

SEXUAL BEHAVIOR OF MALE NORTHERN ELEPHANT SEALS: II. FEMALE RESPONSE TO POTENTIALLY INJURIOUS ENCOUNTERS

by

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Introduction

Females of many species must sometimes contend with males that outweigh them, possess dangerous weapons, and aggressively pursue copulation. Sexual aggressiveness can lead to female injury and death (LE BOEUF & MESNICK, 1990) and increases the cost of mating for females (DALY, 1978). When serious injury and death occur, selection should favor the evolution of female responses that minimize the probability of being victimized. Responses of females to potentially dangerous sexual liaisons include a range of behaviors that differ in the energy required and the probability of insemination: evasion (dabbling ducks, MCKINNEY *et al.*, 1983), resistance (horses, BERGER, 1986), receptivity (dung flies, PARKER, 1979), eliciting protection from mates (white-fronted bee-eater, EMLÉN & WREGE, 1986) or dominant males (orangutans, MITANI, 1985), and morphological adaptations (thicker skin in female blue sharks, PRATT, 1978). Within each species, selection should favor the most efficient strategy enabling females to avoid serious injuries inflicted by males during mating attempts.

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In the northern elephant seal, *Mirounga angustirostris*, adult males are at least four times heavier than females and, during mating, bite the female's neck with their long canines and rest the bulk of their head and neck on the female's back to facilitate intromission. Female elephant seals gather in harems, a behavior that reduces male harassment (LE BOEUF, 1972; LE BOEUF & PETRINOVICH, 1974). Females give birth and nurse their pups in harems for approximately one month. During the final days of lactation, females mate with dominant harem bulls for 1-5 days (LE BOEUF, 1972, 1974; COX & LE BOEUF, 1977).

The danger to female elephant seals occurs when they exit harems to return to the sea at the end of lactation. During departure, females must typically cross several meters of beach and intertidal rocks before reaching the water. The harem periphery is occupied by subordinate males that are excluded from the harem by the male dominance hierarchy. These males compete to intercept and mate with departing females. Nearly all departing females are mounted by peripheral males, and most departing females copulate, typically with the highest ranking male in pursuit. A departing female eludes pursuing males when she reaches deep water and dives (LE BOEUF, WHITING & GANTT, 1972; LE BOEUF & MESNICK, 1991).

The likelihood of female injury is greater during mating attempts on the harem periphery than during mating attempts in the harem. During departure, the female receives many mating attempts in a short time period when she has lost 40% of her body mass by the end of a four-week lactation fast. Neck bites and head slams delivered in haste during attempted matings can cause head injuries, broken ribs, organ damage, and internal hemorrhage. Male-inflicted injuries are the major cause of female mortality during the breeding season. At minimum, one out of every 1000 females is killed by a male during departure from the harem (LE BOEUF & MESNICK, 1991).

The purpose of this study was to test the general hypothesis that female elephant seals behave in a way that reduces the chance of injury or death from sexual encounters with males. We tested two predictions from this hypothesis: (1) *Females departing harems should attempt to evade males during their transit to the sea.* Specifically, we predicted that: a) females would depart in greater numbers at high tide, rather than low tide, when the distance between the harem and the sea is reduced; b) females would depart in greater numbers at night when female movement is concealed by darkness; c) females would utilize distractions on the harem periphery, such as males fighting or another female's departure, to make

their own exits; and d) females would take a direct route to the sea. (2) *If contact with peripheral males cannot be avoided, females should exhibit receptive behavior.* Females accepting male mating attempts, or behaving in a way that facilitates copulation, should receive fewer neck bites and body slams than females that resist.

Methods

This study was conducted at the Año Nuevo rookery in central California, over the course of nine breeding seasons, 1982-1990. During the study period, females resided in 12 harems on Año Nuevo Island and the adjacent mainland. Harems varied in size with a maximum of 1000 females, 55 adult males, and 60 peripheral males (LE BOEUF & MESNICK, 1991). The proximity of harems to the water ranged from 5-100 m. Behavioral observations were made from elevated positions near harems virtually every day during the period of female departures, from late January through late February.

