

**SEXUAL BEHAVIOR OF MALE NORTHERN
ELEPHANT SEALS:
III. THE MOUNTING OF WEANED PUPS**

by

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(With 3 Figures)
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Introduction

It is widely accepted that males are often so highly sexually motivated during reproductive periods that they will direct sexual behavior indiscriminately toward inappropriate objects such as conspecific juveniles, non-estrous females, and males, individuals of other species, and even inanimate objects (TRIVERS, 1985; ALCOCK, 1984). Nevertheless, this phenomenon has received more anecdotal attention than carefully documented study, perhaps because a low threshold for sexual arousal is considered a fundamental trait of the male sex (ORIAN, 1969) and generally appears to be low cost for the indiscriminate males and the objects of their attention. A few studies have shown that male sexual behavior directed toward conspecific juveniles can have considerable impact on the recipient (CAMPAGNA *et al.*, 1988; COOK & HOWELLS, 1981; DALY & WILSON, 1981; ROBINSON, 1988). Because juveniles are generally small and relatively helpless, the result of these interactions may be severe injury or death. It is important, therefore, to direct more careful analysis toward species where sexual behavior toward juveniles occurs relatively frequently.

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One such species is the northern elephant seal, *Mirounga angustirostris*. We have observed male northern elephant seals mounting live and dead weaned pups, yearlings, two-year olds, subadult males, pregnant females, dead females, and dead sea lions (LE BOEUF, 1972; REITER *et al.*, 1978; LE BOEUF & MESNICK, 1991). Of these, weaned pups are the most numerous on the rookery during the latter half of the breeding season. Over the past two decades, researchers at Año Nuevo State Reserve, California have observed weaned pups being mounted frequently by males of various ages.

To put this behavior in context, the breeding behavior of this highly polygynous species is briefly reviewed here. Females arrive singly and continuously over a two-month period in the winter and are highly gregarious, forming harems. They give birth approximately six days after arrival on the rookery, suckle their pups for approximately 28 days, and then depart, abruptly weaning their offspring (LE BOEUF *et al.*, 1972; REITER *et al.*, 1981). Thus, weaned pups begin appearing on the rookery about a third of the way through the breeding season, in mid-January, and their numbers increase rapidly following the peak of the breeding season in early February. Weaned pups move inland, away from the harems, and typically form groups, called pods, of 2 to 30 individuals. Later in the season, aggregations of up to several hundred weanlings may form. Weaned pups fast on the rookery for 10-12 weeks, resting, playing, and learning to swim and dive in shallow water. Their activity patterns are crepuscular (REITER *et al.*, 1978). By late April, most of them depart the rookery on their first pelagic feeding trip.

Yearlings and older juveniles (two and three years old) are present in large numbers before the breeding season (October to early December), but nearly all of them are at sea during January and February. Many of them reappear in mid-March as males depart the rookery (LE BOEUF, 1972; CLINTON, 1990). Thus, interactions between bulls and juveniles are infrequent due to the limited temporal overlap of their terrestrial haul-out periods.

Sexually mature males begin arriving at the breeding rookery in late November, about two to three weeks before the first females. Most of them fast on the rookery for two to three months while attempting to breed (LE BOEUF, 1974; CLINTON, 1990; DEUTSCH, 1990). The bulls engage in ritualized combat on sections of beach traditionally used by females for pupping. As a result, a dominance hierarchy is established, based on age, size, and fighting ability (LE BOEUF & PETERSON, 1969; LE BOEUF, 1974). Subadults and low-ranking adults attempt to enter harems

to copulate but have only limited success (LE BOEUF, 1972, 1974). Some excluded males copulate successfully with estrous females as the females leave the harems at the end of their lactation period (LE BOEUF & MESNICK, 1991; MESNICK & LE BOEUF, 1991). Departing females are probably already inseminated, however, having copulated several times within the harem during the four to five days prior to departure (LE BOEUF, 1972). Most males achieve no copulations during the breeding season (LE BOEUF, 1974; COX, 1983; LE BOEUF & REITER, 1988). It is in this context, with many subordinate males having few breeding opportunities, that weaned pups are mounted.

The specific aims of this study were to determine and describe: (1) the incidence of male elephant seals mounting weaned pups; (2) the costs to weanlings, in terms of severity of male-inflicted injuries and male-caused mortality; (3) the behavior of males and weanlings during mounting attempts; and (4) the characteristics of males that mount weanlings and of weanlings that are mounted. We also report observations of males mounting juvenile elephant seals (one-two years old) and describe cases of male-caused juvenile deaths. Lastly, we speculate on the possible mechanisms and function of this apparently inappropriate behavior.

Methods

Data were collected during five winter breeding seasons spanning 10 years at Año Nuevo State Reserve, San Mateo County, California (1981, 1986, 1987, 1988, and 1990). All observations were made on the Año Nuevo mainland, with the exception of the mortality record, which included data from Año Nuevo Island. The seals on the mainland rookery breed on sloping sandy beaches and inland dunes that are interspersed with dense stands of willow (*Salix lasiolepis*) and other low-growing bushes. The study area is described in detail elsewhere (LE BOEUF & PANKEN, 1977; LE BOEUF & KAZA, 1981). Approximately 200-440 males were present on the mainland at peak season each year. The total number of weanlings produced annually on the mainland rookery increased from about 250 to 1200 over the study period. Four data collection methods were used.

