CALIFORNIA'S CHANNEL ISLANDS:
A ONE-WAY TRIP IN THE TUNNEL OF DOOM

Larry D. Agenbroad

Dept. of Geology/Quaternary Studies, Northern Arizona University, Flagstaff, AZ 86001
(520) 523-2379, FAX (520) 523-9220, E-mail: larry.agenbroad@nau.edu
and
Santa Barbara Museum of Natural History, Santa Barbara, CA 93105
(805) 682-4711, FAX (805) 569-3170

ABSTRACT

Islands have impoverished biological communities when contrasted with continents. Islands are classified as "continental" (being, or having been attached to the mainland), or "oceanic" (separated by deep ocean straits from the mainland). Islands are isolated, their faunas are often described as impoverished, or depauperate, and they often have unique biological forms. Islands are extinction loci. Some islands contain the remains of Pleistocene proboscideans. The Northern Channel Islands of California are compared to island characteristics on the global scale. Extinction of some Channel Islands fauna is documented, and it still may be at work.

Keywords: California Channel Islands, pygmy mammoths, extinction, oceanic islands, Pleistocene.

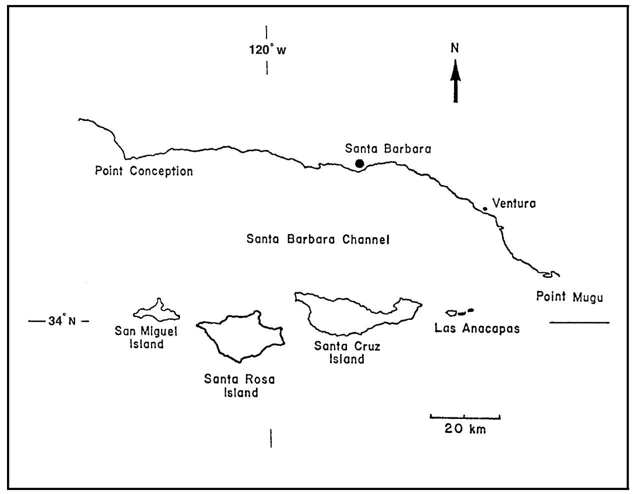

Figure 1. A location map of California's Northern Channel Islands.

INTRODUCTION

"Islands, in general, are biologically anomalous."

"Islands are a haven and breeding grounds for the unique and anomalous."

"They (islands) are natural laboratories of extravagant evolutionary experiments."

"Islands are where species go to die."

".......insular evolution.....tends to be a one-way tunnel towards doom."

The preceding quotes and many similar ones came from a book published in 1996 by David Quammen, entitled, "The Song of the Dodo." The subtitle is, "Island biogeography in an age of extinctions." In the book, Quammen describes and discusses the reasons for the unique biology of islands and why extinction might be considered the "norm" for island biota. The California Channel Islands (Figure 1) are no exception.

There is an extensive history of island research and researchers, many of whom Quammen (1996) discusses or describes. Additional researchers will be discussed in this presentation, beginning with Paul Sondaar, a Dutch scientist interested in fossil faunas of islands, and how they got to the islands, were changed by the islands, and ultimately became extinct.

Let me say, at the onset, that I am not a biogeographer, in the traditional sense of the word. Nor am I a biologist who has studied modern island flora and fauna. I will lay claim to the fact that I am a paleontologist who specializes in mammoths and other extinct Pleistocene megafauna (> 45 kg live weight). It has been my good fortune to become involved in the study of the Northern Channel Islands of California, because three of these islands contain the only pygmy mammoth population in the world!

MATERIALS AND METHODS

I would like to cover some basic facts about islands, island proboscidean biogeography, and island faunas (Table 1). Then I would like to apply these general characteristics to four specific islands: San Miguel, Santa Rosa, Santa Cruz, and Anacapa. What you must keep in mind is that these modern islands do not tell the entire geohydrologic story.

