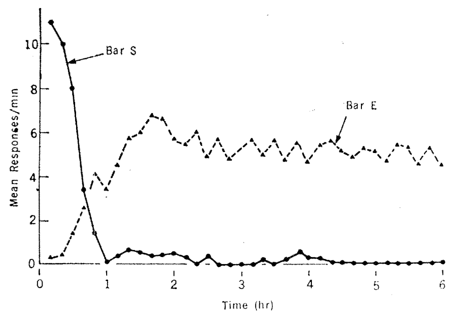

Fig. 1. Response rate (means) on both levers, collected simultaneously, are plotted as a function of time for the first escape session. Bar *S*, the lever on which the rat originally self-stimulated, is now inoperative. A response on lever *E* terminates stimulation for 20 seconds.

and only 6-hour escape session, the escape latencies for the next 19 sessions remained relatively constant (see Fig. 2).

Subsequently subjects were given the opportunity to escape ICS delivered in a regular pattern at the same average rate as their prerecorded self-stimulation. Subjects escaped with shorter latencies from the regular stimulation than from their own prerecorded pattern, which was irregular (Fig. 3). The order of presentation of these conditions was randomized. The differences in average escape latency were consistent over many days.

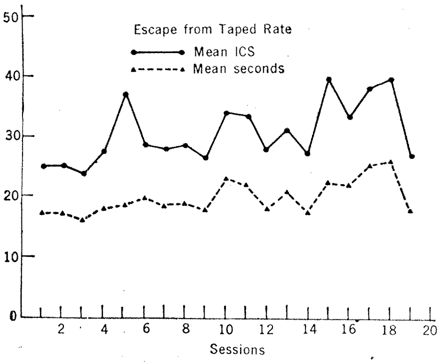

Fig. 2. Mean escape latency and mean number of intracranial stimulation (ICS) trains per trial are plotted over 19 daily 1-hour sessions.

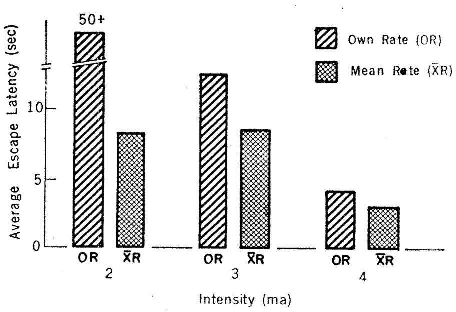

Fig. 3. Mean escape latency is plotted as a function of current intensity. Escape latencies decrease as a function of increasing current intensity. Across all intensities tested, subjects escape the average of their rate of self-stimulation at that intensity ($\bar{X}$R) with shorter latencies than they escape their prerecorded rate (OR).

Each subject was also allowed to escape stimulation presented at twice and at one-half its own taped rate. Escape behavior was not maintained when intracranial stimulation was presented at one-half the subject's taped rate, but could be reinstituted immediately when the original rate was restored. Subjects escaped with shorter latencies when brain stimulation was played at twice the taped rate.

When subjects were given an opportunity both to initiate and to terminate their own taped rate by responding on two levers, they selected an intertrial interval of approximately 4 seconds. Their average escape latencies in this condition were shorter than the condition in which the experimenter initiated stimulation after a 20-second intertrial interval. When the intertrial interval was shortened to 4 seconds, the average escape latencies were similar to those when subjects selected their own intertrial interval.

The escape behavior could not be attributed to superstitious responding. This was demonstrated in the control condition (in which rats had access to two levers) where responding on lever S dropped from a high rate to almost 0 when it no longer affected reinforcement contingencies. In contrast, animals learned to respond on the new lever which did affect reinforcement. It would appear that the escape behavior is learned and maintained because the stimulation becomes aversive (*3*).

The fact that subjects learn to escape their own prerecorded patterns of stimulation casts doubt on results of experiments in which it is assumed that the rate at which the animals take stimulation on one occasion will be rewarding on other occasions. The temporal patterns at which subjects self-stimulate may reflect some ongoing internal event, possibly subconvulsive electrical discharges. This may explain why subjects escape regularly patterned stimulation rates faster than they escape their irregular, self-produced rates of stimulation.

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Social Status and Mating Activity in Elephant Seals

Abstract. *Individually marked male elephant seals,* Mirounga angustirostris, *observed on an island off central California participate in a social hierarchy resembling the peck order of domestic chickens. Individuals achieve status by fighting and maintain it by stereotyped threat displays. The higher the status of a male, the more readily he approaches and copulates with females. Four percent of the males inseminated 85 percent of the females.*

Patterns of social organization in vertebrates have been generally categorized as territories or social hierarchies (*1*). Many pinnipeds are territorial; a few males defend specific sites where breeding females gather in "harems" (*2*). *Mirounga angustirostris* and *M. leonina,* the northern and southern elephant seals, are exceptions. Males of these species establish social hierarchies in which the males of highest rank remain near the breeding females but do not defend specific sites (*3*). Previous studies of the hierarchies were severely limited since few animals were recognizable as individuals, and since an observer must know the members of a group individually to obtain accurate data on social order. During the 1967–1968 breeding season of *M. angustirostris* at Año Nuevo Island, San Mateo County, California, we marked virtually all of the males that landed; thus we are able to provide the first quantitative description of the hierarchy and to relate individual status to breeding success.

