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SEXUAL BEHAVIOR OF MALE NORTHERN ELEPHANT SEALS: I. LETHAL INJURIES TO ADULT FEMALES

by

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(With 2 Figures)
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Introduction

The most direct route to maximizing individual reproductive success is by mating. It follows that the urge to mate, or libido, when translated into mating attempts, must be an advantageous trait that has long been and continues to be subject to strong selection pressure. Among polygynous males, a strong and ready effort to mate is probably highly correlated with frequency of mating with different females and reproductive success (BATEMAN, 1948; TRIVERS, 1972). However, in many mammalian societies, a few males monopolize breeding and the majority of breeding age males are forcibly excluded from mating (CLUTTON-BROCK *et al.*, 1988; LE BOEUF & REITER, 1988). Because conventional access to females is difficult for males of some species, alternative strategies may be used (AUSTAD, 1984; WALTZ & WOLF, 1984) that can be potentially injurious to females (CAMPAGNA *et al.*, 1988). From the female perspective, sexually aggressive tactics increase the cost of mating (DALY, 1978) by decreasing the probability of survival and reproduction.

We present observational data, circumstantial evidence and necropsy results collected over a period of 20 years showing that male northern

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elephant seals, *Mirounga angustirostris*, sometimes injure and kill females while attempting to mate with them. Our thesis is that the majority of injuries and deaths to females on an elephant seal rookery during the breeding season are caused by low-ranking, breeding age males without conventional access to females. We summarize necropsy reports, describe the contexts in which injuries and deaths occur, discuss the implications of these data for elephant seals of both sexes, review similar findings in other animals, and speculate on the general conditions likely to elicit similar behavior in other species.

Male elephant seals of breeding-age are potentially dangerous to females, pups and juveniles because of their great size, large canines, and habit of biting the neck when copulating. The danger is exacerbated because the majority of males in this social system, denied access to females in the harem by the dominance hierarchy, vigorously pursue potential mates, and in certain contexts, outnumber them. The following background information is important for evaluating the results.

Northern elephant seals are extremely polygynous and highly sexually dimorphic. A fraction of the males present on rookeries dominate mating (LE BOEUF & PETERSON, 1969; LE BOEUF, 1974) and variance in estimated lifetime reproductive success among males is over four times that of females (LE BOEUF & REITER, 1988). On average, males are five times heavier than females but in the extreme, a male may be 11 times heavier (2200 *vs* 200 kg) (COSTA *et al.*, 1986; DEUTSCH, HALEY & LE BOEUF, 1990).

Breeding takes place in winter on islands off the coast of California and Mexico. Males fight and threaten each other to gain social status in a dominance hierarchy that confers access to groups of females. One or several of the highest ranking males resides with a group of females and monopolizes mating with them. These males prevent lower ranking males from approaching females. The outcast males, consisting of breeding age subadults and adults, surround harems waiting for an opportunity to mate by sneaking into the group of females or attempting to mate with females as they exit harems (LE BOEUF & PETERSON, 1969; LEBOEUF, 1972). The number of peripheral males around a harem varies from 0 to 60 or more, depending on the location and size of the harem, the terrain and tidal conditions. Most peripheral males congregate on the sea side of harems. Inter-male distance is approximately 5 m with location and spacing determined by dominance relations between the males present. The age composition of peripheral males ranges from mature adults, 8-14 years of age, to developing males, 4-7 years old. The higher

a male's rank the more predictable is his daily presence in the area.

The number of females in a harem varies from a few females up to a thousand. One male, alone, may keep all other male competitors out of a harem of 50 females or less. If entrance into the harem is restricted by the terrain, a single male may control a harem of 100 females. As the number of females in harems increases above 50 or 100, so does the number of males. In a harem consisting of 1,000 females, 20 to 30 males reside within the harem. Harem males are almost always fully grown adults. However, younger males may sneak into harems and reside there temporarily before being chased out.

Females arrive on the rookery pregnant, join a harem and after six days, give birth to a single pup that is nursed daily for four weeks. Females do not feed, drink, leave the harem or enter the water during this time. During the last few days of nursing, a female copulates with the alpha male or the highest ranking male in the vicinity one or several times before she weans her pup and returns to sea. When a female leaves the harem, she is pursued and intercepted by several peripheral males, and perhaps one or more high ranking harem males, who compete aggressively among themselves to copulate with her. Several males may bite her on the neck and copulate with her on the beach or in the water before she gets away (Fig. 1). Once a female reaches the water, it is easier for her to elude her suitors, but on occasion, males will pursue a female for 500 m or more, or until the animals can no longer be seen swimming at the surface (Le Boeuf, 1972, 1974; Le Boeuf, Whiting & Gantt, 1972; Cox & Le Boeuf, 1977).

