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The rise and fall of dialects in northern elephant seals

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Vocal dialects are fundamental to our understanding of the transmission of social behaviours between individuals and populations, however few accounts trace this phenomenon among mammals over time. Northern elephant seals (*Mirounga angustirostris*) provide a rare opportunity to examine the trajectory of dialects in a long-lived mammalian species. Dialects were first documented in the temporal patterns of the stereotyped vocal displays produced by breeding males at four sites in the North Pacific in 1968 and 1969, as the population recovered from extreme exploitation. We evaluated the longevity of these geographical differences by comparing these early recordings to calls recently recorded at these same locations. While the presence of vocal dialects in the original recordings was re-confirmed, geographical differences in vocal behaviour were not found at these breeding rookeries nearly 50 years later. Moreover, the calls of contemporary males displayed more structural complexity after approximately four generations, with substantial between-individual variation and call features not present in the historical data. In the absence of measurable genetic variation in this species—owing to an extreme population bottleneck—a combination of migration patterns and cultural mutation are proposed as factors influencing the fall of dialects and the dramatic increase in call diversity.

1. Introduction

Understanding how animals acquire information from other individuals and identifying the mechanisms that support the transmission of social behaviours are fundamental themes in behavioural ecology and evolutionary biology [1–3]. The topic of vocal dialects among animals has particular significance, owing to its importance in studies of both human language and animal communication. Dialects represent similarities in vocal behaviour that are specific to geographical regions or social groups that typically do not intersect. Among animals, this phenomenon has been demonstrated in birds, primates, bats, rodents, cetaceans and seals (for a review, see [4] and [5]). The examination of vocal dialects enables a consideration of the social, environmental and demographic conditions that promote and maintain behavioural variation among animals [4].

Many descriptions of animal dialects are reported as ‘snapshots’ of divergent vocal patterns for different populations within a given species at a particular time (e.g. [6–8]). However, dialects can be dynamic [9–11]. Like other behavioural traits, they are influenced by changing conditions that may alter an individual’s vocal repertoire. Disentangling the extrinsic factors that influence dialects helps to resolve the selection pressures shaping vocal variation [12]. This kind of work can only be accomplished through long-term studies of populations that capture the stability—or alternatively, the progressive changes—in acoustic behaviour over time [13].

The most comprehensive understanding of dialects comes from studies of passerine birds, which show that there is no singular explanation for the function and evolution of these regional vocal differences [4]. In some cases, geographical

variation is maintained by assortative mating through female choice, which contributes to reduced gene flow between different populations [12,14,15] and eventually leads to speciation [4,16]. In other instances, dialects may be adaptive to varying social or ecological landscapes, and continue to diverge between populations over time [17,18]. Alternatively, dialects may arise as epiphenomena of other evolutionary processes (e.g. learning or patterns of dispersal) [4,12,19,20], and may change over successive generations owing to cultural drift or frequency-dependent selection [3,21]. Few studies have documented the persistence of dialects in mammals [22–24]. This is probably owing to the logistical difficulties of collecting longitudinal recordings from free-ranging animals with extended lifespans, which are required to document changes in vocal behaviour over multiple generations.

The northern elephant seal (*Mirounga angustirostris*) presents a compelling model to examine the persistence and functional significance of dialects. The species was decimated in the late-1800s, with fewer than 20 individuals surviving at a remote breeding colony, Isla de Guadalupe, off the west coast of Baja, Mexico [25]. Northern elephant seals recovered following protection in 1922, eventually recolonizing most of their historic range along the west coast of North America [26]. There are now more than 210 000 individuals, and their population continues to increase by 3–4% per year [27]. It is notable that all living individuals of the species are descendants of the remnant population from only a century ago [28].

Northern elephant seals presently breed at 12 sites along the coasts of Mexico and California [27]. Operating within a system of extreme polygyny, adult males battle to establish dominance hierarchies that determine access to large harems of breeding females [29]. Dominance relationships are maintained through the use of stereotyped displays that include loud vocalizations, elevated visual posturing, and seismic cues produced by slamming their chests against the ground [30]. The exchange of these displays serves to mitigate otherwise costly physical fights between rival males during periods of extended fasting [31]. Significantly, the acoustic component of these ritualized displays remains consistent within each adult male throughout the breeding season, and stable from one year to the next [32,33].