1. Estimating the cumulative percent of weanlings mounted and scoring wound severity.

During the 1981, 1987, and 1990 seasons, an average of 255 weanlings (range 64-442, $N = 23$ surveys) was sexed and examined on the mainland rookery every few days from early February to mid-March for evidence of having been mounted by males. When a male mounts an estrous female, he usually bites her neck, often leaving a mark or wound (LE BOEUF, 1972); neck bites are also observed when males mount weanlings (Fig. 1). Because of their small size, relative to adult females, the "neck bite" sometimes contacts the weanling's head. For each weanling in the sample, we recorded the presence or absence of tooth marks on the dorsal surface of the head, neck, and body, as an indication that the weanling had been mounted by a male.

Male-inflicted tooth marks varied from raked depressions in the fur to multiple contusions that broke the skin, exposing the blubber. Tooth marks were scored for severity on

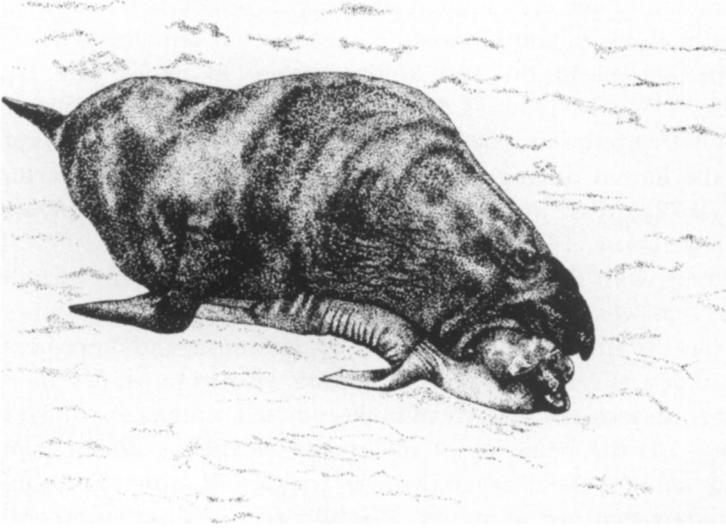


Fig. 1. A subadult male bites the neck of a weaned pup while mounting it. The pup is vocalizing in response to the mount. The illustration was drawn from a photograph.

a three-point scale in 1987 and 1990. Type I injuries included superficial bite marks, surface cuts, or missing fur (no bleeding). Type II injuries were shallow gashes or puncture wounds (Fig. 2a and b). Type III injuries were deep gashes, exposing the blubber, sometimes with profuse bleeding or infection. Fresh marks were not distinguished from old scars; both were taken as evidence that the subject had been mounted by a male. We were confident in attributing these marks to males because adult females bite weanlings on the nose, face, and rump (REITER *et al.*, 1978), but rarely on the neck or back of the head. Male- and female-inflicted marks were further distinguished by the distance between the canines; the diastema in males varies from 8 to 13 cm and in females from 6 to 7 cm (LE BOEUF & MESNICK, 1991).

Weanlings continued to emerge from harems until all females departed by the second week in March and each successive survey probably included previously sampled weanlings. Thus, these surveys provided an estimate of the cumulative percentage of weanlings mounted by males as the breeding season progressed. It is a minimum estimate because some weanlings mounted early in the season may have lost their marks by the time they were sampled again later in the season. In addition, not all mounts included bites and not all bites left a visible mark.

2. Determining weanling and juvenile mortality.

A record of all dead weanlings, yearlings, and older juveniles found on the island rookery was kept during each breeding season for the period 1969-1982; a similar record was kept for the mainland rookery from 1975-1990. Probable cause of death was determined by necropsy, if the carcass was fresh and accessible and skilled personnel were available (LE BOEUF & BRIGGS, 1977). When this was not possible, an external examination was conducted and external injuries were noted.

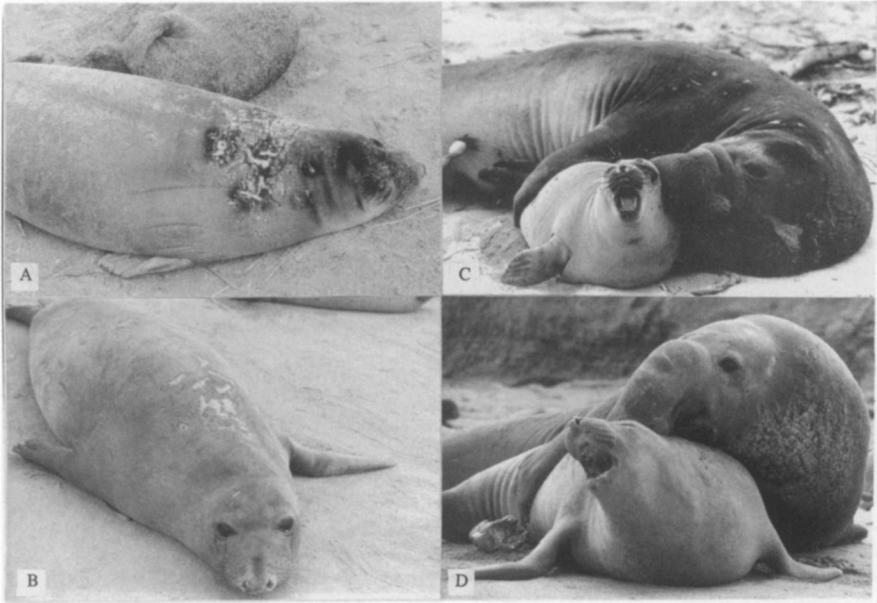


Fig. 2. Similarities in male sexual behavior directed toward weanlings and adult females and its consequences: a) A weanling with male-inflicted cuts and puncture wounds (Type II) on the back of its neck. b) A female with male-inflicted scrapes (Type I) on the neck and back. Note that the wounds are placed farther down the back on the female. c) A subadult male mounting a weanling. d) An adult male mounting a female (photo by Frans LANTING). Note the similarity of weanling and female responses.