Three sampling protocols were used:

1. *Observation of departure.*

The circumstances surrounding 336 female departures were recorded during seven breeding seasons from 1982-1990. Observations were made from 0900-1500 hours at the mainland harems and from 0800-1800 hours at the two island harems. The following information was recorded for each departure: 1) the date, the time, and the tidal height when a female exited the harem; 2) the age of the female, determined from tags attached to the hindflippers shortly after birth (LE BOEUF & PETERSON, 1969); 3) the female's behavioral response to male mounts; 4) the total number of males present at each departure; 5) the number of mounts, the number of copulations, and the number and identity of copulating males (identified by bleach marks on the pelage; LE BOEUF & PETERSON, 1969); and 6) the number of blows (neck bites and body slams) received by each departing female. In addition, we recorded whether a female's departure coincided with another female's departure or with males fighting on the periphery. Data for this latter analysis were collected at the Point harem during 24 days in 1983.

A female's behavioral response to male mating attempts was categorized as either "receptive" or "resisting" based on criteria described by COX & LE BOEUF (1977). A resisting female interferes with male mating attempts by trying to move away, flipping sand backward at the male, and swinging her hindflippers from side to side. She tightens the muscles in the neck and shoulders which may lessen the impact of blows, and she emits croaking vocalizations. A receptive female facilitates intromission by lying quietly and sometimes spreading her hindflippers. Females whose behavior included elements of both reactions were termed either "predominantly receptive" or "predominantly resisting" based on the frequency and duration of each activity.

The males present at a departure were scored as either being in direct or indirect attendance. Those in direct attendance included males that were chasing, mounting, neck biting, or otherwise in contact with the female. Males in indirect attendance included those oriented to and watching the departing female but not in active pursuit. Males most frequently involved in departures were mid to low ranking harem males or subordinate males excluded from the harem by the dominance hierarchy.

2. *Departures during high tide or under the cover of darkness.*

To investigate the effects of tidal height on female departures, we stood watches during the one-hour period before and after high tide and the one-hour period before and after

low tide for 24 days in 1983 and 1988-1990. The watches were conducted at the same harems and on consecutive tides to minimize variation in the number of departures that might be attributable to differences in harem size or date.

To investigate the effect of darkness on female departures, we censused females in harems at dusk to record the number of daytime departures and at the following dawn to record the number of nighttime departures. Counts were made at dawn and dusk over nine different days at the two island harems: six days at the Point harem in 1983, two days at the Cove harem in 1983, and one day at the Point harem in 1984. The watches covered 210 hours, 38% during daylight hours (79 hours or approximately nine hours per day) and 62% during darkness (131 hours or approximately 15 hours per night). We tested the null hypothesis that there is a 0.62 probability of a female departing at night because previous work had shown that elephant seals are as active in sexual, agonistic and locomotory behaviors at night as they are during the day (LE BOEUF, 1972; DEUTSCH, 1990).

3. *The route to the sea and the termination of sexual interactions.*

We determined if departing females moved directly to the water or to males. We identified a female's direction of movement when she initially exited a harem and when she resumed her movement to the sea after being mounted. Observations were made from the Point harem on the island or from one of the four largest mainland harems during 1988 and 1989, from 0800-1800 hours.

We recorded whether females terminated copulations and whether females moved away from males each time a mount or copulation ended. Female behavior during departure mounts and copulations was compared to female behavior during harem mounts and copulations. Observations were collected inside and outside the Point harem on the island during 1983, from 0800-1800 hours. One hundred seventeen harem mounts and copulations and 256 departure mounts and copulations were observed.

4. *The behavior of males that copulate with departing females.*

Observations of male behavior during departure were collected during 1988 and 1989 at the Point harem on the island and at the four largest mainland harems, from 0800-1800 hours. A departing female was said to be "escorted" if a male copulated with her and then followed and defended her (prevented other males from copulating with her) when she resumed her movement toward the water. Escort behavior was similar to the treatment a harem bull exhibited toward females in his harem: the male maintains proximity and fends off the approach of subordinates (LE BOEUF, 1972). To identify escort behavior in peripheral males, we recorded: 1) the identity of each male that copulated with a departing female, 2) whether he followed the female after the copulation, 3) whether he displaced other males away from the female or whether other males displaced him, and 4) whether he copulated with her again.