There are six islands, or island groups that produced the remains of fossil proboscideans (Table 2; Figure 2). These

Table 1. Island characteristics.

a. islands are classed as 'oceanic', or 'continental'
b. islands are biologically impoverished and unbalanced
c. islands are isolate
d. islands are restricted (area, environments)
e. islands are large, or small
f. barren islands acquire biologic populations
g. island fauna undergo size change
h. islands have unique selective pressures
i. oceanic islands lack large carnivores
j. islands are localities of extinction (doom!)

are: 13 islands in the Mediterranean Sea; several islands in the Indonesian archipelago; a few islands in the Philippine archipelago; the Japanese archipelago; Wrangel Island in the Siberian Arctic Ocean; and the Northern Channel Islands of California. Only Wrangel Island and the northern Channel Islands of California have fossil mammoths. A recent article (Thikonov 1997) states that the Wrangel mammoths are no longer considered to be dwarfs. That means the California Channel Islands of San Miguel, Santa Rosa, and Santa Cruz are unique! They have the only pygmy mammoth fossils in the world!

Table 2. Proboscidean fossils on islands or island groups (Shoshani and Tassy 1996; Agenbroad 1998).

Locality	Islands	Proboscidean
Mediterranean Sea	Sardinia, Crete, Sicily, Malta	pygmy elephants
	Cyclades islands, Dodecanese	*Elephas falconeri*
	islands, Cyprus,	*Elephas leonardi*
	Crete	*Elephas mnaidriensis*
Indonesian archipelago	Timor, flores, Sumba, Java,	pygmy stegodons
	Sulawesi	elephants
		Stegodon florensis
		Stegodon sompoensis
		Stegodon tiniorensis
		Stegodon hypsilophus
		Elephas celebensis
		Elephas hysandrindicus
		Elephas maximus
Philippine archipelago	Mindanao	stegodons and elephants
	Luzon	*Stegodon luzonensis*
		Stegodon mindanensis
		Stegodon trigoncephalus
		Elephas beyeri
Japanese archipelago	Ryukyu islands	elephants
	Taiwan*	
Wrangel Island		mammoths
		Mammuthus primigenius
California Channel	San Miguel	mammoths
Islands	Santa Rosa	*Mammuthus columbi*
	Santa Cruz	*Mammuthus exilis*

*Taiwan is not usually considered part of the Japanese archipelago.

RESULTS

Elaboration of Island Characteristics and their Application to the Northern Islands

Classification

Islands are classified as 'oceanic' or 'continental.' (Darlington 1957; Sondaar 1977; Quammen 1996). Continental islands are those that are, or have been attached to the adjacent continent by a land bridge. These islands have a larger, more diverse fauna than oceanic islands. Oceanic islands are those separated from an adjacent continent by a

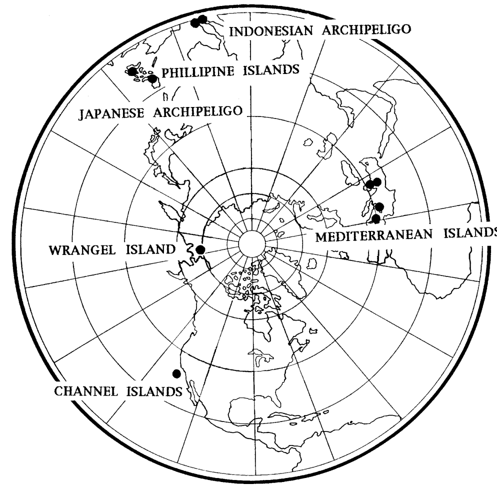

Figure 2. Islands or island groups known to have remains of fossil proboscideans.

deep water strait. They have been uplifted from the ocean floor by tectonic, or volcanic forces. Oceanic islands are depauperate (biologically) as compared to continental islands.