3. Recording male mounting behavior and weanling response.

During February and March in 1986, 1987, and 1988, the rookery was surveyed several times a week for incidents of males mounting weanlings. Individual and groups of weanlings were observed for several minutes at a time, using *ad libitum* sampling. If a mounting attempt began during an observation, male and weanling behavior immediately prior to and during the mounting attempt, duration of the mounting attempt (from initial approach to last contact), and cause of termination of contact were recorded. We also noted the size of the group the weanling was in before the mounting attempt, 1 min after the interaction ended, and 5 min after. Weanlings less than two body lengths apart were considered to be grouped. All mounting attempts were pooled for data analyses. Mounting attempts already in progress were also recorded and the end of some mounting attempts was not observed due to approaching darkness or observer time limitations. For these reasons, sample sizes for analyses varied.

In all years, daily behavioral observations were also made by observers conducting related studies and occasional observations were made by Reserve rangers. These contributed to the recording of unusual mounting episodes, such as those that led to the death of a weanling.

Male mounts of yearlings or juveniles, occasionally present in small numbers during the breeding season, were recorded from January to March 1986 in the same manner as weanling mounts.

4. Describing characteristics of male mounters and mounted weanlings.

Male mounters were assigned to one of five age classes, based on overall body size and the development of the neck shield and proboscis (LE BOEUF, 1974; COX, 1983; CLINTON, 1990). Males undergo puberty at four to six years of age. Subadult-two (SA2) males are approximately five years old, comparatively small, and have almost no neck shield and only a slight elongation of the nose. They rarely engage in serious agonistic encounters with other males or in sexual interactions with females. Subadult-three (SA3) males, approximately six years of age, are more socially active, but are still physically immature. Subadult-four (SA4) males are approximately seven years old and may be competitive in dominance interactions and achieve copulations with estrous females. They have a slightly underdeveloped neck shield and proboscis and have not reached full length. Males who have achieved full length (approximately 4.5 m), with fully developed neck shields and dangling noses, are considered adults (approximately eight years of age and older).

Most males on the rookery were individually identified by marks applied early in the season with a bleaching agent or dye (Nice N' Easy by Clairol or Wellite Cream Bleach by Wella Corp.). In addition to the behavioral data (see above), we collected the following data for each of the observed mounting attempts in 1986, 1987, and 1988: the identity (name) and age class of the male mounter, the mounted weanling's relative size (small, medium, large), and its molt condition. Each male that mounted a weanling was counted only once for age class analyses, regardless of the number of times he attempted to mount a weanling. Each year, about 100 weanlings of known-age females were weighed for a separate study; relative size of mounted weanlings was estimated based on similarity of appearance to these known-mass weanlings, as follows: small weanlings were 60-100 kg, medium weanlings were 100-145 kg, and large weanlings were greater than 145 kg. The sample of known-mass weanlings was used to determine a rookery-wide weanling size distribution with which to compare the mounted weanling size distribution.

Molt condition was categorized as pre-molt, 5-49% molted, 50-99% molted, and completely molted. Weanlings begin molting their black natal pelage within a few days of weaning (REITER *et al.*, 1978), gradually revealing a silvery juvenile coat underneath. Molting occurs over a two to three week period.

In 1988, individual males observed mounting weanlings were monitored for subsequent mounting attempts. After the initial observation, the male was marked on the pelage, if not already marked, and recorded on a master list that was carried in the field daily; when males on this list were subsequently sighted during rookery surveys, they were observed for approximately 10 minutes.

A male census by age class was conducted weekly and the proximity of all marked males to harem females was recorded daily. The percent time individual males spent in harem areas from 6 January to 7 March 1988 was estimated as the percentage of daily sightings within 50 m of a harem. This proximity-to-harem variable was calculated for 29 weanling mounters and 40 non-weanling mounters; individuals that were observed on the rookery for less than 10 days were excluded from the analyses, including seven weanling mounters. The number of successful (≥ 1.5 min) copulations with estrous females throughout the breeding season was also recorded for all marked males.

Results

Timing and incidence of mounting.

Males mounted weanlings as early as the beginning of February. Estimates of the cumulative percentage of weanlings that were mounted

by males increased steadily during the last third of each breeding season, reaching 20% (54/268) to 50% (66/133) by mid-March (Fig. 3). In each year, the increasing incidence of weanlings showing evidence of having been mounted was associated with declining numbers of adult females, the continued presence of males, and increasing numbers of weanlings (Fig. 3). By the first week in March, with many males still present on the rookery, weanlings outnumbered females by about 30:1. By mid-March, however, there were few males mounting weanlings, as most males had left the rookery.

Severity of neck and back bites.

When males bit weanlings during mounting attempts, the resulting injuries ranged from superficial tooth marks and skin abrasions to deep gashes and punctures on the neck and back that bled and exposed the blubber. The injuries sustained by weanlings were also very similar to injuries sustained by females during mounting attempts (Fig. 2a & b). The majority of tooth marks were superficial and serious injuries were rare (Table 1). In 1981, 1987, and 1990, we recorded five, three, and four weanlings, respectively, with severe lacerations or deep puncture

