Title

The Vocal Behavior of the Male Northern Elephant Seal

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Publication Date

2018

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

THE VOCAL BEHAVIOR OF THE MALE NORTHERN ELEPHANT SEAL

A dissertation submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

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December 2018

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THE VOCAL BEHAVIOR OF THE MALE NORTHERN ELEPHANT SEAL

Caroline B. Casey

ABSTRACT

Acoustic communication is a fundamental feature of most animal social systems, and serves to support important behavioral traits such as breeding, foraging, and parental care. Despite many decades of research, detailed information regarding the role that vocal signaling plays in the social lives of marine mammals is scant. This is due in large part to the difficulties of observing the social context in which information exchange between individuals occurs, as these animals live most of their lives beneath the water's surface. As a consequence, many questions regarding the function, ontogeny, and evolution of sounds produced by marine mammals remain un-answered. The northern elephant seal (*Mirounga angustirostris)* presents an opportunity to better understand the role that acoustic communication plays in mediating social interactions between competing males during the breeding season, as they are one of the few species of seal that breed on land in predictable locations each year. In this dissertation, fine-scale acoustic analyses have been paired with close behavioral observations of known adult males in the wild to determine the function of the male vocal display, and the conditions that underpin this species' social system of extreme competition. Additionally, the unique demographic history of the northern elephant seal combined with long-term monitoring of this species offers the opportunity to examine how the vocal behavior of male seals has changed during this species' recovery from near-extinction, and the extent to which these specialized signals have been influenced by factors such population expansion, cultural learning, and the relative abundance of seals at different breeding sites. Finally, to better understand how males navigate this system of tremendous competition, the ontogeny of spatial, social, and communicative behavior among male elephant seals is explored by tracking young males throughout maturation. Taken together, a detailed understanding of the role that vocal signaling plays in the lives of male seals emerges from these studies, and contributes broadly to comparative frameworks for studies of agonistic signaling in other animal systems.

DEDICATION

"You cannot take a few random looks now and then. You must follow hour after hour, at all times and places, lest you miss those odd, distinctive (and often short) events that set a pattern and history for entire species."

– Stephen Jay Gould

To all those—past and present—who share a passion for observing animals in their natural habitat, and provide the subtle yet detailed descriptions that inspire the field of animal behavior.

ACKNOWLEGEMENTS

Where does one even begin when attempting to acknowledge all who have contributed to the completion of a dissertation? I suppose every graduate student must first be introduced to and inspired by a topic that they are willing to contribute the next six years of their life to exploring. So, I will begin by thanking my co-advisor, Colleen, for introducing me to the field of animal behavior. On the beaches of Año Nuevo Colleen exposed me to the wild, tragic, complicated lives of elephant seals, and highlighted the nuanced variation in their behavior which I would ultimately fall in love with. These small but meaningful differences between individuals would end up serving as the foundation of my dissertation. She stoked my enthusiasm for animal communication and learning, instilled great confidence in me as a scientist, and carefully taught me the meticulous tasks associated with data collection, analysis, and writing. Any success in my graduate career is in large part due to her dedication and unwavering support as a mentor. In short, I am the scientist that I am because of Colleen.

A student's dreams of pursuing their own independent research cannot be realized without someone who is willing to open the door and provide them with the rare opportunity to pursue a graduate degree. None of this would have been possible without my advisor Dan Costa. Dan took a huge chance by allowing me to be his student without really knowing who I was or what my plans were. He let me choose my own research path, which encouraged confidence in my own abilities to independently formulate and execute research questions. Over the course of the last six years, he has been a loyal and fierce advocate. I am proud to say that I am a graduate of the Costa lab, and am eternally grateful for all of Dan's support. Thank you also to all of the Costa lab students (past and present, there are far too many to name here) for taking me in as an adopted lab member, and for being such an amazing source of support and guidance over the several years.

I have had an incredible dissertation committee who have spent countless hours helping me to improve my writing and hone my research skills. Dr. Bruce Lyon's own work and passion for animal behavior inspired many aspects of this dissertation, and I am incredibly grateful for his direct and honest feedback. Dr. Peter Tyack provided exceptional guidance on the topics of learning and vocal behavior, and challenged me to think carefully about how the story of elephant seals fits into the broader topic of animal acoustic communication. Additionally, I owe a great deal of gratitude to Dr. Jim Estes, without whom I would have not been able to summarize the findings of my second chapter in a way that was relevant to a broader audience. He enabled me to see why this research is important, and gave me confidence to finish this chapter when I needed it the most.

I would also like to thank Dr. Burney Le Boeuf, whose seminal work on elephant seal behavior laid the foundation for many of my own discoveries. I am grateful for all of his contributions to Chapter 2, and for meeting with me over lunch at Avanti's to discuss the mysteries of elephant seal communication. Thank you also to Dr. Pete Raimondi for providing me with statistical advice throughout this work, and always being available to assuage any fears of doing the “right” kind of statistical tests. I also owe a great deal of gratitude to Drs. Nicolas Mathevon and Isabelle Charrier, who allowed me to be a part of this work nearly 10 years ago, and enabled my leadership role in our collaborative effort exploring the social lives of elephant seals. I am not sure I would have finished my PhD without my time spent with them in France, and I am appreciative of their hospitality and contribution to several parts of this dissertation over the last several years.

Inevitably throughout your graduate career, you hit momentary lulls where you second-guess your own abilities as a scientist and whether you are capable of pursuing a career in academia. It is at this time that you need the un-wavering support of a dedicated friend. I owe a great deal of gratitude to my scientific mentor and academic brother Brandon Southall for providing me with countless opportunities to learn and grow over the past 10 years, and for helping me build my own confidence in this field. Brandon taught me the importance of 1) surrounding yourself with people who you respect and enjoy working with, 2) the value of open, direct, and honest communication, and 3) how to have fun while doing good science.

My work ethic and values have been irreversibly shaped by everyone who is a part of the pinniped lab family (both humans and animals alike). Thank you to all of the volunteers who work tirelessly every day, and who are at the heart of this very special program (all for one, one for all!). I would not have made it through graduate school without Jenna Sullivan; whose love of animals, humor, and dedication to supporting others inspired me every single day of graduate school. I am also grateful for Dr. Jillian Sills, who has served as a role-model for me over the past six years, who edited and provided me with feedback every step of the way, and set an amazingly high bar both with respect to being a skilled scientist and a good human. Additionally, Sarah McKay Strobel served as a steadfast source of support, and provided me with a sense of home and comfort no matter what stage of life I was in. I would also like to thank Sarah Kienle, who always seemed to be on the same roller coaster ride of graduate school as I was, and who continuously offered an ear when I needed to vent or share any small accomplishments. And of course, Sonny Knaub, who provided much-needed company in my final months of writing my dissertation while I was in France, and gave me a ray of sunshine during a challenging period of this work.

I don't think any parent envisions their child pursuing a very obscure and impoverished career in animal behavior and communication, and so I thank my parents—Larry, Amy, and Carrie –for being my biggest fans, celebrating all of my accomplishments (no matter how big or small), and helping me to overcome my failures. Thank you especially to my mom, who took care of my life in Santa Cruz while I went off to live in France and "save the world," as she likes to say. I also thank my sister Tess for always believing in me, and for the countless hours that she spent helping me prepare for my comprehensive exam. I am grateful to my closest friends Kate, Elizabeth, Brie, Maja, Kim, and Tristin for keeping me sane over the past 6 years, for supporting me through some of the most difficult times of my life, and for reminding me who I am outside of graduate school.

The results my dissertation were only made possible by the collective effort of those that I have worked with in the field, who were truly my partners in this research. I would like to start by thanking Selene Fregosi, who contributed a great deal of effort to the contents of Chapter 1 and helped establish the long-term data base on male elephant seals upon which the contents of my dissertation are built on. I also thank Roxanne Beltran, Brad Funari, and Emma Levy for their significant contributions to several aspects of data collection and analysis. I have to pay special gratitude to Claire Nasr and Parker Forman. I never thought anyone could love elephant seals as much as me, but boy was I wrong! Their skills as naturalists, aptitude in the field, and incredible dedication to every single male elephant seal in our study made working with them some of the most memorable, crazy, heart-felt years of my life. I would also like to thank Dr. Dan Crocker for coordinating all research activities, and Dr. Patrick Robinson, Pat Morris, Rachel Holser, and Dr. Guy Oliver for their logistical support while working in the field. In particular, I would also like to express special gratitude to Dr. Fernando Elorriaga-Verplancken, who facilitated our visits to Mexico and enabled much of the data collection presented in Chapter 2. This project was only made possible by piecing together several funding opportunities, including support from the National Geographic Society, Wildlife Acoustics, the Steve and Rebecca Sooy Scholarship, the Mildred E. Mathias Graduate Student Research Grant, and the Friends of Long Marine Laboratory. Additionally, support for my time during the preparation of my dissertation was provided by the

Chancellor’s Quarter Fellowship and the Chateaubriand Research Fellowship.

