Wenner, A. M. and D. L. Johnson. 1980. Land vertebrates on the California Channel Islands: sweepstakes or bridges? Pp. 497-530. *In:* D.M. Power (ed.), The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History: Santa Barbara, CA.

Willimas, D. F. 1983. Population surveys of the Santa Catalina, San Bernadino, and Suisun shrews. Contract No. 11310-1242-2. U. S. Dept. of Interior, Fish and Wildlife Service, Endangered Species Office: Sacramento, CA. 69 pp.

Dwarfism and Variability in the Santa Rosa Island Mammoth (*Mammuthus exilis*): An Interspecific Comparison of Limb-bone Sizes and Shapes in Elephants.

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Abstract – Mammoths (*Mammuthus exilis*) from the Pleistocene of Santa Rosa Island were small and highly variable in size. Linear measurements and principal components analysis scores from humeri and tibiae provide quantitative indices of size and shape for comparisons with the ancestral mainland mammoth,the two Recent species of elephants and another Pleistocene insular dwarf elephant (from Sicily). Adult elephantids appear to follow a single allometric pattern: a large proportion of the total variation is size-related and the remaining variability in shape is not species-specific. Although dwarf mammoths are significantly smaller than their mainland relatives and significantly more variable in size than other elephant species, they do not differ significantly in any index of shape or shape variability; nor do they appear to be achondroplastic. A combination of biological and geographic factors contributed to size reduction and size variability in the island mammoths.

Introduction

Dwarf mammoths (*Mammuthus exilis*), known from Pleistocene fossil deposits on Santa Rosa Island, are among the most intriguing endemics of the California Islands. Unique among mammoths for their small size — the smallest adults attained approximately one-third the shoulder height of their closest relatives on the mainland (Orr 1968) — they exemplify in their dwarfism a trend common among extinct island-dwelling members of the Elephantidae (Hooijer 1967; Sondaar 1977)

The Northern Channel Islands were united for a portion of the time mammoths inhabited them (Vedder & Howell 1980; Madden 1981b; Fergusson & Libby 1962). Fossil mammoth specimens have been found on San Miguel, Santa Cruz and San Nicolas Islands, but by far the most abundant and complete material, and that representing the smallest individuals, is known from Santa Rosa Island. From the perspective of preservational bias, it is perhaps not surprising that the more restricted Quaternary sediments of Santa Cruz Island have yielded mainly large dental specimens. The small number of mammoth specimens known from Santa Cruz and San Nicolas Islands have been described elsewhere (Cushing *et al.* 1984). The limited material available from San Miguel Island is retained in miscellaneous collections and has not yet been assembled or studied in a concerted fashion. For these reasons, I restrict my attention in this paper to material from Santa Rosa Island.

From the available fossils, it is evident that the mammoths, in addition to being small, were highly variable. Although I will here refer to all material from Santa Rosa Island as *M. exilis*, Orr (1968) and Madden (1981a) have suggested that the Santa Rosa Island material represents two or more distinct forms, and possibly two or more species of mammoth. The evidence currently is inconclusive. There is no discontinuity or clustering amongst the material now available (Fig. 1); if more than one mammoth species was endemic to the islands, a larger sample and better stratigraphic control will be needed before a pattern becomes apparent.

It is nevertheless clear that the adults span a remarkable range of sizes. Among mature specimens, for example, the largest individuals are estimated to be twice the shoulder height of the smallest (Orr 1968; Roth 1982).

Intermembral proportions in the dwarfs also vary and appear not to follow the simple size-related trends observed in mammoths from the mainland and both Recent genera of elephants (Roth 1984).

The variability of the island mammoths is interesting not only for what it can reveal about the biology of these animals, or the controversial geographical history of the California Islands (Johnson 1981; Azzaroli 1981), but also for its broader significance. Because dwarfism in the island mammoths is a dramatic manifestation of the island rule for mammalian body size (Foster 1964; Van Valen 1973; Heaney 1978; Lomolino 1985), it may ultimately provide insight on the rates and mechanisms of body size change in mammals (Roth 1992).

In this paper I examine variation in size and shape in some physically mature limb bones of mammoths (*Mammuthus exilis*) from Santa Rosa Island, and compare this with data from: 1) the Columbian mammoth (*M. columbi*), the inferred ancestral stock from the mainland (Madden 1981b; Roth 1982); 2&3) the two Recent species of elephants (*Elephas maximus* and *Loxodonta africana*), which provide indications of the ranges of variation that are observed within single extant species and 4) a Pleistocene dwarf elephant from Sicily (*E. falconeri*).