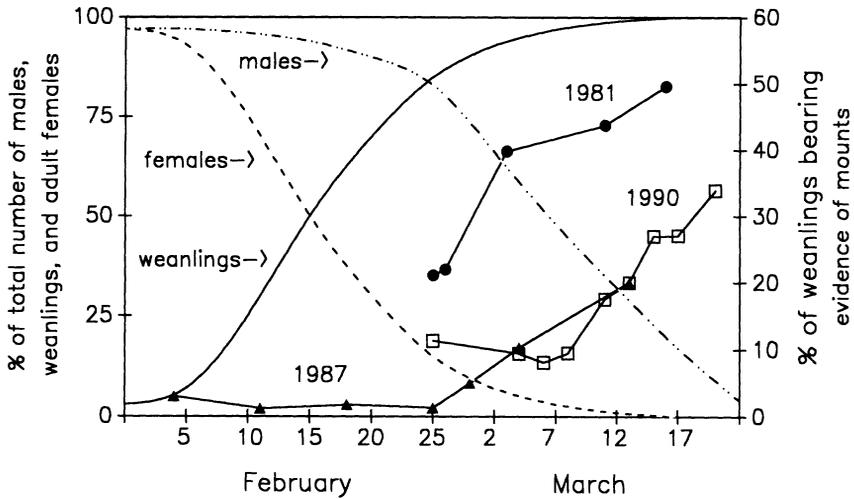


Fig. 3. The percentage of weanlings on the rookery bearing male-inflicted tooth marks, fresh wounds, or scars as a function of date (right axis). The relative frequency (percentage) of the total number of males, weanlings, and adult females on the rookery is also plotted as a function of date (left axis).

TABLE 1. Severity of male-inflicted marks, wounds, or scars on weanlings in 1987 and 1990, given as a percentage of total bitten weanlings

Severity Scale	Percent of Bitten Weanlings	
	1987 (N = 97)	1990 (N = 638)
Type I—superficial wounds, surface cuts, or missing fur (no bleeding)	83.5	93.5
Type II—shallow gashes or puncture wounds	13.4	5.9
Type III—deep gashes, profuse bleeding, or infection	3.1	0.6

N is the number of weanlings scored.

wounds on the neck or back. One individual had a puncture wound above the right eye, apparently caused by a male's canine, as no females were on land at the time of the injury.

Weanling mortality.

From 1969 to 1982, a minimum of 47 out of 7,928 weanlings (0.6%) died on the Año Nuevo rookery (mainland and island) before going to sea (see also REITER *et al.*, 1978). From 1983 to 1990, a minimum of 28 out of 6,531 weanlings (0.4%) died on the mainland rookery alone. Necropsies and descriptions of external injuries indicated that 26 (35%) of the 75 dead weanlings appeared to have been killed by males.

Two weanlings were observed being killed by males attempting to mount them. On 19 February 1980, a seven-week-old weanling was pounded and bitten repeatedly on the neck and head by a subadult male. After the weanling died, the male continued to guard the body and tried unsuccessfully to copulate with it. Four days later, several males were still competing to mount the carcass. On 8 March 1980, a nine-week-old weanling was mounted by a subadult male in a tidepool, pinned underwater, and drowned.

Twenty-four weanlings appeared to have been killed by males. Necropsy results on 16 weanlings revealed trauma—neck bites, head injuries, blood oozing from the nose and mouth, and internal vascular trauma—suggesting that they were killed by males. Eight weanlings were not necropsied, but external examinations indicated good health prior to

death and revealed neck bites apparently inflicted by males. One was found drowned in a shallow pool in 1986 and another appeared to have drowned in 1989. Another weanling in 1989 had a deep puncture wound on the head that appeared to have been the fatal wound. In 1990, a dead weanling was found with two deep gashes on the flank.

For the other 49 of the 75 dead weanlings, no necropsies were performed and cause of death was not determined. However, given their external appearance and apparent good condition prior to death (body mass of 100 kg or more), it was clear that none had died of starvation and unlikely that any had died of disease. Male-induced internal trauma or suffocation was the major suspect, although heat stress (REITER *et al.*, 1978; W. SYDEMAN, pers comm.) may have been involved.

Yearling and juvenile mortality.

At least three yearlings died on the Año Nuevo rookery from male-inflicted injuries during the period 1969-1990. Yearlings are longer and leaner than weaned pups, but they are approximately the same mass (P. MORRIS & B. LE BOEUF, unpublished data). On 26 December 1977, a fresh dead female yearling was found on the periphery of the main breeding beach on the island. Death was apparently caused by a male since large canines punctured the skull above the right eye. On 30 December 1978, a subadult male was observed mounting a yearling on an isolated part of the island. The yearling was found dead on the following day, apparently the result of trauma to the head. On 21 January 1983, a dead yearling was mounted by several males in the surf on the mainland shore; the animal had two male-inflicted puncture wounds on the head, but the cause of death was unclear. On 9 February 1986, a small SA3 male was observed vigorously mounting a female yearling in a willow area away from harems; the male repeatedly bit her neck and slammed her with his forequarters, covering her head and neck with blood. The yearling weakly resisted his aggressive sexual advances and, after the subadult stopped attempting to mate, she moved 10 m away. The yearling was found dead 1.5 hr later, with massive internal hemorrhage and bite wounds on the neck and back. The necropsy also revealed enlarged lymph nodes and a skin condition known as scabby molt, suggesting that the yearling may have been ill at the time of the encounter.

Data were insufficient to calculate yearling mortality rate due to male mounting attempts. However, the risk of death can be placed in perspective with the following figures of yearling abundance taken near the dates

of the above deaths. In 1977 and 1978, the number of yearlings on the island in December ranged from 43 to 157. In 1983 and 1986, no more than 17 yearlings were ever censused on the mainland in January and February.

Two juvenile males (two-three years old) were found dead on 9 December 1985 and 10 December 1986, respectively. Both exhibited broken ribs and seemed to have died from a crushing blow to the dorsum, perhaps inflicted by a larger bull.

Male mounting behavior and weanling response.