Finally, to my husband Ari, to whom I owe a world of gratitude. Ari’s faith in my skills as a scientist have not wavered in all of the years that we have known one another. He has led me when I have needed guidance, followed me when I needed independence, and supported me through endless rejections, revisions, and small victories. How lucky we are to both love our work and share it with one another.

The text of this dissertation includes reprints of the following previously published material; note that small adjustments to the articles reprinted in Chapters 1 and 2 were made to accommodate formatting guidelines for this dissertation. Associated audio and video data can be found online through each respective journal.

Casey C, Charrier I, Mathevon N, Reichmuth C. 2015 Rival assessment among northern elephant seals: evidence of associative learning during mal-male contests. *R Soc. Open. Sci.* **2**(8), 150228. doi: 10.1098/rsos.150228

Casey C, Reichmuth C, Costa C, Le Boeuf B. 2018 The rise and fall of dialects in northern elephant seals. Proc. *R. Soc. Open. Sci.* **285,** 20182176. doi: 10.1098.rspb.2018.2176

Co-author Dr. Colleen Reichmuth directed and supervised the research within this dissertation. Co-author’s Charrier, Mathevon, Costa, and Le Boeuf provided expertise, guidance, statistical advice, and assistance in experimental design and execution. As the first author of both publications and the author of this dissertation, I (Caroline Casey) designed and contributed to all experiments, analyzed all data, and was responsible for manuscript preparation.

GENERAL INTRODUCTION

Understanding the role that acoustic signaling plays in communication is key to interpreting animal behavior, as nearly all animals use sound to transmit and receive information (Hauser 1996). Variation in the acoustic properties of signals emitted by individual animals can convey a wealth of information to listeners, including behavioral state, age, size, strength, and even identity (Bradbury and Vehrencamp, 2011). As a consequence, a listener's ability to successfully discriminate among similar signals from conspecifics can aid in modulating behavior in different social contexts, including kin identification, maintenance of group cohesion, and the accurate assessment of competitive rivals (Owings and Morton, 1998).

Currently our most comprehensive understanding of vocal communication comes from studies of passerine birdsong, where detailed field observations have been paired with careful laboratory experiments to address questions of mechanism, ontogeny, function, and phylogeny of vocal signaling (for a review see Catchpole and Slater, 2003). This holistic approach has resulted in birdsong serving as a model system for understanding the evolution of acoustic communication across several animal taxa, including those only distantly related to birds. Given that many mammal species operate in disparate social environments and differ with respect to basic life-history traits, it seems prudent to search for alternative models when attempting to answer both proximate and ultimate questions relating to mammalian acoustic communication.

Among marine mammals, vocal communication is a critical component of social behavior. Whereas light attenuates quickly with depth—limiting visual contact between individuals—the sound transmission characteristics of the marine environment allow signalers and receivers to remain in contact over large distances. Over the past several decades, advances in underwater sensing technology have provided researchers with the means to record sounds produced by marine mammals while at sea. As a consequence, the field of marine mammal acoustics has expanded considerably, and several studies have provided descriptions of the acoustic repertoire of different species or populations (*e.g.,* Payne and McVay, 1971; Stimpert *et al.,* 2011; Mellinger and Clark 2003; Risch *et al.*, 2013). In some cases, many aspects of the vocal behavior of more cryptic species are now being documented for the first time (*e.g.,* Stafford *et al.,* 2018, Risch *et al.,* 2014).

While the capacity to attribute underwater vocalizations to marine mammal species has improved greatly since the advent of underwater recording technologies, the ability to decipher the meaning of these signals in the social lives of free-ranging individuals remains quite limited. Elucidating the function and/or developmental significance of vocalizations is difficult, as this requires the ability to identify and monitor focal animals, extensive knowledge of the social relationships between individuals, detailed analysis of vocalizations, and the opportunity to experimentally assess the significance of these signals to listeners. Despite their difficulties, these combined approaches are necessary to understanding the specific role that acoustic communication plays in the social lives of marine mammals.

Phocids (true seals) are amphibious mammals that produce an array of acoustic signals both in air and under water. Male seals produce vocalizations during the annual reproductive season that likely aid in male-male competitive interactions and/or as advertisement to estrous females (Schusterman and Van Parijs, 2003). The majority of seal species mate aquatically, making it difficult to associate distinct vocal recordings with individuals of known age, dominance, or reproductive status. In addition to conveying information about reproductive state, call features can also reflect geographic or population-level differences. Among seals, geographic differences in vocalizations have been documented for Weddell *Leptonychotes weddellii* (Thomas and Stirling, 1983), harp *Pagophilus groenlandicus* (Terhune, 1994; Perry and Terhune 1999) leopard *Hydrurga leptonyx* (Rogers and Cato, 2002), harbor *Phoca vitulina* (Van Parijs *et al.,* 2003; Bjørgesæter *et al.,* 2004), elephant *Mirounga angustirostris* (Le Boeuf and Peterson, 1969), and bearded seals *Erignathus barbatus* (Risch *et al.,* 2007). Finally, call features can be unique to individual seals. For example variation in the calls produced by different mature males has been documented for several species including grey *Halichoerus grypus* (Caudron *et al.,* 1998), harbor (Van Parijs *et al.,* 2000), bearded (Risch *et al.,* 2007) and Weddell seals (Thomas and Stirling, 1983). Collectively, these studies offer detailed characterizations of the vocal breeding behavior of males seals of multiple species, and thus creates a foundation for addressing more specific questions regarding the adaptive value (if any) of this documented acoustic variation.

Owing to extreme selection pressures for rival assessment, the northern elephant seal (*Mirounga angustirostris*) provides an optimal social model to explore the role that learning plays in the communication system among males, which can be observed each winter (December-March) at several island and mainland rookeries along the coasts of California and Mexico during the annual breeding season (Lowery *et al.,* 2014). The northern elephant seal is the largest seal in the northern hemisphere, with males weighing between 1500 and 2300 kg, and with females reaching approximately one third the size of males at 400 to 900 kg (Le Boeuf and Laws, 1994). The species is also extremely sexually dimorphic; aside from males being much larger than females, they also develop a long fleshy proboscis and a broad, thick, calloused chest shield that begins to form during puberty.

Reproduction in this species is annually synchronous, and mature female seals aggregate by the thousands on breeding beaches each winter. Reproductively mature males arrive at these terrestrial breeding sites early in the season to establish their dominance status prior to the arrival of adult females. Sub-adult and adult males remain ashore at their breeding colonies until the females have weaned their pups, completed their estrous cycles, and returned to sea —a tenure that may span 100 days without access to food or water (White and Odell, 1971; Le Boeuf 1974, Deutsch *et al.,* 1990). Compared to females, males live much shorter lives (Le Boeuf and Laws,1994). Only 5% survive to physical maturity (Condit *et al.,* 2014), with less than 1% ever gaining reproductive access to females (Le Boeuf and Laws, 1994). This asymmetry in life history and reproductive success underpins one of the most competitive breeding systems known among mammals.

Given their accessibility during the breeding season and the fact that they are minimally disturbed by human presence, the northern elephant seal provides the opportunity for (1) direct observation and close-range recording of acoustic displays emitted by breeding males during competitive interactions, (2) the opportunity to characterize individual and regional differences in vocal behavior, and (3) the ability to experimentally test the significance of these vocalizations to listeners. The overarching goal of this dissertation is to provide a comprehensive assessment of the vocal behavior of the northern elephant seal by attempting to answer questions pertaining to the function, ontogeny, and evolution of vocal signaling by males of this species.

Specifically, Chapter 1 explores the functional significance of the acoustic displays that male northern elephant seals emit during social interactions, and evaluates whether these specialized signals function to convey honest information about an individual's fighting ability, or alternatively, his identity to listeners. Fine-scale acoustic analyses have been paired with close behavioral observations of known individuals to determine the potential functions of these acoustic signals. Using a series of sound analysis and playback experiments featuring natural and modified signals, I show that males do not rely on encoded information about size or dominance status, but rather learn to recognize individual acoustic signatures produced by familiar rivals. In this system of extreme polygyny, it is apparent that a male's knowledge of his social competitors (including their reliable vocal signatures) is imperative to his success within each breeding season. Additionally, these calls appear to reduce the costs associated with fighting while males are fasting during a protracted and energetically demanding breeding season.

