Functions of female aggression during the pupping and mating season of grey seals, *Halichoerus grypus* (Fabricius)

DARYL J. BONESS
Department of Mammalogy, National Zoological Park, Smithsonian Institution, Washington, DC, U.S.A. 20008
SHEILA S. ANDERSON
Sea Mammal Research Unit, Natural Environment Research Council, British Antarctic Survey, Madingley Road, Cambridge, England CB3 OET
AND
CATHLEEN R. COX
Los Angeles Zoo, Los Angeles, CA, U.S.A. 90007
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Aggression of female grey seals *Halichoerus grypus* toward conspecifics was studied during the pupping and mating season on Sable Island, N.S. The responses of 65 individually identified females with pups toward known males and females were recorded throughout each female's stage of lactation. Female aggression varied both quantitatively and qualitatively as a function of the sex of an approaching animal. Males were threatened more often than females even though females outnumbered males. The likelihood of females threatening other females was affected by the location of the threatening female's pup, but aggression towards males was not affected by the pup's position. Females responded aggressively less often in the second half of lactation, when both weaning of the pup and oestrus occur, than in the first half. They were also more likely to threaten transient males than tenured males. However, a male approaching or mounting a female, whatever his status, was more likely to be challenged by another male if the female threatened him than if she did not. These challenges generally interrupted a male's approach or mount and hence a potential copulation. The results are consistent with the hypothesis that female aggression during the lactation period helps to protect the pup and increases the likelihood that a female mates with a dominant male. This latter function may be viewed as a form of mate choice.

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L'aggressivité des femelles du phoque gris *Halichoerus grypus* à l'égard des autres phoques de la même espèce a été étudiée durant la saison des amours et l'époque d'élevage des petits, à Sable Island en Nouvelle-Ecosse. La réaction de 65 femelles avec des petits à l'égard de mâles et de femelles reconnaissables a été enregistrée durant la phase de lactation de chacune d'elles. L'aggressivité des femelles varie quantitativement et qualitativement en fonction du sexe de l'intrus. Les mâles sont menacés plus souvent que les femelles, même si les femelles sont plus nombreuses. La probabilité qu'une femelle menace d'autres femelles est affectée par la proximité de son petit, mais l'agressivité envers les mâles n'est pas affectée par la position du petit. Les femelles sont agressives moins souvent durant la seconde moitié de la lactation, au moment du sevrage et de l'oestrus. Elles sont également plus susceptibles de menacer des mâles de passage que des mâles résidants. Cependant, un mâle qui s'approche de la femelle ou la saillit, quel que soit son statut, est plus susceptible d'être défié par un autre mâle lorsque le femelle est agressive que lorsqu'elle ne l'est pas. Ces défis interrompent généralement l'approche d'un mâle ou sa saillie et coupent donc court à la copulation. Il semble donc vrai que l'agressivité de la femelle au cours de la lactation l'aide à protéger son petit et contribue à augmenter ses chances d'accouplement avec un mâle dominant. Il s'agirait donc en quelque sorte d'une forme de choix d'un partenaire.

[Traduit par le journal]

Introduction

Females of several pinniped species are known to be aggressive toward conspecific males and females during the breeding season (Hewer 1957; Peterson and Bartholomew 1967; Sandegren 1970; Miller 1971; Christenson and Le Boeuf 1978). Aggressive behavior is pronounced following parturition and has intuitively been regarded as defense of the young; indeed, Christenson and Le Boeuf (1978) have provided empirical support for this hypothesis in a study of the northern elephant seal *Mirounga angustirostris*.

In most pinniped species however, females, in addition to caring for their young during the breeding season, also mate before the young are weaned. Anderson *et al.* (1975) suggested that the strong aggressive behavior of grey seal cows who are accompanying pups is part of a mechanism which ensures that cows mate with the fittest males possible. They do not elaborate on the nature of

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this mechanism other than to say that "...in order to mate, a bull requires a strong sexual drive, coupled with the security which a defended position in the breeding group offers" (Anderson *et al.* 1975, p. 190). Cox and Le Boeuf (1977), studying northern elephant seals, also argued that female aggression operates to enhance the likelihood of mating with a dominant male. Their evidence suggests that the mechanism by which this is done is through inciting competition between males. They reported that females respond aggressively to most approaches by males and that this activity usually evokes a threat response from a nearby dominant male. The aggressive reaction from the nearby dominant male frequently prevents a lower ranking male from completing a copulation. Previous studies had shown that the highest ranking males account for most copulations (Le Boeuf and Peterson 1969) and that activity leading to copulation by these males is frequently triggered by the activities of subordinate males (James 1970).