Male courtship is usually direct, aggressive and persistent. On land, where 95% of the copulations occur, a male moves directly to the side of a female, and without preliminaries, puts a foreflipper over her back, bites her on the neck, pulls her strongly to him with his foreflipper, and attempts intromission (Fig. 2). If the female resists or moves away, the male pins her down by slamming the full weight of his head and forequarters on her back one or more times and bites her on the neck more vigorously (Le Boeuf, 1972). Males often try to physically overpower resistant females. This behavior is checked somewhat by the male social structure and mode of competition; most mating attempts are interrupted by higher ranking males in the vicinity (Le Boeuf & Peterson, 1969). Females enhance the probability of male interference and being mated by a high ranking male by vocalizing loudly, flipping sand back and up towards the male with the foreflippers, and making vigorous attempts to move away when mounted (Cox & Le Boeuf, 1977).

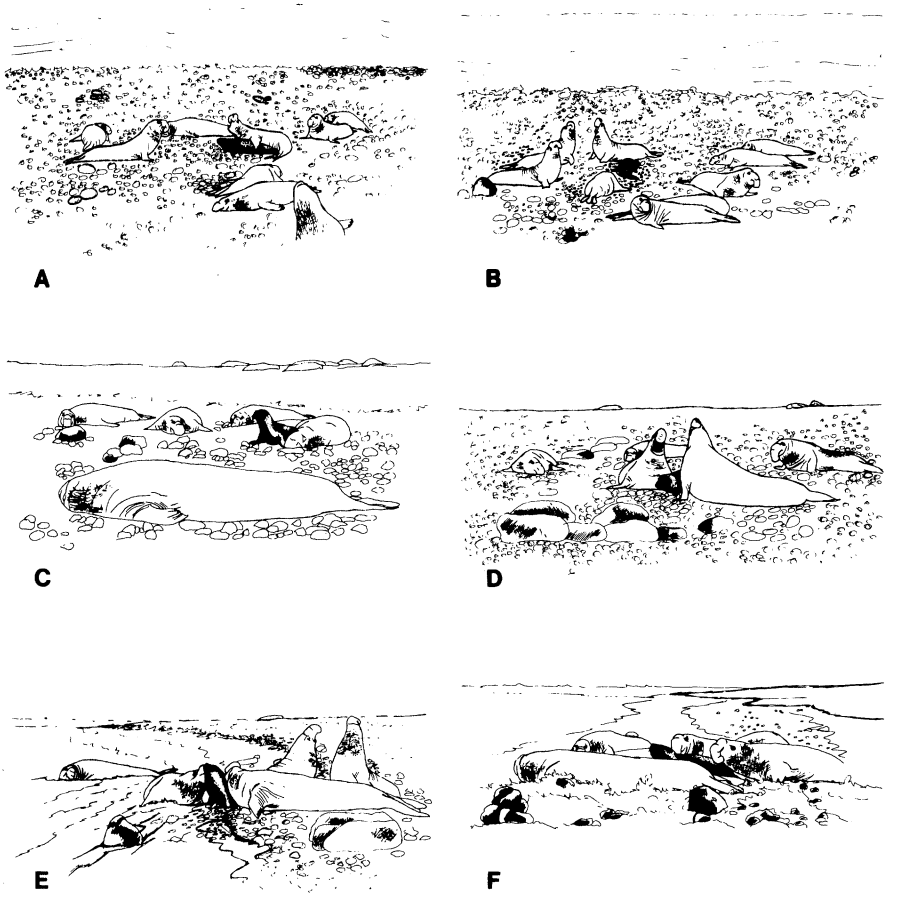

Fig. 1. Line drawings of photographs depicting the departure of a female from the Point harem on Año Nuevo Island. A - The female (the small dark animal) copulates with one of nine males that pursue her as she moves out of the harem (not visible in the foreground). B - At the end of the copulation, males threaten each other, and the female continues her move towards the water. C - Another male copulates with the female as four males watch (the harem is in the background). D - The copulation ends, the female moves towards the water as two males fight over her. E - Two males attempt to bite the female's neck and mount her as she reaches the water's edge; two other males fight in the female's wake. F - The female moves faster as she reaches the water; the males move in closer to her and to each other and continue their pursuit.

Methods

The circumstances and cause of death were inferred from data obtained from females that died on Año Nuevo Island and the adjacent mainland during the period, 1968 to 1987. These data were collected incidental to the conduct of a long term project on reproductive behavior of males and females which included keeping a detailed serial record of the sex-