The unique history of the northern elephant seal combined with long term monitoring of this species also provides the opportunity to document how vocal behavior has changed as this species has recovered from near-extinction, and to what extent these specialized signals can be influenced by factors such as population expansion, cultural learning, and the relative abundance of seals at different breeding sites. As vocal dialects were previously documented in the temporal patterns of the calls produced males at four sites in the North Pacific in 1968 and 1969, Chapter 2 evaluates the longevity of these geographic difference by comparing these early recordings to calls recently recorded at these same locations. I find that while vocal dialects were present among historical populations (confirming early findings), geographic differences in vocal behavior are no longer present at these breeding rookeries nearly 50 years later. In the absence of measurable genetic variation in this species, a combination of migration patterns and cultural mutation are proposed as factors influencing the fall of dialects and the dramatic increase in call diversity among male elephant seals.

In Chapter 3, I characterize the ontogeny of spatial, social, and communicative behavior among male northern elephant seals. I find that with maturation, males occupy smaller, more predictable home ranges, providing the opportunity for more frequent interactions and increased familiarity between competitive rivals. Additionally, while young males exhibit calls that are highly variable with respect to call structure, older males begin producing their stable acoustic signatures once they reach social maturity, at approximately seven years of age. These behavioral patterns suggest that as males get older, they transition towards an established, complex social environment that is conducive to the emergence of individual recognition and associative learning between competitors.

The unique life-history of the northern elephant seal paired with decades of behavioral research conducted through UC Santa Cruz provides an exceptional model to explore the role that vocalizations play in the social lives of male seals, and contributes broadly to comparative frameworks for studies of animal communication.

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CHAPTER 1

RIVAL ASSESSMENT AMONG MALE NORTHERN ELEPHANT SEALS: EVIDENCE OF ASSOCIATIVE LEARNING DURING MALE-MALE CONTESTS

Reprinted with permission from:

Casey C, Charrier I, Mathevon N, Reichmuth C. 2015. Rival assessment among northern elephant seals: evidence of associative learning during mal-male contests. *R Soc. Open. Sci.* **2**(8) 150228.

ABSTRACT

Specialized signals emitted by competing males often convey honest information about fighting ability. It is generally believed that receivers use these signals to directly assess their opponents. Here we demonstrate an alternative communication strategy used by males in a breeding system where the costs of conflict are extreme. We evaluated the acoustic displays of breeding male northern elephant seals (*Mirounga angustirostris*), and found that social knowledge gained through prior experience with signalers was sufficient to maintain structured dominance relationships. Using sound analysis and playback experiments with both natural and modified signals, we determined that males do not rely on encoded information about size or dominance status, but rather learn to recognize individual acoustic signatures produced by their rivals. Further, we show that behavioral responses to competitors' calls are modulated by relative position in the hierarchy: the highest ranking (alpha) males defend their harems from all opponents, whereas mid ranking (beta) males respond differentially to familiar challengers based on the outcome of previous competitive interactions. Our findings demonstrate that social knowledge of rivals alone can regulate dominance relationships among competing males within large, spatially dynamic social groups, and illustrate the importance of combining descriptive and experimental methods when deciphering the biological relevance of animal signals.

INTRODUCTION

Theoretical models of animal conflict predict it is advantageous for males to accurately assess rivals when competing for females (Bradbury and Vehrencamp, 2011; Searcy and Nowicki, 2005). Consequently, signals that encode relevant information about the fighting ability of senders help receivers to determine appropriate behavioral responses, and thus reduce the costs of conflict in terms of energy expenditure, injury, or even death (Bradbury and Vehrencamp, 2011; Kitchen *et al.,* 2003). Rival assessment is often based on signal features that correspond to resource-holding potential (Reby *et al.*, 2005; Kitchen *et al.,* 2013; Wyman *et al.,* 2008) or motivational state (De Villiers *et al.,* 2003). Alternatively, an individual may remember the outcome of previous competitive interactions with an opponent, and learn to associate these consequences with a signal emitted by the individual with whom he previously fought. This information can then be used to influence decision-making during later encounters. The latter situation has been described for species living in small stable social groups, where mechanisms for individual recognition allow for the formation of linear hierarchies based on frequent interactions between group members (Holekamp *et al.,* 2007; Cheney and Seyfarth, 2008). It is unclear whether similar associative learning processes—based on individual recognition—can support structured dominance hierarchies within very large and fluid social groups. However, we can hypothesize that remembering one's previous opponent could be the most secure strategy for rival assessment when both the competition level and the cost of physical fights are extremely high. In a system where great size and strength are traits of any male who survives to adulthood, signals conveying honest information about male quality may not be that informative, and other means for rival assessment may be present.

Due to extreme selection pressures for rival assessment, the northern elephant seal (*Mirounga angustirostris*) provides an optimal social model to explore how signals can be used to mediate competitive behavior among breeding males. Reproduction in this species is annually synchronous, and mature females congregate by the hundreds or thousands on beaches to give birth and breed (Condit *et al*., 2014). Adult males arrive at breeding sites before the females, and remain ashore until after the females have departed—a tenure that may span 100 days without access to food or water (Le Boeuf and Laws, 1994). Compared to females, males live markedly shorter lives: only 5% survive to physical maturity, with less than 1% gaining reproductive access to females (Clinton and Le Boeuf, 1993). This asymmetry in life history and reproductive success underpins one of the most competitive breeding systems known among mammals.

Male northern elephant seals fiercely compete to control access to female harems during the breeding season. While social status is initially established through physical confrontations (Cox, 1981), dominance relationships between familiar individuals are maintained by ritualized displays that include loud vocalizations, elevated visual posturing, and seismic cues produced by slamming the chest against the substrate (Sandegren, 1976; Le Boeuf 1974). The directed displays emitted by higher-ranking males are usually sufficient to control the movements of subordinates relative to female harems. Thus, while behavioral exchanges between competing males are common, physical battles are relatively rare (Sandegren 1976) and extremely costly (Norris *et al.,* 2010).

The vocalizations produced by males during their displays, traditionally called "clap threats," contain 3 to 20 broadband units emitted at high levels with repetition rates of a few pulses per second (Le Boeuf and Peterson, 1969). These signals appear to efficiently transmit information about the level of threat presented by the caller, even in situations where visual cues are unavailable (Shipley and Strecker, 1986). Vocal playbacks have been shown to elicit movement from other males on the rookery (Deutsch *et al.,* 1990) with individual responses to playbacks influenced by both caller orientation (Holt *et al.,* 2010) and relative social status (Insley and Holt, 2011). Early investigators commented on apparent individual differences in the calls of competing males, and indicated that these acoustic differences may be attributable to differences in the size and/or status of callers (Bartholomew and Collias, 1962). Subsequent behavioral and acoustic analyses confirmed the presence of reliable individual differences (Sandegren, 1976; Shipley *et al.,* 1981), but provided no indication that a male's call structure is associated with his dominance status (Shipley *et al.,* 1981). These findings suggested that male calls could function to convey individual identity, and that individuals may learn to associate distinctive features of a threat call with a specific male through learned association (Sandegren 1976; Shipley *et al.,* 1981). At present, it remains unknown whether the acoustic displays of male northern elephant seals function as honest signals that opponents can decode without prior experience, or whether they are individual identifiers which males must learn in order to economize their effort during the energetically demanding breeding season.

To investigate the information contained in the signals emitted by adult male northern elephant seals, we performed a multi-year study that integrated information about the morphological features, spatial relationships, and competitive interactions of known individuals with fine-scale acoustic analyses of their vocal displays. We then applied these results to field playback experiments that explored the extent to which receivers actually used information encoded in vocalizations during conflicts. Specifically, we experimentally tested three alternative hypotheses:

1) Calls encode resource-holding potential, and there are correlations between the acoustic features of an individual's call and his morphological traits and/or dominance rank. Males should thus use these acoustic features to modulate their responses to competitors.

2) Males cannot or do not depend on vocal features signaling phenotype and/or dominance. Individuals then should learn how to respond to rivals from experience only, and a reliable individual vocal signature should support this process.

