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Dietary reconstruction of pygmy mammoths from Santa Rosa Island of California

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ABSTRACT

Microwear analyses have proven to be reliable for elucidating dietary differences in taxa with similar gross tooth morphologies. We analyzed enamel microwear of a large sample of Channel Island pygmy mammoth (*Mammuthus exilis*) molars from Santa Rosa Island, California and compared our results to those of extant proboscideans, extant ungulates, and mainland fossil mammoths and mastodons from North America and Europe. Our results show a distinct narrowing in mammoth dietary niche space after mainland mammoths colonized Santa Rosa as *M. exilis* became more specialized on browsing on leaves and twigs than the Columbian mammoth and modern elephant pattern of switching more between browse and grass. Scratch numbers and scratch width scores support this interpretation as does the Pleistocene vegetation history of Santa Rosa Island whereby extensive conifer forests were available during the last glacial when *M. exilis* flourished. The ecological disturbances and alteration of this vegetation (i.e., diminishing conifer forests) as the climate warmed suggests that climatic factors may have been a contributing factor to the extinction of *M. exilis* on Santa Rosa Island in the Late Pleistocene.

1. Introduction

1.1. Background

Endemic to the California Channel Islands, the pygmy mammoth (*Mammuthus exilis*, Maglio, 1970) was initially discovered on the Island of Santa Rosa and later on Santa Cruz and San Miguel in the Channel Island archipelago of California. *M. exilis* is a small mammoth considered to be a dwarfed form of its likely ancestor, the Columbian mammoth (*M. columbi*), which occupied the mainland of North America (Madden, 1977, 1981; Johnson, 1978). Today, the Channel Islands are comprised of eight islands (Fig. 1). In the Late Pleistocene, the four Northern Channel Islands formed a single super-island, dubbed Santarosae by Orr (1968) and lay closer to the mainland than today's Channel Islands. Even during periods of glaciation in the Pleistocene when sea levels were much lower than they are today, the islands were separated from the California coast by a relatively small water gap of around 6.5–8 km (Roth, 1996; Muhs et al., 2015). As sea levels rose due to the melting of continental ice, 76% of Santarosae disappeared (Johnson, 1972) leaving only the highest elevations exposed – now known as the islands of San Miguel, Santa Cruz, Santa Rosa, and Anacapa. Of these modern islands, all but Anacapa have produced mammoth remains (Agenbroad, 2001). The breakup of Santarosae is believed to have taken place about 11,000 cal. BP (Kennett et al., 2008).

Researchers have long been interested in the Channel Islands for several reasons. First, the islands are part of one of the richest marine ecosystems in the world and are home to over 150 endemic species such as the island fox (*Urocyon litteralis*) – a small fox with six subspecies each unique to the island it lives on. Hence, the Channel Islands are often referred to as the North American

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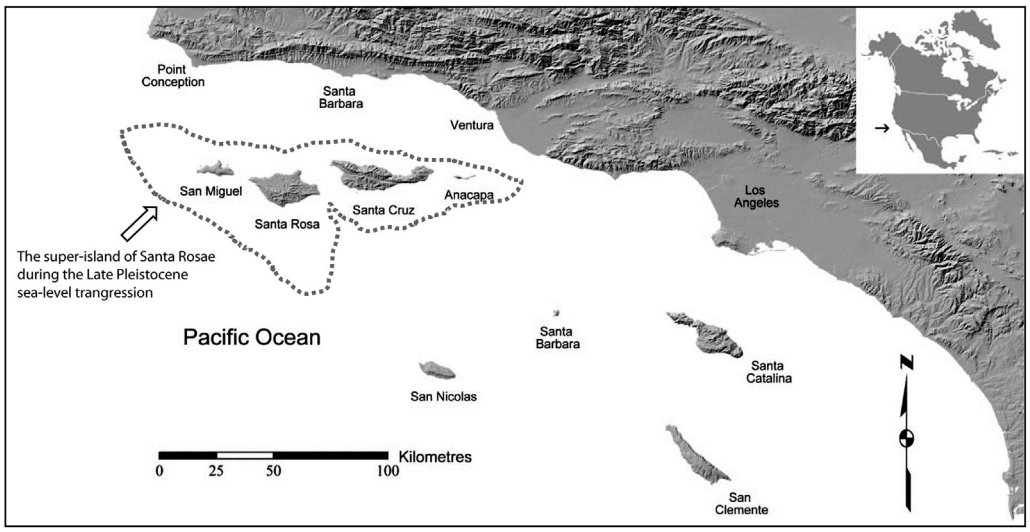

Fig. 1. The Channel Islands and Southern California Coast (Modified from Rick et al. (2012) (Fig. 1)). Dotted line indicates Late Pleistocene shoreline of the "super island" of Santarosae.