Data were analyzed using the SAS statistical package (SAS Institute Inc., Cary, North Carolina) and the MSUSTAT statistical package (Research and Development Institute, Inc., Montana State University). Wilcoxon 2-sample tests were used to compare medians; the binomial exact, Fisher exact and G-tests were used to compare frequencies. The level of significance was $\alpha = 0.05$.

Results

Hypothesis 1.

Partial support for Hypothesis 1, that females should attempt to evade males during their transit from harems to the sea, was obtained.

Tides and female departures.

Females departed more frequently during high tides than during low tides. Of 44 departures observed during tidal watches, 77.3% (34/44) occurred at high tide and 22.7% (10/44) occurred at low tide (one-tailed binomial exact test, $N = 44$, $p < 0.001$).

Females that departed at high tidal heights had less distance to travel to reach the water, their departures were shorter in duration, there were fewer males present and they copulated less frequently (Table 1). There

TABLE 1. Circumstances surrounding the departures of females that left the harem during tidal watches

	Tidal height ¹⁾		Significance ²⁾
	High	Low	
Distance from the harem to the water's edge (m)	1.0 (0-4) 25	22 (15-30) 9	$p = 0.0024$
Duration of departure (min)	7.4 (4-12) 28	36 (18-67) 10	$p = 0.0084$
No. of males in indirect attendance	2 (0.3) 29	6 (4-6) 9	$p = 0.0211$
No. of males in direct attendance	4 (2-5) 29	4 (2-9) 9	$p = 0.7575$
Total no. of males present at departure	6 (5-9) 33	11.5 (8-14) 10	$p = 0.0129$
No. of mounts	1.0 (1-2) 26	2 (1-3) 9	$p = 0.1974$
No. of copulations	1 (0-1) 33	2.5 (2-5) 10	$p = 0.0136$
No. of blows	0 (0-2) 26	1 (0-3) 9	$p = 0.3606$

Values given are the median, 95% confidence interval (in parentheses), and the sample size. ¹⁾ High refers to a tidal height of 2.9 to 6.2 feet; Low refers to a tidal height of -1.1 to 1.3 feet. ²⁾ Wilcoxon 2-sample test, t-test approx.

was no significant difference in the median number of mounts or blows received by females departing during low and high tide.

During low tide, males were widely distributed along the beaches and among the intertidal rocks. More males were alerted by the movement of females on the periphery at low tide and a greater proportion of these males remained in indirect attendance than at high tide. On average, females that departed at low tide completed three copulations before they reached deep water and dove.

At high tide, subordinate males crowded onto the exposed beach or milled about among the breaking waves, patrolling the harem periphery. Females that departed at high tide immediately were chased and mounted by males. Females received blows as males competed with each other to copulate. On average, females copulated once before they reached deep water and eluded pursuers.

The following descriptions from the serial record were chosen to illustrate the contrast between low tide and high tide departures.

10 February 1983: Departure 33-ANI-1983 occurred during low tide and took 52 minutes. The female was pursued by 13 different males, she copulated four times and was mounted an additional three times. She received three neck bites of low-to-moderate severity. Initially, the female moved directly out of the harem and across the beach and headed toward a small inlet of water. DC was the first male to intercept her. He chased off two males, vocalized at a third and exchanged blows with a fourth before he caught the female and put a flipper over her back. She stopped and raised her hindflippers. He copulated with her once, then lost a fight to CHAL. As the males fought, she moved into the intertidal, pursued by three males. SS1, a subadult male, delivered a blow to her neck as he attempted to mount her. DAT displaced SS1 and placed his flipper over the female's back but backed away as CHAL caught up to her again. CHAL mounted her and bit her on the neck twice as he maneuvered himself into position. He copulated with her between the intertidal rocks. After 5 minutes, she moved away from CHAL and headed toward rocks in the intertidal with the open water beyond. CHAL and three other males followed her. KHM approached from the water and vocalized. The males stopped their forward motion except 109M, who put his flipper over her back briefly and attempted to mount her. KHM moved closer, displaced the males, and copulated with her. Eight minutes later, he turned to vocalize at an approaching male and she moved away. He followed her, fending off the approach of two males, and copulated again in deep water.