Fortuitously, the calls of northern elephant seals were recorded when the recovering population was less than a third of its present size. Le Boeuf & Peterson [34] compared the vocal displays of adult males at four primary breeding colonies (Año Nuevo Island, San Miguel Island, San Nicolas Island and Isla de Guadalupe) in 1968 and 1969, and found that the pulsed calls produced by the seals were notably similar within breeding sites, but differed from one site to another. The geographical dialects were demonstrated by common temporal patterns in the vocalizations specific to each breeding colony—providing, to our knowledge, the first evidence of vocal dialects for any non-human mammal [34]. With the exception of the Isla de Guadalupe source population, these historical recordings were obtained within one generation¹ of seals breeding again at these sites, thus capturing the initial inception of dialects at each of the observed breeding colonies.

Given the extreme population bottleneck this species endured [36], Le Boeuf and Peterson proposed that it was unlikely that the observed geographical variation in vocal patterns were related to genetic differences between regions [34]. Le Boeuf & Petrinovich [32] further suggested that dialects arose as a by-product of the manner in which

northern elephant seals recolonized their historic range: early dialects would have been maintained by isolation given limited dispersal of animals among breeding sites. Given no stabilizing function, the authors predicted that as the population expanded and immigration increased, vocal differences between the founding colonies would decline and eventually disappear.

Our aim in this study was to compare the calls of contemporary male northern elephant seals with those calls collected at the same breeding colonies nearly a half century ago. We tested the prediction that the dialects originally described in this species were an epiphenomenon of recolonization patterns that would diminish with time. Alternatively, these dialects may have persisted despite continued population growth and immigration because they serve an important function in the social lives of these seals. The availability of both recent and historic recordings provide a rare opportunity to examine how vocal dialects respond to changing social and demographic conditions in a long-lived mammal. Furthermore, the extraordinary degree of relatedness among individuals owing to inbreeding in this species [36–39] compounded by extreme polygyny [40], enables consideration of the non-genetic factors that contribute to both geographical and individual variation in acoustic communication.

2. Methods

(a) Historical recordings

The calls of individual males collected by Le Boeuf and Peterson during the 1968 and 1969 elephant seal breeding seasons (December–March) were converted from reel-to-reel audio recordings to digital format. The original recordings had been obtained with a Uher Report L recorder (48 kHz sampling rate) and Uher M514 microphone [34]. To prevent resampling the same individuals twice, males in this study were systematically recorded on a unidirectional path through the colony at each study location during a single day. At the Año site, individual males had been dye-marked to prevent re-sampling. The comments embedded in each recording included the caller's location, identity and age. In 2015, we resampled the reel-to-reel audio tape with a Fostex FR2 digital recorder (48 kHz sampling rate). Complete vocalizations and associated annotated information were extracted using AUDACITY (version 2.1.3).

(b) Individual identification and acoustic recordings of contemporary males

Acoustic displays produced by contemporary adult males were recorded during the breeding season at the same four breeding colonies visited by Le Boeuf & Peterson in 1968 and 1969. The locations and years sampled were Año Nuevo (2014), San Miguel Island (2015), and San Nicolas Island (2014) in California, and Isla de Guadalupe in Mexico (2015) (figure 1a). Each site was visited for a period of 4–6 days and sampling intensity was similar at all sites, resulting in comparable proportions of males recorded at each breeding colony. Acoustic recordings were collected at distances of 5–15 m and between 0 and 90 degrees orientation from spontaneously calling males, using a Neumann KMR 82i condenser shotgun microphone with Rycote suspension and windscreen (0.02–20 kHz, 21 mV Pa⁻¹) attached to a Fostex FR2 Field Memory Recorder (24-bit/48 kHz sampling rate), or a Brüel & Kjær 2250 Sound Level Meter (24-bit/48 kHz sampling rate) with a calibrated 4189 free-field microphone (0.06–20 kHz, 50 mV Pa⁻¹) with a Brüel & Kjær