3) There is a mixed system in which males respond differently to the calls of familiar versus unfamiliar individuals. In this case, males may depend on acoustic cues linked to resource-holding potential to modulate their responses to unknown

competitors, while relying on individual vocal signature and previous experience when responding to familiar rivals.

The results of this work provide insight into the function of this specialized acoustic signal, and demonstrate its role in maintaining dominance relationships within relatively large social networks that are not spatially predicable. Our findings also shed light on the outstanding question of behavioral flexibility in decision-making during male-male contests.

METHODS

Study animals

We worked at Año Nuevo State Park (37.1086 N, -122.338 W) from December through February for four consecutive years from 2009-2013, and 300 km south at San Simeon State Park (35.6512 N, -121.2196 W) during the 2011-2012 breeding season (Fig. 1a). At Año Nuevo, we dye-marked 30 to 51 adult males (aged 8 to 14 years) annually upon their first sighting in our study area —a 1 km long section of sandy beach used by approximately 300 adult females. A subset of adult males also had flipper tags for inter-annual identification. We took calibrated photographs of the males and recorded their location each observation day to determine proximity to female harems as well as to assess site fidelity, movement patterns, and rival familiarity. Fewer than 20 adult males were reliably re-sighted at the Año Nuevo study area during each breeding season. At the San Simeon site, we marked and photographed 15 adult males.

Determining the dominance status of males

To evaluate the dominance status of each individual, determine the relative size of his social network, and quantify the use of vocalizations during competitive behavior, at least two experienced observers scored dyadic interactions between identified males throughout each breeding season (season specific sampling effort is given in Table I). For each interaction, we recorded the identity of the apparent winner, whether he had vocalized, and how far he had moved. The same information was recorded for the apparent loser. We also recorded whether there was physical contact between the two males (Fig. 1b), and if so, scored the intensity of the interaction (from single blows to sustained combat). The dominance status of males, including those that had not directly interacted with one another, was then determined by applying an Elo-rating approach to these data, which assigns a quantitative score to individuals based on the probability of one individual beating another in a two-player game (Elo, 1978; Albers and de Vries, 2001; Briffa *et al.,* 2013). Each male was assigned an initial Elo score of 1000, as every individual began the season with the same presumed probability of winning a dyadic competitive interaction. We then adjusted individual Elo scores after each observed interaction by an amount proportional to the expected outcome, such that their subsequent win/lose probabilities changed with their adjusted rating. Relative probability (E_a) that individual 1 would beat individual 2 was determined using the equation $E_a =$

$1/1 + 10^{\left(\frac{Rank_2 - Rank_1}{400}\right)}$, where $Rank_2$ and $Rank_1$ are the ranks of individuals 2 and 1 prior to the observed interaction. Ratings were modified in proportion to the deviation from the anticipated outcome, and new Elo scores were determined using the formula $R'_A = R_A + K(S_A - E_a)$, where R'_A = new rank, R_A= previous rank, K = constant, S_A = actual score (1 for winner, 0 for loser), and E_a is the probability of each individual winning that interaction. Elo calculations were executed in R (custom code developed in R Development Core Team 2004, www.R-project.org).

Elo scores provided an instantaneous measure of dominance as well as an overall (seasonal) dominance score for each individual. At the end of each breeding season, the final Elo score for each male in the sample was validated against his corresponding descriptive rank, which in turn was qualitatively based on his repeatedly sampled proximities to female harems. Alpha males held stable positions within female harems, beta males held flanking positions relative to harems, and peripheral males were totally excluded from access to harems (Fig. 1c, 1d). Elo scores were calculated for focal males both at the Año Nuevo and San Simeon field sites.

Assessment of morphological traits and age

To estimate the size of focal males, we analyzed digital photographs obtained with a scale bar positioned on axis with the midline of the animal. The photographs were taken while individuals were lying at rest with straight (supine) body posture on flat terrain. The images were analyzed with ImageJ (v1.34, National Institutes of Health) to determine four parameters of body size: length, vertical height, body perimeter, and head perimeter (Fig. 2). The age class of focal males was determined in the field based on scarring of the chest shield, development of the proboscis, and body length (as in Le Boeuf, 1972; Clinton 1994); age class estimates were later verified from scaled photographs by experienced, independent observers.

Recording calls

To provide a large data set of male vocalizations for acoustic analysis, we opportunistically recorded males from 5-15 m during stereotyped displays using a Neumann KMR 82i Condenser Shotgun Microphone (with Rycote suspension and windscreen) connected to a Fostex FR-2 Field Memory Recorder (24-bit/48 kHz). Additionally, to determine call source levels, we used a calibrated Brüel and Kjær 4189 condenser microphone (with UA-1650 windscreen) held at 1 m from, and on-axis with, the head of the animal. Signals were received by a Brüel and Kjær 2250 sound level meter (24-bit/48 kHz). Recordings were obtained throughout the breeding season. To determine the stability of an individual's call across different behavioral states, the social context of every recorded vocalization was categorized as either directed (emitted toward another male) or non-directed (produced when not interacting with another individual). It was possible to record vocalizations at close ranges without disturbance to male seals, as adults typically completed each acoustic display once initiated, regardless of external cues or the presence of researchers.

Acoustic analysis of calls

Measurements

To examine individual variation in call structure, we characterized the calls of focal adult males (>8 years old) using the acoustic recordings obtained during competitive interactions. These males held mid-to-high ranks in the dominance hierarchy, including alpha, beta, and peripheral positions (Fig. 1c, 1d). All recorded calls were evaluated and subjectively scored for quality. Only calls with low background noise and without overlapping acoustic signals were used in subsequent analyses. To avoid possible replication of individuals in the study over multiple years, we used only calls from identified individuals recorded within a single season (2010-2011) for this analysis.

Based on the quantity and quality of the available recordings, we described the calls of 16 individuals in both the temporal and spectral domains (mean: 15.8 calls/individual, range: 9-25 calls/individual). We selected acoustic parameters that could be applied to all calls. To assess temporal features, we used Avisoft SAS Lab Pro to perform a pulse train analysis on the normalized envelope of the main (rhythmic) portion of the call, excluding introductory and terminal snorts (smooth: 41 pts, frequency range 0-6 kHz), and measured the following parameters: call duration (s), total number of pulses (n), and the average repetition rate (pulse rate, Hz) (Fig. 3a). The transient and broadband structure of the entire call precluded a traditional analysis of energy distribution among frequencies. Several spectral features were measured over the same portion of the call with the Seewave R package (Mundry, 2007): the centroid of the frequency spectrum (Hz), the 25%, 50% and 75%

frequency quartiles (1st quartile: “Q25”, 2nd quartile: “Q50” and 3rd quartile: “Q75”, in Hz), the frequency bandwidth within which the energy falls within 12 dB of the maximal frequency peak (Hz), and the frequency of maximal energy (Hz) (Fig. 3b). Individuals showed reliable substructure within the repeatable units comprising the rhythmic portion of each call; these patterns were identified and descriptively coded but not included in subsequent analyses. In contrast to analyses of the calls of the congeneric southern elephant seal (*Mirounga leonina*) (Sanvito *et al.,* 2007), we did not assess frequency information such as F0 or formant structure in this study—the calls of northern elephant seals are discrete pulses rather than long roars, and therefore preclude such measures.

Fifteen individuals from the same season had at least four high-quality source level recordings and measurements. Given the impulsive nature of these calls, amplitude was reported as dB_{peak} at 1 m (referenced to 20 μPa) rather than as dB_{rms} sound pressure level.

Individual signatures

To determine whether there were reliable differences among the calls of individuals, we used a cross-validated and permuted discriminant function analysis (pDFA, Mundry, 2007; Boersma and Weenink 2013; customized script written in R). A fitting data set (2/3 of the calls from each individual) was used to generate linear discriminant functions on the basis of the acoustic features describing the calls. The remaining 1/3 of the calls were used as a cross-validation set to measure the percentage of correctly classified vocalizations. The mean effect size was calculated from 100 random iterations. From the cross-validation results, we extracted a confusion matrix to show the conditional probability that a call emitted by the individual *i* was in fact emitted by *j*: *confusion(i,j)=p(i|j)*. To determine the significance of the effect size calculated by the cross-validation step, we created data sets where the identity of calls was randomly permuted between individuals (permuted DFA). For each of these randomized sets, we followed the same steps—training and validation—as with the non-randomized sets. After 1000 such iterations, we calculated the proportion of randomized validation data sets with the number of correctly classified calls being at least as large as the effect size obtained with the non-randomized validation data set. This proportion gives the significance of the level of discrimination and is equivalent to a *p*-value (McGregor, 1992).