12 February 1983: Departure 51-ANI-1983 occurred during high tide and took 1.2 minutes. GIN, a 9 year-old female, exited the harem when an especially large wave crashed onto the beach and washed into the harem. Four males were instantly alerted by her movement and gave pursuit. She was mounted briefly by SAM and KAYA. SAM displaced KAYA but lost his grip on her when a second wave broke. The female dived, escaping from her pursuers. She did not copulate and received no blows.

Cover of darkness and female departures.

Our census at dawn and dusk showed no tendency for females to depart in greater numbers at night. Controlling for differences in the duration

of daylight and darkness during the observation period, the number of daytime departures (63) was not significantly different from the number of nighttime departures (78; one-tailed binomial exact test, $N = 141$, $p = 0.9574$).

Social distractions on the harem periphery and female departures.

At the Point harem in 1983, a mean of 5.9 ± 4.8 female departures and approximately 5 fights between peripheral males occurred per day over a 24-day period. Few of the 145 departures observed during this period coincided with these events. Five females (3.4%) exited the harem coincident with the departure of other females and 10 females (6.9%) exited the harem during male fights on the periphery.

The route to the sea.

Every one of 52 departing females took a direct route to the water, moving only briefly around rocks or males. Gullies between sand dunes, channels between intertidal rocks, and small inlets of water became common pathways for many departing females and minimized the distance to the water's edge. No female took an indirect route to the sea by heading towards males that were away from the water.

Hypothesis 2.

Support for Hypothesis 2, that departing females should exhibit receptive behavior when males cannot be avoided and, as a result, should receive fewer blows than when they resist, was obtained.

Table 2 shows that receptive behavior was much more common among departing females than resisting behavior. For every female whose departure was characterized as "predominantly resisting", the departures of 7 females were characterized as "predominantly receptive". When we analyzed female responses during individual mating attempts ($N = 190$ mating attempts observed during the departures of 101 females), 64.2% were receptive, 17.5% were both receptive and resisting, and 17.9% resisted throughout. Moreover, this represents a significant increase in receptivity when the behavior of estrous females residing in harems 3 to 5 days prior to departure is compared with the behavior of departing females, 13% vs 64.2% receptive, respectively ($G_{\text{adj}} = 90.9$, $df = 1$, $p < 0.001$). A similar increase is observed when the behavior of estrous

TABLE 2. The duration and median number of sexual and aggressive interactions sustained by departing females as a function of their response, receptive or resisting, to male mating attempts

	Female response to male mating attempts		Significance ¹⁾
	Receptive	Resisting	
Duration of departure (min)	14.3 (11-17.5) 108	9.3 (5-22) 14	p = 0.3768
Total no. of males present at departure	8 (7-9) 75	7 (4-23) 7	p = 0.9470
Total no. of mating attempts (mounts plus copulations)	3 (2-3) 75	3 (2-5) 9	p = 0.5508
No. of mounts	1 (1-2) 75	3 (2-4) 9	p = 0.0137
No. of copulations	1 (1-2) 75	0 (0-1) 9	p = 0.0368
No. of copulating males	1 (1-1) 73	0 (0-1) 9	p = 0.0825
No. of blows	0.5 (0-1) 100	2.5 (2-4) 10	p = 0.0029 ²⁾

“Receptive” includes predominantly receptive and totally receptive females; “Resisting” includes predominantly resisting and totally resisting. Values given are the median, 95% confidence interval (in parentheses), and the sample size.

¹⁾ Wilcoxon 2-sample test, t-test approx., two-tailed test unless otherwise noted.

²⁾ One-tailed Wilcoxon 2-sample test.

females during their last day in the harems is compared with the behavior of departing females, 50% vs 64.2% receptive, respectively ($G_{adj} = 15.3$, $df = 1$, $p < 0.005$).

Table 2 shows that receptive females received significantly fewer blows than those that resisted. Receptive females also received fewer mounts. However, receptive females copulated more frequently and with more males.

When males had difficulty copulating, most females resumed their movement to the water. For example, six females that departed from the Point harem in 1983 vigorously resisted male contact. All of these females were mounted by males ($\bar{x} = 3.0 \pm 1.6$ mounts per female). Five females received blows during the mating attempts. Yet, of the six, five eluded their pursuers and departed without copulating. The sixth female protested but did not elude males. She copulated and also received blows. Thus, resisting may have increased the chance that a female departed without copulating but the behavior increased the probability of receiving blows.

