References and Notes

1. D. J. Lehmer, *Middle Missouri Archeology* (National Park Service, Washington, D.C., 1971), pp. 28, 29, and 61.
2. R. W. Neumann, *Plains Anthropol.* **9**, 173 (1964).
3. Five reservoirs with a surface area of nearly 3600 km² have drowned more than 80 percent of the 1200-km length of the Missouri River in the Dakotas (*1*, p. 19).
4. C. R. Falk and F. A. Calabrese, *Plains Anthropol.* **18**, 336 (1973).
5. A. H. Coogan and W. H. Irving, *Proc. Iowa Acad. Sci.* **66**, 317 (1959).
6. The site No. 39WW203 in the Smithsonian River Basin Survey system, is at 45°24′45″N, 100°16′30″W, 495 m above mean sea level.
7. U.S. Department of Agriculture, Soil Conservation Service, *Soil Classification; A Comprehensive System* (Government Printing Office, Washington, D.C., 1960), 7th approximation.
8. L. Clayton, S. R. Moran, W. B. Bickley, Jr., in preparation.
9. J. H. McAndrews, *Mem. Torrey Bot. Club* **22**, 51 (1966); R. P. Wodehouse, *Pollen Grains* (Hafner, New York, 1959), p. 439.
10. H. T. J. Irwin, thesis, Harvard Univ. (1968).
11. C. Irwin-Williams, H. Irwin, G. Agogino, C. V. Haynes, *Plains Anthropol.* **18**, 40 (1973); W. Mulloy, *Am. Antiquity* **25**, 112 (1959); E. M. Davis, *Spec. Publ. Univ. Nebraska State Mus. No. 3* (1962).
12. J. B. Wheat, *Am. Antiquity* **37**, 157 (1972).
13. H. T. Irwin and H. M. Wormington, *ibid.* **35**, 24 (1970).
14. More specifically, the points represent a variation of the Hanna type [see R. P. Wheeler, *Plains Anthropol.* **1**, 7 (1954); G. Frison, *ibid.* **15**, 1 (1970)].
15. S. A. Ahler, in preparation; C. R. Falk, in preparation.
16. L. Clayton, W. B. Bickley, Jr., W. J. Stone, *Plains Anthropol.* **15**, 282 (1970).

17. Support for this research was provided by the Midwest Region of the National Park Service and the Division of American Archeology of the University of Missouri at Columbia. We thank J. E. King and W. E. Klippel for reading the manuscript and L. K. Lischer, J. Livingstone, W. Nelson, and J. Johnson for technical assistance.

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Elephant Seals: Genetic Variation and Near Extinction

Abstract. *Blood samples from northern elephant seals* (Mirounga angustirostris), *representing five breeding colonies in California and Mexico, were surveyed electrophoretically for protein variation reflecting underlying genetic differences. No polymorphisms were found among 21 proteins encoded by 24 loci. This uniform homozygosity may be a consequence of fixation of alleles brought about by the decimation of this species by sealers in the last century.*

What are the genetic consequences for a species of reduction in numbers to near extinction? We have approached this problem by examining genetic variation in the northern elephant seal (*Mirounga angustirostris*) whose numbers have varied enormously over the last 150 years.

In the mid-1800's, northern elephant seals were hauled-out by the thousands at numerous breeding rookeries along 2700 km of the coast of California and Baja California, Mexico (*1*). From 1820 to 1880 they were heavily exploited by man for oil. Because of a biological necessity to breed and give birth on land, the seals were more vulnerable than whales; hunters could quickly slaughter hundreds of adults and pups. The commercial harvest was so extensive and indiscriminate that by 1884 the species was considered virtually extinct (*2*). Only the most remote population survived—that on a nearly inaccessible beach on Isla de Guadalupe, 240 km west of Baja California (*3*). Estimates based on early census data indicate that this remnant population may have consisted of as few as 20 individuals in the early 1890's and the total number remained less than 100 individuals until at least 1900 (*4*). Under the protection of the Mexican and U.S. governments, the northern elephant seal slowly increased in numbers and, by the early 1930's, began to establish additional breeding colonies (*5*). Since then, the species has reoccupied its former breeding range and now numbers more than 30,000 (*6*). Thus the genetic reconstruction of this species was influenced by two factors: (i) the northern elephant seal suffered a severe "bottleneck" in numbers and (ii) its present genetic resources were derived from a single isolated population possessing but a fraction of the total variability of the predecimation species.