Aggression by female grey seals occurs under contexts similar to those reported for northern elephant seals (Boness and James 1979). Grey seal females might therefore incite competition between males too. However, since pups are still with their mothers at mating time and female aggression may well serve to protect pups from other animals, one must take into account the possible effects of pup protection when examining the possibility of incitation of male competition. We did this by observing female aggression towards both approaching males and females. If female aggressive behavior served only to protect pups, one might expect no difference in aggression towards males and females or greater aggressiveness towards females since they appear to be more likely than males to bite or injure another's pup. If, on the other hand, female aggression served just to incite males or served both functions, predictable differences in the females' responses toward each sex would be found. The specific predictions will be described in each section of the results.

Methods

Grey seals breeding on Sable Island, N.S., were observed continuously during daylight hours from 2 to 17 January, 1977. This period covers the first half of the breeding season; within 1 or 2 days of the 17th, the number of females present begins to decline rapidly. Observations were made from hides overlooking an area of approximately 1500 m^2 between Long Dune and Steeple Dune. This area is described in detail by Boness and James (1979) and corresponds to part of areas A and D in their Fig. 1. All individuals in the study area were identified either by brand marks (applied in previous seasons by employees of Fisheries and Marine Service, Environment Canada) or by distinctive variations in hair coloration or scars. The stage of lactation and the proximity to oestrus of each female was either known directly, because her pup's birth was observed, or could be estimated from the pup's size and development. Males were divided into two categories as described by Boness (1979) according to their length of stay; those present in the study area for less than 2 consecutive days were described as "transient" males, whereas those seen on 2 or more consecutive days were considered "tenured" males. Data were collected from a total of 65 known females and 35 known males. To determine the identity of each female's nearest male neighbor, we scanned the study area at hourly intervals and noted which male was the closest to each female. These observations were collated at the end of each day, and for each female the male which had been recorded most frequently was called her nearest neighbor for that day. If two males were recorded an equal number of times, both males were considered nearest male neighbors to that female.

Female aggression was identified by the occurrence of one or more of the following behavioral items: (1) an open mouth threat (see Fig. 1 in Miller and Boness 1979), (2) a rapid up-and-down movement of a foreflipper (flippering), (3) a wailing vocalization, (4) an abrupt move towards the approaching animal, (5) a swift extension of the neck and head toward the approaching animal (lunge), and (6) biting.

Aggressive behavior was sampled in the following manner: two to four observers scanned subsections of the study area for instances of males or females moving towards a known female who was clearly aware of the approaching animal. Instances involving females who were, in the observers' opinion, asleep or distracted by other events were not included. The identities of both individuals involved in a potential encounter were recorded, and the set of data collected was based on the female's response and the sex of the approaching animal. For all encounters, several variables were recorded: the distance between the approaching animal and both the female and her pup, the position of the pup relative to the female and the approaching animal, and the outcome of the encounter. If the female responded aggressively to the approaching animal, other observations recorded included the components of the aggressive response, the duration of the response, and whether the response was constant or intermittent. If the animal approaching was a male and he mounted the female, the duration of the female's aggressive response while being mounted and the total time from the beginning of mounting to intromission or termination of the mount (whichever occurred first) were also recorded. Distances between animals were estimated by comparison with the known lengths of adults and pups (Mansfield and Beck 1977).

