of the domestic bitch in estrus). Minute amounts of a chemical substance released by the virgin silk moth, *Porthetria monacha*, attracts males from as far away as a few miles (Schneider 1969). Some female fishes release pheromones into the water, which attracts courting males (Tavolga 1956). However, it is not clear whether these chemical signals simply advertise a female's receptivity or whether they also incite males to compete, with the result being that the winner is most apt to fertilize the signaler. As in many insects, it may be simply a matter of first come, first served.

Finally, some females may affect the potential genotype of their offspring after mating has occurred. In insects in which sperm competition occurs within the reproductive tract of the female after several males have copulated, Parker (1970) reasons that the female might have evolved postmating mechanisms to influence which sperm will fertilize her eggs. The favoring of any sperm character

over another within the female's reproductive tract would serve to intensify sperm competition, i.e., male competition.

Laboratory studies of the female's role in courtship are often misleading. Observations are usually restricted to a heterosexual pair in an enclosed area. The female is given no choice of partners. Elements of her behavior pattern which might normally function to signal other males to compete are apt to be misinterpreted as being irrelevant, a sign of solicitation, or an indication of unreceptivity, e.g., darting away, earwiggling, and tail vibrating in the laboratory rat, *Rattus norvegicus*. The most unnatural aspect of the standard laboratory study of courtship and mating is allowing one male uninterrupted access to an estrous female who cannot get away. This is like giving the male subject alpha-male status or his own territory. The male can force the issue without the threat of male interference. Some females are even killed by the male when they cannot get away (e.g., white-tailed deer [Severinghaus 1955]). In nature, this one-to-one situation is probably a rarity, since most vertebrates are polygynous.

In conclusion, we agree with the thrust of Fisher's statement (1930, p. 147) that some naturalists may have been overly concerned with the distinction between the two processes of sexual selection, especially the possibility that the female process involves will or choice, and this has detracted from the potentially more important study of the element common to both processes, i.e., competition between members of each sex.

SUMMARY

Females that mate with the most fit male available leave more viable offspring than females that mate with males of lesser fitness. We describe a mechanism by which females facilitate mating with a superior genotype, as reflected by age, social rank, and sexual experience, without exerting choice. Female elephant seals increase the probability of mating with a mature, high-ranking male by simply rejecting all copulatory attempts during early estrus. Females protest loudly when mounted; this signals all nearby males and activates the dominance hierarchy. The probability that the mounting male will be interrupted by another male is a function of the mounter's social rank. The lower his rank, the higher the probability of interruption. The result is that mature males of high social rank have more time and freedom to attempt copulation, and they succeed in doing most of the mating. The behavior of the female intensifies this monopoly by making it more difficult for young, subordinate males to copulate. A similar female strategy seems to operate in several species where the female is courted by several males. Influencing the genotype of her offspring is an important means by which a female can increase her inclusive fitness. This aspect of sexual selection has been neglected.

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