To assess the possible consequences of this species-wide decimation and subsequent recovery, we surveyed proteins electrophoretically for polymorphisms reflecting underlying genetic differences at structural gene loci (*7*). Blood samples were collected from 159 seals of both sexes at five rookeries: Año Nuevo Island ($N = 67$), San Miguel Island ($N = 24$), San Nicolas Island ($N = 20$), Isla de Guadalupe ($N = 25$), and Islas San Benito ($N = 23$) (*8*). Starch-gel electrophoresis was performed for 21 proteins encoded by 24 presumptive gene loci (*9*). No individual or populational differences were found; all proteins were monomorphic.

Is an apparent absence of genic heterozygosity unique to this species or is it also characteristic of other pinnipeds? For perspective we can look at the northern elephant seal's nearest relative, the southern elephant seal (*Mirounga leonina*), which is subantarctic in distribution. This species was also hunted extensively in the last century, but the effects were not as catastrophic as for the northern elephant seal (*10*). McDermid *et al.* (*11*) demonstrated five polymorphisms among 18 proteins examined electrophoretically in 42 individuals from Macquarie Island. From their data, we estimate genic heterozygosity at 0.028. Another population studied by Seal *et al.* (*12*) showed no variation in six proteins in 18 animals, but these proteins were among those found to be monomorphic by McDermid *et al.* (*11*).

The electrophoretic analysis of genic variation in pinnipeds other than *Mirounga* has been very limited (*13*). Multiple phenotypes of transferrin were demonstrated in 8 of 12 species of pinnipeds studied (*14*), and other polymorphic proteins include haptoglobin in 2 species, lactate dehydrogenase in another, and a rare variant of hemoglobin in a fourth (*15*).

Electrophoretic studies have convincingly demonstrated that a high level of genic variation is maintained as a normal equilibrium condition in most natural populations of plants and animals. In 22 species of vertebrates surveyed, genic heterozygosity averaged 0.0584 and the proportion of polymorphic loci ranged from 10 to 20 percent (*16*). The northern elephant seal apparently is genetically depauperate relative to its southern congener and other vertebrates, and indeed may be entirely monogenic. Whether this situation represents a reduction in genetic diversity from the level existing prior to the bottlenecking of the species is problematical. It is likely, however, that the genetic constitution of this species has changed as a consequence of decimation. It has been suggested that the magnitude of genetic change could be assessed by comparing means and variances of dimensions of museum specimens collected in the last century and more recently (*4*).

The roles of natural selection and random drift are complementary in bringing about a reduction in overall diversity in small and isolated populations. The uniformity of the marine environment throughout the range of the northern elephant seal provides little opportunity for the proliferation of genetic variability by natural selection. It is reasonable to assume that a rela-

tively low level of genetic variability would be maintained within single small and isolated breeding colonies; discontinuities in the distribution of neutral or weakly selected alleles between breeding colonies would be largely a function of the "founder effect" (*17*). At the time of its bottleneck, the effects of random drift and inbreeding on the population as a whole would have been amplified because of the small size of the remnant herd and the slow rate of recruitment. The only immigrants to the Isla de Guadalupe population would have been survivors from other populations forsaking their traditional breeding grounds. Additionally, the highly polygynous mating system of elephant seals, wherein as few as 14 percent of the males inseminate all the females, would greatly reduce the effective population size (*18*).

Dramatic reductions in genetic variability as an apparent consequence of isolation and the "founder effect" are known in natural populations of several organisms (*19*). Although genetic drift has generally been invoked to account for reduced variability in small and isolated populations, it is possible that the effect results in part from density-dependent selection or adaptation to a narrow range of environmental heterogeneity (*20*). In any event, however, the absence of protein polymorphisms in the northern elephant seal indicates that genic variability is not essential for the continued existence of animal species. Our results also suggest that the northern elephant seal, now lacking a pool of variability with which to adapt to changing conditions, is especially vulnerable to environmental modification.