Mounting attempts ranged from casual approaches by males, with limited physical contact, to vigorous and repeated attempts to achieve intromission. Duration of mounting attempts, from initial approach to last contact, ranged from 5 seconds to over 32 minutes, with an overall mean duration (\pm one SD) of 170 ± 303 sec (median = 180 sec, $N = 81$). In a typical mounting attempt, a male initially approached a weanling resting nearby; he then moved alongside the weanling and placed a pectoral flipper over its back (FOB). The weanling protested by vocalizing and vigorously attempting to move away from the male. The male exhibited various stereotypical female-mounting behaviors (see LE BOEUF, 1972), including neck rests (pressing his neck heavily and steadily on the weanling's neck), neck bounces (dropping his head and neck forcefully on the neck or back of the weanling), and neck bites, to subdue the weanling and prevent its escape (Figs 1, 2c). A weanling usually escaped a male's grasp within two to three minutes and moved directly away, whereupon the male did not pursue the weanling. Male mounts of weanlings appeared very similar to male mounts of females (Fig. 2c & d).

Immediately prior to a mounting attempt, about half of the males (47%) were active; 15% were interacting with another weanling (Table 2). Both subadult and adult males spend at least 90% of their time on the rookery resting during the latter third of the breeding season, when most mounts were observed (DEUTSCH, 1990). This suggests that the probability of a male mounting a weanling increased if he was already active. Approximately one-quarter of the weanlings were active prior to a mounting attempt. Diurnal activity budgets of weanlings have not been determined; however, qualitative observations indicate that weanlings were active much less than 25% of the time (pers. obs.; J. REITER, pers. comm.). This suggests that, although weanling movement was not

TABLE 2. Activity of males and weanlings immediately prior to a mounting attempt, given as a percentage of the number of observed mounts

Activity	Year			Totals
	1986	1987	1988	
<i>Males:</i>				
Resting	39	62	55	53
Moving	31	38	6	24
Interacting with weanling	15	0	28	15
Interacting with male	15	0	0	4
Swimming	0	0	11	4
Sample size	13	16	18	47
<i>Weanlings:</i>				
Resting	80	88	57	76
Moving	20	12	36	22
Swimming	0	0	7	2
Sample size	10	17	14	41

Sample size indicates the number of mounts.

required to attract the attention of a male, an active weanling may have had an increased probability of being mounted.

Table 3 shows the frequency of various male behaviors and weanling responses during a mounting attempt. The most frequently observed behaviors for males were neck rests (observed in 61% of interactions), flipper-over-back (48%), and neck bounces (38%). Males bit weanlings in 21% of the mounts. Penile extrusion, which is observed prior to intromission with an estrous female (LE BOEUF 1972), was observed in 10% of the mounts. Some males persistently, but always unsuccessfully, attempted intromission. The male often pinned the weanling to the ground with a neck rest or neck bounce, so that the weanling could not move. Some weanlings appeared to have difficulty breathing in this situation.

Weanling response to a mounting attempt was generally similar to that of an unreceptive female being mounted (LE BOEUF, 1972); 97% protested, which included attempting to move away and vocalizing (Table 3). Twenty-seven percent of the weanlings slapped their hind-flippers against the male, a vigorous hind-quarter swinging motion displayed by females that refuse to copulate (COX & LE BOEUF, 1977). Many weanlings retracted their heads, bunching the skin and blubber on the top of the neck; this neck contraction is also exhibited by females and may offer

TABLE 3. Percentage of mounting attempts in which various male and weanling behaviors occurred

Behavior	Year			Totals
	1986	1987	1988	
<i>Males:</i>				
Neck rest	69	33	71	61
FOB ¹	43	38	67	48
Neck bounce	17	67	52	38
Bites	17	19	33	21
Nose touch ²	7	14	24	13
Penile extrusion	7	14	10	10
Sample size	42	21	21	84
<i>Weanlings:</i>				
Moves away	86	81	67	83
Vocalizes	72	100	48	73
Attempts to move away	42	48	33	41
HF slap ³	25	10	48	27
OMT ⁴	8	0	24	10
Bite male	3	10	0	4
Totally protesting	55	81	54	64
Predominantly protesting	38	19	36	33
Predominantly passive	7	0	0	3
Sample size	36	21	21	78

Sample size refers to the number of mounts. ¹FOB = flipper-over-back. ²Nose touch = male touches weanling's body with his nose. ³HF slap = hind-flipper slap. ⁴OMT = open-mouth threat.

TABLE 4. Causes of termination of mounts, given as a percentage of the number of observed weanling mounts

Cause of termination	Year			Totals
	1986	1987	1988	
Weanling moves away-male stops	48	67	59	56
Male threatened by neighboring male	24	14	14	18
Male terminates voluntarily	7	14	18	12
Observer disturbance	7	5	5	6
Male threatens neighboring male	11	0	0	5
Male redirects to another weanling	3	0	4	3
Sample size	38	21	22	81

Sample size refers to the number of mounts.

some protection from bite-caused injuries to the neck and back (LE BOEUF, 1972; LE BOEUF & MESNICK, 1991).

Most mounts (56%) ended when the weanling broke away and the male did not pursue the weanling (Table 4). In 12% of the mounts, the male terminated the interaction voluntarily. Twenty-three percent of the mounts ended when the mounting male engaged in an agonistic interaction with a nearby male.

Males usually did not persist in their mounting attempt once a weanling escaped and weanlings generally moved only a short distance (<5 m) before coming to rest again after an interaction ended. The mean \pm one SD group size of weanlings accosted by males was 3.3 ± 3.1 (median = 2.0, N = 27) and this did not change significantly in the subsequent 5 min (Kruskal-Wallis Test, $H = 0.005$, $df = 2$, $p = 0.99$).

Males mounting yearlings and juveniles.