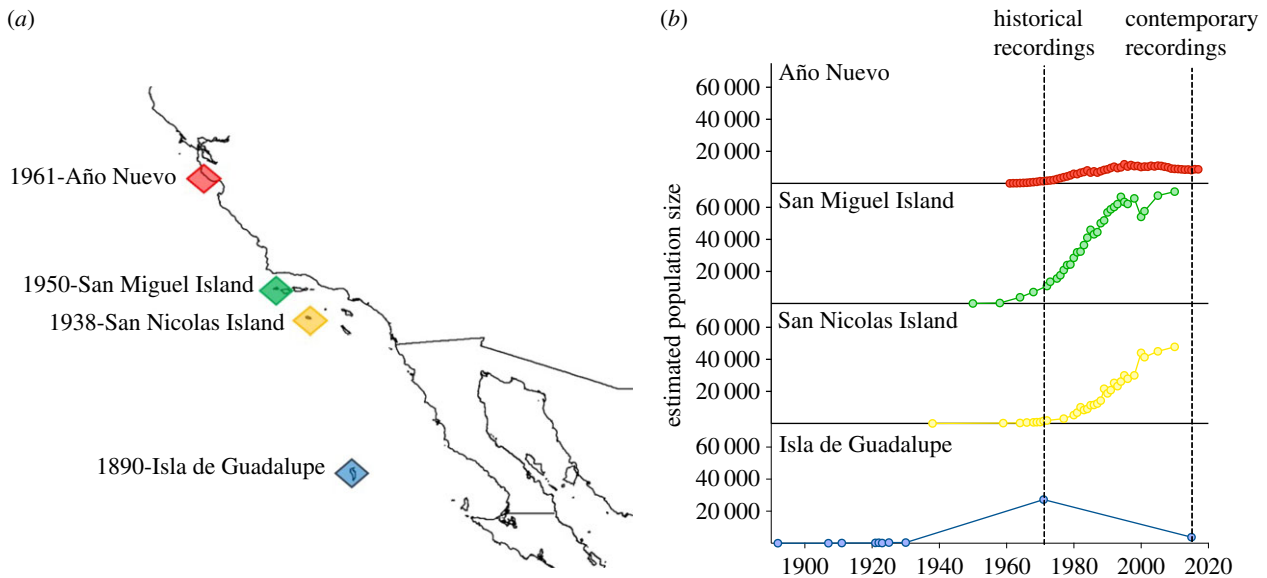


Figure 1. Study locations and associated populations trends at each breeding location. Panel (a) illustrates the four breeding sites (and corresponding colonization dates) along the United States and Mexican coasts sampled during 1968–1969 and 2014–2015. Panel (b) presents the population trends at each location following exploitation. Dotted vertical lines indicate when recordings were obtained for the historic and contemporary datasets: Año Nuevo, San Miguel, San Nicolas [27], and Isla de Guadalupe [28,41].

UA-1650 windscreen. To enable identification and prevent pseudo-replication, each male was dye-marked with a temporary alphanumeric code on his back after he was recorded. Comments appended to each recording included location, age and identification, microphone orientation, and distance to the caller. The age class of focal males was determined in the field based on chest shield scarring, proboscis development and body length [40,42]. Additionally, photographs were taken of each marked and recorded individual, and an independent observer later confirmed the age-class of males.

(c) Acoustic analysis

Previous research confirmed the stability of an adult male's display vocalization across motivational contexts, within seasons, and across years [32,33]. Therefore, only adult calls were analysed, and individuals whose age class was not specified in the recordings were excluded. A minimum of one and a maximum of 16 calls were collected for each individual in the historic and contemporary data, and a subsample of one call per individual was randomly selected for analysis. As adult male calls are extremely stable and exhibit little variation [33,43], we consider one call to be an adequate sample.

Among male northern elephant seals, temporal rather than frequency-related characteristics of vocalizations are the most reliable call features [33,34,43,44]. To characterize the temporal features of each call, we defined a call bout as the entire vocalization produced by a male, including any introductory or terminal snorts and rumbles (figure 2a). We identified the rhythmic portion of the vocalization as the bout component that had a defined pattern, which often consisted of repeating intervals (figure 2b). Each repeating interval of the bout's rhythmic portion was defined as a unit, measured from the onset of the first sonic element in the unit to the onset of the following unit (figure 2c). Each unit contained individual elements, which were defined as perceptually discrete sonic components (figure 2d). Elements were divided into two types based on duration: elements less than 200 ms were considered pulses, whereas elements more than 200 ms were considered bursts. This duration criterion was selected based on perceptual differences between the sounds to human listeners.