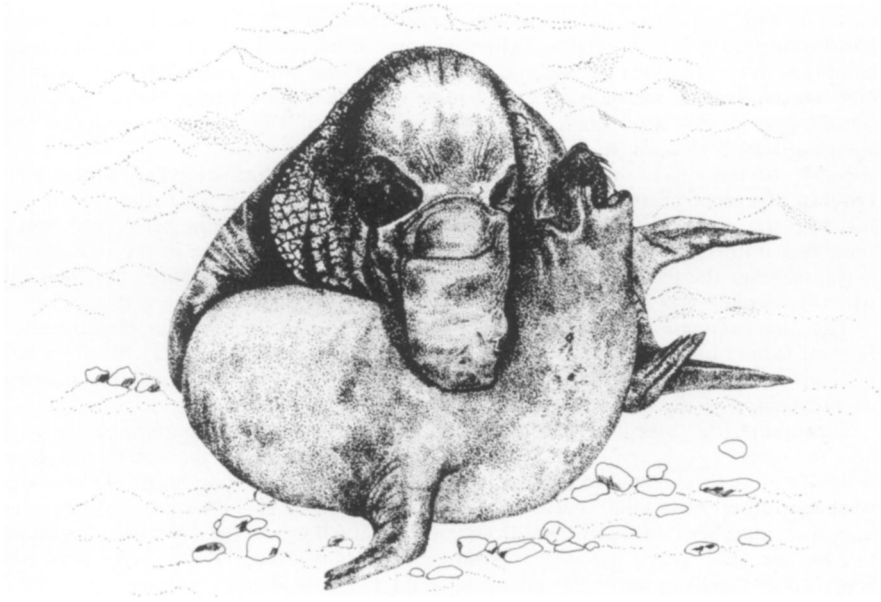

Fig. 2. As a prelude to copulation in elephant seals, the male bites the female on the neck. The bite may be maintained throughout copulation. Line drawing from a photograph.

ual activity of marked individual males and females (Cox & Le Boeuf, 1977; Reiter *et al.*, 1978, 1981; Le Boeuf & Reiter, 1988). During this period, females gathered in two principal harems on the island and up to ten harems on the mainland. The number of females that gave birth to pups on the island increased from 188 to 1194 during this period. The number of pups produced on the mainland increased from one in 1975 to 808 in 1987.

Virtually every day of each three-month-long breeding season, the perimeter and beaches of the island and mainland were censused for living and dead animals. The identity, and location of each corpse was noted, and, when possible, a necropsy was performed *in situ* (Le Boeuf & Briggs, 1977) and an attempt was made to ascertain the cause of death. The necropsy was performed by a veterinarian or trained physiologist. The aim was to determine whether death was caused by trauma, to differentiate *premortem* from *postmortem* trauma, and to infer from inspection of the corpse, the source of the trauma. The protocol included the following: 1) A description of the nature and extent of external wounds including a search for gunshot wounds, boat propeller injuries, shark bites, edematous swellings indicative of trauma under the skin, and bites (raked skin or puncture wounds) produced by conspecifics. In the case of the latter, bites of breeding age males were distinguished from those of adult females by the diastema between the canines. The diastema range is 8 to 13.5 cm in males and 6 to 7 cm in females. 2) An estimate of the time since death based on the temperature of the corpse or the stage of *rigor mortis*. 3) Inspection of the viscera and major organs for disease or vascular trauma. All ribs and rib connections were inspected for evidence of breakage. 4) Evidence of external wounds or hematomas. The head was given special attention. Besides describing obvious trauma, such as puncture wounds to the rostrum or eyes, skulls were collected,

cleaned and inspected for punctures and fractures. 5) Standard measurements (ANONYMOUS, 1967) and weights. When this procedure could not be conducted, carcass condition was described as well as possible and all other potentially relevant circumstances were recorded. Age of the female was either known from tags affixed to the hindflippers shortly after birth (LE BOEUF & PETERSON, 1969) or was estimated from standard length (REITER *et al.*, 1981).

Since observations of some areas were nearly continuous during daylight hours, a description of events preceding death was sometimes available in the serial record. The record of the area where the female resided was checked to determine behavioral interactions that immediately preceded death, noting especially, the stage in the reproductive cycle, whether the female copulated, with whom, and the circumstances that prevailed when the female was last seen alive.

The thoroughness of necropsies varied greatly depending on the circumstances. Several factors impeded the process: fading light, carcass inaccessibility (in the middle of a group of females), belligerent adult males guarding the carcass, and advanced decomposition of the carcass.

During the 1983 breeding season, the departure of females from harems on the island and mainland beaches was studied. The aim was to describe the social and sexual behavior of males directed to females departing harems. Three harems on the mainland were monitored from 0900 to 1500 hours every day from 10 January to 2 March; one harem on the island was monitored from 0800 to 1700 hours every day from 2 December to 2 March. Each time a female was observed departing a harem for the water, the event was recorded, paying particular attention to the female's identity and age, time of day, latency to reach the water, distance to the water, mounts and injuries received, number of males in attendance and their dominance status, number of males mounting and copulating with the female, and the response of females to mounting (receptive or resistant).

The three harems differed in size, location and distance to the water. The Año Nuevo Point harem on the mainland (MP harem) contained 358 females at peak season and was located in sand dunes above the beach; females had to travel 50-150 m to reach the water, depending on tidal conditions. The South Beach harem on the mainland (MBS harem) contained 133 females at peak season and the harem periphery was located on the beach within 2-20 m from the water. The point harem on the island (IP harem) contained 956 females at peak season and was very crowded (REITER *et al.*, 1981). These harems were representative of other harems in the area. A "mount" was recorded when a male put a foreflipper over the departing female's back. "Time to depart" was calculated as the interval between the female's exit from the harem and her disappearance in the water. "Males in attendance" was defined as males orienting to, chasing or physically contacting the departing female.