Variability over years and across social contexts

To assess the long-term reliability of call structure, we recorded a subset of individuals over two successive years (*n*=10 males, 5.8 calls/individual/year, range: 5-6), and measured both the centroid of the frequency spectrum and the pulse rate (main parameters shown to support the individual signature—see Results). We then calculated Euclidian distances in the two-dimensional space defined by these two parameters after transforming them into *Z*-scores. Three categories of distances were computed: within the calls recorded during year 1 for each individual, between the calls of years 1 and 2 for each individual, and between the calls of year 1 of each individual and all the other calls of all other individuals from year 1. We then evaluated whether the average distance between an individual's calls during year 1 was shorter than the average distance between its year 1 and year 2 calls. We also calculated densities of the distribution of the three categories of Euclidian distances. We followed a similar procedure to assess the stability of vocal signatures between calls produced in directed versus non-directed social contexts (n = 8 males, 4.7 calls/individual/social context, range: 2-6).

Correlations between acoustic cues, body size and dominance

To investigate whether spectral, temporal, and/or acoustic features were linked to morphological traits or dominance score among the focal males, we performed linear correlations (lm function in R Statistical Package). We also assessed whether the morphological traits of the focal males were correlated with their dominance scores.

Playback experiments

General procedure

Playback tests were performed during periods of high male responsiveness corresponding to the females' oestrous. Adult males were tested once or twice a day, with at least 3 h separating each test to avoid habituation. We used a similar method to that described by Holt *et al.,* 2010. Playback signals were projected from a self-powered Premio 8 PA sound system or paired Advent AV570 speakers capable of replicating the amplitude and spectral components of the recorded calls. The speaker was placed 7 ± 1 m from the focal male, except as noted in section 3.7.3 (experiments on alpha males). To control for possible directionality effects, the speaker was placed on axis with the focal animal (maximum deviation 90 degrees). Males were challenged after a minimum period of 2 min of not having interacted with other males, and with no other males within a 7 m radius. Each playback included three different calls separated by 3 s of silence and broadcast at 116 ± 1.5 dB_{peak} at 1 m. For playback experiments using modified calls (described below), we built each series with only two repetitions of a single call; this was done to limit habituation since each of the ten adult males was tested with up to seven different signals.

Testing the use of size-related acoustic cues

To evaluate the biological relevance of acoustic features that scaled with body size, we challenged ten adult males from Año Nuevo, ranging in eye-to-tail length from 3.2 to 3.6 m, with playbacks of signals derived from those recorded in a distant colony (Piedras Blancas, San Simeon, California) to avoid familiarity with senders. We mimicked either smaller males (< 3.2 m) or larger males (> 3.6 m) by changing the characteristics of natural calls that were shown to be correlated with size: pulse rate, the number of pulses, or the frequency spectrum (see Results). Temporal modifications of natural calls were made by deleting or adding pulses to alter the pulse number, and by shortening or lengthening the inter-pulse interval to alter the pulse rate. Spectral content (modified Q25) was manipulated by re-synthesizing natural calls using a PSOLA-based algorithm in PRAAT (Boersma and Weenink, 2013).

In the first set of experiments, we played back calls with modified pulse rates (1, 1.7 or 3 Hz, corresponding to small, medium and large males respectively), while the number of pulses per call remained fixed (14 pulses, a rate corresponding to average-sized males). In the second set of experiments, we modified the number of pulses per call (7, 14 or 21 pulses, corresponding to small, medium and large males respectively) while maintaining an average pulse rate (1.7 Hz). Finally, we challenged the same males with signals showing both fixed pulse rate (1.7 Hz) and number of pulses (14) but with modified spectral content (either a low Q25 of 536 Hz or a high Q25 of 804 Hz; these low and high Q25 values correspond to mean Q25 values ± ~20%, representing large and small males respectively). These experiments were conducted during the 2011-2012 breeding season.

Testing the effect of social rank and familiarity

To assess whether alpha and beta males have the same responsiveness to the dominance status and/or the familiarity of the callers, we performed three sets of playback experiments. First, we tested whether beta males respond differently to calls from known dominant and subordinate males. We challenged ten beta-ranking males at Año Nuevo with calls from both dominant and subordinate familiar rivals. Target males were sighted for at least 10 days before the experiments and their social ranks determined (harem-flanking males with Elo scores of 964-1713). The playback treatments for each target male were selected based on at least three observed interactions in which the familiar rival had called, and there was a clear approach or retreat response by the target male. These experiments were conducted during the 2010-2011 breeding season.

In a subsequent experiment, we tested whether the observed responses of males to the calls of familiar rivals were dependent on prior experience with an individual. In this test, we used the calls from the same dominant-subordinate playback treatments to challenge ten different beta males from a distant colony (San Simeon). We took great care to match the dominance status of these naïve males with the ten beta males tested previously. These experiments were conducted during the 2011-2012 breeding season.

Finally, due to their high dominance status on the rookery, alpha males could not be tested with both familiar dominant and subordinate treatments. Rather, to evaluate their responsiveness to imposing males on the rookery, five alpha males from Año Nuevo (harem-holding males with Elo scores of 1056-2047) were challenged with calls from neighboring alphas, familiar (flanking) betas, and unfamiliar alpha males (males recorded the same year but in another area of the breeding colony and never seen at our study site). We performed these playbacks at four successive distances along a linear transect from the border of the alpha's harem (40, 30, 20 and 10 m) to simulate intrusion of an approaching adult male. These experiments were conducted during the 2010-2011 breeding season.

Analysis of responses to playbacks

The behavioral responses of target males to playbacks were measured over a 90 s period from the onset of the playback, and characterized by six measures: latency to orient towards the loudspeaker (s), latency to change posture (s), latency to vocalize (s), number of emitted calls, latency to move towards or away from the loudspeaker (s), and distance moved (m). Rather than separately analyzing these six non-independent measures of response, they were collapsed using a principal component analysis (PCA, varimax rotations (Kitchen *et al.,* 2013; Charrier *et al.,* 2011; Sokal and Rohlf, 1995). The PC scores of components showing eigenvalues > 1 were used to compare responses to different stimuli. For playbacks using modified calls and those with dominant/subordinate pairs, we used non-parametric tests (Wilcoxon matched-pairs tests (Barr *et al.,* 2013). To cope with the 2 x 2 fully crossed design (playback type x distance) of the test on alpha males, we used a linear mixed model (function lmer in R lme4 package), after transforming data to meet the model assumption (exponential transformation), and checking the distribution of the residuals with respect to normality and homoscedasticity (fixed effects: playback type and distance; random effects: intercepts for tested males, males random slopes for the effect of playback type, and distance (Barr *et al.,* 2013). *P* values were obtained with likelihood-ratio tests comparing the fit of the full model with reduced models lacking playback type or distance.

RESULTS

Social interactions and the use of vocalizations

We observed and scored 2445 male-male dyadic competitive interactions over four breeding seasons (Table I). Most interactions involved approach and/or multi-modal display behavior after which one individual assumed a submissive posture and retreated. Vocal displays from at least one individual of the pair were observed in 76% of interactions. Winners called during 95% of interactions that included vocalizations, much more frequently than losers (29%). Only 5% of interactions led to physical contact. Sustained fights comprised less than 2% of the interactions, and occurred most often when neither male backed down from an escalating dispute. The majority of these battles involved vocalizations from both individuals and all occurred between males of similar dominance status that had not fought previously that season. Within a given season, alpha and beta male elephant seals engaged competitively with an average of 38 and 26 other males, respectively (Fig. 1c).

Relationships between acoustic cues, body size and dominance

Call pulse rate and the total number of pulses per call were positively correlated with most body measurements (Table II). Further, the first frequency quartile (Q25) decreased with body size, with larger animals having lower-frequency calls (Table II). None of the acoustic parameters were correlated with dominance score among breeding age males (Table II). There was also no correlation between dominance score and morphological traits among adult males (Table III).

