ACTIVITY BUDGET OF MALE GRAY SEALS, *HALICHOERUS GRYPUS*

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ABSTRACT.—Breeding activity budgets of male gray seals were estimated to determine how they are fine tuned to changing demands and to determine whether or not the limited body reserves produced by fasting act to minimize energetically demanding activities. Behaviors were divided into nonsocial and social activities with each category including both active and inactive behaviors. The overall frequency of social behavior did not change throughout a male's tenure but aggressive behavior decreased while sexual behavior increased. Even though resting accounted for the greatest proportion of activity, males that were most active had the greatest copulatory success, suggesting that fasting does not place severe limitations on their activity levels.

Activity budgets should reflect a balance between the costs and benefits of expending energy. A general characteristic of male pinnipeds is that they fast during the breeding season (Bartholomew, 1952; Laws, 1956; Peterson, 1965; Peterson and Bartholomew, 1967; Gentry, 1970; Miller, 1975; Boness and James, 1979), building up fat reserves before the season begins (Schusterman and Gentry, 1971). Many pinnipeds are polygynous and males must compete for access to females; this activity requires expending energy on aggressive as well as sexual activity.

It has been argued that if males can enhance their reproductive success by increasing their length of stay at the breeding grounds, the fixed energy supply produced by fasting should act as a strong selective force to minimize energy demanding activities (Sandegren, 1976*a*). Gray seals, *Halichoerus grypus*, fast during the breeding period, are polygynous, and the longer a male remains on the breeding grounds the greater the number of females he mates (Anderson et al., 1975; Boness and James, 1979). This species therefore provides an excellent opportunity to examine the above prediction.

METHODS

This study was conducted on Sable Island (45°55′N, 60°00′W), a vegetated sand bar located about 288 km ESE Halifax, Nova Scotia. The island is approximately 35 km long and 1.5 km wide and serves as traditional breeding grounds for harbor seals, *Phoca vitulina*, in spring (Boulva and McLaren, 1979) and for gray seals in winter (Mansfield, 1967; Mansfield and Beck, 1977). The major breeding concentration of gray seals is on the east spit of the island, where females give birth between the last week of December and the last week of January (Boness, 1979). Females nurse their pups for 17 days and come into estrus 15 days postpartum, just before weaning their pups. Males arrive at Sable Island in synchrony with the females, the larger, older males taking up positions amongst females. These males, called tenured males, may defend positions for as long as 30 days continuously (Boness and James, 1979; Miller and Boness, 1979). The study site consisted of a 3,132-m^2 area located between two dunes on the east end of the island (fig. 1 in Boness and James, 1979). Daily observations were made between 30 December and 28 January 1976, covering most of the breeding season. During each of four sampling periods (0900, 1130, 1330, 1530 h), up to seven males were scanned in sequence, from an observation blind 10–30 m away. The behavior of each male as he was scanned [scan sampling according to Altmann (1974)] was recorded. Forty-five scans were made during a sampling period. The time to complete one scan took approximately 25 s so each sampling period lasted about 20 min. Individual males were identified by natural pelage markings, and scars made from intraspecific aggression or shark attacks. Once a male was chosen to be sampled, he was observed for the duration of his tenure in the study area. Three males established in the study area when sampling started on 30 December were used, and each newly established male was included until seven males were being sampled. From that point on, when one of these males departed for the season, the most recent male to have arrived in the study area was added to the sample. In this way the activity budgets of 11 males were obtained.

TABLE 1.—*Number of observations and relative frequencies of activities of tenured male gray seals.*

Activity	Number of times observed	Percent total observations
Nonsocial		
Resting	24,827	88.8
Grooming	197	0.7
Alert	3,616	12.9
Lying	21,014	75.2
Moving	584	2.1
Total	25,411	90.9
Social		
Male aggression	1,766	6.3
Stationary threat	1,365	4.9
Locomotory threat	349	1.2
Fight	52	0.2
Sexual	769	2.8
Approach	359	1.3
Mount	256	0.9
Copulation	154	0.6
Total	2,535	9.1
All activity	27,946	100.0

The copulatory success of each male was determined by noting all copulations involving those males scanned. A male was considered likely to have fertilized a female if he was the first male to copulate with her. Previous work (Boness, 1979; Boness et al., 1982) showed that the first male to copulate with a female usually mated with her several times over a 2-day period before another male might breed her.