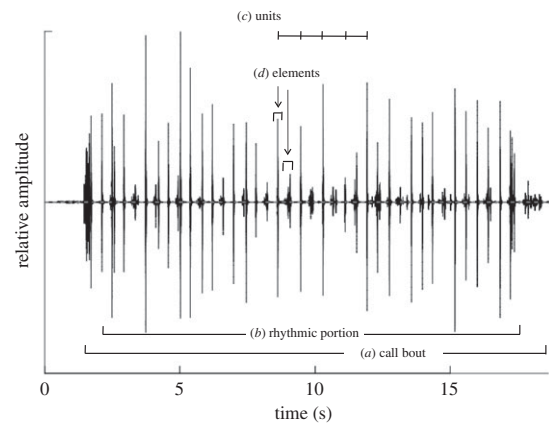


Figure 2. Waveform of a representative adult male northern elephant seal call, and terminology used for temporal analysis of call substructure. Variables measured include (a) the call bout, (b) rhythmic portion of call, (c) call unit, and (d) call elements (see text for details).

Each call was measured manually from the waveform to obtain the following temporal variables: unit duration (ms), duration of the sonic portion of each unit (ms), number of elements in each unit, number of different element types in each unit, unit repetition rate (Hz)—measured as the mean number of units per second calculated over the rhythmic portion of the bout, and degree of isochronicity within the call—measured as the standard deviation of the unit duration, with lower values corresponding to a greater consistency in tempo (RAVEN PRO 1.4). The duration of the silent portion of each unit (ms) was calculated based on the difference between unit duration (ms) and the duration of the sonic portion of each unit (ms). For discrete parameters, we report the mean and standard deviation of each variable; for continuous data, we report the mode and range.

(d) Analysis of acoustic variation

We conducted a multivariate discriminant function analysis (DFA) with all measured call features (RSTUDIO version 1.1.456) to evaluate differences in call features between sites. We classified calls by location, with breeding site as the group identifier and acoustic measures as discriminant variables. This approach