Materials and Methods

I concentrated on the tibia and humerus, because they were the most abundant long bone elements available in museum collections. Fusion of the epiphyses to the diaphysis (fusion scores greater than or equal to two at each epiphyseal-diaphyseal junction; Roth 1984) signalled physical maturity in the tibiae and humeri I measured for this study. For all specimens for which complete and associated skeletons were available (the two Recent species, and some of the mainland mammoths), I measured bones from one side of the body only.

Although comparisons of variability at the level of single populations are highly informative (see Yablokov 1974), they were not possible with the material available. Populations of the fossil taxa were difficult to define: records of stratigraphic position do not exist for most of the island mammoth specimens, and the systematics of mainland mammoths is problematic (Kurtén & Anderson 1980; Madden 1981a; Roth 1982; Graham 1986). Specimens are not abundant: the largest accumulations of mammoths on the mainland (see Dutrow 1980) have yielded small numbers of any one skeletal element. Physically mature specimens moreover constitute a small proportion of any population (or museum collection) of elephants, because the lengthy growth period of an elephant can extend into the fourth decade (Sikes 1971; McKay 1973). Even specimens of the Recent species are few, because they are not retained in quantity by museums: bones of such large size present storage problems.

Samples of the two Recent species included individuals of both sexes, some individuals with no data, some that were caught in the wild and others that were maintained in captivity (for varying periods of time). Source localities (where known) varied, and the sample of *Loxodonta africana* included at least one of the small "forest" forms from western central Africa (Brown 1934; Sikes 1971). The assortment of specimens was therefore diverse; if it was not clearly representative of any single population, it nevertheless gave an indication of the range of variation expressed within these species.

Of all the taxa considered here, *Elephas falconeri* is represented by the closest approximation of a population sample. The source of data for all but one individual of this species was Ambrosetti (1968) and his specimens derived from an exceptionally large accumulation in Spinagallo Cave, Sicily. Dimorphism in size, which Ambrosetti inferred to be intraspecific and sexual, is apparent in the distributions of his data.