It has been stated, repeatedly, in the literature that the Northern Channel Islands were connected to the coast of California by a land bridge. That notion was based on the premise that elephants could not swim, and since elephant (mammoth) remains were found on the Northern Channel Islands they must have been connected to the mainland (Fairbanks 1897; Stock and Furlong 1928; Chaney and Mason 1930; Stock 1935, 1943; Valentine and Lipps 1967; Von Bloecker 1967; Weaver and Doerner 1967; Hooijer 1976; Madden 1977; Azzaroli 1981). Wenner and Johnson (1980) provided sufficient evidence to conclude that the Northern Channel Islands are to be classed as "oceanic" islands. They were never connected by a land bridge—at least in the mammoth period (the late Pleistocene).

Biologic Impoverishment

Oceanic islands have only a small representation of the species diversity of the nearest mainland (Johnson 1983). Wenner and Johnson (1980) provided tables of southern California fauna as contrasted to the Northern Channel Islands. They indicate at least 127 species of mainland land vertebrates (excluding avifauna). In contrast, they list the Northern Channel Islands as having only 12 or 13 species native to the island, including extinct ones. Table 3 provides a list of fossil fauna from the islands. Extant, endemic land mammals on Santa Rosa Island include the island fox (*Urocyon littoralis santarosae*), the spotted skunk (*Spilogale gracilis amphias*), and the deer mouse (*Peromyscus maniculates streatori*) (Orr 1968). Three other species of living deer mice are proposed from Santa Cruz Island and one extinct form (*Peromyscus anyapahensis),* from Anacapa Island. This provides a total of thirteen fossil species and up to seven species of extant vertebrates (omitting extant snakes).

Either assessment is sufficient to illustrate the extreme biological impoverishment of the Channel Islands as compared to coastal southern California. Isolation is easily demonstrated by a deep water strait present between the Northern Channel Islands and the California coast (Wenner and Johnson 1980). This was so, even in the eustatic sea level fluctuations of the Pleistocene. During an ice age, sea level was lowered by as much as 100 m by the fact that precipitation was stored on the continents as snow and ice, creating the ice sheets, glaciers, permafrost, and snow fields characteristic of an "Ice Age." The lowering of sea level by as much as 100 m made a drastic change to the Pleistocene coastline of California, and an even more impressive change to the shoreline of the Ice Age island named Santarosae (Figure 3) by Phil Orr (1968). The modern Channel Islands are simply the subaerial mountain tops of Pleistocene Santarosae. Using a simplistic map of the Santarosae land area compared to the land area of the modern islands, approximately

Table 3. Fossil vertebrate, terrestrial fauna from the Northern Channel Islands (Guthrie 1998).

Land Vertebrates	
Columbian mammoth	*Mammuthus columbi*
pygmy mammoth	*Mammuthus exilis*
ornate shrew	*Sorex ornatus*
"giant" deer mouse	*Peromyscus nesodytes*
"giant" meadow vole	*Microtus miguelensis*
Anacapa deer mouse	*Peromyscus anyapahensis*
Avifauna	
Condor (?)	*Gymnogyps californicus*
vampire bat	*Desmodus stocki*
caracara	*Caracara prelutosa*
flightless goose	*Chendytes lawi*
owl	*Asio prelutosa*
gannet	*Morus reyanus*
auklet	*(currently undescribed)*
Reptiles	
(Pacific) San Miguel rattlesnake	*Crotalus viridis*

Note: (?) remains on San Miguel w/extinct vole (condor is "extinct" on the islands).

76% of ancient Santarosae was submerged, as sea level rose with the post-Pleistocene warming and resultant meltoff, returning water to the ocean. During sea level lowering the strait separating Santarosae was reduced to approximately 6 to 9 km. It has been demonstrated (Wenner and Johnson 1980) that elephants (and probably mammoths) could easily have swum the strait formed by Pleistocene sea level lowering.