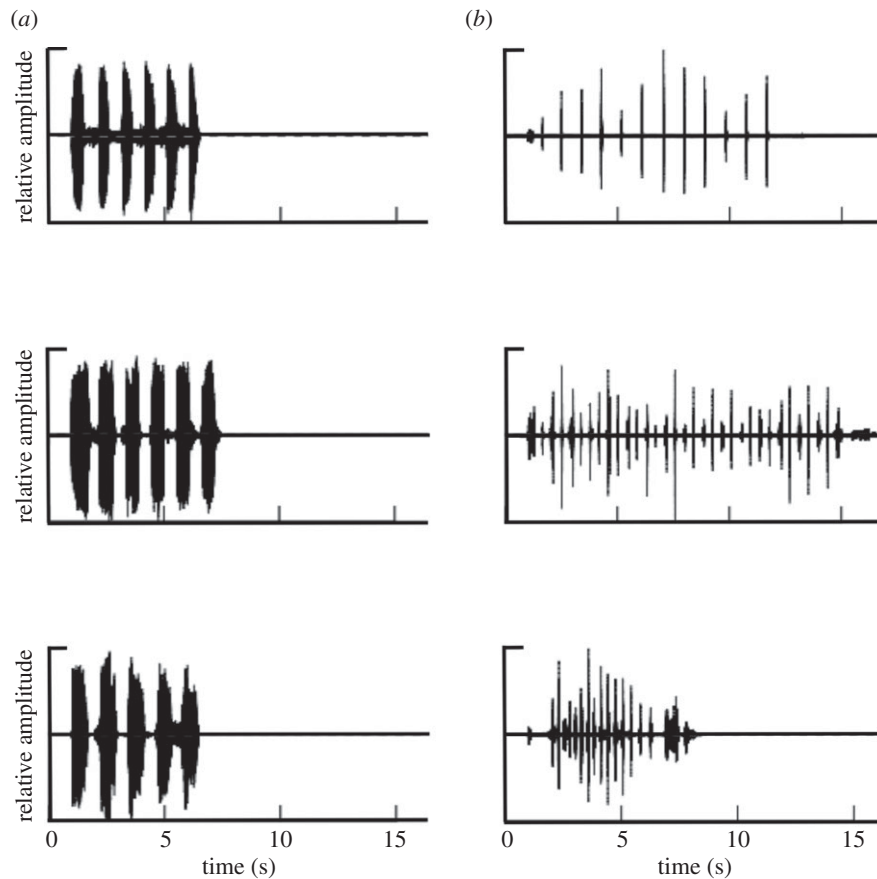


Figure 3. Waveform comparison of representative signature calls produced by three adult male elephant seals in 1968 (*a*), and three adult males in 2014 (*b*) at the Año Nuevo breeding colony. Recordings of these calls are provided in the electronic supplementary material (audio S1 and S2). Time (s) is shown on the *x*-axis, and relative amplitude is shown on the *y*-axis.

produced canonical discriminant functions representing the combinations of the acoustic variables that provide the maximum separation among groups in multidimensional acoustic space [45]. Per cent correct classification, obtained from the classification matrix, served as a metric of how well the measured variables separated between sites. Site-specific per cent-correct scores were compared with a $N-1$ chi-squared test to determine whether calls from males at historical sites had different per cent-correct scores than those recorded recently at the same locations. To rule out potential confounding effects of differences in sample size between the two recording periods, we randomly subsampled the males from the current dataset to match the sample size at each of the historic sites to support the DFA.

We conducted a principal components analysis (PCA) to evaluate the relationship between call characteristics and geographical location. Our aim was to construct a reduced set of orthogonal factors (principle components) that would summarize the major dimensions of acoustic variation between males across sites. To produce a relative index of individual variability for both the historic and current data, we calculated the 90% density volume of between-individual variation within a site. We then plotted this variation as a transparent cloud over the data resulting from the PCA analysis. The greater the vocal diversity within a site, the greater spread in acoustic space between individuals and the larger relative volume of these variation clouds. Relative cloud volumes were then compared to determine whether there had been a change in acoustic variation within each site over time. This analysis was conducted with all the males across both sampling periods using MATLAB (R2015b).

To provide a statistical assessment of the PCA data, we performed a distance-based test of homogeneity of multivariate dispersions at each site across the two sampling periods using RSTUDIO (version 1.1.456). Analogous to Levene's test for

homogeneity, this approach determines the distance in multivariate space between each point and the site-specific group centroid [46]. We then applied a one-way ANOVA to these scores to confirm the increase in variation at each site over time.

3. Results

(a) Call description

The calls from 105 historical adult males from the four breeding sites (figure 1*a*; Año Nuevo Island, $n = 24$; San Miguel Island, $n = 14$, San Nicolas Island, $n = 9$, Isla de Guadalupe, $n = 58$) were reanalysed. A descriptive assessment of these recordings indicate that the temporal features of the historic calls were markedly similar within each site, but varied considerably between locations, supporting Le Boeuf and Peterson's original account of vocal dialects in the pulse rate pattern in this species. Specifically, calls produced at each site had similar unit durations, unit repetition rates, and sonic portions of each unit, yet showed discernible differences in these features between sites (electronic supplementary material, table S1 and audio S1; figure 3*a*). Historic calls had strong isochronicity, measured as consistency in tempo throughout the call duration. Historic calls also had simple structure—without notable substructure components—featuring regularly repeating units of only a single acoustic element.