The frequency of female aggressive encounters was sampled during 26 observation periods, each 0.5 h, made between 11 and 17 January, 1977. Between one and five samples were obtained on each of these days, with a minimum of 1.5 h between sampling periods on any one day. For all instances of female aggression in the study area, we recorded the identity of the participant and whether or not the aggression was provoked by the approach of another animal. The number of females present at the start and at the end of the 0.5-h sampling period was noted. Not all aggressive interactions have a discrete beginning and ending, so when two animals which had been threatening one another put their heads down briefly before starting again only one threat bout was counted. If, on the other

TABLE 1. Frequency of female threats which were spontaneous or were provoked by an approaching animal. Figures represent threats per female per hour ± SE and the number of observations (in parentheses)

	Provoked by an approaching animal	Unprovoked	Total
Encounters between two females	0.22±0.03[a] (85)	0.09±0.02[a] (36)	0.31±0.04[b] (121)
Encounters between a female and a male	1.78±0.03[c] (659)	0.37±0.04[c] (137)	2.15±0.13[b] (796)
Total	2.00±0.13[d] (744)	0.46±0.03[d] (173)	2.46±0.07 (917)

[a] $t = 4.06$, df = 25, $p < 0.001$.
[b] $t = 14.17$, df = 25, $p < 0.001$.
[c] $t = 10.96$, df = 25, $p < 0.001$.
[d] $t = 40.55$, df = 25, $p < 0.001$.

hand, one animal moved away from a threat and then returned to threaten again, two bouts were counted.

Statistical analyses included standard t-tests and χ^2 tests. However, for testing the equality between two proportions we used the test recommended by Sokal and Rohlf (1969, p. 608). In this test the data are subjected to an arcsine transformation before a t-test is done.

Results

Components of female aggression

Frequency of aggressive encounters

Not all aggression by females is triggered directly by the approach of another animal. To determine how frequently female aggression occurs and to determine what proportion of aggression was being sampled by recording only those encounters arising from approaches by other animals, we counted the number of interactions during the 0.5-h periods as described above. Table 1 summarizes the results of these observations. The overall frequency of aggression by females was 2.46 encounters per female per hour. Females threatened one another much less than they threatened males, even though there were more females than males ($\bar{X}$ sex ratio = 2.0 ± 0.08). Table 1 shows that aggression provoked by an approaching animal occurred significantly more frequently than that which was unprovoked, for both female–female and female–male encounters. Given that about 80% of the 917 observed threat encounters were ones in which females responded to the approach of another animal, it would appear that by selecting this type of interaction we still account for a large proportion of female aggressive behavior.

Distance between interacting animals

Female aggression was more likely to occur the closer a male or female was to the female it was approaching, although males tended to be threatened over greater distances than females (Table 2). The mean distance at which a female first showed aggression, however, was similar for both males and females. Also, the distance between the approaching animal and the cow's pup when she began to threaten was the same whether the approaching animal was female or male ($\bar{X}$ = 1.63 vs. 1.83; $t = 1.43$, df = 496, $p > 0.05$).

TABLE 2. Proportion of observations in which approaching animals were threatened as a function of how far they were from the female being approached. The numbers in parentheses refer to the number of observations

Sex of approaching animal	Distance class (m) 0–1	1–2	2–3	3–4	>4	χ^2	$p <$
Female[a]	0.65 (55)	0.59 (80)	0.40 (70)	0.46 (24)	0.33 (12)	12.0	0.025
Male[b]	0.88 (177)	0.85 (301)	0.71 (221)	0.49 (76)	0.30 (37)	106.5	0.001

[a] Mean distance, 1.3 ± 0.08.
[b] Mean distance, 1.4 ± 0.04.

Duration of encounters

A single aggressive interaction may include the use of more than one of the behaviors listed in the Methods section. In spite of this, aggressive bouts tended to be brief, regardless of the sex of the approaching animal. The median duration of an interaction was 15 s. Threats typically ended when the approaching animal moved away. However, sometimes an animal stopped approaching and the approached animal terminated her threat.

Factors affecting the likelihood of aggression towards an approaching animal

Relative position of pup

Insofar as female aggression serves to protect pups, one would expect the likelihood of its occurrence to be affected by the position of the pup relative to the

positions of the approaching animal and the pup's mother. To examine this, the aggressive bouts were divided into three groups: those in which the pup was between the approaching animal and its mother, those in which the pup was to the side of its mother, and those in which the pup's mother was between it and the approaching animal.