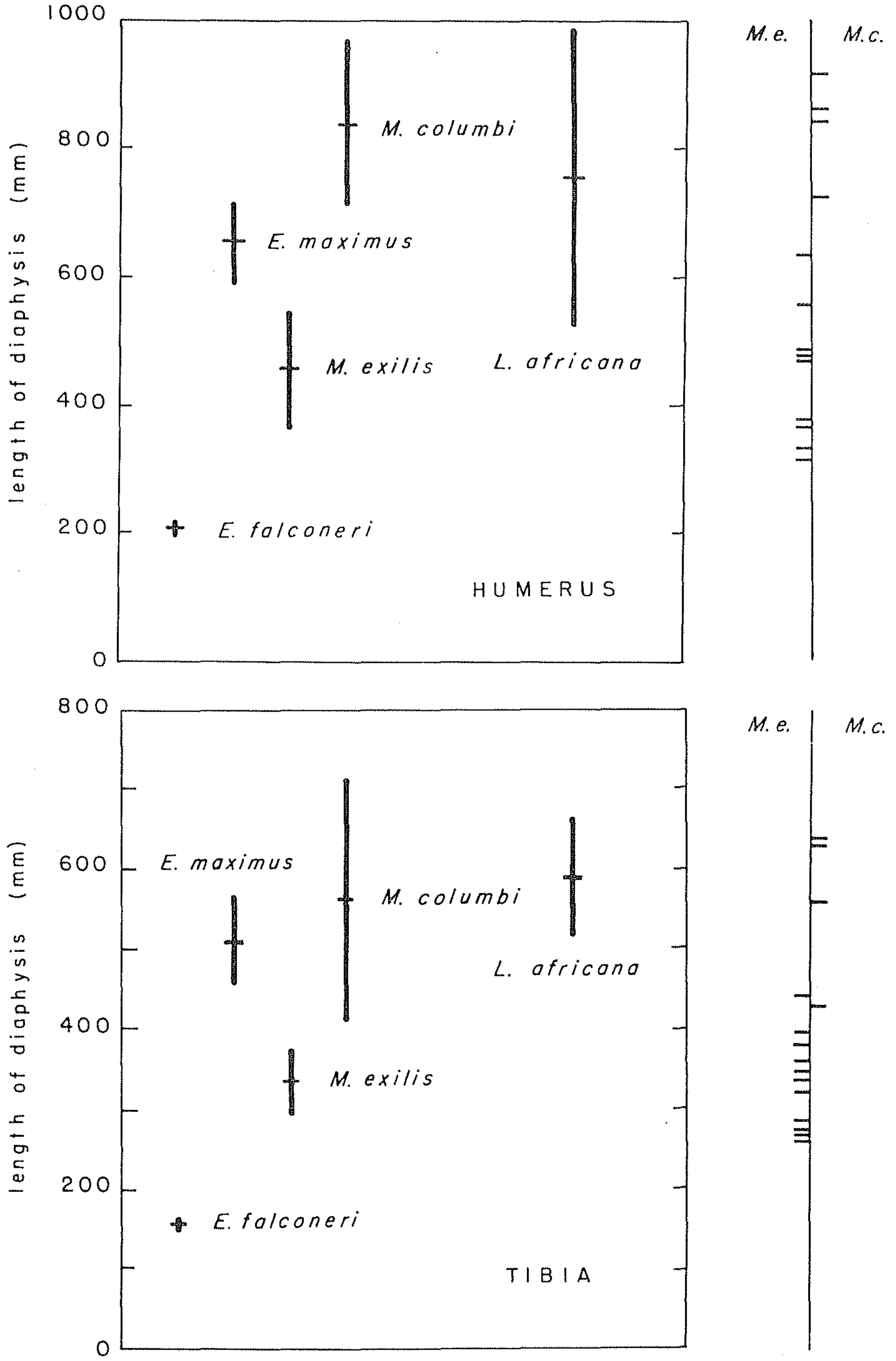

Figure 1. Diaphysis lengths for humerus and tibia of taxa examined in this study. Average lengths, L_1, and L_2 (95% confidence limits of the mean) are shown in the rectangular graphs at the left. To the right, the distributions of lengths of specimens of *Mammuthus exilis* (M.e.) and *M. columbi* (M.c.) may be examined for evidence of clustering and overlap. (Sample sizes are listed in Table 1.)

Although the samples used in this study were small and heterogeneous, they nonetheless (as I will show) provided a context for interpreting variability in the island mammoth.

Data were collected from the following sources: *Loxodonta africana* - American Museum of Natural History (AMNH), Smithsonian Institution (USNM), Philadelphia Academy of Natural Sciences (ANSP); *Elephas maximus* - AMNH, USNM, ANSP, Yale Peabody Museum (YPM), Field Museum (FMNH), University of Nebraska State Museum (UNSM); *E. falconeri* - UNSM, Ambrosetti's (1968) published account; *Mammuthus columbi* - UNSM, Los Angeles County Museum (LACM), Florida State Museum (UF), University of California Museum of Paleontology (UCMP), Cleveland Museum of Natural History (CMNH); *M. exilis* - LACM, Santa Barbara Museum of Natural History (SBMNH).

I took the following measurements on tibiae:

A. Widths:
  1. maximum antero-posterior diameter of the proximal end
  2. maximum transverse diameter of the proximal end
  3. minimum transverse diameter of the diaphysis
  4. maximum antero-posterior diameter of the distal end
  5. maximum transverse diameter of the distal end

B. Lengths:
  1. total length
  2. length of diaphysis

and the following measurements on humeri:

A. Widths:
  1. maximum transverse diameter of the proximal end
  2. maximum transverse breadth of diaphysis across the deltoid crest
  3. minimum transverse diameter of the diaphysis
  4. maximum transverse breadth of the distal end

B. Lengths:
  1. total length
  2. length of diaphysis
  3. length of (lateral) supinator crest

C. Other measurements:
  1. transverse diameter of proximal articular surface
  2. antero-posterior diameter of proximal end
  3. transverse breadth of distal articular surface

Statgraphics (Statistical Graphics Corporation) software was used for all statistical and principal components analyses.

I considered tibiae and humeri separately, and used three criteria to assess size for each. One criterion was simply the length of the diaphysis. The two other indices of size were principal axis (PC1) scores from two principal components analyses (PCAs), which I ran on covariance matrices of log-transformed values of: a) all the data and b) the width measurements (as defined above) only. After the eigenvectors are calculated but before PCA scores are computed, Statgraphics standardizes data by subtraction of the mean and division by the standard deviation of each measurement. Eigenvalues for the principal axes in all cases exceeded 0.97 and loadings of the variables were uniform and positive, justifying use of this axis as a measure of the overall size of a bone. Data for *Mammuthus columbi*, *M. exilis*, *Elephas maximus*, and *E. falconeri* were pooled for the PCAs and PCA scores subsequently were grouped by species and compared using Mann-Whitney-Wilcoxon (nonparametric) tests. The four aforementioned species together constitute two pairs of congeners, with one insular dwarf per pair. *Loxodonta africana* was omitted from the PCAs because *Mammuthus* and *Elephas* are more closely related (Shoshani *et al.* 1985).