In December of each year male elephant seals land at Año Nuevo Island, and many of them remain there continuously until March (*4*). In January, after many males have been on land for several weeks, the adult females come ashore, give birth, suckle their

Fig. 1. Two northern elephant seal bulls fighting.

Table 1. Social rank and copulation frequency of highest ranking males on area 17. Each male dominates those listed below it; deviations from a linear hierarchy are indicated by arrows. Dotted arrows denote a change in relation which occurred toward the end of the 10-day period. Copulation frequencies are in parentheses.

21 Dec. to 30 Dec.	30 Dec. to 8 Jan.	9 Jan. to 18 Jan.	19 Jan. to 28 Jan.	29 Jan. to 7 Feb.	8 Feb. to 17 Feb.	18 Feb. to 27 Feb.	28 Feb. to 8 Mar.	Total copulations (No.)
NIC	NIC	CLS*	NIC(1)	GL(6)	GL(15)	GL(19)	GL(5)	46
UG	UG†	NIC	GL(1)	CLS(13)	CLS(7)	CLS(9)	CLS(1)	31
GL	GL	GL*	CLS(2)	NIC‡	GLS(4)	GLS(8)	GLS(1)	15
WN	WN	GLS	GLS(1)	GLS(5)	TWO(2)	PIN	PIN	8
HSN	TWO	TWO	TWO(2)	TWO(1)	PIN(3)	YLN(3)	YLN	9
TWO	YDB	PIN	PIN	PIN	YLN(3)	TWO‡	BLB	3
BRS	PIN	YLN	YLN	YLN(1)	BO	BLB(2)	BO	3
Copulations (No.)								
0	0	0	7	26	34	41§	7	
Females present (range)								
0–2	2–21	24–58	66–102	70–89	54–79	19–51	6–15	
Males present (range)								
15–27	19–26	19–28	22–29	24–34	24–34	23–35	24–31	

* Indeterminate relation during period despite two bloody fights. † Moved to area 3 after losing fight to YLN at end of period. ‡ Left island during period and did not return. § Three other copulations were observed during this period; two by BO, one by WN.

Table 2. Correlates of social rank in four males on area 17 during the period when GL was the alpha male.

Males (in order of rank)	Times other males moved by threats (No.)	Mounts prevented by male (No.)	Copulations interrupted by male (No.)*	Mounts prevented by others (%)	Copulations interrupted by others (%)
GL	726	213	15	0	0
CLS	332	52	5	24	15
GLS	332	23	1	71	47
YLN	215	9	0	83	57

* Taken from all copulations observed, a total of 152.

young for an average of 28 days, breed, and depart. We observed this population, on an average, for 6.0 hours per day, from 10 December 1967 to 15 March 1968, from blinds overlooking two beaches. We put individual markings on 93 of approximately 115 males as they landed on the island, and on 46 of 225 females (*5*). The males that we did not mark were immature transients rarely seen near the females.

As they came ashore, the adult males exhibited mutual rivalry which kept them apart from each other. Rivalry was evidenced most often by stereotyped threat patterns; a male elevated his forequarters, reared back his head allowing his proboscis to hang into his opened mouth, and emitted a series of loud, low-pitched, gutteral sounds (*6*). Normally, the threatened male halted his approach or retreated. If, instead, he held his ground or answered the display with one of his own, a confrontation often followed in which the males came together and attempted to butt, bite, and slash each other on the neck (Fig. 1). We saw only 90 clashes, but more than 6000 threat displays. Fights lasted from a few seconds to 15 minutes and ended when one participant turned and fled.

We determined the direction of dominance between pairs of marked animals by noting which individual retreated after every threat or fight. Some pairs of individuals interacted as often as 65 times in 10 days. The social rank of an individual was determined by the number and identity of animals from which he retreated when threatened.

The relations between the seven top-ranking males on area 17, one of the two study areas, when displayed at 10-day intervals, demonstrates the dynamic nature of the social system (Table 1). The hierarchies were either linear (28 February to 8 March, Table 1), or complicated by triangular relations. An example of the latter occurred from 19 to 28 January when subject NIC moved subject GL, GL moved CLS, and CLS moved NIC. The direction of dominance between a pair of males did not change unless a fight occurred between them. The relation reversed when the previously dominant male retreated. The animals recognized each other individually.

The most important animal in the system was the alpha bull, the male that dominated all others on the beach. Activity centered around him since he usually remained in or near the aggregation of females toward which the other males were also oriented. Much of the alpha bull's activity involved keeping other males away from the females.