Paul Sondaar (1977) presents data that suggests oceanic islands are represented by only a few large mammals. Large mammals found most often on oceanic islands are good swimmers. They include elephants, deer, and hippopotami. Similarly, such islands lack large carnivores (poor swimmers). He goes further, to state that if an oceanic island has one or more members of his "elephant-deer" fauna, they got there by a "sweepstakes" route (Sondaar 1977; Wenner and Johnson 1980). Quammen (1996) makes a more definitive statement, "Every terrestrial animal on an oceanic island, and every plant, is descended from an animal or plant that arrived there by cross-water dispersal after the island was formed." The smaller animals were most likely castaways (or waif migrants) which clung to debris from mainland floods until they arrived at the island. This would have been even more feasible during lowered sea level. There is, however, no known Pleistocene record for foxes nor skunks on the islands.

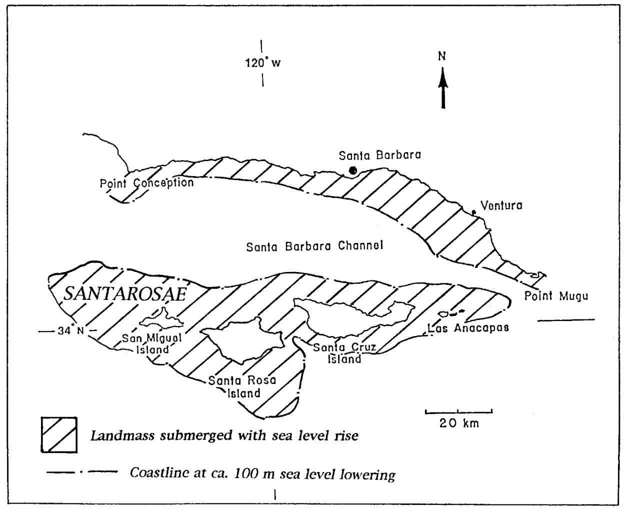

Figure 3. The modern Channel Islands compared to the Pleistocene island Santarosae. The Pleistocene coastlines of Santarosae and the mainland are due to approximately 100 m sea level drop. The modern islands represent the mountains of Santarosae after post-Pleistocene eustatic sea level rise.

Orr (1968) reported the collection of one fox skull he collected from the upper part of the Tecolote Formation (± 16,000 yr BP). He goes on to state the specimen was "lost at sea." Paul Collins (SBMNH) found the specimen in other collection material, compared it with fox specimens from San Miguel and Santa Rosa islands, and found it to be within the range of modern specimens (Collins 1993). Until the skull is dated, it is uncertain as to whether it is a Pleistocene fox, or a Holocene fox whose den was in Pleistocene sediments.

Island foxes have low genetic variability (Roemer et al. 1994), are threatened by canine diseases, and are classed as a threatened species by the California Department of Fish and Game (Crooks and Van Vuren 1994).

Island Fauna and Size Change

Darwin noted that on islands, large mainland animals often became smaller, whereas small mainland animals often became larger. He attributed dwarfism to a process of pathologic degeneration (Sondaar 1977). The change of size noted above is commonly known as "Foster's Rule" (Foster 1964). Sondaar (1977) suggests that rather than degenerate forms, that smaller large mammals and larger small animals may be an adaptive response producing an animal better suited for island life. In the absence of carnivores, large size loses its adaptive value and selective pressures for becoming smaller are: 1) increased mobility, 2) less food consumption, and 3) a reduction in range requirement. He (Sondaar 1977) also notes that a common development of island elephants, deer, and hippos is a shortening of the distal part of the legs. This fact allows for low speed locomotion in a varied, mountainous environment (Sondaar 1977). The overall size reduction also lowers the center of gravity of the animal (over its mainland ancestral form) which is advantageous (and a selective advantage) in a rugged mountainous island, allowing negotiation of steeper slopes, giving access to rugged grazing areas.