Size information and its influence on rivals' behavior

We determined whether focal males utilized the morphological information encoded within vocalizations by modifying the body-size-linked acoustic features of call (pulse rate, total number of pulses per call, and first frequency quartile) during playback experiments. Only the first two components of the PCA (PC1 and PC2) performed on the six behavioral measurements showed eigenvalues > 1, and explained 55% and 18% of the total variance respectively (Fig. 4). All the behavioral variables except latency to orient were strongly correlated to PC1, with distance moved and number of calls negatively correlated to PC1 (factor loadings: latency to orient: 0.151; latency to change posture: 0.697; latency to vocalize: 0.885; latency to move towards or away from the loudspeaker: 0.799; distance moved: -0.742; number of emitted calls: -0.904). Negative PC scores thus indicate a strong reaction, with shorter latencies, close approach to the speaker and calls in response to the playback. When we modified call pulse rate, males responded equally to the three experimental signals (Fig. 4b; Wilcoxon matched pairs tests on PC1 scores: $n = 10$, $Z = 0.051$, $p = 0.959$ for 1.7 Hz *vs* 1 Hz; $Z = 0.357$, $p = 0.721$ for 1.7 Hz *vs* 3 Hz; $Z = 0.15$, $p = 0.878$ for 1 Hz *vs* 3 Hz; for PC2 scores $p= 0.241$, $p = 0.203$ and $p = 0.444$ respectively). When we modified the number of pulses per call, we similarly observed no significant differential responses from the tested males, although there was a trend for males to respond more strongly when the number of pulses was higher (Fig. 4c; Wilcoxon matched pairs tests on PC1 scores: $n = 10$, $Z = 0.42$, $p = 0.674$ for 14 *vs* 7 pulses; $Z = 1.78$, $p = 0.074$ for 14 *vs* 21 pulses; $Z = 1.68$ $p = 0.09$ for 7 *vs* 21 pulses; for PC2 scores $p = 0.401$, $p = 0.074$ and $p = 0.721$ respectively). Males did not show differential responses to signals with modified spectral composition (Fig. 4d; Wilcoxon matched pairs tests, PC1 scores: $n = 10$, $Z = 1.07$, $p = 0.284$; PC2 scores: $n = 10$, $Z = 0.968$, $p = 0.333$).

Individual vocal signatures

Our qualitative observation that experienced observers could identify males solely by their calls was supported by a quantitative cross-validated and permuted discriminant function analysis. The results of the cross-validation step showed that individual identification on the basis of six spectral and three temporal acoustic parameters was highly reliable (average rate of correct classification = 61.3%, range: 35.9 - 99.5%; chance = 6.3%; $n = 16$ adult males with 15.8 ± 3.5 calls/individual, range: 9-20; $p < 0.001$; see classification matrix in Fig. 5a). The two main acoustic factors separating individuals on the first discriminant function were one temporal and one frequency parameter: call pulse rate and the centroid of the call frequency spectrum (Table IV). The combination of these two cues was sufficient to characterize the unique acoustic space of each individual (Fig. 5a), even without further consideration of notable differences in fine-scale pulse structure.

By recording ten individuals over consecutive years, we found that their vocal signatures were stable over at least two seasons (Fig. 5c, Table V). Further, comparisons of Euclidian distances for calls recorded for eight individuals within and between social contexts (undirected *vs*. directed calls) showed that an individual's call exhibited the same signal structure and amplitude regardless of the social condition during which it was emitted (Fig. 5b, Table V).

The influence of social knowledge on the behavioral responses of males

Beta males presented with calls from familiar dominant and subordinate rivals responded aggressively to the calls of their subordinate opponent by approaching the loudspeaker and vocalizing (*i.e.,* negative PC scores), while they quickly moved away without calling (*i.e.,* positive PC scores) upon hearing the calls of their dominant rival (Wilcoxon matched pairs test on PC1 scores, $n = 10$, $Z = 2.1915$, $p = 0.028$; on PC2 scores: $n = 10$, $Z = 1.68$, $p= 0.09$; Fig. 6). The first two components of the PCA performed on behavioral measurements showed eigenvalues > 1, and explained 53% and 28% of the total variance, respectively. Distance moved, latency to vocalize, and number of calls were correlated to PC1 (all positively except latency to vocalize), while latency to orient and latency to move were positively correlated to PC2. In a subsequent experiment, the same dominant-subordinate treatments were presented to ten beta males of similar status from a distant colony. In this case, the focal males were unfamiliar with the callers. We observed no differential response to the calls of high-ranking and low-ranking strangers (Wilcoxon matched pairs test on PC1 scores, $n = 10$, $Z = 0.652$, $p = 0.515$; on PC2 scores: $n = 10$, $Z = 0.059$, $p = 0.952$; Fig. 6).

Alpha males that were challenged with calls from nearby alpha males, familiar beta males, and unfamiliar alpha males did not exhibit differential responses ($\chi^2 = 0.257$, n = 5, df = 2, $p = 0.879$; Fig. 7). Only the distance of the playback significantly influenced their reactions to intruders' calls ($\chi^2 = 8.04$, n = 5, df = 1, $p = 0.005$), with post-hoc comparisons indicating that behavioral responses were strongest (*i.e.,* negative PC scores) when the loudspeaker was closest, at 10 m (Tukey tests, between 20-10 m: $p = 0.005$, 30-20 m: $p = 0.748$, 40-30 m: $p = 0.975$; Fig. 7).

DISCUSSION

Exploring the mechanisms that sustain dominance hierarchies in animal groups is necessary to understand the dynamics of social interactions in situations where individuals compete for resources. The present study reveals that signals produced by male northern elephant seals during rival assessment do not necessarily convey information about the motivational state or resource-holding potential of individuals. Instead of using signals to assess aggressive intention or fighting ability, individuals may need only to learn to associate the outcomes of previous interactions with reliable cues emitted by competitors. This social knowledge based on individual recognition enables competitors to choose between alternative behavioral responses (*e.g.,* attacking, retreating or observing), thereby increasing opportunities to gain access to desired resources under the least costly conditions. In the social system of the northern elephant seal, the few alpha-status males defend their harem from any intrusion, while less dominant beta males recognize their opponents and respond conditionally on the basis of prior experiences. Here, we discuss the selection pressures that favor such a communication system, which relies on individual signatures and associative learning. We also consider how competitors assess and manage information about their social network, and emphasize the importance of combining descriptive and experimental methods when attempting to understand signaling strategies.

Reproduction in northern elephant seals combines an extreme level of intra-sexual competition with an extended period of fasting, and therefore imposes enormous energetic costs on males (Norris *et al.,* 2010). Individuals must balance their time between vigorously competing for access to females while minimizing energy and water loss, as well as avoiding harm. Substituting fighting and chasing with calling may represent the most efficient strategy in this system. We have shown that the acoustic displays produced by males serve as identity signals—that is, signals requiring only that senders and receivers have prior knowledge of one another and that they remember the outcome of previous competitive interactions (Laidre and Johnstone, 2013). While this kind of recognition has been observed to sustain dominance relationships within stable, territorial groups (Temeles, 1994), far fewer studies have evaluated the role of individual recognition in maintaining these relationships in more fluid, non-territorial social environments.

The finding that male northern elephant seals can rely on individual acoustic signatures to assess their opponents is surprising given the more “honest” signaling systems of mammals that compete for access to females groups rather than territories (*e.g*., Reby *et al.,* 2005). From a strictly correlational standpoint, while some acoustic features of northern elephant seal displays were associated with morphological traits, there was no predictive relationship between these call parameters and the social dominance of callers. The extent to which size and status are linked is less clear: while we found no correlation between morphological traits and dominance rating among adult males, another study reports a positive association (Haley *et al.,* 1994). Irrespective of the relationship between phenotype and dominance, the present study provides direct experimental evidence that—while some call features encode morphological traits—males *do not* attend to the available honest information during competitive encounters. Thus, it appears that hierarchical structure among the elite males that survive to physical maturity may be more influenced by the dynamics of social interactions than the advantages associated with size or strength (Chase *et al.,* 2001, Tanner *et al.,* 2011, Correa *et al.,* 2013). In this highly competitive system, cues associated with phenotype or motivation may not be informative enough for males to discriminate between the few top contenders. Signals conveying individual identity are apparently more informative, and a male’s success appears to rely on his ability to effectively manage this social knowledge throughout the breeding season.

To function effectively, such a system based on associative learning requires fidelity to a given breeding location, stable individual vocal signature, and the ability to recognize and remember the vocal signatures of other males. Northern elephant seal males show strong breeding-site fidelity (Le Boeuf and Laws, 1994). This allows males the opportunity for repeated interactions with individuals in a given social hierarchy, as shown in this study. Reliable vocal signatures encode the identity of callers, regardless of social context. This benefits male callers through ease of recognition by subordinate rivals who are likely to retreat from contests. Males also use vocalizations to recognize more dominant, familiar opponents, and thus avoid conflicts that they are likely to lose. Paired with associative learning capabilities that allow individuals to link acoustic signatures to social consequences, the use of identity signals may produce an evolutionary stable strategy within the context of dominance interactions within relatively large, social groups (Tibbetts and Dale, 2007). Moreover, since individual vocal signatures remain stable over successive years, it is possible that males may recognize familiar rivals across breeding seasons. Prior to each season, the relative dominance status of individuals may thus be influenced by the long-term memory of past competitors. However, multi-year recognition of rivals warrants further investigation in this species.

