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18. This work was made possible through the outstanding cooperation and performance of a singularly unique *Tursiops truncatus* that we named "Tuffy" because of his humanlike frailty of occasionally displaying an ill temper. We thank F. G. Wood who aided in all phases of the project; Drs. J. G. Simpson and J. Collins, and R. Pierce who reviewed the manuscript; T. Dohms and Dr. H. Chiodi who performed the Haldane analyses; and J. Walton and the Naval Missile Center's photographic unit for the pictures.

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Dialects in Elephant Seals

Abstract. *Threat vocalizations of male elephant seals* Mirounga angustirostris *vary among four populations on islands off the coast of California and Baja California, Mexico. Males at San Nicolas Island in Southern California emit sound pulses at more than double the rate of males at Año Nuevo Island, 528 kilometers north. Mean pulse rates at San Miguel Island and Isla de Guadalupe (408 and 944 kilometers south of Año Nuevo, respectively) are intermediate to these two. Pulse rate is homogeneous within each population and consistent in the same individual. Other properties of the calls which separate populations are pulse duration and embellishment of the initial or terminal pulse in a series. These geographical differences in vocal behavior resemble local dialects in birds and humans.*

Consistent differences in the predominant song or call of adults from different populations of the same species are called local dialects. The phenomenon has been described and studied most intensively in birds and has significance for diverse topics such as speciation, learning, and social communication (*1*). The only mammal in which dialects have been demonstrated is man (*2*). We now report differences in the threat vocalizations of males from different breeding populations of northern elephant seals *Mirounga angustirostris*.

During their 3-month breeding season, adult males haul themselves out of the water on island rookeries along the coasts of California and Mexico, and compete aggressively with each other for status in social hierarchies. Threat behavior is important in maintaining hierarchical relations between males. High-ranking bulls also threaten lower ranking bulls to keep them away from females. As a result, a few of the highest ranking males in each hierarchy do most of the breeding (*3*). A male threatens another male by elevating his head and forequarters and emitting a series of approximately 3 to 15 sound pulses which are loud, low-pitched, and guttural (*4*). After a pause in which the elevated posture is maintained, the vocalization may be repeated. The usual result is that the threatened animal moves away. Thus, threat calls enable one male to displace another with a minimum expenditure of energy. They are the predominant vocalizations of males and occur frequently throughout the breeding season.

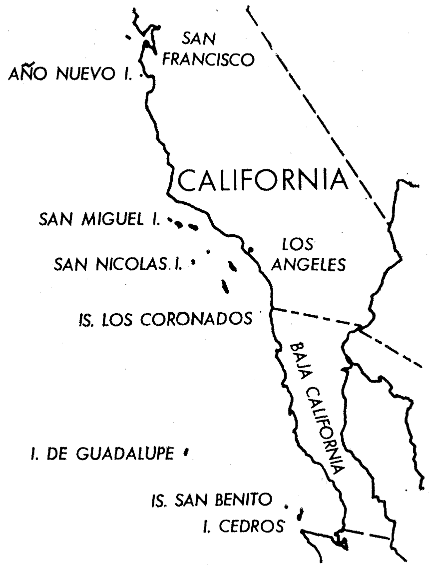

Fig. 1. Islands where northern elephant seals were known to breed in 1969.

We recorded threat vocalizations of full-grown males during the 1968 and 1969 breeding seasons at four major rookeries (*5*): Año Nuevo Island, San Miguel Island, San Nicolas Island, and Isla de Guadalupe (Fig. 1). The only large rookery not sampled is located on Islas San Benito, off the coast of central Baja California. Tape recordings were made from December through February with a Uher Report L recorder and a Uher M514 microphone; overall frequency response of the system was from 70 to 14,000 hz. Marked individuals were identified on the tape when possible.

Temporal analysis of all records was made by displaying uninterrupted series of pulses, called "bursts," on a Tektronix type RM 564 storage oscilloscope. The number of discrete pulses in a burst was counted, and the duration of each burst measured directly on the oscilloscope face as the interval between the peak of the first and last pulse. Wave-form analyses of recordings selected for minimum background noise were made with a Fairchild model 708A oscilloscope, and sound spectrograms were made with a Raytheon Rayspan spectrum analyzer and a Granger model 9010 electrostatic recorder.