Activities were categorized as social and nonsocial behavior. Social activity included all behavior directly involving at least two individuals whereas nonsocial activity involved only the animal being observed. Each major type of activity was divided into more detailed categories. Nonsocial behavior included: (1) Resting—the male was stationary and in a prone position with most of his ventral, dorsal or lateral surface in contact with the ground. During resting the male may have been grooming, alert (head up) or lying (head down and no body movements). (2) Moving—the male moved his entire body, either crawling on the ventrum or rolling. Social activity included: (1) Male aggression—the male directed visual or auditory threats toward another male. These responses may have involved local body movements while stationary (stationary threat), movement toward a male (locomotory threat), or vigorous physical combat (fight). (2) Sexual—the male directed his actions toward a female. These actions may have involved approaching (approach), mounting (mount), or coitus (copulation). I have included "approaching" under sexual behavior because unless the male retreated after being threatened by the female or chased by another male, one of which usually happened, he subsequently tried to mount her.

Statistical analyses included a test for equality of two proportions (using an arcsine transformation), chi square goodness of fit test, Spearman's rank correlation test, and Pearson's correlation test (Sokal and Rohlf, 1969). The significance level for all analyses was 0.05.

RESULTS

Overall activity budget.—The data were first analyzed to determine whether or not time of day affected a male's activity. This was done by using a chi square goodness of fit test on social behavior separately. The null hypothesis was that the relative frequency of a given type of behavior was the same for each time period. No effect of time of day was found for either social ($\chi^2 = 4.42$, d.f. $= 3$, $P > 0.05$) or nonsocial behavior ($\chi^2 = 6.47$, d.f. $= 3$, $P > 0.05$) so for all further analyses the data from each sampling period were combined.

The relative frequency with which each of the activities occurred is summarized in Table 1. Nonsocial activities were far more prevalent (90.9%) than social ones (9.1%). Most time was spent (88%) resting, 76% of which was with eyes closed. Among social activities, males spent more time engaged in aggression (6.3%) than in sexual (2.8%) activity ($t_s = 20.5$, d.f. $= \infty$, $P <$ 0.05).

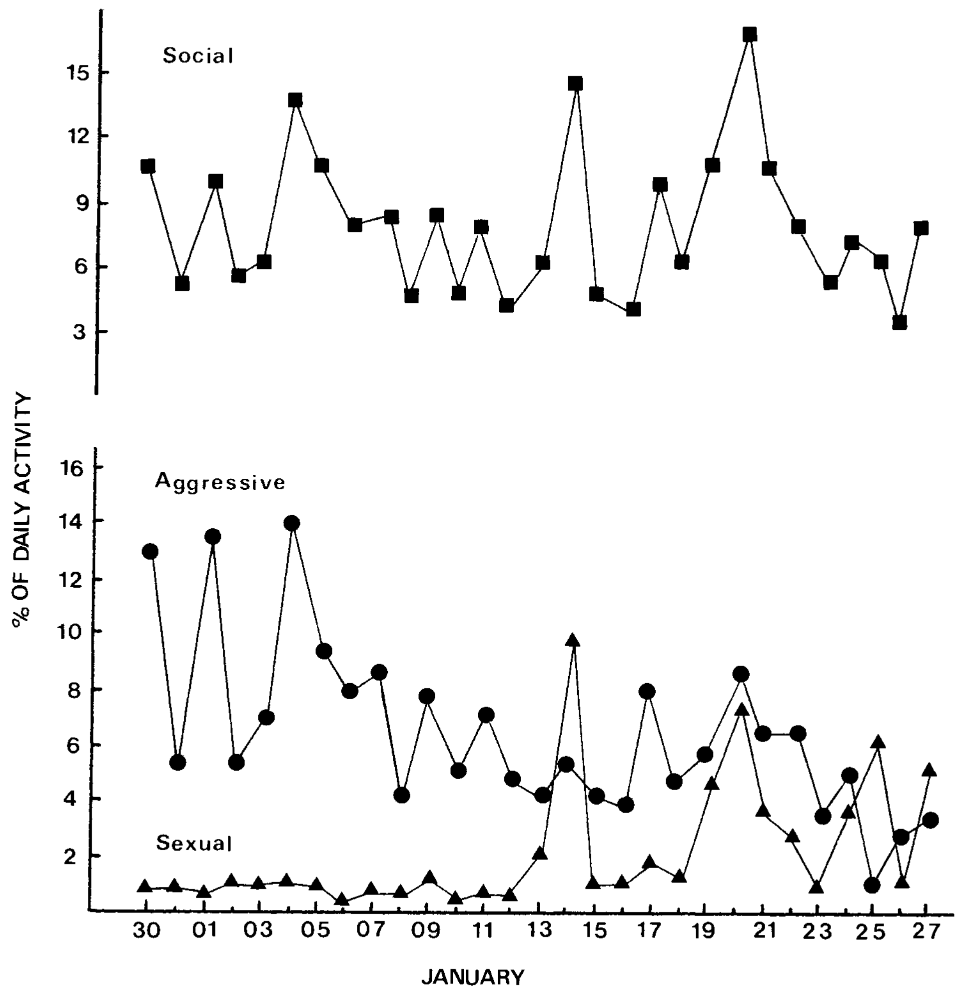

FIG. 1.—The average relative frequency of all social activities combined and aggressive and sexual behavior separately for 11 tenured males during their stay on the breeding grounds.