Copulation frequencies (in parentheses, Table 1) show that social rank was highly correlated with breeding success (*7*). We estimate that four of the highest ranking males (GL, CLS, GLS, and YLN), representing 6 percent of 71 individuals observed in area 17, inseminated 88 percent of the 120 females on that beach. The alpha bull from 29 January to 8 March (GL) copulated more frequently than any other male.

Among the four males that copulated most frequently, high rank was positively correlated with (i) demonstrating dominance over other males, (ii) preventing others from mounting and copulating, and (iii) mounting and copulating without interruption (Table 2).

On the other beach under study, area 3, one individual maintained the alpha position during the entire breeding season. This bull was involved in 73 percent of the copulations observed on area 3.

The extent to which social structure restricted mating to only a few males is illustrated by the combined statistics of the entire island. The four highest ranking males on area 17, plus the alpha bull on area 3, accounted for 123 of 144 copulations observed during the season. Thus 4 percent of the males apparently inseminated 85 percent of the females.

Social hierarchies exist in several mammalian species (*8*), but the type we observed in male elephant seals is especially comparable to that of domestic fowl (*9*). In both systems, the hierarchy may be linear, or may show triangular relations. The relations between individuals are stable unless fighting leads to reversals. However, among male fowl, high status confers access to food and roosting and nesting sites as well as to females, whereas in elephant seals the competition during the breeding season relates primarily to females. A male elephant seal shows no preference for a particular site, except one close to the females. As the females shift location, the males follow them. High-ranking males do not eat during the 3-month haul-out, and therefore do not compete for food. In addition, all the male elephant seals in our population exhibited a dominance relation with each other, whereas "no-contest" relations occur between some individuals in chicken peck orders.

A social system in which only a few males mate might have important genetic consequences for the evolution of the species, particularly if the same males continue to mate for more than one season. We do not know how many seasons one male successfully competes for females, or whether he fertilizes all those with whom he mates (*10*).

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5. Our best marks were obtained by slowly dripping 30 percent hydrogen peroxide, mixed with a cosmetic emulsifier, on the pelage of sleeping animals. The marks were easily recognizable from the blinds and lasted throughout the breeding season. We thank Clairol, Inc., for providing the emulsified "Lady Clairol Ultra Blue."
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7. Copulation frequencies include only the first of a female's copulations that we observed. Additional copulations by the same female are excluded because we assumed that insemination occurred most likely as a result of the initial mating.
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10. We attached permanent monel metal tags to many of the seals to identify them in future seasons and study the reproductive rates of males and females.
11. Our studies in Año Nuevo State Reserve were authorized by the California Department of Parks and Recreation, W. P. Mott, Jr., director; and permission to tag seals was granted by the California Department of Fish and Game, W. T. Shannon, director. We acknowledge the field assistance of M. Skeel, D. Ramsey, G. Eaton, and R. Gentry.

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Colobus guereza: Territoriality and Group Composition

Abstract. *Troops of the black and white colobus* Colobus guereza *in the Budongo Forest, Uganda, average eight animals with a typical composition of one adult male, four adult females, two subadults, one juvenile, and one infant. Solitary males and small all-male groups also occur. Troops of mixed sexes have well-defined territories which coincide roughly with the home range. Territories of five groups averaged 0.062 square mile (0.137 km²) in area, agreeing closely with territory-sizes of Asian Colobine monkeys. Adult males have a roar that is concerned with maintaining territorial spacing, but not with actual territorial defense. The territories of these arboreal, forest animals are much smaller than the home ranges of more terrestrial and nonterritorial open-country primates.*

Among the Colobine monkeys of the Old World, the gray langur, *Presbytis entellus*, seems to be territorial, at least in certain areas (*1*). In Africa, two investigators have reported territoriality in the black and white colobus monkey *Colobus guereza* (*2, 3*). The black and white colobus, observed in the Budongo Forest, Uganda, at irregular intervals between 15 October 1964 and 27 May 1965, moved in the tree tops in close-knit groups averaging 8 animals in the 14 troops accurately counted, with a range from 2 to 13 individuals. In an average troop there is a single adult male, four adult females, perhaps one subadult male and a female, a juvenile, and perhaps one infant. There are rather smaller troops in the southern part of the Queen Elizabeth National Park but with a similar basic composition (Table 1). Solitary males and small all-male troops are difficult to detect and may be more common than our two cases indicate. Ullrich (*2*) describes a troop of 13 animals in Tanzania with the same composition. Schenkel and Schenkel-Hulliger (*3*) report on four troops in Kenya, two containing 6 animals, one 12, and one 15 animals. The numbers of adult males and females indicated are equal, whereas we found a preponderance of females. However, they do not distinguish between adults and subadults. Some variation may be a result of differences in the criteria for sexing animals. Ullrich mentions sex difference in