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References and Notes

1. C. M. Scammon, *The Marine Mammals of the North-western Coast of North America, Described and Illustrated: Together with an Account of the American Whale-Fishery* (Carmany, San Francisco, 1874), pp. 115–123.
2. In 1884, C. H. Townsend collected 16 specimens of the northern elephant seal at San Cristobal Bay on the Baja California mainland for the U.S. National Museum. No subsequent sightings of the northern elephant seal were reported until 1892 when Townsend discovered eight elephant seals on "elephant seal beach," Isla de Guadalupe, seven of which were taken for museum specimens. C. H. Townsend, *Proc. U.S. Mus.* **8**, 90 (1885); in *The Fur Seals and Fur Seal Islands of the North Pacific Ocean*, D. S. Jordan *et al.*, Eds. (Government Printing Office, Washington, D.C., 1899), p. 265.
3. Charles Harris visited Isla de Guadalupe in 1907 and counted 40 elephant seals at elephant seal beach, 14 of which were collected as museum specimens. At this same location in 1911, C. H. Townsend found 125 northern elephant seals. [C. M. Harris, *Pacific Monthly* **21**, 331 (1909); C. H. Townsend, *Zoologica* **1**, 159 (1912).]
4. All known counts or estimates of the Isla de Guadalupe population are summarized by G. A. Bartholomew and C. L. Hubbs [*Mammalia* **24**, 313 (1960)]. The historical background of this species and the genetic implications of its decimation are discussed by G. A. Bartholomew [*Univ. Calif. Publ. Zool.* **47**, 422 (1952)].
5. A. W. Anthony, *J. Mammal.* **5**, 145 (1924); K. W. Radford, R. T. Orr, C. L. Hubbs, *Proc. Calif. Acad. Sci.* **31**, 601 (1965).
6. R. S. Peterson and B. J. Le Boeuf, in *Transactions of the Thirty-Fourth North American Wildlife and Natural Resources Conference* (Wildlife Management Inst., Washington, D.C., 1969); B. J. Le Boeuf, D. G. Ainley, T. J. Lewis, *J. Mammal.*, in press.
7. J. L. Hubby and R. C. Lewontin, *Genetics* **54**, 577 (1966); H. Harris, *Br. Med. Bull.* **25**, 5 (1969); R. K. Selander and S. Y. Yang, *Genetics* **63**, 653 (1969).
8. Blood was collected during the breeding season in the winter and early spring of 1970, 1971, 1972, and 1973. Eighty percent of the samples were taken from weaned pups. Becton-Dickinson "Vacutainer" glass tubes, holders, and adapters were used with 18-gauge veterinary needles 3 inches long (1 inch = 2.54 cm). Blood was drawn from the extradural vein of sleeping seals, frozen whole on Dry Ice, and later stored at −68°C until analysis.
9. For the 21 proteins, except as noted, the sample size was 124 seals. Buffer systems employed in electrophoresis are indicated by numbers in parentheses assigned by R. K. Selander, M. H. Smith, S. Y. Yang, W. E. Johnson, J. B. Gentry [*Stud. Genet.* **6**, 49 (1971) (University of Texas Publ. No. 7103)]. N is the number of seals. The proteins assayed were: malate dehydrogenase (buffer system 2); two lactate dehydrogenases (2); 6-phosphogluconate dehydrogenase (9; $N = 84$); glucose-6-phosphate dehydrogenase (9; $N = 92$); sorbitol dehydrogenase (8); phosphohexose isomerase (8); phosphoglucomutase (8); glutamic oxaloacetic transaminase (5); indophenol oxidase (2); peptidase (9); leucine aminopeptidase (2; $N = 72$); creatine kinase (histidine buffer; $N = 35$); adenylate kinase (histidine buffer; $N = 35$); aldolase (histidine buffer; $N = 35$); two esterases (1 and 2); hemoglobin (presumably two loci; several buffer systems; $N = 159$); transferrin (2; $N = 159$); albumin (2; $N = 159$); two postalbumins (2); and haptoglobin (2).
10. L. H. Matthews, *Discovery Rep.* **1**, 233 (1929).
11. E. M. McDermid, R. Ananthakrishnan, N. S. Agar, *Anim. Blood Groups Biochem. Genet.* **3**, 85 (1972).
12. U. S. Seal, A. W. Erickson, D. B. Siniff, R. J. Hofman, in *Symposium on Antarctic Ice and Water Masses* (Tokyo, Japan, 1970), p. 77. Samples were collected near Palmer Station across the Antarctic continent from Macquarie Island.