During the 1983 and 1990 breeding seasons, we observed marked females in the harems for 30 minutes on the day they departed, recording the number of blows (neck bites, butts and body islams) received, mounts and copulations.

Results

Incidence of mortality.

We counted 17 dead females during the 20 years monitored. Since 18,837 births were recorded during this period, the female mortality incidence on the rookery was about one death per thousand females giving birth. The first female death was observed in 1976, after nine

years of making observations. Deaths were distributed rather evenly over the period 1976 to 1986.

Cause of death and circumstances.

Four carcasses are excluded from the present analysis, three because no clue to the cause of death was available because of advanced decomposition, and a fourth, because of an unusual accident. This female became lodged in a crevice and drowned during the incoming tide.

Table 1 summarizes data from 13 females examined within an estimated 24 hrs after death. The major finding is that most females (11 of 13) showed evidence of traumatic injury, an indication that most deaths were not from natural causes. Necropsies revealed that the most likely cause of death for most females was a blow or bite to the head or spine, or crushing which caused broken ribs, organ damage and massive internal bleeding. Of the two remaining females, one had a severe bacterial infection at the time of death, and the other's death may have been associated with difficulties in giving birth.

All but one of the deaths occurred during the breeding season. Only one death occurred during the spring molt, when as many females were present on the rookery as during the breeding season. The majority of the females that died were not pregnant and died on the harem periphery or the nearshore waters. When first observed, most carcasses were being guarded or mounted by males.

Deaths were evenly distributed across a broad age range, from 3 to 11 years. Of the 13 necropsied animals (Table 1), the estimated age distribution, with frequencies in parentheses, was: 3 (1), 4 (1), 5 (3), 6 (1), 7 (1), 8 (3), 9 (1), 10 (1), and 11 (1). One five-year-old and ten-year-old were known age; the ages of the rest were estimated from standard lengths (REITER *et al.*, 1981).

Males as the source of trauma to females.

The external appearance and necropsy findings, plus direct and indirect observation, support the hypothesis that males inflicted the injuries that caused at least 11 of the deaths. The following points and data are consistent with this conclusion:

1. The trauma and types of injuries observed could only have been caused by males because of their teeth, size and behavior. The species-specific behavior of a courting male is to bite and hold the female on the

TABLE 1. The physical condition of female carcasses examined and circumstances evident at the time of death

	Proportion	Percent
I. *Physical condition of carcass*		
A. No trauma[1])	2/13	15.4
B. Trauma[2])	11/13	84.6
1. External		
a. Bitemarks[3]) on neck and back, lacerations, punctured eyes	8/11	72.7
2. Internal		
a. Broken bones (skull, spine, ribs)	7/9	77.8
b. Blood in mouth, nasal cavity, anogenital area	3/9	33.3
c. Organ damage (*e.g.*, ruptured liver, lacerated lungs)	6/9	66.7
d. Vascular trauma	9/9	100.0
e. Blood in blubber[4])	3/9	33.3
II. *Circumstances*		
A. Period of death		
1. Breeding season (January & February)	12/13	92.3
2. Molt period (April)	1/13	7.7
B. Location		
1. In a harem	1/13	7.7
2. On harem periphery or beyond[5])	12/13	92.3
C. Reproductive condition		
1. Pregnant[6])	2/13	15.4
2. Not pregnant	11/13	84.6
D. Carcass guarded by a male when found	8/13	61.5

An N of less than 13 indicates lack of data due to incomplete necropsy or carcass condition.

[1]) Necropsies performed on both carcasses. [2]) Complete necropsies performed on nine carcasses; partial necropsies on two carcasses. [3]) Distances between parallel neckbites were 8 to 12.5 cm, equal to the diastemas between the upper canines of males seven years old or older. [4]) Indicative of premortem trauma. [5]) Nine carcasses were found on the harem periphery suggesting that trauma occurred during departure from the harem to the water; two carcasses were found on non-breeding beaches. [6]) One pregnant female received a traumatic injury on her way to a harem; the other female may have died from complications during parturition.

neck to facilitate mating. When necessary, a male butts the female with the lower part of his head, neck and upper torso to pin her down and restrain her (Fig. 2). Bitemarks on the neck or back of eight dead females matched the diastema between male canines and not those of female canines (Table 1). Misplaced bites or female movement could have resulted in male bites landing on the head or back. Bites to the head were

of a severity to cause lethal brain damage. In some cases, bites to the back punctured the large extradural, intravertebral vein. Head and body slams, which courting males may often alternate with neck bites, were most likely to have caused broken ribs, organ damage and internal hemorrhage.

There is no other plausible cause for the type of trauma observed. Females cannot inflict these types of injuries on each other, given their smaller dentition and similar size. Shark injuries are easily distinguished from the ones we observed (LE BOEUF *et al.*, 1982) and can be excluded. It is unlikely that humans caused the injuries since the rookery was off limits and under nearly continual surveillance; it was clear that gunshot wounds were not involved. The type of trauma observed, and the timing of deaths in relation to weather, was not consistent with the idea that females were killed by being pounded into rocks by strong surf.