By contrast, calls from 171 contemporary males recorded at the same four sites 47 years later (figure 1*a*; Año Nuevo Island, $n = 42$; San Miguel Island, $n = 38$; San Nicolas

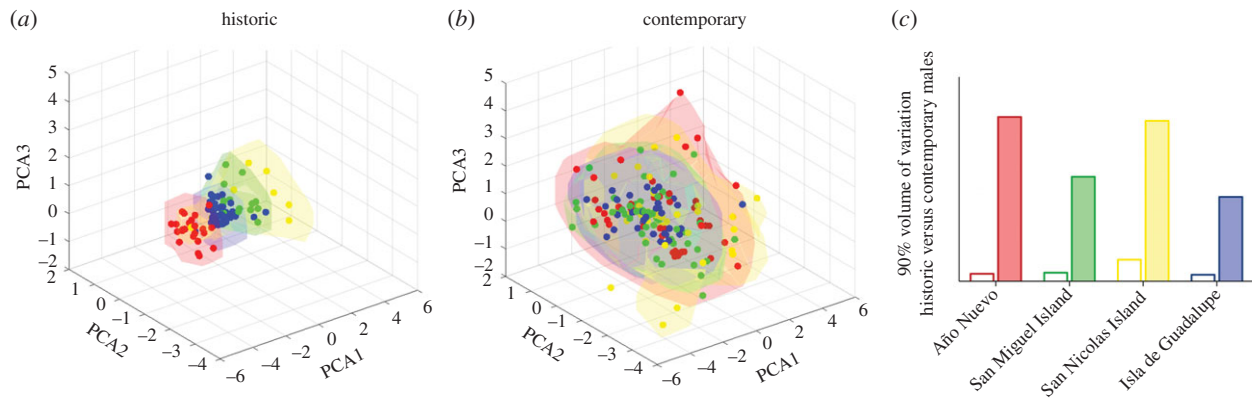


Figure 4. Comparison of between-individual call variation between historical and contemporary sampling periods. Panels illustrate the results of the PCA of the measured call variables plotted using the three principle components that captured 90% of the variance observed in the data. Panel (a) represents the calls of males within and between the four historic sites ($n = 105$) while panel (b) shows the calls of contemporary males ($n = 171$) from the same four locations. Panel (c) shows a comparison of the 90% cumulative density volume of the measured between-individual call variation for both the historic (1968–1969) and contemporary (2014–2015) data.

Island, $n = 59$; Isla de Guadalupe, $n = 32$) did not show regional differences in call features, indicating that dialects were lost completely over time. Moreover, the individuals recorded at each location had more diverse calls, with new call variants not observed in the historical data (figure 3b; electronic supplementary material, audio S2). Modern-day males displayed substantial between-individual call variation within each site (electronic supplementary material, table S1 and audio S2; figure 3b). While many males called with a regular temporal interval, some males at each site possessed characteristic calls with complex tempos, progressively speeding up or slowing down the emission of acoustic units over the duration of the call. Additionally, in contrast to historic males, calls from some contemporary males at all sites contained repeating units with more than one acoustic element that varied in both duration and structure (electronic supplementary material, table S1 and audio S2; figure 3b).

(b) Call analysis

The DFA analysis revealed that males from the historic dataset could be accurately assigned to each site with an average correct classification rate of 82% (Año Nuevo = 100%, San Miguel = 80%, San Nicolas = 56%, Isla de Guadalupe = 90%; compared to chance levels from 14% to 55%). By contrast, a matched sample of the contemporary data showed an overall reduction in average classification rate to 32% (Año Nuevo = 23%, San Miguel = 11%, San Nicolas = 22%, Isla de Guadalupe = 73%; compared to chance levels of 14–55%). Per cent correct classification declined significantly for Año Nuevo, San Nicolas, and San Miguel (N-1 chi-squared $\chi^2_1 = 37.6, 3.1, 63.8, p < 0.0001$). Isla de Guadalupe exhibited a relatively high classification rate for both the historical and contemporary data (90% and 73% respectively), however, males from this colony still exhibited a decrease in per cent correct classification (N-1 chi-squared $\chi^2_1 = 4.4, p < 0.04$) between the two sampling periods.

The PCA analysis extracted two factors that explained 68% and 64% of the variance from both from the historic and contemporary data, respectively (electronic supplementary material, tables S2 and S3). Vocal displays from the historic dataset were well separated in acoustic space

according to location, as seen by the clustered distribution of calls within each site (figure 4a, coloured points) and confirmed by the results of the DFA. Furthermore, there was more overlap among males from different contemporary colonies (figure 4b, coloured points), indicating that individual males no longer cluster in acoustic space according to breeding site.

