

Long-Term Stability of Vocal Dialects in Northern Elephant Seals

Caroline Casey, *Ecology and Evolutionary Biology, University of California Santa Cruz, California, USA, cbcasey@ucsc.edu*

Colleen Reichmuth, *Institute of Marine Sciences, University of California Santa Cruz, California, USA*

Dan Costa, *Ecology and Evolutionary Biology, University of California Santa Cruz, California, USA*

Burney Le Boeuf, *Ecology and Evolutionary Biology, University of California Santa Cruz, California, USA*

Species-typical acoustic signals may vary dramatically between individuals and across geographically isolated populations, yet the selective pressures that drive these differences are often unknown. Examining situations in which acoustic differentiation occurs over time within a species and measuring the extent to which different factors are associated with variation in vocal behavior can provide insight into the adaptive significance of acoustic differentiation—both between individuals and across geographic regions.

Northern elephant seals (*Mirounga angustirostris*) provide an unparalleled opportunity to examine environmental and demographic factors that may contribute to divergence in animal vocal signals. Historical populations of northern elephant seals were rapidly and systematically extirpated along the coastlines and offshore islands of North America beginning in the early 1800s, to satisfy demand for rendered oil. More than 200,000 seals had been killed by the turn of the century, and the species was considered extinct by 1884. A small remnant population, re-discovered in 1911 on Isla de Guadalupe (150 miles from mainland Mexico), likely consisted of less than 20 individuals. Following the collapse of the sealing industry, these survivors enabled the population to recover to more than 210,000 animals, which can be observed each winter (December-March) at eight main island or mainland rookeries along the coasts of California and Mexico during the annual breeding season.

Elephant seals engage in an extremely competitive breeding system in which adult males fight to establish dominance hierarchies that determine access to large aggregations of females on breeding beaches. Intra-sexual vocal communication is critical to breeding success, as ritualized vocal exchanges mitigate otherwise costly physical fights between competing males during periods of extended fasting. Male threat calls comprise broadband, high-amplitude pulses that are emitted at regular rates. Historical recordings of these calls identified the presence of vocal dialects (temporal patterns in calls specific to a geographic region) among four discrete founder populations. In contrast, more recent findings from one colony indicate that males produce individually unique vocal signatures, and that temporal variation between individuals supports accurate recognition of rivals. Since the original recordings were obtained for the species in 1968 and 1969, no study has re-examined the persistence of vocal dialects across their geographic range as the species has recovered from near extinction.

Several unique conditions enable the long-term stability of vocal dialects in the northern elephant seal to be examined as well as the influences of non-genetic factors on acoustic differentiation. These conditions include 1) availability of historic recordings from four founder populations, 2) evidence of extraordinarily low genetic variability due to the bottleneck, compounded by extreme polygyny over multiple generations, 3) documentation of the species' recovery and re-colonization of breeding sites

since the historic recordings were obtained, and 4) opportunity to obtain acoustic recordings at the four original founder colonies plus four additional (more recently established) breeding sites.

Our initial aims were to confirm the presence of vocal dialects in the historical data set, and to determine whether the vocal behavior of male northern elephant seals had changed over the subsequent 45 years. To this end, we re-analyzed the calls of 107 males recorded in 1968 and 1969 at the four founder colonies; these recordings had been obtained when the population was one-third of its current size. We confirmed that the calls of these historical males could be readily classified by their geographic location. We then compared these historic recordings to the calls of 315 males recorded between 2013 and 2016 throughout the present-day range of the species; this included the four original sites as well as four more recently established breeding colonies. We found that vocal dialects diminished while variation between individuals increased at most sites. Specifically, males recorded recently at the four original colonies could not be appropriately assigned to their geographic region based on the characteristics of their call. Further, males recorded recently at all sites exhibited more complex call structure and variation in tempo than the calls of the historical males. Additionally, we found differing amounts of acoustic variation at the eight contemporary breeding sites - call differentiation among males was most pronounced at older colonies with relatively high density. This is likely the result of elevated competition between individuals at crowded rookeries, and more time available for new call patterns to emerge at these locations.

These findings demonstrate geographic and generational changes in acoustic signaling within a genetically constrained and rapidly recovering population, and help to identify the potential drivers of signal divergence in animals that rely on acoustic communication. [Supported by National Geographic Society]