When the approaching animal was a female, the occurrence of aggression was related to the position of the pup ($\chi^2 = 7.19$, df = 2, $p < 0.05$), The relationship is as one would expect; the likelihood of aggression was greatest when the pup was between the approaching female and its mother and was least when the mother was between her pup and the other female (Fig. 1). In contrast to these results, when the approaching animal was a male, there was no significant relationship between a pup's position and aggression by the female ($\chi^2 = 4.93$, df = 2, $p < 0.10$). Males tended to be threatened regardless of the relative position of the pup.

Stage of lactation

As lactation proceeds, female grey seals approach both weaning and oestrus. The average weaning date of Sable Island grey seals is 17 days after parturition, and the first observed copulation occurs 2 days earlier (Boness and James 1979). To determine whether female aggression changes as oestrus approaches, we divided the maximum observed lactation period of 20 days in half and recorded the proportion of interactions in which females responded aggressively toward the approaching or mounting animals (Table 3). For male approaches only, there was no difference in the relative frequency of aggression between the two halves of the lactation period. In contrast, aggression toward approaching females and toward males who succeeded in mounting females decreased in the second half of the period.

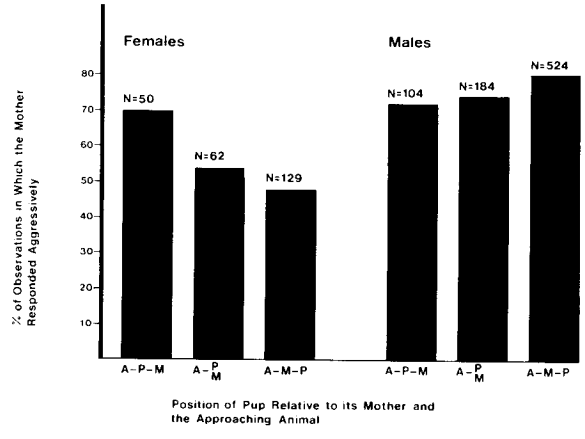

FIG. 1. The effect of a pup's position (P) relative to its mother's (M) on the likelihood of the mother threatening an approaching animal(A).

TABLE 3. The relationship of relative frequency of female aggression to stage of lactation, as a function of the approaching animal's sex. The values indicate proportions and total number of observations (in parentheses)

	Days after parturition			
	0–9	10–19	t_s	$p <$
Male approach	0.76 (403)	0.78 (483)	1.02	ns
Male mount	1.00 (26)	0.85 (162)	3.74	0.001
Female approach	0.58 (149)	0.45 (106)	1.94	0.05

Status of males

On Sable Island most female grey seals copulate with the tenured male that is nearest to them when they come into oestrus (Boness and James 1979). Some females copulate with tenured males that are not their nearest male neighbor and a few females copulate with transient males. With this in mind, we examined whether or not a female was less likely to respond aggressively toward her nearest tenured male than toward one with which she might be less familiar or toward a transient.

When approaches and mounts are considered separately, the relationship between male status and the likelihood of an aggressive response by a female is not clear (Table 4). For approaches, nearest tenured males were threatened less often by females than were other tenured males and transient males, but the difference between the nearest tenured male and a transient male was not significant. In contrast, for males mounting females, both nearest tenured males and other tenured

TABLE 4. The proportion and number of observations (in parentheses) in which females responded aggressively toward approaching or mounting males as a function of male status

	Approaches	Mounts
Nearest tenured male	0.75^a (462)	0.82^b (82)
Other tenured males	0.82^a (321)	0.74^c (81)
Transient males	0.79 (135)	$1.0^{b,c}$ (22)

NOTE: Comparisons unless indicated were not significantly different.

[a] $t_s = 2.35$, $p < 0.02$.
[b] $t_s = 3.65$, $p < 0.001$.
[c] $t_s = 4.46$, $p < 0.001$.

males were significantly less likely to be threatened by the females they mounted than were transient males. There was, however, no difference between the two groups of tenured males in the likelihood of being threatened.