There was a clear predominance of nonlocomotory behavior in both social and nonsocial activities. Resting (88.8%) occurred by far more often than moving (2.1%) ($t_s = 258.8$, d.f. $= \infty$, $P < 0.05$), and stationary threats were more frequent than locomotory ones ($t_s = 4.63$, d.f. $= \infty$, $P < 0.05$).

Seasonal changes in activity.—For the first 2 weeks of the breeding season there are no females in estrus and then for the next 2–3 weeks the number will reach a peak before declining. This change in the males' surrounding environment should be reflected in their activity budget. To examine this, Spearman's rank correlation test was performed on the frequency of nonsocial and social behaviors. Among nonsocial behaviors the level of alertness changed over the course of the season, showing a very weak increase as the season progressed ($r_s = 0.44$, $t = 2.53$, d.f. $= 26$, $P < 0.05$); nonsocial moving ($r_s = -0.34$, $t = 1.86$, d.f. $= 26$, $P > 0.05$) and lying ($r_s = -0.05$, $t = 0.26$, d.f. $= 26$, $P > 0.05$) did not change. There was also no change in the overall level of social activity ($r_s = -0.11$, $t = 0.58$, d.f. $= 26$, $P > 0.05$) (Fig. 1). However, a separate analysis

TABLE 2.—*A comparison of activity budgets of tenured gray seal males on the Monach Isles and Sable Island.*

Activity	Percent of on-land activity	
	Monach Isles	Sable Island
Nonsocial		
Resting	87.8	88.8
Moving	4.4	2.1
Total	92.2	90.9
Social		
Sexual	5.5	2.8
Aggression	2.2	6.3
Total	7.7	9.1

of aggressive and sexual behavior revealed that male aggression decreased ($r_s = -0.64$, $t = 4.44$, d.f. $= 26$, $P < 0.05$) while sexual behavior increased ($r_s = 0.77$, $t = 6.01$, d.f. $= 26$, $P < 0.05$). The increase in sexual behavior occurred abruptly, beginning the 16th day (13 January) after the first pup was born in the study area (Fig. 1). This corresponds closely to the expected time of the first females coming into estrus—15.2 days after the first births (Boness and James, 1979).

Relation between copulatory success and activity budget.—If fat reserves are a limiting factor to reproductive success and a male's reserves are depleted by activity, one might expect to find that males whose copulatory success is high are least active (e.g., use stationary threats more than moving ones) except in their copulatory behavior. To examine this, a Pearson's product-moment correlation test was performed on the number of females mated by each of the 11 known males and both the percent of activity involving locomotion (nonsocial moving, moving threat and fighting) and the percent of nonlocomotory activity (resting and stationary threat).

The results do not support the hypothesis. There is no significant correlation between number of females mated and locomotory behavior ($r = 0.05$; $t = 0.42$, d.f. $= 9$, $P > 0.05$), regardless of whether one examines social and nonsocial behavior separately or in combination. Also, the most successful males spent the least amount of time resting and using stationary threats ($r = -0.67$, $t = 10.81$, d.f. $= 9$, $P < 0.05$), the opposite of what is predicted by the above hypothesis.

Because one might expect maximum copulatory success to be the result of a balance between the apparent conflicting advantages of competitive activity and length of stay, I re-analyzed the relationship between number of mates and activity levels, controlling for length of stay, by using partial correlation coefficients. There still was no significant relationship between copulatory success and locomotory behavior ($r = 0.01$, $t = 0.03$, d.f. $= 9$, $P > 0.05$) and the relationship between copulatory success and nonlocomotory activity was still negative ($r = -0.70$, $t = 2.94$, d.f. $= 9$, $P < 0.05$).