Female response to males as a function of female age.

A higher proportion of females ≥ 6 years of age (prime-age) were receptive to male mating attempts than were younger, less experienced females ≤ 5 years of age (Table 3). Nevertheless, prime-age females did not receive significantly fewer bites and blows than young females (Table 3).

The termination of sexual interactions.

Females pulled away from males and broke off interactions at a higher frequency during departure copulations than during harem copulations. Fifty percent (51/102) of departure matings were terminated by females as they resumed their movement to the sea, whereas only 13% (17/131) of harem copulations were terminated by females ($G_{\text{adj}} = 38.7$, $df = 1$, $p < 0.001$). Similarly, after mounts and copulations ended, females moved away from their mates more frequently during departures than during matings inside the harem. Females moved away from their mates and resumed their movement to the sea after 89.8% (230/256) of departure mounts and copulations, whereas only 10.3% (12/117) of females moved more than 2 m from their mates after harem mounts and copulations ($G_{\text{adj}} = 253.6$, $df = 1$, $p < 0.001$).

The behavior of males that copulate with departing females.

Seventy-eight percent (53/68) of males that copulated with 48 departing females escorted the female all or part of the way to the water. Escorting reduced the number of males that came into contact with a departing female. The presence of a dominant male in proximity to a departing

female deterred the approach of 58.1% (61/105) of the males in pursuit. The approaching males stopped their movement toward the female or turned and moved away. The escort physically thwarted the approach of the remaining 41.9% (44/105) of pursuing males with aggressive interactions, such as threat vocalizations or blows. Of the escorts that remained with a female from the time they copulated with her until the time she disappeared in the water, 50% (10/20) copulated with the female again ($\bar{x} = 1.7 \pm 0.2$ additional copulations per male).

The remaining 22% of the males that copulated with departing females did not escort their mates. These males either remained at the site of the copulation—falling asleep in place, or watching but not moving—or they followed the female but were unable to maintain their position because they were moved by the arrival of a more dominant male.

Discussion

We found only partial support for Hypothesis 1. Females did little to evade males surrounding harems. They did not leave in greater numbers at night, in groups, or during disturbances. Females left harems more frequently at high tide but they also departed at moderate and low tides as well. Except for some females that departed at the highest tides, females were not successful in avoiding the males surrounding harems with any of the behaviors we analyzed.

Hypothesis 2 was substantiated. Faced with not being able to evade males, most departing females were receptive to male mating attempts and the majority of females copulated at least once on the periphery before completing their departures (LE BOEUF & MESNICK, 1991). Females were more receptive on their way to sea than they were during their estrous periods in harems. Mating appeared to be an especially effective means of reducing the potential for injury because of its dual effect on male behavior. First, males did not need to subdue receptive females with bites and blows in order to facilitate copulation and second, males that were able to intercept and mate with departing females clearly dominated other males in the vicinity. These males were able to successfully defend the female as she moved toward the sea. Departing females that were receptive to males received fewer blows and bites than females that resisted.

The explanation of female behavior during departure that is most consistent with our data is that *the behavior exhibited by departing females is a means*

of ensuring safe conduct to the sea. It is clear that the females were eager to leave the rookery. All females moved directly toward the water and rarely stopped their forward motion except when approached by males. Encounters with males and copulations en route appeared to be only momentary interruptions in their transit to the sea. Females departed harems most frequently a high tide which minimized the distance and transit time to the sea. Receptive responses by females to males on the egress route appeared to be attempts to decrease male aggressiveness during mating attempts. Sexual receptivity minimized the probability of injury and maximized the probability of associating with a dominant peripheral male, a male likely to escort the female to the water. In effect, females that copulated on the harem periphery traded sex for protection from male harassment. In this context, copulation was a behavior that not only may have increased female reproductive success but also may have increased the probability of female survival.

We address two alternative explanations of female behavior during harem departures.