Each breeding site showed a marked increase in 90% cloud volume (figure 4a,b), corresponding to an increase in acoustic variation between the two sampling periods (figure 4c). Modern males at the Año Nuevo breeding colony exhibited the greatest total cloud volume, while modern males at Isla de Guadalupe demonstrated the lowest levels of variability. The greatest relative rise in call variation over time occurred at Año Nuevo (2044% increase in cloud volume), followed by Isla de Guadalupe (1143% increase), San Miguel Island (1106% increase) and San Nicolas Island (643% increase). The increase in call variation between the historic and contemporary datasets occurred along with substantial changes in population size at each breeding colony (figure 1b). Significant differences in acoustic variation at each site between the two sampling periods were present at the Año Nuevo, San Miguel, and Isla de Guadalupe colonies (Año Nuevo: $F_{1,46} = 63, p < 0.0001$, San Miguel = $F_{1,15} = 8, p < 0.001$, Isla de Guadalupe: $F_{1,24} = 27, p < 0.001$), based on the analysis of homogeneity of multivariate dispersions.

4. Discussion

After 50 years, the dialects originally described in this species were lost completely. The calls of modern males now exhibit more between-individual variation, with the emergence of novel call characteristics not previously described as part of the acoustic repertoire. In comparison to historic calls, contemporary individuals differ from one another in discernible ways within each site, and males can no longer be assigned to their breeding colony simply on the basis of their call features.

This long-term study raises the question of why dialects at each site initially emerged and eventually disappeared, and whether the observed increase in vocal diversity between

individuals plays an important role in male elephant seal social behaviour. There is probably no singular underlying explanation for the rise in acoustic variation among male northern elephant seals. Changes in vocal dialects of other species, including passerine birds, have been attributed to the interaction of multiple factors, including patterns of migration, cultural drift, sexual selection and genetic variation [12,47]. Here, we explore a theoretical explanation for the mechanisms that may have eroded vocal dialects in northern elephant seals across breeding locations, and the potential factors that may have maintained—and even promoted—vocal diversity between males at each site.

While social learning is a plausible explanation for the rapid increase in between-individual variation observed in this study [2,47], it is usually not possible to exclude genetic contributions to such differences in vocal behaviour. In this case, there are several notable factors that suggest the rapid rise in vocal diversity cannot be driven by genetic variation. In this relatively long-lived species, the time between sampling intervals covered only four generations. Additionally, modern northern elephant seals retain extraordinarily low genetic variability [36,38,39], with the lowest levels of microsatellite variability reported for any mammalian species [37]. Thus, learning appears to be a possible mechanism that would support this pattern.

Little is known about the ontogeny of vocal displays in northern elephant seals, and the degree to which these signals are shaped by learning and auditory/social experience. While the display vocalizations of mature males are both stereotyped and individually unique, the same calls produced by adolescent males are highly variable and unstructured [48]. This suggests that the calls of young male elephant seals—like those of juvenile songbirds—undergo a transitional period during development before becoming relatively fixed beyond a certain age [49]. This crystallization process, at least in passerine birds, is a proximal phenomenon based on learning through auditory experience [21,49–51]. While there is some anecdotal evidence to suggest that learning is also important to the formation of elephant seal acoustic displays (see [52] for review), additional research is needed to fully resolve the mechanisms that supports vocal development in the species. If learning is critical to call development, then copying errors (i.e. cultural mutations) during maturation could introduce new call characteristics into the population, as observed in songbirds (e.g. [53–56]). Studies tracking the acoustic behaviour of known individuals through their lifetime would reveal the timing of call fixation during maturation. Additionally, observing the vocal development of male elephant seals raised in captive settings would clarify whether learning from conspecifics is critical to the development of these specialized acoustic displays.