Within species, I employed the following measures of size variability for each of the two bones. (1) The ratio of the largest to the smallest diaphysis length is one expression of the range of sizes represented in a sample. (2) Coefficients of variation (V) are commonly used as a measure of variability that is independent of absolute size; because samples were small, I used Haldane's (1955) correction factor (1 + 1/[4n]) to obtain nearly unbiased estimates. (3) The variances (s^2) of log-transformed data also have the property of size-independence, with the advantage that the significance of differences in variability can easily be computed from F-ratios (Lewontin 1966). Lastly (4&5), I computed variances for PC1 scores obtained from the two PCAs described above.

PCA scores also served as indices of shape. For each of the PCAs, high-ranking axes other than the principal axis (*i.e.*, PC2 and PC3; see Table 2) were readily interpretable as aspects of shape: the patterns of positive and negative loadings reflected contrasts in bone proportions that were easy to recognize visually and to describe in simple terms. I considered the axes in rank order; once I encountered an axis that was difficult to interpret intuitively, I examined no further axes from that analysis. PC2, PC3 and sometimes other axis scores, were used as measures of shape and the variances of these scores as measures of shape variability within species. As with the PC1 scores, Mann-Whitney-Wilcoxon tests and F-ratios were used to evaluate the significance of differences between species in shape and shape variability.

Results

For both the tibia and the humerus, all measures of size (PCA scores, diaphysis lengths) produced the same ranking of *Mammuthus* and *Elephas* species: *M. columbi* is

Table 1. Variability of bone size. For each of the measures of variability listed below, species are listed in order of the magnitude of their variability, from most to least variable. For 3, 4 and 5, variability of *Mammuthus exilis* was compared with that of the two *Elephas* species, with the following significance levels indicated: $P < 0.05$: *; $0.10 < P < 0.05$: @. (Sample sizes for a single species may differ because PCAs require complete, undamaged bones, whereas diaphysis lengths do not.)

	Index of Variability (*n*)			
Bone	Most Variable Species	....	....	.... Least Variable Species
1. Ratio of smallest to largest diaphysis length in each sample.				
	M. exilis	*E. falconeri*	*L. africana*	*E. maximus*
Humerus	0.58 (9)	0.62 (25)	0.70 (4)	0.80 (6)
Tibia	0.61 (11)	0.63 (72)	0.65 (7)	0.71 (7)
2. Coefficient of variation of diaphysis length (with Haldane's [1955] correction).				
	M. exilis	*L. africana*	*E. falconeri*	*E. maximus*
Humerus	27 (9)	21 (4)	17 (25)	9 (6)
Tibia	17 (11)	14 (7)	13 (72)	12 (7)
3. Variance of log-transformed diaphysis lengths.				
	M. exilis	*L. africana*	*E. falconeri*	*E. maximus*
Humerus	0.063 (9)	0.037 (4)	0.023* (25)	0.006* (6)
Tibia	0.028 (11)	0.020 (7)	0.014* (72)	0.012 (7)
4. Variance of PC1 score; PCA on all data (logs, cov.m.).				
	M. exilis	*M. columbi*	*E. falconeri*	*E. maximus*
Humerus	2.5 (6)	1.4 (2)	0.85 (25)	0.44* (6)
	E. maximus	*M. columbi*	*M. exilis*	*E. falconeri*
Tibia	1.04 (11)	0.88 (4)	0.81 (7)	0.41@ (51)
5. Variance of PC1 score; PCA on width data only (logs, cov.m.)				
	M. exilis	*M. columbi*	*E. falconeri*	*E. maximus*
Humerus	1.4 (6)	1.0 (2)	0.49@ (11)	0.15* (6)
	M. exilis	*M. columbi*	*E. maximus*	*E. falconeri*
Tibia	0.88 (9)	0.78 (4)	0.71 (11)	0.30* (51)

on average larger than *E. maximus*, which is similar to, but slightly larger than, *M. exilis*; *E. falconeri* is smallest of all (Fig. 1). The size difference between *M. exilis* and *M. columbi* was consistently significant ($P \leq 0.05$), except in one comparison ($P < 0.07$) for which the sample of *M. columbi* was very small ($n = 2$).