The behavior exhibited by departing females is a continuation of harem mating behavior, behavior that evolved in the context of facilitating copulation with harem bulls. As the estrous period proceeds, the frequency of receptive responses increases and receptivity is the most common response on the day of departure (COX & LE BOEUF, 1977). Therefore, receptivity outside harems may be simply a continuation of the physiological and behavioral manifestations of estrus. However, the different responses of females to males inside and outside harems suggest that the context alters female behavior. Females more frequently terminated departure copulations than harem copulations. Moreover, a higher ratio of females were receptive outside harems than inside them. Receptive behavior on the harem periphery in the presence of several eager male suitors was extreme compared to that in the harem. Before onrushing males reached them, departing females often raised and spread their hindflippers, a pose that facilitated intromission (COX & LE BOEUF, 1977). This argues for female behavior at departure being context specific rather than a continuation of harem mating behavior.

The behavior exhibited by departing females is a means of ensuring fertilization. We do not know when female elephant seals ovulate, or whether the sperm count of harem bulls declines after they copulate repeatedly throughout the breeding season. If departure copulations were a means of ensuring fertilization, as COX & LE BOEUF (1977) suggested, we would predict that females would remain *in copula* as long as possible to facilitate

sperm access to the female reproductive tract, that females would move toward males during departures, and that females would depart at low tide when they would be more likely to encounter and copulate with males. None of these predictions was supported by our data.

The resistance of the mating attempts of males by some departing females is partially explained by female youth and sexual inexperience (Table 3).

Females of other species cope with potentially dangerous sexual liaisons in a variety of ways (Table 4). Female responses to aggressive male mating can be divided into four categories: I) evasion and resistance, II) acceptance, III) eliciting protection from a mate or domi-

TABLE 3. The circumstances surrounding the departures of females as a function of their age and experience

	Age and experience of female		Significance ¹⁾
	Prime-age females (≥ 6 years)	Young females (≤ 5 years)	
Duration of departure (min)	22 (16-27) 33	18.7 (13-32) 29	$p = 0.9496$
Tidal height (ft)	2.5 (1.0-3.1) 26	2.0 (1.5-2.7) 21	$p = 1.000$
Total no. of males present at departure	8 (6-9) 30	7 (5-9) 26	$p = 0.3855$
Proportion of females receptive to male mating attempts	100% (34/34)	82.6% (25/29)	$p = 0.0400^2)$
No. of mounts	1.5 (1-2) 20	2 (1-3) 18	$p = 0.5143$
No. of copulations	2 (1-2) 34	1 (1-2) 28	$p = 0.1416$
No. of blows	1.5 (1-2) 30	1 (0-2) 26	$p = 0.2015^3)$

Values given are the median, 95% confidence interval (in parentheses), and the sample size, unless otherwise noted. All Wilcoxon 2-sample tests were non-significant at the $\alpha = 0.05$ level.

¹⁾ Wilcoxon 2-sample test, t-test approx., two-tailed test, unless otherwise noted.

²⁾ Fisher's exact test, $df = 1$. ³⁾ One-tailed Wilcoxon 2-sample test.

TABLE 4. Classification of female responses to sexual harassment and potentially dangerous mating encounters with males