There are several potential mechanisms by which the original dialects were introduced to each breeding site. Le Boeuf and Petrinovich suggested that the dialects they discovered may have resulted from founder effects, with site-specific vocal patterns arising as a by-product of how seals recolonized their former range [32]. Following the population bottleneck, the displays of northern elephant seals were preserved within the few surviving individuals (less than 20) on Isla de Guadalupe, with very few males probably present in that remnant population [26,41]. Indeed, when Townsend searched Isla de Guadalupe during the 1884 breeding season, he noted that of 15 seals remaining, only one was a male; he then collected these individuals for ‘scientific

purposes’ and declared the species extinct [41]. Thus, it is probable that juvenile males in subsequent years lacked significant (if any) exposure to adult males, and developed their calls without adult exemplars. This could help to explain the simple temporal patterns present in the calls of male seals recorded by Le Boeuf and Peterson [34].

With an initially low level of movement between sites, the historical dialects present in the 1960s may have persisted while the population continued to recover. However, as colonies reached carrying capacity, individuals migrated to less-dense breeding areas. For example, tagging studies confirmed that elephant seals born at the San Miguel and San Nicolas Islands became the major source of growth at the Año Nuevo colony during the 1960s [26]. Concurrent with the arrival of new immigrants, novel calls were probably introduced into the acoustic environment of these rookeries. Dialects would not be maintained if they had no selective benefit to males, as migration paired with cultural mutation would have probably introduced vocal variation. This process may have ultimately led to the erosion of site-specific patterns over successive generations.

If cultural mutation and increased migration between sites led to the dissolution of dialects, what factors helped to maintain or even promote acoustic diversity among modern male elephant seals? We previously showed that vocal variation between adult males is essential in mediating male–male competition—each male possesses a unique acoustic signature, and vocal variation among males supports individual recognition through the process of associative learning [33,44]. The rhythmic features of these calls are of particular importance, as males can remember subtle differences in call sub-structure and unit repetition rate, allowing them to use these call features to discern between familiar competitors [44]. Thus, in this system of extreme polygyny, powerful selection pressures for avoiding harm and conserving energy favour the accurate assessment of competitive rivals. This recognition process requires individual differences in acoustic signals, which, at a population level, appears to promote vocal variation regionally.

While the relationship between social structure and signal design has previously been evaluated with respect to parent–offspring discrimination in breeding colonies of birds (e.g. [57–59]), fewer studies consider how interactions among males competing for resources influence signal design and increased signal complexity (e.g. [60,61]). Social systems with high levels of male–male competition promote individual variation when there are severe consequences for misidentifying competitors and strong benefits for recognizing familiar rivals. This has been demonstrated in studies of iguanid lizards, where signal complexity improves opponent assessment under conditions of increased male–male competition [60]. Thus, as the number of rivals each male elephant seal encounters during the breeding season increases (owing to population growth), small structural differences between the calls of familiar opponents probably become increasingly useful to the recognition process. Future research should evaluate the relationship between acoustic diversity and social organization at different breeding locations, enabling a more precise consideration of how signal structure is influenced by male–male competition in this species.

Our findings with northern elephant seals underscore the view that vocal repertoires are not fixed, but change in response to both demographic and social conditions. To our

knowledge, this is the first study to document changes in the vocal behaviour of a species concurrent with significant changes in population structure. The observed increase in acoustic diversity despite extreme genetic similarity in this case presents an unparalleled opportunity to evaluate the factors that facilitate the formation and maintenance of dialects over time.

Ethics. Animal research was conducted with authorization from the Institutional Animal Care and Use Committee at UCSC and NMFS permits 14636 and 19108. Site-specific permissions were granted by Año Nuevo State Reserve (Año Nuevo), Channel Islands National Park (San Miguel Island), NAVAIR Point Mugu, Naval Base Ventura (San Nicolas Island), and the Comisión Nacional de Áreas Naturales Protegidas (Isla de Guadalupe).

Data accessibility. Data—including digital sound files—are archived at the University of California Santa Cruz, and are available by contacting the corresponding author.

Authors' contributions. C.C. designed the study, secured funding, collected contemporary recordings, analysed the data and wrote the manuscript. C.R. designed the study, secured funding, collected contemporary recordings and wrote the manuscript. D.P.C. secured necessary permits and wrote the manuscript. B.L. designed the study, collected historical recordings and wrote the manuscript.

Competing interests. The authors declare no competing interests.

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Endnote

¹As elephant seals may live to approximately 14 years of age, we define generational time as the mean age of reproductive males—estimated to be 10 years—plus one additional year for their prolonged gestation [35].

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