Males also mounted yearlings and older juveniles (two to three years old) and, on occasion, even four-year-old males. Although there were few of these animals in relation to weanlings, males behaved as if they preferred to attempt to mate with the larger, older juveniles. On several occasions, a male moved past several weanlings in order to mount a two-year-old.

The behavior of males and juveniles (one yearling and seven two-year-olds) during 10 observed mounting attempts in 1986 was qualitatively similar to that described above for males mounting weanlings. The duration of juvenile mounts (mean \pm one SD = 120 ± 124 sec, median = 49 sec, N = 9) was not significantly different from the duration of weanling mounts observed in the same season (169 ± 395 sec, median = 30 sec, N = 39; Mann-Whitney U-test, t-test approx.: $N_1 = 39$, $N_2 = 9$, $U = 215.5$, $p > 0.20$). The age distribution of the nine males observed mounting juveniles in 1986 was as follows: 2 SA2, 4 SA3, 1 SA4, and 2 adults.

Although the sample size was small, there appeared to be a few behavioral differences between weanling and juvenile mounts. Males placed their flipper over the back (FOB) of the juvenile in 80% (8/10) of the interactions and they bit the juvenile in 50% (5/10) of the mounting attempts; these frequencies were greater than those observed for weanlings mounts (compare Table 3). The response of juveniles to being mounted was similar to the response of weanlings, except that juvenile movements were more coordinated and more likely to resemble those of an adult female. For example, they slapped their hindflippers against the

male in 62% (5/8) of the mounts, which was more often than exhibited by weanlings (see Table 3).

Characteristics of male mounters.

The age distribution of weanling mounters did not reflect the relative proportions of male age classes present on the rookery (Table 5). Ninety-one percent of the males observed mounting weanlings were subadults, although subadults comprised only 46 to 68% of the males present during February and March (Table 5). Only seven different adult males were seen mounting weanlings over the three-year study period, significantly fewer than expected based on their numbers on the rookery. SA3 males comprised one-third or less of the male population on the mainland, yet over half of the male mounters were of this age category during the study period. SA4 males accounted for about one-quarter of all known mounters. Only 10% of weanling mounters were SA2 males, but the number of SA2 males present on the rookery was low during the time of weanling emergence, especially after the 1986 season (Table 5).

As is characteristic of male elephant seals in general (Cox, 1983; DEUTSCH, 1990), the percentage of time (mean \pm one SD) that weanling mounters spent in harem areas in 1988 increased with male age class: 5% for 1 SA2 mounter, 48% \pm 13% for 9 SA3 males, 54% \pm 15% for 8 SA4

TABLE 5. Age distribution of weanling mounters in the 1986, 1987, and 1988 breeding seasons, given as a percentage of the total number of different individuals observed mounting weanlings in a given year

Age class	Year			Totals
	1986	1987	1988	
SA2	13 (12)	10 (2)	7 (-) ¹	10
SA3	77 (35)	33 (25)	48 (-)	56
SA4	7 (21)	47 (19)	31 (-)	25
Adult	3 (32)	10 (54)	14 (-)	9
Sample size	31	19	29	79
χ^2	27.26	21.93	--	
df	3	3	--	
significance	p < 0.0001	p < 0.001	--	

The percentage of each age class present on the mainland rookery during February and March is given in parentheses. χ^2 goodness-of-fit tests were performed to test the null hypothesis that the age distribution of weanling mounters reflected the relative proportions of male age classes present. ¹no information available.

males, and $80\% \pm 12\%$ for 4 adults. SA3 and SA4 weanling mounters in 1988 spent the same amount of time in harem areas as their non-weanling mounter counterparts (Mann-Whitney U-test, t-test approx.: SA3 - $N_1 = 9$, $N_2 = 20$, $U = 91.0$, $p > 0.20$; SA4 - $N_1 = 8$, $N_2 = 20$, $U = 104.0$, $p > 0.10$). Although the sample sizes for SA2 and adult males were too small to perform statistical comparisons, their percent time near harems was in the general range of males of the same age class (DEUTSCH, 1990).

Males that mounted weanlings were usually unsuccessful in copulating with adult females. Of 21 weanling mounters that were marked before the peak estrous period in 1988, five (24%) were observed to copulate successfully with at least one estrous female: 0 of 1 SA2 males, 1 of 8 SA3 males, 1 of 8 SA4 males, and 3 of 4 adults. Again, the sample sizes for SA2 and adult males were too small for comparison, but the copulatory success of SA3 and SA4 weanling mounters was not significantly different from that of non-weanling mounters of the same age classes (Fisher's Exact test: SA3 - $N_1 = 8$, $N_2 = 20$, $p = 0.42$; SA4 - $N_1 = 8$, $N_2 = 20$, $p = 0.26$).

Mount duration did not vary significantly among male age classes (Kruskal-Wallis Test, $H = 3.05$, $df = 3$, $p = 0.39$). Interactions between males and weanlings lasted 90 ± 99 sec (median = 60 sec) for 7 SA2 mounts, 197 ± 391 sec (median = 60 sec) for 44 SA3 mounts, 167 ± 159 sec (median = 120 sec) for 24 SA4 mounts, and 80 ± 49 sec (median = 60 sec) for 6 adult mounts. All five mounts that exceeded 10 minutes in duration were by SA3 males.