Of all of the taxa examined, *Mammuthus exilis* exhibited the greatest variability in size, by nine out of ten measures (Table 1). *Elephas maximus* was the most variable species in its PC1 score for tibial measurements, but its variance was not significantly greater than that of *M. exilis* ($0.25 < P < 0.5$). By contrast, *M. exilis* was often significantly more variable than *E. falconeri* and *E. maximus* (Table 1). The difference in variability between *M. exilis* and *E. maximus* was greatest for measurements on the humeri ($P < 0.05$, consistently).

The principal component axes used as indices of shape are listed in Table 2 with their interpretations. The eigenvalues were all small and superficially they may appear to be insubstantial. To take an example, PC2 in the analysis of all humerus data accounted for 1% of the total variance. If one calculates the amount of variation in the original measurements that this represents, however, the 1% is equivalent to a coeffient of variation of 17. (If this seems counter-intuitive, note that we are dealing with a large total variance – total length, for example, varies by a factor of five – and with log-transformed data.) PC3 from the same analysis accounted for a proportion of the total variance equivalent to a coefficient of variation of 12 in the original measurements and even the small eigenvalue (0.19 %) associated with PC4 on all data from the tibia corresponds to a coefficient of variation of 5. Thus, although size-related variation predominates within this sample of four species, and accounts for a large proportion of the total variance, variability in shape is appreciable in absolute terms.

The variation in shape was not species-specific, however. *Mammuthus exilis* was not statistically distinguishable from the other taxa in any measure of shape of the bones: average scores on the principal components axes described in Table 2 showed no significant differences ($P > 0.05$ in all cases, and with only one exception $P > 0.4$). Moreover, although *M. exilis* varied greatly in size (Table 1), it was often less variable than *E. maximus* in bone shape (Table 3).

Discussion

The analyses described above indicate that adults of two large species of elephants, *Mammuthus columbi* and *Elephas maximus*, and their insular dwarfed congeners, *M. exilis* and *E. falconeri*, follow a single allometric pattern in the shapes of their humeri and tibiae. A large proportion of the total variation is size-related, and the remaining variability in shape is not species-specific. Although none of the species consistently shows more variation in bone shape than the others, the dwarf mammoth from the California Islands is distinctive in being extraordinarily variable in size.

Range estimates for shoulder heights may be derived from the sizes of individual bones. Orr (1968) estimated that shoulder heights of the adult, living *Mammuthus exilis* ranged from 4-8 ft (approximately 120-240 cm) with a mode at 6 ft (180 cm); Stock (1935) had judged them to be between 6-8 ft or 9 ft (180-270 cm). Although these authors did not state how they obtained these estimates, my own calculations of height, derived from *Elephas maximus* and *Loxodonta africana* skeletons comprising elements similar in size to available *M. exilis* specimens, are consistent with them (Roth 1982): skeletal height (a measurement which differs from shoulder height by an amount equivalent to the thickness of the soft tissues) ranged from 105-235 cm.

Dwarfism in the island mammoths may have been the consequence of a combination of processes. (1) Stunting. The restricted habitat offered by an island imposes resource limitations; food shortages are exacerbated by

Table 2. Indices of bone shape. Measurements with heavy positive or negative loadings are listed with a verbal description of the contrasts they reflect. (a) = axes on which achondroplastic individuals should have extreme scores.

Bone	PCA	Axis	% Total Variance Explained	Contrast Reflected (measurement #s)	
Humerus					
	All Data	PC2 (a)	1.01	long; large articular surfaces (C1,C3,B2,B3)	short; stout midshaft (A2,A3)
	"	PC3 (a)	0.52	long & narrow (B1,B2,B3)	short & broad (C1,C2,C3,A1, A3, A4)
	"	PC4	0.27	short with large distal end (A4,B3,C3)	long with large prox end & midshaft (B1,B2,C1,C2,A1,A3)
	Widths Alone	PC2	0.98	broad distal & proximal ends (A1,A4)	stout diaphysis (A2,A3)
Tibia					
	All Data	PC2 (a)	0.41	short, wide & thick (A1,A2,A3,A4,A5)	long & narrow (B1,B2)
	"	PC3	0.21	large distal ends (A3,A4,A5)	large proximal ends (A1,A2)
	"	PC4	0.19	large A-P dimensions (A1,A4)	large transverse dimensions (A2,A5)
	Widths Alone	PC2	0.28	large distally (A5,A4,A3)	large proximally (A1,A2)
	"	PC3	0.26	transverse proximal end large (A2)	other measurements large

Table 3. Variability of bone shape. Variances of PCA scores for *Mammuthus columbi*, though computed, were based upon small samples; they are not listed here, in order to highlight comparisons between *M. exilis* and the two *Elephas* species.