We have found that male northern elephant seals are capable of accurately identifying familiar competitors on the basis of their calls, and show flexibility in their responses to threats depending on their dominance status and the familiarity of the caller. Beta males show a conditional behavioral strategy in response to challengers, responding appropriately to familiar males of known relative hierarchical status, while showing no specific reaction to the calls of strangers. We do not propose the males exposed to unfamiliar calls were indifferent, but rather, that lack of response may represent the safest strategy when assessing the calls of unfamiliar challengers. Mid-ranking males may have a good deal to gain by asserting dominance over new contestants, but a substantial amount to lose if their new opponent is far larger or more motivated to attack. This dichotomy in motivation to respond may leave mid-ranking males at a draw when first assessing the calls of unfamiliar opponents, and in these cases males may require additional information (including visual or seismic cues) about their opponent before deciding to attack or retreat. Once a male has reached alpha status and has gained a harem-controlling position, his motivation to defend against encroaching males is amplified. Alpha males appear to be highly responsive to the calls of any males, regardless of familiarity or social status, once they perceive an immediate threat. The behavioral plasticity of males highlights the importance of individual strategy in this system, and warrants further investigation in other breeding systems in which males compete for access to breeding rights.

In our study, male elephant seals were observed to engage with as many as 43 opponents over the course of a single breeding season. An individual’s success within this relatively large and dynamic social system depends on managing knowledge of dominance relationships, regardless of whether this information is obtained through interaction or observation. As the amount of information stored by individuals may be limited, males could sort competitors into different relative social categories, and continuously update these categories throughout the breeding season. For example, a beta male could classify familiar competitors into a few functional categories, such as "alphas," "higher-ranking males," and "lower-ranking males" (Daniels *et al.,* 2012; Schusterman, 1978). and respond similarly to the different individuals within each category. The level of accuracy and persistence of this kind of social knowledge remains to be investigated in this species.

CONCLUSIONS

The communication system of male northern elephant seals emphasizes the role that signaling plays during contests over resources, as well as conditional behavioral strategies for conflict resolution gained from social experience. An initial look at this system would suggest that the maintenance of hierarchical relationships relies on acoustic cues conveying resource-holding potential (Kitchen *et al.,* 2013; Charlton *et al.,* 2010; Taylor *et al.,* 2010; Ilany *et al.,* 2013). While we found positive correlations between body size and a few acoustic features, playback experiments showed that male northern elephant seals do not use these phenotype-linked cues to assess their rivals. Rather, listeners attend to and remember individual vocal signatures experienced during previous contests. These findings demonstrate the importance of using experimental approaches to confirm the biological function of animal acoustic signals. Several recent studies have used correlational approaches alone to argue that phenotypically "honest" signals are used to settle conflicts between competitors (*e.g.,* Wyman *et al.,* 2008; Mathevon *et al.,* 2010; Sanvito *et al.,* 2007; Taylor *et al.,* 2010; Ilany *et al.,* 2013). Given the growing interest in status signaling and selective pressures influencing the structure of animal social networks (Arnott and Elwood, 2009; Szamado, 2011; Pinter-Wollman *et al.,* 2014), we advocate that further studies combine both descriptive and experimental methods to establish a true understanding of the information gained by the exchange of specialized signals.

ACKNOWLEDGEMENTS

We gratefully acknowledge the efforts of Selene Fregosi, who contributed to behavioral data collection, analysis of social dominance, and experimental design, Brandon Southall who contributed to acoustic recording and source level measurements, Roger Mundry for statistical advice, and Rob Harcourt, Burney Le Boeuf, Bruce Lyon and several anonymous referees for their helpful comments on a previous version of the manuscript. We thank Trashon Boudreaux, Roxanne Beltran, Claire Nasr, Bradley Funari, Ari Friedlaender, Patricia Morris, Guy Oliver, and Brendan Wakefield for technical and logistical support. We also thank Dan Costa and Dan Crocker for coordinating research activities. We dedicate the present work to the late Ron Schusterman, who brought our team together.

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TABLES AND FIGURES

Breeding Season Event	**2010**	**2011**	**2012**	**2013**	**TOTAL**
Days with Observations	23	49	31	24	**127**
Hours of Opportunistic Sampling	43	191	82	90	**406**
Number of Calls Recorded	800	1468	584	759	**3611**
Unique Males Identified	74	177	79	142	**320**
Unique Adult Males Identified	30	50	40	51	**171**
Unique Males Observed Interacting	48	127	61	116	**352**
Interactions Observed	383	1177	786	482	**2445**
Unique Males with > 5 Interactions	24	64	36	30	**130**
Unique Males with > 10 Interactions	16	42	33	26	**101**
Winner Vocalized Interactions	-	863	590	334	**1787**
% Winner Vocalized Interactions		73.3%	75.8%	69.3%	**73.4%**
Loser Vocalized Interactions	-	255	186	105	**546**
% Loser Vocalized Interactions		21.8%	23.7%	21.9%	**22.4%**
Neither Vocalized Interactions	-	258	179	136	**573**
% Neither Vocalized Interactions		22.1%	22.8%	28.3%	**23.5%**
Both Vocalized Interactions	-	242	175	105	**522**
% Both Vocalized Interactions		21.5%	22.5%	21.8%	**21.4%**
Physical Contact Interactions	-	65	35	24	**124**
% Physical Contact Interactions		5.6%	4.5%	5.0%	**5.1%**
Sustained Physical Contact Interactions	-	21	11	12	**44**
% Sustained Physical Contact Interactions		1.8%	1.4%	2.5%	**1.8%**
Sustained Physical Contact Interactions - Both Vocalized	-	10	6	8	**24**
% Sustained Physical Contact Interactions - Both Vocalized		47.6%	54.5%	66.7%	**54.5%**
Sustained Physical Contact Ends Without Decision	-	7	2	0	**9**
% Fights End as Draw		33.3%	18.2%	0.0%	**20.5 %**

TABLE I. Summary of observed frequency of events within and across breeding seasons, including the relative proportions (%, by type) of male competitive interactions. (Unique males are those that have been marked at the primary field site during a given season, a subset of these are present across two or more seasons. Consistent scoring of vocal behavior throughout each breeding season indicated that the observed trends in vocal signalling by winners and losers during competitive interactions were similar year- to-year.)

	Acoustic parameter	N	R^2 (adjusted)	Equation	P value
Correlations with vertical height	Duration (s)	16	-0.057	4.72x + 6.10	0.665
	Pulse rate (Hz)	**16**	**0.425**	**3.11x – 0.68**	**0.004**
	Number of pulses	16	0.138	29.6x – 6.47	0.086
	Fmax (Hz)	**16**	**0.282**	**676x - 152**	**0.020**
	Centroid (Hz)	16	0.059	575x + 1294	0.185
	Q25 (Hz)	**16**	**0.413**	**1693x - 642**	**0.004**
	Q50 (Hz)	16	0.040	695x + 699	0.221
	Q75 (Hz)	16	0.002	731x + 1877	0.329
	-12 dB Bandwidth (Hz)	16	-0.070	0.124x + 1.0	0.891
	dB$_{peak}$ re: 20μPa @ 1m	15	-0.027	-4.99x + 130	0.425
Correlations with body length	Duration (s)	16	0.090	5.01x – 7.14	0.137
	Pulse rate (Hz)	**16**	**0.489**	**1.11x – 2.26**	**0.002**
	Number of pulses	**16**	**0.263**	**12.8x – 28.5**	**0.024**
	Fmax (Hz)	16	0.171	152x - 221	0.062
	Centroid (Hz)	16	-0.003	118x + 1294	0.346
	Q25 (Hz)	**16**	**0.262**	**-169x - 1233**	**0.033**
	Q50 (Hz)	16	0.041	197x + 517	0.221
	Q75 (Hz)	16	-0.036	143x + 1903	0.500
	-12 dB Bandwidth (Hz)	16	-0.069	0.057x + 0.906	0.861
	dBpeak re: 20μPa @ 1m	15	-0.129	-2.76x + 5.49	0.123
Correlations with body perimeter	Duration (s)	16	-0.021	1.57x – 2.26	0.420
	Pulse rate (Hz)	**16**	**0.454**	**0.677x – 3.55**	**0.003**
	Number of pulses	**16**	**0.250**	**6.44x – 33.7**	**0.028**
	Fmax (Hz)	16	0.187	120x - 599	0.053
	Centroid (Hz)	16	-0.022	63.6x + 1219	0.426
	Q25 (Hz)	16	0.161	-73.2x + 1205	0.138
	Q50 (Hz)	16	-0.007	90x + 508	0.359