We measured variation in pulse rate within individuals and between individuals both during a single season and from one season to the next, using 317 recordings of 43 adult males at Año Nuevo Island. Pulse rate was constant for each individual; 12 males for which we obtained 20 to 45 records apiece exhibited mean pulse rates of approximately 1.0 pulse/sec and standard deviations ranging from 0.04 to 0.09. Change in pulse rate from one year to the next was determined in two ways: by selecting randomly a single vocal burst from each of 23 males in 1968 and comparing this distribution to one similarly collected on 20 different males in 1969, and by comparing the pulse rates of 7 males on which we had records in two consecutive years. The first comparison yielded a mean rate of 0.97 pulse/sec with a standard deviation of 0.06 in 1968 and a slightly faster rate in 1969 of 1.04 pulse/sec with a standard deviation of 0.13 ($t = 2.10$, d.f. $= 41$, $P < .05$). The pulse rates of males measured in both years did not change substantially from one season to the next. As only the first comparison revealed a change in pulse rate, and because this change was slight, we have combined samples taken in two breeding seasons in the population comparisons below (Table 1).

Table 1. Parameters of male northern elephant seal vocalizations from four rookeries (means and standard deviations).

Rookery	Sample size (No.)	Estimated population (No.)	Pulse rate* (pulse/sec)	Burst duration† (sec)	Pulses per burst‡ (No.)
Año Nuevo Island	43	50	1.02 ± .11	6.10 ± 2.1	6.1 ± 1.8
San Miguel Island	33	500	1.88 ± .41	6.50 ± 3.6	11.7 ± 6.2
San Nicolas Island	9	42	2.53 ± .60	5.63 ± 4.3	13.4 ± 10.6
Isla de Guadalupe	236	1000	1.77 ± .39	5.80 ± 2.9	9.9 ± 4.7

* All comparisons except San Miguel Island as against Isla de Guadalupe are significantly different from each other ($P < .05$, *t*-tests). † No significant differences between any two rookeries. ‡ Año Nuevo Island differs from all other rookeries, and San Nicolas Island and Isla de Guadalupe differ from each other.

The mean pulse rate differed significantly from one population to the next and each population sample was relatively homogeneous (Table 1). The pulse rate was slowest at Año Nuevo Island, averaging 1.0 pulse/sec, and fastest at San Nicolas Island, averaging about 2.5 pulse/sec. Mean burst duration was similar in all populations. Therefore, the differential pulse rates between rookeries were produced by variation in the number of pulses in bursts of similar length.

The Año Nuevo population differed from the other populations in two other respects. Analysis of 11 spectrograms from each of three of the populations revealed a median pulse duration of 0.56 second at Año Nuevo Island, significantly longer (Mann-Whitney *U* tests, $P < .05$) than the median pulse duration of 0.14 second characteristic of the San Miguel and Guadalupe populations (Fig. 2). The small amount of data from San Nicolas Island suggested a mean pulse duration of approximately 0.20 second. Second, some males from all populations except Año Nuevo emitted prolonged terminal pulses (SM-1, SM-2 and SN-1, SN-2 in Fig. 2). Some individuals from Guadalupe sustained the first as well as the last pulse in a burst, and some San Nicolas males set the first pulse apart from subsequent pulses in a burst by as much as 1 second (SN-2 and SN-3 in Fig. 2).

Wave-form analyses of individual pulses revealed no consistent differences in fundamental frequency (approximately 250 to 750 hz) or rise time (approximately 5 to 50 msec) in vocalizations of males from the four rookeries.

These geographical variations in vocalizations of male elephant seals resemble the dialects reported in populations of birds such as white-crowned sparrows *Zonotrichia leucophrys* (*6*), chaffinches *Fringilla coelebs* (Thorpe, *1*), and tree creepers *Certhia brachydactyla* (*7*). Like these avian songs, the elephant seal threat call is discrete and highly stereotyped, which makes small variations stand out in sharp relief