Comparison with another gray seal colony.—Activity patterns have been sampled on the Monach Isles in the Outer Hebrides (Harwood, in litt.), using a form of scan sampling. Gray seal males on the Monachs spent about 60% of their time in the water off the beach, while on Sable males remained on land continuously during their tenure. To compare the activity budgets (at least the on-land budgets) of animals at the two breeding colonies, I excluded the time spent at sea for males at the Monachs and calculated the proportion of the total on-land activity for each class of activity (Table 2). The main differences are that nonsocial moving occurred about twice as often on Monach Isles as it did on Sable Island ($t_s = 500$, d.f. $= \infty$, $P < 0.05$). Also, on the Monachs, the frequency of aggression was low compared to that of sexual behavior ($t_s = 5.20$, d.f. $= \infty$, $P < 0.05$), while on Sable sexual behavior was infrequent compared to aggression ($t_s = 7.95$, d.f. $= \infty$, $P < 0.05$). Harwood also found seasonal variation in activity. Like Sable Island, males on the Monach Isles showed a rapid increase in sexual activity that was closely associated with the presence of females in estrus. Aggressive behavior at the Monachs remained constant for the early part of the season, decreased during peak sexual activity and increased again as sexual activity diminished. This is in contrast to the gradual decrease in aggressive activity on Sable. Levels of alertness increased as the season progressed at the Monachs, although the increase was more marked than at Sable.

Discussion

The most striking aspect of the activity budget of male gray seals is the disproportionately large part which is given to resting. The only pinniped known to demonstrate a higher proportion of time resting is another phocid, the northern elephant seal, which rests for 95% of its time on the breeding ground (Sandegren, 1976*a*). The southern elephant seal male, *Mirounga leonina*, rests for about the same amount of time as gray seals (87.3%; McCann, 1983). The activity budgets of otariids suggest that these species tend to spend less time resting than do the two phocids. The New Zealand fur seal, *Arctocephalus forsteri,* the Guadalupe fur seal, *A. townsendi,* the Steller's sea lion, *Eumetopias jubatus* and the Amsterdam fur seal, *A. tropicalis* only spend 72%, 76%, 80% and 81% of their time respectively, resting on the breeding grounds (Stirling, 1971; Sandegren, 1976*b*; Bester, 1977; Pierson, 1978).

This generally high level of inactivity for carnivores is possible because during breeding male pinnipeds fast and do not devote energy to the search for food. The reasons for the apparent differences between the phocids and otariids are not clear. It is possible that the phocids which generally are under greater thermal stress because of winter breeding in temperate to polar climates (Pierotti and Pierotti, 1980), must be more conservative in the use of energy. Alternatively, but not mutually exclusive, the general otariid mating system, where males acquire females by holding a territory, might require a greater activity level in order to re-affirm boundaries and to keep females confined to the territory. In contrast, spatially more flexible systems as those of the gray seal (Boness and James, 1979) and northern elephant seal (Le Boeuf, 1974) do not require the constant patrolling of borders or herding of females. The added energetic costs of maintaining a territory could indeed be part of the reason a territorial mating system is not found among phocids that mate on land.

The overall activity budgets of breeding gray seals on Sable Island and the Monach Isles differ considerably because the latter animals move back and forth between the sea and land. The on-land activity budgets, however, were similar and the differences in aggressive and sexual behavior which do exist may be accounted for by the movement to and from sea as well as a greater female:male sex ratio on the Monach Isles (Harwood and Anderson, in litt.).

Variation in activity budgets during the breeding season has also been reported in southern elephant seals (McCann, 1983). Unlike gray seals, aggressive activity increased as the season progressed, reaching a peak at the same time sexual activity reaches a peak. The reasons for this difference are unclear. McCann (1981) suggested that it may be because most elephant seal aggression takes the form of stationary vocalizations. However, the same is true of gray seals on Sable Island (from Table 1).

Sandegren (1976*a*) hypothesized that fasting during breeding in pinnipeds should have led to the evolution of a restricted energy regime. Although the high level of inactivity in the gray seal and other pinnipeds tends to support this hypothesis, there are other data which contradict it. As shown in this study, there is not a positive correlation between a male's copulatory success and the amount of time spent inactive. Nor is there a negative correlation between copulatory success and the amount of time spent active; indeed, just the opposite was found. Both of these are logical predictions that follow if a male's fat reserves are a limiting factor on reproduction. The relationship between activity budget and copulatory success of northern and southern elephant seals appears to be the same as for gray seals. The most dominant males, which are also the ones that mate with the majority of the females, spend a greater proportion of their time active than do the less dominant males (Sandegren, 1976*a*; McCann, 1983). The results presented here for gray seals and the observations for northern and southern elephant seals thus suggest that fasting does not place severe limitations on the activity of males; instead the advantages of being active appear to outweigh the costs.

A similar conclusion was reached for an otariid species through indirect evidence. Miller (1971) argued that the absence of a negative correlation between the duration of tenure and the ability to sustain a challenge suggests that fat reserves in New Zealand fur seals are not depleted enough throughout a male's tenure to affect his activity budget. It would appear that at least some pinnipeds have reconciled the trade-off between length of stay on the breeding grounds, amount of fat reserves and the activities which are prerequisites for acquiring females.

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