Galapagos. Second, because island species are generally regarded as more susceptible to human-induced extinctions than those on continents, and the Channel Islands were initially occupied by humans during a period of extensive extinction in North America (and elsewhere) around 13,000 cal. BP (Erlandson et al., 2011), data from such islands has proven useful for providing context for late Quaternary extinctions on continents such as the Americas and Australia (Steadman and Martin, 2003; Wroe et al., 2006). Third, islands are invaluable for studying evolution and diversification, including the effects of insularity on fauna (Palombo, 2008) such as the so-called "Island Rule". The Island Rule was first stated by Foster (1964) after comparing numerous island species to their mainland varieties. He proposed that the body size of a species becomes smaller or larger depending on the resources available to it in its environment. The Island Rule posits that certain island species evolve larger size when predation pressure is relaxed (due to the absence of some mainland predators), while others evolve smaller size due to resource constraints regarding availability of food and land area (Whittaker, 1998; McNab, 2010).

The history of the discovery and excavation of pygmy mammoths from the islands is chronicled in Agenbroad (2001). Mammoth remains have been known from the Northern Channel Islands of Santa Rosa, San Miguel, and Santa Cruz since 1856 (Stearns, 1873). A spectacular find was made in 1994 by Park Service researchers led by Larry Agenbroad (a Santa Barbara Museum research associate at the time) of a nearly complete adult male *M. exilis* skeleton – a mature male of about 50 years of age (Agenbroad, 1998). After this discovery, a thorough pedestrian survey of the islands using GPS was begun, to document and pinpoint each discovery. More than 160 new localities were recorded with the majority of localities found on Santa Rosa Island (Agenbroad et al., 2007). Several mainland-size mammoth (*Mammuthus columbi*) elements in addition to remains of *M. exilis* were recovered as a result of this survey. The survey of Santa Rosa revealed a ratio of approximately 3:10 large mammoth:small mammoth remains (Agenbroad, 2012).

As many as three species ostensibly of different sizes have been proposed by researchers over the years (Orr, 1956a,b, 1968; Roth, 1982, 1996). However, Agenbroad (2009) showed convincingly, using less fragmentary material, that only two species are likely present – *M. columbi* and *M. exilis* (Fig. 2).

There has been much speculation regarding the origin of mammoths on the Northern Channel Islands, and the finding of Columbian mammoth remains is intriguing given that these remains may represent remnants of an ancestral population, unless they represent later migrants to the island. The oldest remains are found in the basal conglomerate of the Garanon Member of the Santa Rosa Island Formation. U/Th results formerly suggested an age of at least 200 ka (Orr, 1968), but these are not now considered reliable and new U/Th data indicate an age of ca. 80 ka (Muhs et al., 2015). Mammoth remains attributed to both *M. columbi* and *M. exilis* have been found throughout the entire Formation (the latest calibrated direct radiocarbon date on *M. exilis* being 10,700 ± 90 BP (B-14660), equivalent to c. 12,600 cal BP (Agenbroad, 2012).

Also intriguing is the speculation as to how mainland mammoths arrived on the islands. Initially, it was assumed that the ancestral form of *M. exilis* was either *Mammuthus* (formerly *Archidiskodon*) *imperator* or *Mammuthus columbi*. It has now been shown that *M. imperator* and *M. columbi* are conspecific (Slaughter et al., 1962; Miller, 1971, 1976; Agenbroad, 2003) and further research has suggested that *M. columbi* represents the likely ancestor of *M. exilis* (Johnson, 1978; Madden, 1981; Roth, 1982, 1996). This suggests that *M. exilis* evolved according to the Island Rule (Foster, 1964). That is, a large continental species (*M. columbi*) adapted to an island environment becoming in time a new smaller species – *M. exilis* (Fig. 2).

The question remains – how did Columbian mammoths reach the islands? Historically, it was assumed that ancestral mammoths could not have swum to the islands. Consequently, various land bridges linking the Northern Channel Islands to the mainland have long been hypothesized (e.g., Clements, 1955; Van Gelder, 1965; Valentine and Lipps, 1967; von Bloeker, 1967; Remington, 1971). This early idea, that insular mammoth remains proved the existence of a land bridge, persisted for many decades (see synopsis by Johnson, 1978). The idea was deeply entrenched but began to give way in light of accumulating geological and biological evidence (Savage, 1967; Johnson, 1978). For example, Johnson (1972, 1978) pointed out that a land bridge was not a *sine qua non* for explaining mammoths on the Northern Channel Islands, citing research that elephants are excellent distance swimmers, among the best of all land mammals and highly skilled at crossing water gaps. Hence, currently it is now understood that sea-level fall brought the