			Variances (*n*)		
Bone	PCA	Axis	Most Variable Species	....	Least Variable Species
Humerus	All Data	PC2	*M. exilis* 0.141(6)	*E. maximus* 0.080(6)	*E. falconeri* 0.061(11)
	"	PC3	*E. maximus* 0.097(6)	*M. exilis* 0.029(6)	*E. falconeri* 0.0095(11)
	"	PC4	*E. maximus* 0.030(6)	*E. falconeri* 0.016(11)	*M. exilis* 0.010(6)
	Width Data	PC2	*E. maximus* 0.065(6)	*E. falconeri* 0.024(11)	*M. exilis* 0.006(6)
Tibia	All Data	PC2	*E. maximus* 0.062(10)	*M. exilis* 0.015(6)	*E. falconeri* 0.013(50)
	"	PC3	*M. exilis* 0.034(6)	*E. maximus* 0.023(10)	*E. falconeri* 0.013(50)
	"	PC4	*E. maximus* 0.030(10)	*M. exilis* 0.023(6)	*E. falconeri* 0.008(50)
	Width Data	PC2	*M. exilis* 0.029(9)	*E. maximus* 0.013(10)	*E. falconeri* 0.013(50)
	"	PC3	*E. maximus* 0.044(10)	*M. exilis* 0.011(9)	*E. falconeri* 0.007(50)

destruction of habitat (Laws 1970; Johnson 1972, 1980). (2) Maternal effects. In mammals, females that are small (for whatever reasons), tend to give birth to small offspring. Even in small, polytochous species like rodents, the effects are measurable (Roth & Klein 1986); in larger monotochous forms (and hence, probably elephants) the effects often persist into adulthood (Snow *et al.* 1981). (3) Natural selection for small body size. Given 1 and 2 above, individuals capable of attaining reproductive maturity on a low plane of nutrition should be favored. The result, potentially, would be a genetic assimilation of stunting (Bonner 1968; Waddington, Marshall & Corruccini 1978). (4) Release from selection against small body size. Large predators capable of preying upon small elephants were absent from the California Islands (Kurtén & Anderson 1980).

Prothero & Sereno (1982) invoked achondroplasia, a form of dwarfism with a simple genetic basis, as a mechanism (presumably in conjunction with either natural selection or genetic drift) allowing rapid size reduction in insular mammals. The achondroplastic condition is marked by premature cessation of longitudinal growth in long bones, but continuation of periosteal deposition (Maroteaux & Lamy 1964; Rimoin *et al.* 1970); hence achondroplastic individuals would appear as extreme scores on principal component axes that contrast short, robust bones with longer, slenderer ones. Neither *Mammuthus exilis* nor *Elephas falconeri* scored particularly high, or showed consistently greater variability on the relevant PCA axes (Table 3), so achondroplasia must be ruled out for these dwarf elephants.

A combination of factors may explain the variation in size of the dwarf mammoths. (1) Because the fossil record samples through time, a population in the process of dwarfing, fluctuating or increasing in body size will appear highly variable. (2) With changing sea level, the islands united or subdivided, and their land area fluctuated. Variation in the geography of the islands would isolate populations, permitting divergence, and change environmental conditions and selection pressures (Orr 1968; Johnson 1978). (3) Periodic invasion by large individuals from the mainland could result in introgression and contribute large specimens to the sample (Wenner & Johnson 1980). (4) Relaxation of selection for large body size, as a result of absence of predators (see above) could also contribute variation.

Mammoths from Santa Rosa Island varied markedly in intermembral proportions (Roth 1984), as well as in size. In striking contrast, the shapes of single limb bones do not vary greatly: there is no evidence that variation in tibiae or humeri differs qualitatively or quantitatively from that observed within other species of elephants, and a single size-related trend predominates.

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Literature Cited

Ambrosetti, P. 1968. The Pleistocene dwarf elephants of Spinagallo (Syracusa, south-eastern Sicily). Geol. Rom. 7:277-398.

Azzaroli, A. 1981. About pigmy mammoths of the northern Channel Islands and other island faunas. Quat. Res. 16:423-425.

Bonner, J.T.B. Size change in development and evolution. J. Paleontol. 42:1-15.