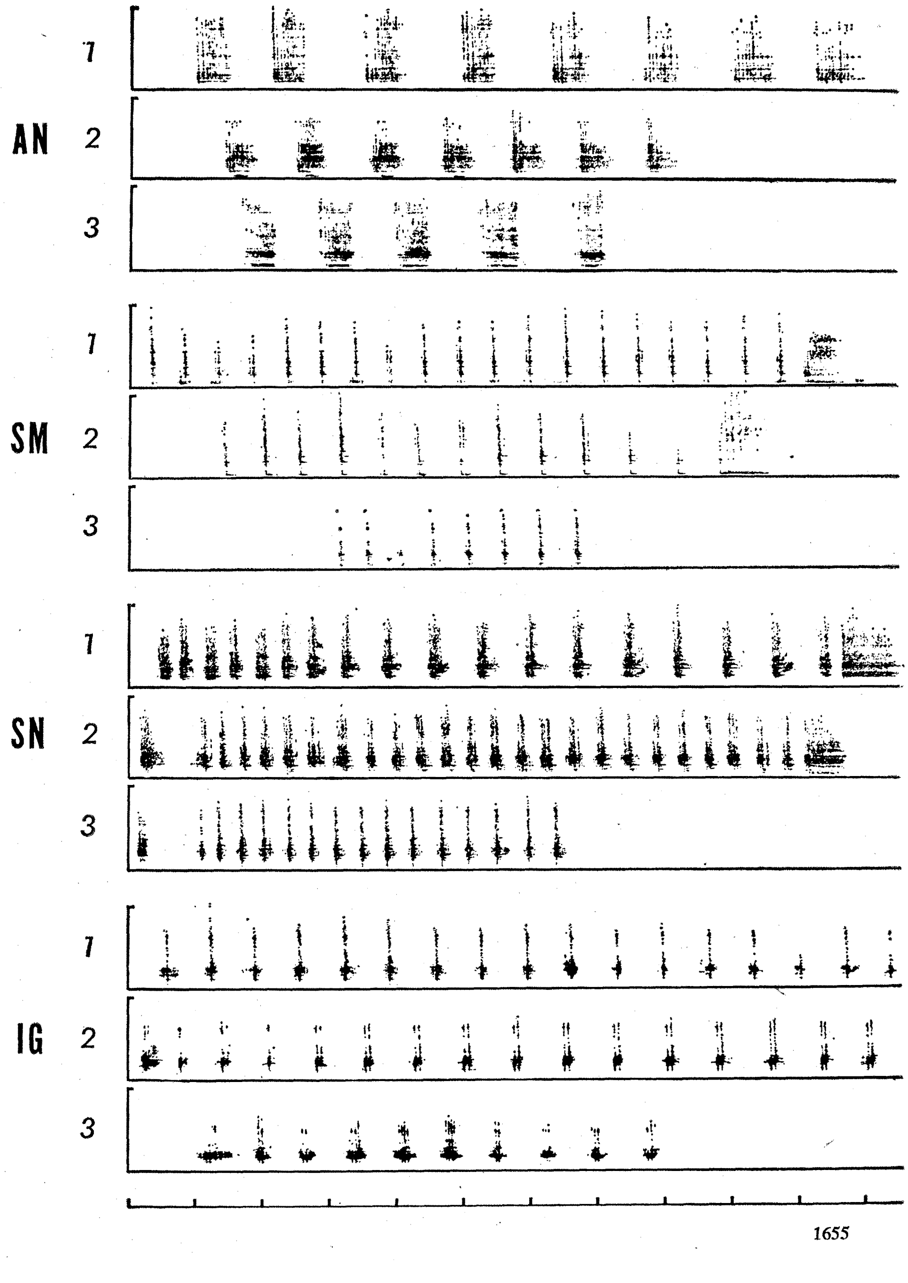

Fig. 2. Threat vocalizations of 12 males recorded at four different rookeries. AN 1-3, males from Año Neuvo Island. SM 1-3, males from San Miguel Island. SN 1-3, males from San Nicolas Island. IG 1-3, males from Isla de Guadalupe. The horizontal time scale is marked at 1-second intervals; the vertical frequency scale is arithmetic and ranges from 0 to 6 khz for each spectrogram. The analyzing filter bandwidth was 16 hz.

(Marler and Hamilton, *1*). That local dialects have not been demonstrated in other mammals except man may be due to the extensive gradation and acoustic complexity of most mammalian vocalizations, especially those of higher primates.