DISCUSSION

All of the features, discussed above, are demonstrable for *Mammuthus exilis* on the Channel Islands. It is my theory that as sea level rose, reducing the resource area(s), crowding the remaining island, that mainland size mammoths (*M. columbi*) that originally colonized Santarosae were selected against, giving rise to their smaller (pygmy) descendents who could reach resources that were unavailable to the larger forms. The ratio of *M. columbi* remains to *M. exilis* is approximately 1 to 10 in the on-going controlled survey for mammoth remains, initiated in 1996.

Island environmental pressures were selective for smaller, more mobile mammoths that could reach rugged resources unavailable to the larger form and which needed a smaller amount of those resources for survival, than did the ancestral, mainland form.

Extinction

Three causes of extinction on oceanic islands are discussed by Sondaar (1977). They include: 1) introduction of new, mainland species by way of a land bridge; 2) arrival of humans; and 3) periodic overpopulation leading to overgrazing of vegetation resulting in malnutrition and starvation. An additional category, with similar results would be drought, or lightning strike fires.

The first two causes have little to do with the pygmy mammoths of the Northern Channel Islands. However, the arrival of humans was Orr's (1968) favorite theory for the extinction of island mammoths. Results of the third cause would be dramatic population reduction, limiting the surviving genetic diversity of the survivor's gene pool, and selection for traits advantageous to the island environment. Sondaar (1977) feels this would cause rapid evolution of the island forms but make them more susceptible to extinction.

Quammen (1996) gleaning from others, cites four sources of "population uncertainty:" 1) demographic: variation in birth rates, death rates, and ratio of sexes; 2) environmental: fluctuation of weather, food, disease, competition; 3) natural: floods, droughts, wild fires; and 4) genetic: reduction of allelles in the gene pool increasing the frequency of harmful traits, and inbreeding of surviving populations.

There is another negative factor which has been alluded to in the previous discussions, that is dividing or splitting habitats. It is generally accepted that small populations in fragments of former habitat are especially vulnerable to the four sources of population uncertainty.

Recall now that Santarosae is being inundated by the post glacial melt of continental ice. Approximately 11,000 years ago, the modern four islands became separate (isolate) and are the mountainous remainder of ancient Santarosae. The extinction causes, or "population uncertainties" are focused on small, isolated, inbreeding populations, and, as we know, *Mammuthus exilis* is extinct!

Is the "Tunnel of Doom" Still Active?

My answer is "yes." The most recent victim, in my opinion, is the Island fox (*Urocyon littoralis*). There is one tentative report of the fox in the Pleistocene (Orr 1968), however it may have represented a den <u>in Pleistocene sediments</u>, rather than a Pleistocene fox. There is no question this charming little animal was (and is) present in the Holocene. It has been suggested that it may have been brought to the islands as pets, by Chumash people (Orr 1968; Johnson 1983), and they are as early as 11,700 Yr BP according to the record in Daisy Cave, San Miguel Island (Erlandson et al. 1996; Guthrie 1998).

The possible Pleistocene specimen was the same size as extant animals, which led to some question of its Pleistocene antiquity (Collins 1993). Those remains were thought to have been "lost at sea" (Orr 1968; Guthrie 1998), however, it was relocated by Paul Collins (Johnson 1983). Whether Pleistocene or Holocene, the indications of last August are that the Island Fox has become very scarce on the islands. National Park Service fox trapping efforts during my August 1998 stay on the island of Santa Rosa yielded scant results—a sharp contrast to August 1994, or August 1996. The suspected cause of declining fox numbers is heartworm. But isn't that (disease, not heartworm) one of the extinction factors that Quammen (1996) postulated for island animals. The disease appears to be transferred from the mainland to the island by mosquitos (Paul Collins, pers. comm. 1998).

There are possibly other examples I could cite, but as I said at the beginning of this presentation, I am not a biological or zoological researcher working on extant populations. My research subjects, the pygmy mammoths (*Mammuthus exilis*), have already made their trip through the tunnel! They met DOOM! They are extinct!