System	Female response to sexual harassment and potentially dangerous mating encounters with males	Reference
I. Evasion and resistance		
common murre	run away; attempt to dislodge male; attack	BIRKHEAD <i>et al.</i> , 1985
dragonfly	perch motionless, perhaps unseen by males	JACOBS, 1955
herring gulls	adopt a hunched posture, walk away,	MACROBERTS, 1973
lesser black-backed gulls	threaten, snap at male	
mink	arch back to prevent intromission	ENDERS, 1952
mountain sheep	run away; jump; turn; head for cliffs	GEIST, 1971
orang-utan	hide	MACKINNON, 1974
scorpionfly	flee; fight vigorously to escape	THORNHILL, 1984
sea otter	leave vicinity; struggle	FISHER, 1939; FOOT, 1970
waterfowl	sneak to avoid detection; hide in vegetation when males are nearby; evasive flight; twist, turn, sudden plummet, alight on water; dive; run away; characteristic hunched, ruffled postures with loud broody calls; peck; attack; fight	AFTON, 1985 BARASH, 1977 MCKINNEY <i>et al.</i> , 1983 MCKINNEY & STOLEN, 1982 MINEAU & COOKE, 1979 WERSCHKUL, 1982
white ibis	refuse to raise tail; attempt to dislodge male	FREDERICK, 1987
wild horse	run away; kick	BERGER, 1986
II. Acceptance		
chimpanzee	lacking opportunity to escape, or threatened by aggressive retribution, females may not safely risk the struggle and are submissive	YERKES, 1939 GOODALL, 1986
dung fly	receptivity saves time and energy; may account for the evolution of the passive phase in insects	PARKER, 1979
nesting birds	females incubating eggs are perhaps better off to accept forced copulation attempts in order to prevent egg breakage	FUJIOKA & YAMAGISHI, 1981 MCKINNEY <i>et al.</i> , 1984 MINEAU & COOKE, 1979 WERSCHKUL, 1982
III. Eliciting protection from mates or dominant males		
dragonfly	when their mates hover overhead and repulse intruders, females are able to oviposit longer	SHERMAN, 1983
dung fly	mounted males deflect other males from approaching the female	PARKER, 1970, 1979
elephant seal	authors suggest that females mate with subordinate males on the harem periphery to reduce the probability of injury	this paper
fallow deer	authors suggest that females leave densely-populated feeding grounds to mate in an area where they can be effectively defended by a single male; one of the possible explanations for the evolution of leks	CLUTTON-BROCK <i>et al.</i> , 1988
hammer-headed bats		WRANGHAM, 1980
sage grouse		
Uganda kob		

TABLE 4. Continued

System	Female response to sexual harassment and potentially dangerous mating encounters with males	Reference
Galapagos sea lion	authors propose that females form harems to reduce harassment from marginal males	TRILLMICH & TRILLMICH, 1984
Galapagos fur seal		
orang-utan	females that travel with dominant adult males experience reduced rates of forced copulation by subadult males	MITANI, 1985
white-fronted bee-eater	females utter a vocalization before leaving the nest chamber to which their mates respond; "escorted" females are rarely the target of sexual harassment	EMLEN & WREGE, 1986
IV. Morphological adaptation		
blue shark	females were found to have thicker skin than males; authors propose that this trait is an adaptation to accommodate aggressive male mating behavior	NORDELL, 1990
round stingray		PRATT, 1978

nant male, and IV) morphological adaptation. Each response has a different cost in terms of the energy required and a different probability of insemination by the harassing individuals.

Evasion and resistance represents a range of behaviors in which females reduce the chance of injury by avoiding contact with males. Included are females that: avoid males by hiding; move away from males by running, diving, or flying; adopt repelling postures that make it difficult for the male to achieve intromission; and attack. These strategies can be costly in time and energy, *e.g.*, the long and wild aerial flights of female dabbling ducks that are pursued by males attempting to force copulations (McKINNEY *et al.*, 1983). If effective, however, these behaviors result in females avoiding matings with younger or marginal males (BARTHOLOMEW, 1970).

When females cannot avoid males effectively or efficiently, receptivity to male mating attempts may reduce the chance of injury. This response necessitates sexual contact with males and the risk of potential insemination in exchange for protection. It has been suggested that females mate to prevent injury to their unborn offspring (MINEAU & COOKE, 1979), to prevent injury to themselves (YERKES, 1939), or to avoid the loss of time and energy that resisting requires (PARKER, 1979).

Females that elicit protection from a mate or dominant male set the male against the harassing individuals. This strategy should be especially

likely to evolve in species with marked sexual dimorphism. Males in these species, typically well equipped in size and weaponry, are better suited for combat with other males than females are suited to deflect male suitors. Females in this category exchange copulation, or the possibility of future matings, for protection from male harassment.

TRILLMICH & TRILLMICH (1984) suggest that female Galapagos sea lions and fur seals choose an area already defended by a dominant male (forming harems) rather than expend their own time and energy in fending off sexual harassment from overly zealous males. As a result, dominant harem bulls fend off approaching males and copulate with harem females.