Brown, C.E. 1934. Captive pigmy elephants in America. J. Mamm. 15:248-250.

Cushing, J., M. Daily, E. Noble, V.L. Roth and A. Wenner. 1984. Fossil mammoths from Santa Cruz Island, California. Quat. Res. 21:376-384.

Dutrow, B.L. 1980. Metric analysis of a late Pleistocene mammoth assemblage, Hot Springs, South Dakota. M.S. thesis, Southern Methodist University, Dallas, TX. 165 pp.

Fergusson, G.J. and W.F. Libby. 1963. UCLA Radiocarbon dates II. Radiocarbon, 5:1-22.

Foster, J.B. 1964. Evolution of mammals on islands. Nature 202:234-235.

Graham, R.W. 1986. Taxonomy of North American mammoths. Pp. 165-169 *In:* G. C. Frison and L. C. Todd (eds.), The Colby mammoth site – taxonomy and archaeology of a Clovis kill in northern Wyoming. University of New Mexico Press: Albuquerque, NM.

Haldane, J.B.S. 1955. The measurement of variation. Evolution 9:484.

Heaney, L.R. 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of southeast Asia. Evolution, 32:29-44.

Hooijer, D.A. 1967. Indo-Australian insular elephants. Genetica 38:143-162.

Johnson, D.L. 1972. Landscape evolution on San Miguel Island, California. Ph.D. dissertation, University of Kansas, Lawrence, KS. 622 pp.

_____ 1978. The origin of island mammoths and the Quaternary land bridge history of the northern Channel Islands, California. Quat. Res. 10:204-225.

_____ 1980. Episodic vegetation stripping, soil erosion, and landscape modification in prehistoric and Recent historic time, San Miguel Island, California. Pp. 103-122. *In:* D.M. Power (ed.), The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History: Santa Barbara, CA. 787 pp.

_____ 1981. More comments on the northern Channel Islands mammoths. Quat. Res. 15:105-106.

Kurtén, B. and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press: New York, NY. 442 pp.

Laws, R.M. 1970. Elephants as agents of habitat and landscape change in East Africa. Oikos 21:1-15.

Lewontin, R. C. 1966. On the measurement of relative variability. Syst. Zool. 15:141-142.

Lomolino, M.V. 1985. Body size of mammals on islands: the island rule reexamined. Amer. Nat. 310-316.

Madden, C. T. 1981a. Mammoths of North America. Ph.D. dissertation. University of Colorado, Boulder, CO. 271 pp.

_____ 1981b. Origins(s) of mammoths from northern Channel Islands, California. Quat. Res. 15:101-104.

Maroteaux, P. and M. Lamy. 1964. Achondroplasia in man and animals. Clin. Orthopaed. & Related Res. 33:91-103.

Marshall, L.G. and R.S. Corruccini. 1978. Variability, evolutionary rates, and allometry in dwarfing lineages. Paleobiology 4:101-119.

McKay, G.M. 1973. Behavior and ecology of the Asiatic elephant in southeastern Ceylon. Smithsonian Contrib. Zool. 125:1-113.

Orr, P.C. 1968. Prehistory of Santa Rosa Island. Santa Barbara Museum of Natural History: Santa Barbara, CA. 253 pp.

Prothero, D. and P.C. Sereno. 1982. Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain. Paleobiology 8:16-30.

Rimoin, D.L., G.N. Hughes, R.L. Kaufman, R.E. Rosenthal, W.H. McAlister and R. Silberberg. 1970. Endochondral ossification in achondroplastic dwarfism. New England J. Medicine 238:728-735.

Roth, V.L. 1982. Dwarf mammoths from the Santa Barbara, California Channel Islands: size, shape, development and evolution. Ph.D. dissertation, Yale University, New Haven, CT. 277 pp.

_____ 1984. How elephants grow: heterochrony and the calibration of developmental stages in some living and fossil species. J. Vert. Paleo. 4:126-145.

_____ 1992. Inferences from allometry and fossils: dwarfing of elephants on islands. Pp. 259-288 *In:* D. Futuyma and J. Antonovics, (eds.), Oxford surveys in evolutionary biology. Vol. 8. Oxford University Press: Oxford, ENGLAND.

______ and M.S. Klein. 1986. Maternal effects on body size of large insular *Peromyscus maniculatus*: evidence from embryo transfer experiments. J. Mamm. 67:37-45.