I, for one, regret their loss. Imagine a 1 to 2 m tall mammoth—one I refer to as a "house mammoth," or an "attack mammoth." I would love to have seen the reaction of a German Shepherd, or Rottweiler that jumped the fence into my yard!

The world's only island-inhabitating mammoth! I only missed it by ± 11,000 to 12,000 years. We still do not know the events that shaped this exceptional creature. It will take more field research, and many more absolute dates to understand the timing and sequence of events that took place in transit, through the tunnel. In particular, the timing (rate) of dwarfing; the possible causes of population pressures, if there are more than we have already discussed (and I think I've seen hints, in the field, that can be dated). The possibility of contemporaneity with the earliest Chumash; the final date of mammoth extinction.

I am often asked, "Won't you be excited when you find a mammoth bone with a spear point in it?" My response is, "I've got a different perspective. I'm looking for a human ribcage with a tusk in it." A second common question is, "How is your research relevant (to modern times)?" Well, I feel it shows us what has happened in an oceanic island environment in very recent time (geologically speaking) and may be still at work, as in the case of the Island fox. The Tunnel of Doom is still functioning (Figure 4).

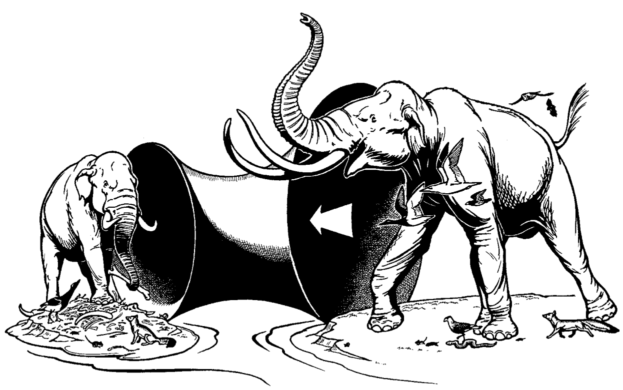

Figure 4. A schematic of the one-way trip through the "tunnel of doom." Selected mainland forms enter the island (tunnel) to become modified by island adaptations and finally become extinct. (Artwork by Carl Buell).

LITERATURE CITED

Agenbroad, L. D. 1998. Pygmy (dwarf) mammoth of the Channel Islands of California. The Mammoth Site of Hot Springs, South Dakota, Inc. Hot Springs.

Azzaroli, A. 1981. About pigmy mammoths of the Northern Channel Islands and other island fauna. Quaternary Research 16:423-425.

Chaney, R. W. and H. L. Mason. 1934. A Pleistocene flora from Santa Cruz Island, California. Carnegie Institution of Washington. Publication 415.

Collins, P. W. 1993. Taxonomic and biogeographic relationships of the Island Fox (*Urocyon littoralis*) and Gray Fox (*U. cinereoargenteus*) from western North America. Pages 351-390 *in* Hochberg, F. G. (ed.), Third Channel Islands Symposium: recent advances in research on the California islands. Santa Barbara Museum of Natural History, Santa Barbara.

Crooks, K. R. and D. Van Vuren. 1994. Conservation of the Island Spotted Skunk and Island Fox in a recovering island ecosystem. Pages 379-385 *in* Halvorson, W. L. and G. J. Maender (eds.), The Fourth California Islands Symposium: Update on the status of resources. Santa Barbara Museum of Natural History. Santa Barbara.

Darlington, P. J. 1957. Zoogeography: the geographical distribution of animals. John Wiley and Sons, Inc. New York.

Erlandson, J., D. Kennett, B. Ingram, D. Guthrie, D. Morris, D. Tveskov, G. West, and P. Walker. 1996. An archaeological and paleontological chronology for Daisy Cave (CA-SMI-261), San Miguel Island, California. Radiocarbon 38:1-19.

Fairbanks, H. W. 1897. Oscillations of the coast of California during the Pliocene and Pleistocene. American Geologist 20:213-245.