13. G. Naevdal, *Fiskeridir. Skr. Ser. Havunders.* **14**, 37 (1966); P. D. Shaughnessy, *Aust. J. Biol. Sci.* **22**, 1581 (1969); *Aust. J. Zool.* **18**, 331 (1970); U. S. Seal, A. W. Erickson, D. B. Siniff, D. R. Cline, in *Antarctic Pinnipedia*, W. H. Burt, Ed. (American Geophysical Union, Washington, D.C., 1971), p. 181.
14. *Lobodon, Leptonychotes, Arctocephalus* (two species), *Phoca, Pusa, Pagophilus*, and *Histriophoca* show transferrin polymorphisms.
15. *Cystophora* and *Pusa* show haptoglobin polymorphisms, and *Pusa* additionally has an albumin polymorphism. A rare variant of hemoglobin has been found in *Pagophilus* and a possible polymorphism of lactate dehydrogenase has been reported in *Lobodon*.
16. R. K. Selander and W. E. Johnson, in *Proceedings, 17th International Congress on Zoology*, in press; R. K. Selander and D. W. Kaufman, *Proc. Natl. Acad. Sci. U.S.A.* **70**, 1875 (1973).
17. In the absence of detectable phenotypic differences, the evidence of discontinuity in the gene pool of the northern elephant seal is circumstantial. Tagging studies have shown that adults apparently return to the same breeding colony year after year. Less than 1 percent of the tagged animals found on Isla de Guadalupe during winter breeding seasons were tagged elsewhere (B. J. Le Boeuf, personal communication).
18. B. J. Le Boeuf, *Am. Zool.*, in press. In a population of 100 elephant seals with a balanced sex ratio and with 20 percent of the males inseminating all the females, the effective population size would be only 33. See also J .F. Crow and M. Kimura, *An Introduction to Population Genetics Theory* (Harper & Row, New York, 1970).
19. F. J. Ayala, J. R. Powell, Th. Dobzhansky, *Proc. Natl. Acad. Sci. U.S.A.* **68**, 2480 (1971); S. Prakash, R. C. Lewontin, J. L. Hubby, *Genetics* **61**, 841 (1969); S. Prakash, *ibid.* **72**, 143 (1972); T. P. Webster, R. K. Selander, S. Y. Yang, *Evolution* **26**, 523 (1972); J. C. Avise and R. K. Selander, *ibid.*, p. 1.
20. B. Charlesworth and J. T. Giesel, *Am. Nat.* **106**, 402 (1972); B. Clarke, *ibid.*, p. 1; J. Maynard Smith, *ibid.* **104**, 487 (1970); K. P. V. Sammeta and R. Levins, *Annu. Rev. Genet.* **4**, 469 (1970); M. Soulé, *Taxon* **20**, 37 (1971).
21. Authorization for studies was provided by the California Department of Parks and Recreation, U.S. National Park Service, U.S. Navy, and Direccíon General de Pesca y Industrias Conexas. We thank C. L. Hubbs and D. M. Robinson for assistance in reaching rookeries and B. J. Le Boeuf for advice and support. Research supported by NSF grants GB-16321 and GB-37690, and NIH grant GM-15769.

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Carnosine in the Primary Olfactory Pathway

Abstract. *Carnosine (β-alanyl-L-histidine) is present in mouse olfactory bulbs and nasal olfactory epithelium at concentrations exceeding that previously reported for any brain region of any species. After peripheral deafferentation, carnosine concentrations in the olfactory bulbs decrease to less than 10 percent that of normal, while other amino compounds are unaffected. Carnosine appears to be highly localized to the primary olfactory pathway.*

Two naturally occurring dipeptides of histidine, carnosine (β-alanyl-L-histidine) (*1*) and homocarnosine (γ-aminobutyryl-L-histidine) (*2*), have been known as constituents of excitable tissue for many years. Nevertheless, virtually nothing is known of their function. While studying the effect of peripheral deafferentation on amino acid pools in the primary olfactory pathway of mice, I observed specific changes in the concentrations of carnosine measured by chromatographic and electrophoretic techniques. These observations may eventually lead to elucidation of the function of these dipeptides.

Extracts for analysis were prepared