In 1988, 20 (69%) of the 29 males that mounted weanlings were observed to do so only once. Seven males (24%) mounted weanlings two or three times. These data must be interpreted with caution because it is likely that only a small proportion of the actual number of mounting episodes was observed, due to several factors: the brief duration of most mounts; the fact that observations typically lasted only 5 to 6 hr per day; and the large area over which males and weanlings were distributed. Nevertheless, one SA4 male named "Bank7" exhibited exceptional behavior, mounting weanlings at least 15 times over a 33-day period! His mounting attempts were persistent, incorporating all of the typical female-mounting behaviors (see above), including penile extrusion and pelvic thrusts in an attempt to copulate. This male returned to the rookery in 1989 and was again observed mounting weanlings, as well as departing females and non-estrous females returning to the rookery to molt at the end of the breeding season. Bank7 lost his tag during the 1989

summer molt and so we do not know if he returned to the rookery in 1990. There were no reports of an unusually persistent weanling mounter during the 1990 breeding season.

Characteristics of mounted weanlings.

Sixty-two percent (24/39) of the mounted weanlings were of medium size (estimated mass of 100-145 kg). Small and large weanlings were mounted less frequently (18% and 20%, respectively). This size distribution was no different from the expected size distribution based on known-mass weanlings ($\chi^2 = 1.421$, $df = 2$, $p = 0.504$), indicating that the probability of a weanling being mounted was independent of its size. Sixty percent (31/52) of mounted weanlings had completely molted their black natal pelage. Only 15% of those mounted were less than half molted.

A cumulative total of 2080 weanlings (50.3% male, 49.7% female) was sexed and examined for evidence of having been mounted during February and March in 1990. Nineteen percent (74/391) of the sample showed evidence of having been mounted; of these mounted weanlings, 52.2% were male and 47.8% were female, a nonsignificant sex difference ($\chi^2 = 0.685$, $df = 1$, $p = 0.58$).

Discussion

The relatively high incidence of male elephant seals mounting weanlings seems best explained at the proximate level by a combination of factors. Strong libido, coupled with sexual inexperience and limited access to estrous females, stimulate males to generalize their sexual response from adult estrous females to weanlings. This statement is supported by a number of observations. Males that mounted weanlings had an apparently strong urge to mate, as evidenced by their presence in and around harems during the breeding season and by the resemblance of their weanling mounting behavior to male sexual behavior directed to estrous females. Males that mounted weanlings were sexually inexperienced; very few weanling mounters were observed copulating with estrous females. The age category of males with the highest incidence of mounting weanlings was six-year-old subadults (SA3), males that rarely succeed in copulating with females (LE BOEUF, 1974; LE BOEUF & REITER, 1988). Most males on the rookery, but especially the younger and less dominant ones, had limited access to estrous females throughout the breeding season because of the power structure in harems. At the end

of the breeding season, it was even more difficult for the subordinate males to approach females because of the latter's diminishing numbers. These circumstances led to a shift of male attention to the increasingly numerous weaned pups. Some males directed sexual responses to weanlings that they usually directed to adult females. That is, males exhibited stimulus generalization (HOVLAND, 1937), responding sexually to a stimulus that resembles the appropriate one. When sexual drive is high, the gradient of stimulus generalization is increased (MEDNICK & FREEDMAN, 1960). In other words, when libido is high, the less the generalized stimulus need resemble the standard (see also BAERENDS *et al.*, 1955; EIBL-EIBESFELDT, 1970).

It is not surprising that weanlings were treated as "female substitutes" because at this age, both sexes bear a remarkable resemblance to adult females in the shape of the body and the head. The differences between adult females and weanlings are graded; weanlings are on average one-third to one-half the size of adult females and have a silver coat instead of the tan to brown coat of breeding adults. Consistent with the above logic is the fact that males did not discriminate between the sexes when mounting weanlings and most mounted weanlings had lost the black natal pelage. Most weanling mounts were brief and desultory and most males were observed to mount only one weanling. These observations suggest that males learned quickly that the stimulus was inappropriate. However, males may not actually be mistaking weanlings for females; subadult males are known to mount peers during bouts of play-fighting (DEUTSCH, 1990), clearly not a case of mistaken identity. It could simply be that males are stimulated by this abundant female-like object, but with habituation, they cease to respond.

Further evidence for stimulus generalization comes from the observation that males appeared to mount the longer and larger (and hence, more adult-like) two-year-olds more readily than weanlings, even though the latter were far more abundant. This logic suggests that males should have preferentially mounted large weanlings, but weanlings were mounted independent of their size. This may have been because differences in size among weanlings were minor compared to differences between weanlings and females or between weanlings and juveniles. Thus, it appears that sexually motivated but inexperienced young males approached and mounted weanlings frequently, because they were the most abundant and accessible female-like stimulus at the end of the breeding season.

At the functional level, weanling mounting may benefit males if such

indiscriminate mounting behavior is occasionally reinforced by a copulation with an ovulating female. Approximately one-third of the females at Año Nuevo give birth for the first time at age three, meaning that these females were inseminated as virgin two-year-olds the previous year (LE BOEUF & REITER, 1988). There are also two records of females giving birth for the first time at age two, once in 1976 and again in 1991 (LE BOEUF & REITER, 1988; J. REITER, pers. comm.). Therefore, selection for indiscriminate mounting of female-like objects may occasionally enhance a male's reproductive success. There should be little if any selection against the behavior, as costs to weanling mounters are probably negligible (see also ROBINSON, 1988). Less than a quarter of the mounting attempts resulted in agonistic interactions with another male, none of which were observed to escalate into actual fights. Mounters are not likely to be closely related to their victims; regardless of relatedness, severe injuries to weanlings were rare and deaths even rarer. Thus, the fitness of males is not likely to be adversely affected by weanling mounting.

Other investigators have suggested that males may gain practice and experience from mounting juveniles, improving their ability to control and inseminate females later in life. CAMPAGNA *et al.* (1988) made this argument for southern sea lions, *Otaria byronia*, where adult males sequester females and subadult males abduct, sequester, and mount dependent pups. ROBINSON (1988) suggested that subadult male yellow-rumped caciques, *Cacicus cela*, which chase and mount fledglings, may gain conditioning benefits and practice in consorting with and defending females as adults. However, given the lack of persistence of weanling mounting attempts, it does not seem likely that elephant seal males gain much sexual experience.