2. The location of most dead females on the periphery of harems, their post-parous condition, and the behavior of males to females entering or leaving harems, provide strong circumstantial evidence that males mortally injured the females while attempting to mate with them. Table 2 presents data indicating the circumstances females encountered during one breeding season when exiting harems to return to sea. Several points are relevant: a) Nearly all departing females were intercepted and mounted by males; not one female escaped from the two mainland harems without being mounted or bitten on the neck by at least one male. b) Most departing females copulated; copulation occurred on the harem periphery or in the nearshore water. Multiple copulations and copulations with as many as three different males were common. For example, during departures at South Beach harem, six females copulated twice, one female copulated three times, two females copulated four times and one female copulated seven times. c) Departing females were pursued and mounted by several males while others of lower rank attended nearby. The number of males that mounted departing females varied with the number and composition of males in attendance and the dominance relations between them. d) Departure times, calculated from the harem edge to when the female reached deep water, varied with the harem site and males in attendance.

Competition among males attending a female departure is especially keen and this makes the situation dangerous for the female, the center of attraction. Pursuing males vacillate between detaining the departing female, by pinning her down or biting her neck in order to mate with her, and fighting off competing males. Table 3 presents comparative data on

TABLE 2. Statistics on female departures from three harems at the Año Nuevo rookery during the 1983 breeding season

	Mainland Point Harem (MP)	Mainland South Beach Harem (MSB)	Island Point Harem (IP)
Peak no. females in harem	358	133	956
No. departures observed	23	20	106
No. males in attendance ($\bar{X} \pm$ sd)	10.4 ± 4.6	7.6 ± 2.5	8.9 ± 6.2 (104)
Percent females mounted	100	100	87.7
Percent females copulating	91.3	75	53.8
Blows per female ($\bar{X} \pm$ sd)	2.0 ± 1.9 (21)	2.7 ± 2.7 (19)	0.8 ± 1.8 (75)
Departure duration ($\bar{X} \pm$ sd min)	30.3 ± 23.4	19.2 ± 12.2	12.9 ± 10.6

An N of less than the number of departures (in parentheses) indicates lack of data.

the rate of mating and aggressive interactions in harems and outside harems when females are returning to sea. The data show clearly that during the relatively short departure period (a mean of less than 30 min, Table 2), females received over 20 times more blows (neck bites, butts and head slams), mounts, and copulations than they did in the harem shortly before they began to leave. This was so despite the fact that the number of blows per mount was no different in the two locations. Note also that the sex ratio reversed abruptly as females departed the harems. As a result, females were at greater risk of encountering males, and hence, being injured, on the periphery. Lastly, even after death, female carcasses were an object of avid competition among males (Table 1).

3. On one occasion (January 20, 1986, Point harem, Año Nuevo island), we observed a male kill a lactating female. At 0934 hrs, an 8-year-old male, Dino, lost a fight with another male then was threatened by yet another male. Dino responded with a counterthreat (elevated posture and vocalization) but instead of striking the male, he bit a nearby female on the back and shook her back and forth. The female began bleeding immediately from a puncture wound slightly off midline in the lumbar region and the area began to swell. Within two hours, she was dead. In the interim, the same male fought again and bit two more females. It could not be determined if these females suffered serious injury. This observation was unusual in that it involved the only female

TABLE 3. The sex ratio and rates of sexual and aggressive interactions inside harems and outside harems during female departures

	Inside Harems	Outside Harems
Sex ratio[1]) (male : female)	1:10.6 (21)	8.2:1 (163)
No. of mounts/hour	0.28 ± 0.14 (36)	5.35 ± 0.42 (226)
No. of copulations/hour	0.16 ± 0.08 (36)	3.98 ± 0.27 (223)
No. of blows/hour	0.06 ± 0.06 (36)	4.41 ± 0.48 (199)

Inside harem data were obtained from 30 minute focal periods of 36 estrous females in 11 harems on the Año Nuevo Rookery during the breeding seasons of 1983 and 1990. Outside harem values are based on the departures of 226 females during the 1982-1986 breeding seasons and a mean departure duration of 22.6 minutes. Values shown are the mean ± S.D. N is in parentheses.

[1]) The inside harem sex ratio was calculated from censuses of males and females recorded at the time each focal period was conducted. During 21 counts recorded at 11 harems, the mean number of females was 171.2 ± 220.0 and the mean number of males was 16.1 ± 24.4 (171.2/16.1 = 10.6). The outside harem sex ratio was calculated from counts of males made during 163 departures; the mean number of males pursuing each departing female was 8.2 ± 4.9.

that died in a harem. However, it provides support to our first point that males have the potential to kill females.