Tenured males tend to be more vigilant when females in the area are in oestrus, and tenured males prevent transients from approaching or mounting oestrous females (Appendix C of Boness 1979). It is, therefore, possible that proportionately more transient male than tenured male observations occurred when females were in early stages of lactation, which is also when females are more likely to be aggressive (see Table 3). The relationship between the status of mounting males and the occurrence of female aggression, shown in Table 4, could therefore be spurious. To eliminate this possible bias, we examined the likelihood of aggression as a function of male status, using only those observations in which the female involved was copulating or had already copulated ($N = 219$). The results of this analysis revealed that nearest tenured males were indeed the least likely to be responded to aggressively by oestrous females ($\chi^2 = 11.71$, df = 2, $p < 0.005$).

Effects of female aggression

A direct outcome of aggression by females was to increase the distance between the approaching animal and both the female and her pup (Table 5). The data for males and females were combined in Table 5 because the results were the same regardless of the sex of the approaching animal. When a female responded aggressively towards an animal, the distance between the approaching animal and both herself and her pup usually increased. On the other hand, when the female did not respond aggressively, there tended to be no increase in either of these distances.

TABLE 5. The relationship of distance between an approaching animal and a female and her pup to female aggression. The values represent proportions and number of observations (in parentheses)

Distance between approaching animal and:	Female threatened	Female did not threaten
Female increased but pup did not increase	0.05 (26)	0.01 (2)
Female did not increase but pup increased	0.05 (26)	0.01 (2)
Female and pup increased	0.70 (381)	0.08 (25)
Female and pup did not increase	0.20 (109)	0.90 (263)
Total	1.00 (542)	1.00 (292)

In nearly one-third (244 of 865 observations) of the aggressive interactions between a female and a male, a second male entered the interaction by threatening the first. However, in female–female threat bouts, males virtually never became involved. This contrasts with otariid males which frequently interrupt female interactions (e.g., *Arctocephalus forsteri*, Miller 1974; *Eumetopias jubatus*, Gisiner 1977; *Zalophus californianus*, D. J. Boness, unpublished observations).

To assess further this apparent effect of female aggression on the behavior of males, we examined the occurrence of males challenging other males as a function of whether or not a female responded aggressively toward the approaching or mounting male and as a function of the status of the approaching male (Table 6). For all classes of males, the proportion of approaches and mounts that were challenged by another male was significantly greater when the female responded aggressively than when she did not. This supports the hypothesis that the female's aggressive behavior is indeed affecting that of the males. It may also be seen from Table 6 that transient males were more likely to be challenged by another male than were tenured males. This is true whether or not a female responded aggressively. However, if one subtracts the proportion of challenges that occurred despite the lack of a female threat from the proportion of challenges that occurred when the female threatened the approaching animal, challenges of transient males are still proportionately greater than are those of nearest tenured males or other tenured males (0.32 vs. 0.12 vs. 0.14, respectively). This suggests that the relationship of male challenges to male status is, at least in part, a result of female aggression.

Most approaches by males and mounts that were challenged by other males were interrupted (84.7% of

TABLE 6. Proportion of observations in which either an approaching or mounting male was challenged by another male as a function of the status of the first male. The total number of observations is given in parentheses

	Female responded aggressively	Female did not respond aggressively
Nearest tenured male	0.14 (412)	0.02 (132)
Other tenured male	0.33 (324)	0.19 (78)
Transient male	0.64 (129)	0.32 (28)

NOTE: The combined effects of female aggression and male status on the probability of challenges occurring was tested statistically using sets of 2 × 2 contingency tables in which the data were transformed to a logit scale (pp. 253–256 in Snedecor and Cochran 1967). The results are significant ($z = 5.245$, $p < 0.001$).