What are the consequences for weanlings of being mounted by males? The worst case is that some weanlings are killed during these sexual encounters, just as adult females are sometimes killed during aggressive mating attempts outside of the harem (LE BOEUF & MESNICK, 1991). Direct and circumstantial evidence leads to the conclusion that the aggressive sexual behavior of males is the principal cause of death of weanlings during the 2.5-month period on the rookery between weaning and going to sea, although heat stress and disease are other possible explanations. Unfortunately, assigning cause of death and estimating its incidence in nature is difficult. In our judgement, the maximum weanling mortality due to males was about 1 in 200 and the minimum was approximately 1 in 600.

A mortality risk of approximately 0.5% may result in significant selection pressure for behaviors that minimize that risk (ENDLER, 1986; LE BOEUF & MESNICK, 1991; MESNICK & LE BOEUF, 1991). Observations show that weanlings may employ strategies that have the effect of reducing the incidence of male mounts. Aggregating into pods may decrease the probability of male harassment to individuals, as appears to be the case for females (LE BOEUF, 1972; TRILLMICH & TRILLMICH, 1984), although weanlings form groups in the absence of males for other possible reasons, such as thermoregulation. In addition, through mid-March, weanlings are frequently observed on the tops of high dunes or deep within willow clumps, areas relatively inaccessible to bulls. Lastly, weanlings resist mounts vigorously by trying to get away and vocalizing loudly. As is the case when a female is mounted, loud resistance attracts the attention of other males (COX & LE BOEUF, 1977) who may displace the mounter, sometimes giving the mountee an opportunity to escape.

Reports of males injuring, abusing, and killing conspecific young have been described in a variety of contexts in various species of mammals. Males use infants as shields in aggressive encounters with other males and as "passports" to gain access to resources (*e.g.* non-human primates: HRDY, 1976; PACKER, 1980; STRUM, 1984). They redirect aggressive behaviors intended for male competitors toward neonates (*e.g.* Australian sea lions, *Neophoca cinerea*: HIGGINS & TEDMAN, 1990) and kill non-related infants in order to hasten the estrous cycle of females (*e.g.* non-human primates: HRDY, 1974; STRUHSAKER & LELAND, 1987; lions, *Felis leo*: PACKER & PUSEY, 1983) or exploit young as food (*e.g.* chimpanzees, *Pan troglodytes*; NISHIDA & HIRAIWA-HASEGAWA, 1987; ground squirrels, *Spermophilus beldingi*: SHERMAN, 1981). Males also abduct and sequester young as female substitutes when denied access to reproductive females (*e.g.* hamadryas baboons, *Papio hamadryas*: KUMMER, 1968; southern sea lions, *Otaria byronia*: CAMPAGNA *et al.*, 1988) and in general may direct sexual behavior toward young conspecifics (*e.g.* humans, *Homo sapiens*: COOK & HOWELLS, 1981; DALY & WILSON, 1981; New Zealand sea lions, *Phocarctos hookeri*: MARLOW, 1975; southern elephant seal, *Mirounga leonina*: CARRICK *et al.*, 1962; mountain sheep, *Ovis canadensis* and *O. dalli*: GEIST, 1971; Hawaiian monk seals, *Monachus schauinslandi*: ALCORN, 1984; C. J. DEUTSCH, pers. obs.; yellow-rumped caciques, *Cacicus cela*: ROBINSON, 1988). All interactions between sexually mature males and weanlings in the northern elephant seal fall into the final category of mating attempts. We conclude that the weanling mounting phenomenon in this species is a by-product of selection for high sexual motivation among sexually inexperienced males.

Summary

1. Up to 50% of weaned northern elephant seal pups, *Mirounga angustirostris*, present on the Año Nuevo mainland rookery at the end of the breeding season showed evidence (tooth marks and injuries on the neck) of having been mounted by males.

2. Male-inflicted injuries on weanlings ranged from superficial tooth marks to deep gashes and punctures that bled and exposed the blubber. Most marks were superficial.

3. Approximately 0.5% of all weaned pups died on the rookery from 1969-1990; about 35% of the dead weanlings showed physical evidence that they were killed by males and males were suspected of having killed most of the rest.

4. Males mounting weanlings displayed many behaviors that are characteristic of male sexual behavior toward adult females and most weanlings responded like non-estrous females. Weanling mounts lasted an average of 2.8 min (N = 81) and were usually terminated when the male did not pursue an escaping weanling. There was no bias in the sex or the size of mounted weanlings.

5. Males also mounted conspecific juveniles (one and two years old), although these interactions were relatively infrequent because most juveniles were at sea during the breeding season. The behavior of males and juveniles during mounting attempts was qualitatively similar to weanling mounts; rarely, yearlings were killed by males.

6. Most mounters (91%) were subadult males and were observed to mount weanlings only once in a breeding season. Occasionally, a male persisted in mounting weanlings repeatedly, within a season and across years. Weanling mounters did not differ from other males in their proximity to harems or in their copulatory success.

7. The proximate factors leading to weanling mounts appear to be male sexual inexperience, high libido, limited access to adult females, and stimulus generalization. Functionally, male sexual behavior toward weanlings appears to be a low-cost by-product of high male sexual motivation that may enhance a male's reproductive success. Weanlings exhibit behaviors, such as grouping into pods, seeking microhabitat refuges, and resisting mounts, that may reduce the chance of being mounted by a male or of being injured during a mounting attempt.

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