4. Summaries of three case histories provide additional information implicating males as the cause of death of departing females:

a) A 9-year old female named B was observed daily throughout the nursing period during the 1976 breeding season. She copulated in the Point harem on Año Nuevo Island on February 22, 24, 25 and 26, and was last observed alone at 1700 on 27 February. On February 28, she was found dead in the shallow water near the Point harem with several bulls competing to mount the corpse. Inspection of the corpse revealed four deep, paired cuts, approximately 10 cm long, with 8 cm between them, across the left side of her face. Her left eye was missing and there were numerous lacerations on the other side of her face. There was blood in the body cavity. Subsequent inspection of the skull revealed a broken zygomatic arch and fractures of the maxilla and nasal. It was concluded that death was due to a blow to the head at or near the time that the female was leaving the rookery to go to sea.

b) On february 21, 1981, a 5-year-old female, J, weaned her pup and was seen leaving the North Point harem at 1000 hrs, pursued by several peripheral males as well as the alpha male of the nearby harem. The alpha male kept other males at a distance and mounted the female several times on her way to the water but he failed to copulate with her at this time. When the female reached the water at 1015, the alpha male returned to his harem 20 m inland. Five to seven males continued pursuing the female as she entered the water. As the female entered the surf zone, observations were discontinued.

At 1145 hrs she was found dead in the nearby surf with a 7-year old male attempting to mate with the corpse. Inspection revealed an edematous, roughly circular swelling 25.5 cm in diameter above the spine 12.5 cm posterior to the axilla. Cutting through the edematous area above the spine revealed a large hematoma in and below the blubber layer, the result of venous trauma. A broken vertebral spine was noted beneath the hematoma. A longitudinal incision of the ventrum revealed massive hemorrhage in the body cavity apparently due to injury of the intravertebral vein which was the principal cause of death. Death occurred during the short period that the female was in the water. Hair was missing on the neck indicating that the female had been bitten and mounted by males. Sperm were found in the reproductive tract.

c) On January 22, 1982, a 5 ± 1 year-old, post-parous female with milk in the mammary glands was found on South Beach, Año Nuevo Mainland. Her right eye was punctured and there was a deep puncture wound in the skull 12 cm above the right eye near the midline. There was considerable bruising and blood in the blubber above the head and neck near the puncture wounds indicative of *premortem* trauma. There were ten broken ribs on each side of the body, each rib broken close to the dorsal midline. Because of the absence of bruising or blood in the blubber at this level of the spine, it appears that the body was crushed *postmortem*, probably by a large male mounting the carcass. No other external injuries. The female was in good condition prior to death. Probable cause of death was a blow to the head and neck.

Premortem *vs* postmortem trauma.

Necropsies revealed trauma that occurred both before death and after death, sometimes in the same individual. One of the best indicators of premortem trauma was blood in the blubber beneath an injury (*e.g.*, to the head, neck or spine), an indication that the vascular system was functioning at the time of the blow. In contrast, some carcasses had all ribs on one or both sides broken at the dorsal heads; we interpreted this trauma to have occurred after death, owing to the lack of resistance of the flaccid body to a body slam by a mounting male. We interpreted ribs broken distal to the dorsal heads (*e.g.*, in the center of the rib) to have been caused by a premortem blow. For some injuries, it was not possible to distinguish whether they occurred before or after death.

Discussion

The context of females departing harems at the end of lactation is such that several factors make them vulnerable to serious injury by males. These can be summarized briefly: 1) The female is outnumbered by males. The operational sex ratio on the periphery of harems is seldom less than 4:1 and may be as high as 25:1. 2) Males on the periphery of harems are eager to mate, but cannot do so in the harem and are left with the alternative strategy of competing with each other to intercept departing females. The high libido of the males and the great number of them

increases the probability of lethal injury. 3) Departing females have just lost 36 to 42% of their mass following a 34 day fast and four weeks of lactation (COSTA *et al.*, 1986; DEUTSCH *et al.*, 1990). Consequently, their blubber layer is thinnest at this time of year, meaning less protection from blows to the body, especially for the large extradural vein which runs the length of the spine. 4) Because departing females are moving away or making side to side evasive actions, male bites directed to the female's neck may land on the female's back or head. When females are in motion and their bodies are extended, as when moving over boulders, the spine and adjacent extradural vein is particularly susceptible to injury. Vulnerability to injury by males appears to be age-invariant.

This study adds support to E. O. WILSON's dictum that some important behaviors may not be apparent until the observation time devoted to the species passes the 1000 hour mark (WILSON, 1975). We did not observe a dead female on Año Nuevo Island during the first eight breeding seasons monitored and an estimated 7,200 hrs of observation. However, during the period 1976 to 1986, 11 breeding seasons, we counted 13 female deaths, most of which we attribute to adult males. Although the low incidence of female deaths observed makes study difficult, this does not diminish its importance. Like infanticide (HAUSFATER & HRDY, 1984), the phenomenon involves lethal behavior that has important implications for both sexes and the species.