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

Guthrie, D. A. 1998. Fossil Vertebrates from Pleistocene Terrestrial Deposits of the Northern Channel Islands, Southern California. Pages 187-192 *in* Weigand, P. W. (ed.), Contribution to the Geology of the Northern Channel Islands, Southern California. Pacific Section American Association of Petroleum Geologists.

Hooijer, D. A. 1976. Observations on the pygmy mammoths of the Channel Islands, California. Pages 220-225 i*n* Churcher, C. S. (ed.), Athlon: Essays on palaeontology in honor of Loris Shano Russel. Miscellaneous publications of the Royal Ontario Museum. Ontario.

Johnson, D. L. 1972. Landscape evolution on San Miguel Island, California. Ph.D. dissertation, Univeristy of Kansas, Lawrence, Kansas.

Johnson, D. L. 1978. The origin of island mammoths and the Quaternary land bridge history of the Northern Channel islands, California. Quaternary Research 10:204-225.

Johnson, D. L. 1980. Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. Journal of Biogeology 7:383-398.

Johnson, D. L. 1983. The California Continental Borderland: landbridges, watergaps, and biotic dispersals. Pages 381-527 *in* Masters, P. M. and N. C. Fleming (eds.), Quaternary Coastlines and Marine Archaeology: towards the prehistory of land bridges and continental shelves. Academic Press, New York.

Madden, C. T. 1977. Elephants of the Santa Barbara Channel Islands, Southern California. Geological Society of America Abstracts with Programs, 1977 Annual Meeting. Pages 458-459.

Orr, P. C. 1968. Prehistory of Santa Rosa Island. Santa Barbara Museum of Natural History. Santa Barbara.

Quammen, D. 1996. The Song of the Dodo. Touchstone Publishers. New York.

Roemer, G. W., D. K. Garcelon, T. J. Coonan and C. Schwemm. 1994. The use of capture-recapture methods for estimating, monitoring, and conserving Island Fox populations. Pages 387-400 *in* Halvorson, W. L. and G.

J. Maender (eds.), The Fourth California Islands Symposium: Update on the status of resources. Santa Barbara Museum of Natural History. Santa Barbara.

Shoshani, J. and P. Tassy (eds.). 1996. The Proboscidea: Evolution and palaeoecology of elephants and their relatives. Oxford University Press. Oxford.

Sondaar, P. 1977. Insularity and its effects on mammal evolution. Pages 671–707 *in* Hecht, M. K., P. C. Goody, B. M. Hecht (eds.), NATO Advanced Study Institute Series Number 14. Plenum Press. New York.

Stock, C. 1935. Exiled elephants of the Channel Islands, California Scientific Monthly XLI:205-214.

Stock, C. 1943. Foxes and elephants of the Channel Islands. Los Angeles County Museum of Natural History Quarterly 3:6-9.

Stock, C. and E. L. Furlong. 1928. The Pleistocene elephants of Santa Rosa Island, California. Science LXVIII:140-141.

Thikonov, A. 1997. (Brief report). Zoological Institute Russian Academy of Sciences, St. Petersburg, Russia. Department of History of Fauna. UroMam Newsletter 4:14-15.

Valentine, J. W. and J. H. Lipps. 1967. Late Cenozoic history of the southern California Islands. Pages 21-35 *in* Philbrick, R. N. (ed.), Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden. Santa Barbara.

von Bloeker, J. R., Jr. 1967. The land mammals of the southern California Islands. Pages 245-266 *in* Philbrick, R. N. (ed.), Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden. Santa Barbara.

Weaver, D. W. and D. P. Doerner. 1967. Western Anacapia—a summary of the Cenozoic history of the Northern Channel Islands. Pages 13-20 *in* Philbrick, R. N. (ed.), Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden. Santa Barbara.

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

SOURCES OF UNPUBLISHED MATERIALS

Collins, Paul, Vertebrate Zoology, Santa Barbara Museum of Natural History, 2559 Puesta del Sol, Santa Barbara, CA 93105. Personal Communication September 1998.