It is unlikely that variations in dialect are primarily genetic in origin. Año Nuevo Island was first reestablished as a breeding colony in 1961 by a few adults (*8*). The 50 full-grown bulls living there in 1968 and 1969 could not have been born there because (i) it takes 10 years or more for males to attain full size (*9*), and (ii) none of these males bore tags like those attached to most of the pups born on the island each year since 1961 (*10*). Clearly, most of these adult males must have immigrated from other rookeries, like the original settlers in 1961. These data, the uniformity of calls in the Año Nuevo population, and the minimal drift from one year to the next, suggest that immigrants adopted the vocal peculiarities or dialect of the breeding males already in residence. Indeed, one adult male first seen at Año Nuevo in 1969, consistently threatened other males by first emitting a burst of pulses at the rate of 4.7 pulse/sec immediately followed by another series at 1.0 pulse/sec (like other Año Nuevo males) (*11*). We know from tagging studies that interchange of animals occurs between colonies, particularly during the first year of life (*12*).

Young male elephant seals may copy some of the threat call characteristics of adult males in the colony where they find themselves. Such a mode of transmission would account for the rapid development of dialects in separated geographic areas and their apparent perpetuation from one generation to the next. Thus, it is also possible that man is not the only mammal in which normal vocalizations are learned from other species members.

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11. Because this male had two distinct pulse rates, he was excluded from other analyses reported in this paper.
12. Numerous marked pups born on one island land on another (as far away as 944 km) 3 to 4 months after birth. Although we have tagged only pups extensively, we have observed subadult males on Isla de Guadalupe that were tagged on San Miguel Island and vice versa. We do not yet know whether these are temporary movements or permanent relocations.
13. Studies in Año Nuevo State Reserve authorized by California Department of Parks and Recreation, W. P. Mott, Jr., Director; in Mexico by Dirección General de Pesca e Industrias Conexas, J. L. Cifuentes, Subdirector; and on the Channel Islands by the U.S. Navy Pacific Missile Range. We thank C. L. Hubbs, J. B. Stoddard, R. F. Dwyer, and D. M. Robinson for assistance in getting to the seal rookeries, L. J. Bidinian, D. H. Ramsey, and T. A. Babb for field assistance, and T. C. Poulter, G. W. Boudreau, and L. J. Underkofler for help in data analysis.

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Climate and Evolutionary Rate

Stehli, Douglas, and Newell (*1*) present the thesis, previously advocated by Darlington (*2*) in a slightly different form, that evolutionary rates tend to be greater in tropical areas than in temperate ones. While this thesis may be correct, the evidence given needs examination. My competence is greatest for mammals and so I will emphasize this group.

Stehli *et al.* compare the earliest records of all extant mammalian families in central west Africa with those of northern Eurasia. There is an important bias here. The fossil record is very much poorer in the former area than in the latter, and this is generally true for comparisons between tropical and temperate regions. Therefore families which have been endemic to the present-day tropics throughout their existence will have a poorer chance of being found at a time near their origin than will families which have occurred in areas that are now temperate. The high proportion of tropical families not known earlier than the Pleistocene (Fig. 1) and the complete absence of such families in the cooler north temperate region illustrate this point. Bats, which have an unusually poor fossil record, are disproportionately numerous in the tropics. It is invalid to infer that families unknown before the Pleistocene originated relatively recently. For example, the Tupaiidae had no known fossil record at all until 1965, when a genus probably referable to that family was reported from the Middle Paleocene (*3*).

With the above-mentioned point of view, I have therefore analyzed the major tropical and north temperate faunas of recent mammals (*4*). Data on distribution are from Darlington (*2*), with a few modifications from standard regional checklists. Data on ages are from Romer (*5*) unless specifically noted otherwise. I have subjectively distinguished between families for which there is reason to believe the origin was appreciably earlier than the first record, and the remainder. I have included, in a distinguishable form, families regionally extinct after the last glaciation, because of the possibility that man contributed to their extinction (*6, 7*). Only the marine whales are excluded. The list of families (*8*) permits modification of my results by others using different criteria or data. Absence of such data and of geographic boundaries precludes detailed comparison with the results of Stehli *et al.* (*1*).

It is obvious from comparison of parts A to D in Fig. 1 with parts E and F that there is no tendency for tropical