274 observations); that is, males approaching females backed off and males which were mounting females dismounted and did not succeed in copulating at that time. Whether or not a challenged male was interrupted, however, depended on the status of the male; nearest tenured males were interrupted least often and transient males were interrupted most often (67%, $N = 60$ vs. 96%, $N = 93$; $t_s = 5.26$, $p < 0.001$). Other tenured males were interrupted significantly more often than nearest tenured males (84%, $N = 121$; $t_s = 3.05$, $p < 0.01$) but less often than transients. Aggressive reactions to both approaches and mounts therefore had a greater effect (in terms of interrupting potential copulations) on transient males than they did on tenured males.

Discussion

The evidence presented here is generally consistent with the hypothesis that female aggression serves both to protect pups and to increase the likelihood of mating with a dominant male by inciting male competition. The female's aggressive behavior towards males differed from that displayed towards females. Protection of pups is inferred from the fact that a female is more likely to threaten an approaching female if her pup is between her and the approaching female than if it is not (see Fig. 1). One might also expect the need for maternal protection to diminish as the pup becomes more viable and approaches independence at weaning. Aggression toward approaching females and mounting males did diminish in the second half of lactation. This latter result, however, is not free of ambiguity since there was no effect of stage of lactation on male approaches. Cox and Le Boeuf (1977) found a similar reduction in aggressiveness associated with the approach of weaning, but they argued that this simply reflects the increased "receptivity" of the female as she comes into oestrus. This study does not allow us to distinguish between these two explanations.

The evidence suggesting that female aggression on Sable Island serves to maximize the likelihood of mating with a fit male by inciting male competition is straight forward. In contrast to the effect of pup position on aggression between two females, females respond aggressively towards males regardless of the position of their pups (see Fig. 1). Transient males are more likely to be threatened than tenured males when they are trying to mount females (see Table 4). A male approaching or mounting a female is more likely to be challenged by another male if the female responds aggressively than if she does not (see Table 6). Transient males are more likely to be challenged as a result of the female's aggressive response than are tenured males. Even though this latter result would occur as a natural consequence of the typical social organization of grey seal males (Boness and James 1979), when one controls for the effect of male organization by subtracting the proportion of challenges occurring without female aggression from those which did involve aggression, transient males are still more likely to be challenged than tenured males. Furthermore, as shown in earlier work (Boness and James 1979), the net result of challenges is that the precopulatory behavior of transient males is more likely to be interrupted than is that of tenured males.

The existence of an increased postpartum aggression has been documented in a variety of mammalian species (Bartholomew 1952; King 1958; Ross *et al.* 1963; Wilson and Boelkins 1970; Gandelman 1972), but most of the work has been aimed at understanding the proximate mechanisms, not the adaptive value, of it. Wilson and Boelkins (1970) do report a general relationship between the occurrence of injuries and deaths and the birth season in *Macaca mulatta*. Christenson and Le Boeuf (1978), in a study of northern elephant seals, found a negative correlation between female aggressiveness and the number of times a pup was bitten by alien females. Although they were unable to show a negative correlation between mortality and aggression, a previous study (Le Boeuf and Briggs 1977) showed that one of the major causes of death in northern elephant seal pups is bite wounds.

It should, nonetheless, be pointed out here that the incidence of grey seal pups being bitten by alien females is markedly less than in elephant seals. Mortality induced by males trampling pups during male–male aggression is also not of the same magnitude in grey seals as it is in elephant seals (cf. Anderson *et al.* 1979 and Le Boeuf and Briggs 1977). Pup protection may therefore be less crucial in grey seals than in elephant seals.

Incitation of male competition by females appears to be a mechanism of female choice, whereby the female enhances the fitness of her male offspring as well as her inclusive fitness by mating with the fittest male available. Darwin (1871) first proposed the hypothesis that females have peferences for males with certain traits. He argued that choosing mates created a strong selection pressure favoring those traits of males being chosen by females. Darwin did not, however, consider the advantages of mate choice to the female. It was Fisher (1930) who subsequently argued that females who mate with males which have "attractive" traits to females in general will produce attractive sons insofar as the traits are heritable. McLaren (1967), in proposing an hypothesis to explain the adaptive significance of female gregariousness, was first to suggest that mate choice operates in this fashion in pinnipeds.

A crucial assumption in this argument is that the fitness of males is heritable. This assumption has been questioned recently (Williams 1975; Maynard Smith

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