In birds, females can manipulate the behavior of their mates to gain protection from harassment by non-mates. Female bee-eaters utter a vocalization before exiting their nest chamber so that their mates will accompany them and fend off the hordes of males that attack unescorted females (EMLEN & WREGE, 1986). LUMPKIN (1981) argues that females may control the onset of mate-guarding in monogamous species of birds because of the benefits they derive from it, such as protection from the time consuming courtship of other males. She suggests that explanations for the evolution of mate-guarding must take into account not only the benefits to males (generally, the avoidance of cuckoldry) but also the benefits to females. MCKINNEY (1986) shows that one of the benefits to females in monogamous paired dabbling ducks is the presence of a vigilant male escort to protect the female from harassment by courting males. He suggests that females control the onset of pairing early in the season and also asks whether females control dabbling duck mating systems by forcing males to be monogamous.

PARKER (1970, 1979) argues that there is little that female dung flies can do to avoid the persistent advances of males. He found that receptivity saved females time and energy. In addition, males paired to females in the passive phase (when a male is attached to but not *in copula* with a female insect as she oviposits) benefited the female because the mated male kept other males from approaching. He suggests that the evolution of the passive phase, presumed to be a product of selection on males to avoid cuckoldry, may be controlled by the female. Similar protection occurs in female dragonflies that are guarded by males during oviposition (SHERMAN, 1983). In this species, the mate hovers overhead and defends against advances of other males, which enables the female to oviposit four times longer than if she were not guarded.

WRANGHAM (1986) and WRANGHAM & RUBENSTEIN (1986) suggest that

sexual harassment can promote the evolution of sociality in some mammalian species. Sociality can be explained by the significant measure of protection that females gain by traveling in groups with dominant, adult males; the authors' "hired gun" principle. In adult orangutans, the only common form of sociality is sexual consortship. Females that travel with dominant males experience reduced rates of forced copulation which otherwise occur at high rates, despite intense female resistance (MITANI, 1985).

WRANGHAM (1980) and CLUTTON-BROCK *et al.* (1988) suggest that sexual harassment can explain the evolution of leks in some species. In sage grouse, hammer-headed bats, Uganda kob (WRANGHAM, 1980) and European fallow deer (CLUTTON-BROCK *et al.*, 1988) females mate on leks where dominant males can effectively defend them from interference by subordinate males. Both authors predict that lekking is likely to evolve in species with high population densities where females might otherwise expend considerable time and energy deflecting unwanted male suitors. Sexual harassment may cause estrous females to move off densely populated foraging grounds to mate in areas where they can be defended by dominant males.

Morphological adaptation to aggressive male mating has been suggested in two chondrichthian fishes. As a prelude to mating, both female blue sharks and round stingrays receive numerous bites from males. PRATT (1978) showed that the skin of female sharks is twice as thick as the skin of male sharks and is thicker than male teeth are long. NORDELL (1990) found that the disc of female round stingrays is thicker than that of males. Both authors suggest that these traits are adaptations to prevent serious injury from male biting during courtship.

In conclusion, females that copulate, or that make the probability of copulating likely, can shape the behavior of males and affect the distribution of matings among males within a population. Selection acting on females to reduce the probability of injury should be considered in discussions on the evolution of sociality, mate-guarding, harems, and leks.

Summary

During mating attempts by males, female elephant seals, *Mirounga angustirostris*, are sometimes injured or killed as they return to sea at the end of lactation. We tested two predictions from the general hypothesis that females behave in a way that reduces the possibility of injury or death from sexual encounters with males: 1) departing females attempt to avoid males, and 2) if males cannot be avoided, departing females exhibit sexually receptive behavior to males, and thereby reduce the threat of injury from aggressive mating attempts.

Circumstances surrounding the departure of 336 females from harems on the Año Nuevo rookery in central California were recorded over the course of nine breeding seasons from 1982-1990.

Females did little to avoid encounters with males surrounding harems; they did not leave in greater numbers at night, in groups, or during disturbances on the harem periphery. They did, however, leave harems preferentially at high tide which reduced the distance to the water and shortened transit time.

Most departing females did not resist the mating attempts of peripheral males but, rather, they were unusually receptive. Receptive females received fewer blows capable of producing injury than resisting females. We conclude that receptive behavior in this context "buys safe passage". It is an effective means of reducing male aggression and the probability of injury; a male has no need to restrain a receptive female with blows, and should the most dominant male in the area copulate with a departing female, he frequently escorts her to sea and defends her from other males.

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