The evolutionary implications of the phenomenon described in this paper hinge on its incidence. Male induced female mortality during the period 1976 to 1986 was at minimum 11/14,419 = .0008. Assuming similar colony numbers, this is the probability of an individual female being killed by a male during any single breeding season. If three females, whose bodies were decomposed and could not be necropsied, are added to the total of male induced mortalities, the seasonal probability increases to .001. This could be significant selection pressure (ENDLER, 1986) that might have the effect of shaping the behavior and morphology of females to avoid being victimized. Moreover, we emphasize that the incidence of female mortality we report is a minimum estimate. It is very likely that some female deaths are never counted because they occur in the nearshore waters where the corpse sinks or drifts out to sea, or the female is injured during departure and dies at sea several days later.

The risk of injury or death increases the cost of mating for females (DALY, 1978; PIANKA & PARKER, 1975) and selection should act on females to reduce this cost by taking evasive action. Behaviors are observed which appear to have this effect. Females gather together in

groups during their stay on land which reduced exposure to males while putting them in a position to mate with a male of demonstrated fitness (TRIVERS, 1972; COX & LE BOEUF, 1977). Accepting copulation readily or facilitating copulation while en route to the water appears to reduce male aggressiveness and the probability of injury at a time and in a situation when the female is vulnerable. Indeed, a female's readiness to copulate while departing differs radically from her resisting response to males in the harem. One gets the impression that departing females buy safe conduct to the water by copulating (MESNICK & LE BOEUF, 1990). To reject mating attempts while departing elicits even more aggressive mating attempts by males, whereas this same behavior in the harem increases the probability that she will be mated by the highest ranking adult male in the vicinity (COX & LE BOEUF, 1977).

We think it unlikely that males are under strong selective pressure to moderate their aggressive courtship so as to lower the incidence of female deaths. Selection favors males that attempt to copulate with fertile females by whatever means. If aggressive courtship leads to fertilization and is not too costly, the behavior will endure. It is not known whether copulations by peripheral males, forced or unforced, are effective in fertilizing females since females copulate in the harem for one to four days before they depart (LE BOEUF, 1972). Nevertheless, peripheral males compete vigorously to mate with departing females because this is their only alternative. The context demands that copulation be effected quickly which may lead to misdirected blows. The time and energy expended that results in the death of an occasional female does not seem to provide sufficiently strong selection pressure to check male libido. Indeed, the same high libido leading to mortal injury of females on the harem periphery may bring about the insemination of numerous females within the harem. The net reproductive success of a male in his lifetime is what counts and high libido seems to serve this purpose well.

Aggressive mating behavior of males occurs in other pinnipeds. Female southern elephant seals, *M. leonina*, are sometimes killed during attempted copulation by inexperienced bulls who bite the head instead of the neck and crush the skull (CARRICK & INGHAM, 1962). Neck scars due to male mounts are so common in this species that MCCANN (1982) used the degree of scarring to differentiate primiparous from multiparous females. JOHNSON & JOHNSON (1979) saw two male monk seals, *Monachus schauinslandi*, mount a female repeatedly, grasping her around the back with foreflippers and securing a back bite posterior to the shoulder. This behavior continued for several hours during which intromission occurred

several times. At the end of the episode, large sections of skin and blubber were removed from the female's back. The female was not seen again and it was assumed that she died from injuries sustained during mating. Similar observations were made by C. DEUTSCH in 1982 (pers. comm.) and are reported by ALCORN & BUELNA (1989). Indeed, "mobbings", where adult male monk seals kill females during mass mating attempts are considered an explanation for the slow recovery rate of this species on some islands. Roger GENTRY (pers. comm.) saw an adult male Steller sea lion, *Eumetopias jubatus*, kill a female during copulation on Año Nuevo Island in 1968. The female resisted being mounted and kept turning to bite the male. Her neck was broken as the male attempted to pin her down. When high surf washed the body to sea, the male retrieved the corpse and copulated with it. Southern sea lion males, *Otaria byronia*, may injure and kill females during abductions (CAMPAGNA *et al.*, 1988). Alaska fur seal males, *Callorhinus ursinus*, compete for females on the border between territories. Occasionally, two males seize a female with their teeth and injure or kill her by pulling in opposite directions (D. COSTA, R. GENTRY, pers. comm.).

Males injure or kill females during mating attempts in many other species. In rhesus monkeys, *Macaca mulatta*, estrous females are often severely wounded by males (CARPENTER, 1942; VANDERBERGH & VESSEY, 1968). Female orangutans are struck and bitten during forced copulations by subadult males (MACKINNON, 1974; GALDIKAS, 1978) and, in humans, violent rape is reported in many cultures with the woman being frequently injured but rarely killed (CHAPPEL *et al.*, 1977; MCCAHILL *et al.*, 1979; SYMONS, 1979; THORNHILL & THORNHILL, 1983). In several carnivores, females are sometimes killed during mating. In viverrids and mustelids, mating is typically violent and of long duration. Males are larger than females and the male bites the female on the neck during copulation. In martens, *Martes martes*, the male drags the female around by the neck until she assumes the mating position (EWER, 1968). ENDERS (1952) recorded incidents in which male mink, *Mustela vison*, kill females when, taking an improper neck grip during mating, their canines puncture the base of the skull to the brain; the likelihood of accidental death is increased by female resistance. Continued harassment by males also causes female deaths (HATLER, 1976). Occasionally, female felids are wounded or killed during mating (LEYHAUSEN, 1956). In mountain sheep, *Ovis canadensis*, males pester ewes so much that the latter are often forced to flee into dangerous areas on a cliff face to escape pursuing males (GEIST, 1971). American bison cows, *Bison bison*, are sometimes injured