Shoshani, J., L.M. Lowenstein, D.A. Walz and M. Goodman. 1985. Proboscidean origins of mastodon and wooly mammoth demonstrated immunologically. Paleobiology 11:429-437.

Sikes, S.K. 1971. The natural history of the African elephant. Weidenfeld and Nicolson: London, ENGLAND. 397 pp.

Snow, M.H.L., P.P.L. Tam and A.L. McLaren. 1981. On the control and regulation of size and morphogenesis in mammalian embryos. Pp 201-218. *In:* S. Subtelny and U. K. Abbot (eds.), Levels of genetic control in development. A.R. Liss: New York, NY. 255 pp.

Sondaar, P.Y. 1977. Insularity and its effect on mammal evolution. Pp. 671-707 *In:* M.K. Hecht, P.C. Goody and B.M. Hecht (eds.), Major patterns in vertebrate evolution. Plenum Press: New York, NY. 908 pp.

Stock, C. 1935. Exiled elephants on the Channel Islands, California. Sci. Monthly 41:205-214.

Van Valen, L.M. 1973. Pattern and the balance of nature. Evol. Theory 1:31-49.

Vedder, J.G. and D.G. Howell. 1980. Topographic evolution of the Southern California Borderline during Late Cenozoic time. Pp 7-31. *In:* D. M. Power (ed.), The California Islands: Proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History: Santa Barbara, CA. 787 pp.

Waddington, C.H. 1975. The evolution of an evolutionist. Cornell University Press: Ithaca, NY. 328 pp.

Wenner, A. and D.L. Johnson. 1980. Land vertebrates on the California Channel Islands: sweepstakes or bridges? Pp. 497-530. *In:* D. M. Power (ed.), The California Islands: Proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History: Santa Barbara, CA. 787 pp.

Yablokov, A.V. 1974. Variability of mammals. Amerind Publishing Co.: New Delhi, INDIA. 350 pp.

Control of Feral Sheep (*Ovis aries*) on Santa Cruz Island, California

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Abstract. - Overgrazing by feral sheep (*Ovis aries*) has contributed to soil erosion and reduction in native plant populations on Santa Cruz Island since sheep were introduced in the mid-1800's. After The Nature Conservancy acquired an interest in the western 90% of the island in 1978, contract research was undertaken leading to a sheep eradication program commencing in 1980. Partitioning of the island into 23 pastures by repairing existing fences followed by systematic hunting resulted in the near elimination of sheep on TNC property by 1989. Hunting in the boundary area will continue to prevent recolonization of sheep from the eastern portion of the island. Extensive vegetation and photo monitoring to document the recovery of the landscape was instituted in 1980.

Introduction

Islands, isolated by time and distance from neighboring landmasses, often support natural communities that exhibit unique characteristics. Island flora and fauna may evolve with considerably lessened selective pressures than face similar taxa on the mainland, making them particularly vulnerable to deliberate or accidental introductions of non-indigenous species (IUCN 1984). Insular ecosystems that have evolved without the presence of large herbivores may exhibit drastic reductions in populations of endemic plants when subjected to grazing (Carlquist 1974; Coblentz 1977).

While the presence and impacts of goats (*Capra hircus*) and sheep (*Ovis aries*) on a number of the world's islands have been investigated during the past decade (Rudge 1970; Coblentz 1978), the documentation of control programs is minimal (Stone 1986).

Management of feral sheep on Santa Cruz Island, the largest of the eight California Channel Islands, has been of concern to landowners and biologists for many years. The feral sheep control program undertaken by The Nature Conservancy (TNC), provides an excellent opportunity to examine a successful management strategy and to document the elimination of an introduced herbivore.

Geographical Setting and History

Santa Cruz Island is located about 39 km south of Santa Barbara, California. Thirty-eight km long and ranging from 3-11 km wide, the island encompasses about 248 km^2. The island's large central valley is bordered on the north by a mountain range oriented on an east-west axis and has an average elevation of about 610 m and a maximum elevation of nearly 750 m. The north shore is rugged with steeply dissected ridges and slopes up to 30° while the south range with a maximum elevation of 464 m has gentler slopes and broader drainages.

The Mediterranean climate is characterized by hot, dry summers and mild, wet winters. Annual rainfall of about 51 cm falls mainly between November and April (Santa Cruz Island Ranch records 1977 *in* Brumbaugh 1980). Mean temperatures in the central valley range from 12-21° C (Brumbaugh 1980).

Of the estimated 625 plant species found on Santa Cruz Island, about 480 are assumed to be indigenous. Forty-three plant taxa are endemic

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