by males as they dismount following copulation (LOTT, 1981). The bull's hooves strike the cow's back a few inches on either side of the spine, occasionally removing patches of skin. By their 7th or 8th year, most cows have patches of hairless scar tissue on their backs. Yvette MCCULLOUGH (pers. comm.) saw a bison male kill a female during a long, persistent mating attempt. Male sea otters, *Enhydra lutris*, bite females on the nose during aquatic copulations; some females die as a result of drowning or infections following lacerations to the nose and face incurred during mating (FISHER, 1939; FOOTT, 1970; Jack AMES, pers. comm.). Courtship in the wild ass, *Equus asinus*, involves the male pursuing the female, biting and kicking her until she stands (ANTONIUS, 1937).

Courtship and copulation is especially perilous for some female sharks. In several species (*e.g.*, blue shark, *Prionace glauca*, SUDA, 1953; STEVENS, 1974; PRATT, 1979; sandbar shark, *Carcharhinus milberti*, SPRINGER, 1960; gray reef shark, *Carcharhinus amblyrhyncos*, CLARK, 1981), males bite the backs of females between the first and second dorsal fins as a prelude to mating. The dermal lacerations that result can be severe. CLARK (1981) observed and photographed numerous females that were "badly bitten". "Mating scars" are so reliable in female blue sharks that they are used to determine sex and sexual maturity (PRATT, 1979). An adaptation that appears to have evolved in response to the male's aggressive mating behavior is that the skin over most of the body of the mature female is more than twice as thick as that of the male (see Fig. 17 in PRATT, 1979).

Forced copulation is common in many ducks, especially *Anas* species (BARASH, 1977; MCKINNEY *et al.*, 1983) and geese (MINEAU & COOKE, 1979) and the possibility of injury is high. In woodfrogs, *Rana sylvatica*, a swarm of 10 to 15 males may compete to amplex a single female and during these contests females may be killed (HOWARD, 1980). Similar observations occur in several insect species. For example, yellow dung flies, *Scatophaga stercoraria*, arriving at a fresh cow dropping (the site of mating and oviposition) may attract several males and a struggle ensues; females sometimes drown in the liquid dung or are badly torn in the process (PARKER, 1979). Two dragonfly males, *Plathemis lydia*, may seize an ovipositing female at the same time and injure her or cause her to drop into the water where she is captured and eaten by wolf spiders (JACOBS, 1955).

Although high motivation to mate may be generally beneficial in enhancing male reproductive success (FARR, 1980), it clearly can have opposite effects for females of many species. The evidence we present on male elephant seals inflicting lethal injuries on adult females of the

species, combined with observations of males injuring and killing suckling pups (LE BOEUF & BRIGGS, 1977), weanlings and yearlings (LE BOEUF *et al.*, 1972; REITER *et al.*, 1981), and each other (LE BOEUF, unpubl. obs.), demonstrates that males are a dangerous force on the rookery with the potential to shape the behavior of conspecifics.

We hypothesize that mortality risk to a female during mating is highest in species having one or more of the following characteristics: 1) males much larger than females, 2) adult males more numerous than adult females, 3) a male mating pattern involving the use of force or potentially dangerous weapons, and 4) a social system in which a few males monopolize mating and prevent the majority of males from mating by controlling females directly (such as in elephant seals) or by controlling resources important to them such as food (*e.g.*, scorpion flies, *Panorpa*, THORNHILL, 1980) or birthing sites (Steller sea lions, *Eumetopias jubata*, GENTRY, 1970). The above traits are characteristic of many highly polygynous species but are not exclusive to them.

Summary

Adult female mortality of northern elephant seals, *Mirounga angustirostris*, was monitored daily throughout the breeding season and weekly during the non-breeding season at Año Nuevo, California, during the period 1968 to 1987.

Behavioral observation and necropsy findings were collected and circumstantial evidence was compiled to determine the cause of death.

Female deaths on the rookery were rare; only 17 female deaths were recorded over the 20 year period. Cause of death could not be estimated in three cases because of advanced decomposition, one female died from an accident, and two others had no apparent trauma. The majority of deaths (11) were caused by traumatic injuries inflicted by males during mating attempts as the females departed harems for the sea at the end of lactation. Mortalities caused by males were distributed across a broad age range.

Based on the observed incidence of female mortality in relation to females present on the rookery, the probability of a female being killed by a male during the breeding season is about one in a thousand. Females are expected to evolve adaptations to reduce injurious encounters with males.

Females are injured and killed by males during mating attempts in a variety of species. A hypothesis concerning the conditions under which female animals sustain potentially lethal injuries during mating is advanced.

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