	Q75 (Hz)	16	-0.049	74x + 1832	0.591
	-12 dB Bandwidth (Hz)	16	-0.062	-0.05x + 1.46	0.731
	dB_{peak} re: 20μPa at 1m	15	0.162	-1.91x + 141	0.096
Correlations with head perimeter	Duration (s)	16	-0.063	-2.44x + 10.6	0.737
	Pulse rate (Hz)	16	0.106	2.13x + 0.20	0.117
	Number of pulses	16	-0.070	-2x + 13.45	0.884
	Fmax (Hz)	16	-0.056	290x + 81.1	0.662
	Centroid (Hz)	16	-0.052	152x + 1607	0.621
	Q25 (Hz)	16	-0.069	-129x + 731	0.601
	Q50 (Hz)	16	-0.066	101x + 1121	0.787
	Q75 (Hz)	16	-0.034	350x + 2188	0.488
	-12 dB Bandwidth (Hz)	16	-0.071	0.011x + 1.08	0.990
	dB_{peak} re: 20μPa at 1m	15	-0.081	1.11x + 126	0.755
Correlations with dominance rating	Duration (s)	16	0.053	-0.0044x + 15.2	0.197
	Pulse rate (Hz)	16	0.051	-0.0005x + 2.03	0.201
	Number of pulses	16	-0.04	-0.0031x + 16.7	0.528
	Fmax (Hz)	16	-0.070	-0.0098x + 257	0.940
	Centroid (Hz)	16	-0.070	-0.004x + 1700	0.970
	Q25 (Hz)	16	-0.050	0.1x + 532	0.144
	Q50 (Hz)	16	-0.060	0.056x + 1103	0.704
	Q75 (Hz)	16	-0.065	-0.05x + 2452	0.777
	-12 dB Bandwidth (Hz)	16	-0.069	0.00006x + 1.01	0.852
	dB_{peak} re: 20μPa at 1m	15	-0.081	1.11x + 126	0.755

TABLE II. Correlation of acoustic parameters with morphological measures and dominance rating (note that significant correlations are shown in bold).

	N	R^2 (adjusted value)	Equation	P value
Vertical height	16	0.038	-1279x + 2300	0.228
Body size	16	-0.015	-311 x + 2463	0.391
Body perimeter	16	-0.0008	-199x + 2900	0.337
Head perimeter	16	-0.068	146x + 1342	0.839

TABLE III. Correlation of dominance status (Elo score) with morphological measures.

Acoustic parameter	**N**	**Number of calls per male ± SD (range)**	**Group mean ± SD**	**Range of mean values for individuals**	**LD1**
Temporal					
Duration (s)	16	15.8 ± 3.5 (9-25)	10.3 ± 3.7	5.7 – 19.5	0.192
Pulse rate (Hz)	16	15.8 ± 3.5 (9-25)	1.73 ± 0.5	0.94 – 2.84	-0.795
Number of pulses	16	15.8 ± 3.5 (9-25)	15.6 ± 7.5	7.8 – 35.7	-0.411
Spectral					
Fmax (Hz)	16	15.8 ± 3.5 (9-25)	460 ± 161	232 – 725	-0.067
Centroid (Hz)	16	15.8 ± 3.5 (9-25)	1700 ± 175	1574 – 1902	0.656
Q25 (Hz)	16	15.8 ± 3.5 (9-25)	643 ± 127	263 – 781	0.064
Q50 (Hz)	16	15.8 ± 3.5 (9-25)	1209 ± 216	543 – 1473	-0.028
Q75 (Hz)	16	15.8 ± 3.5 (9-25)	2367 ± 296	1624 – 2774	-0.426
-12 dB Bandwidth (Hz)	16	15.8 ± 3.5 (9-25)	1077 ± 347	241 – 1578	-0.074
Amplitude					
dB$_{peak}$ re: 20μPa at1m	15	4	126.2 ± 3.3	120.4 - 130.2	

TABLE IV. Summary of acoustic parameters measured (note that LD1 gives the loadings of acoustic parameters for the first discriminant function used to classify calls from different individuals).

	Mean Euclidian distances[a]	
Individual	**Within year**	**Between years**
X579	1.257	1.898
25C	0.932	0.934
GL	1.36	1.011
4C	1.25	0.986
6Z	0.668	0.799
9R	1.21	1.413
2BR	1.009	0.984
3TC	0.554	0.868
3MX	0.906	0.774
6097	0.502	0.791
Comparison[a]	$P > 0.05$	
	Within directed context	**Between directed and undirected contexts**
2BR	0.701	0.574
3MA	1.196	1.016
3MX	0.898	0.981
3TC	0.318	0.252
6LI	0.766	0.769
6RA	0.680	0.735
8IC	1.884	1.559
6097	0.651	0.545
Comparison[b]	$P > 0.05$	

TABLE V. Comparison of individuals' calls between years and across social contexts.

[a] Euclidian distances, calculated in the two-dimensional space defined by calls' centroid of the frequency spectrum and pulse rate, were determined for the calls from males recorded on two successive years or on two different social contexts (*e.g.,* calls directed and non-directed to a particular individual).

[b] There is no significant difference between the distance separating an individual' s calls recorded in the same year and the distance between calls recorded in two consecutive years (n = 10 males, Wilcoxon matched-pairs test, z = - 0.64, $P > 0.05$). Similarly, there is no difference in calls emitted in the directed context, relative to those emitted in non-directed context (n = 8 males, Wilcoxon matched-pairs test, W = 22, $P > 0.05$).

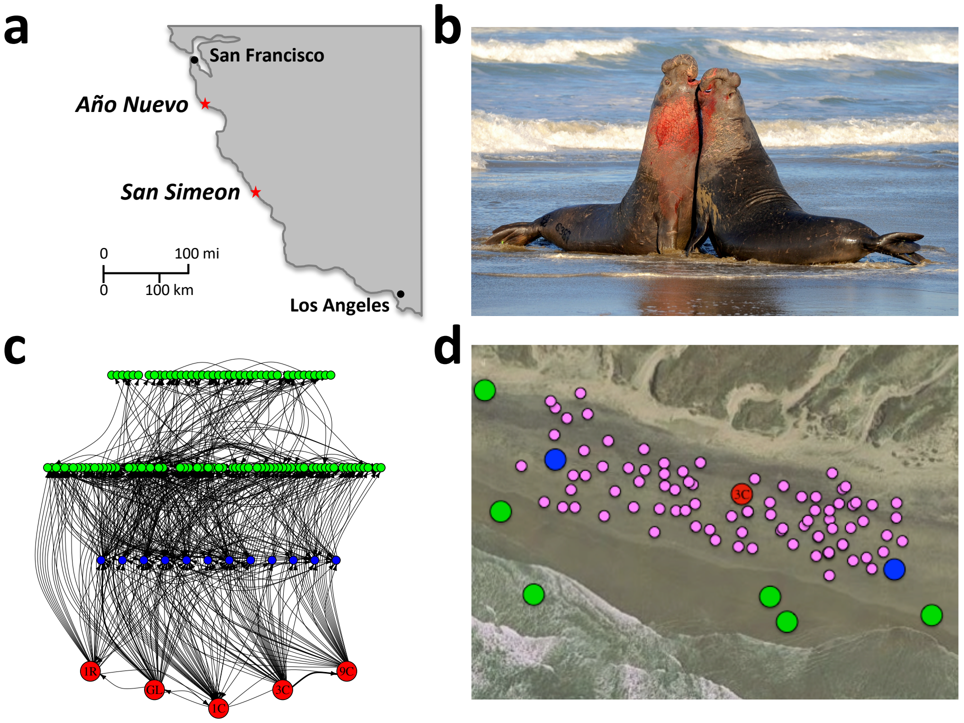


FIG. 1. (**a**) Locations of the primary (Año Nuevo) and remote (San Simeon) study sites. (**b**) Example of male-male physical conflict following exchange of displays. (**c**) The social network of northern elephant seal males as it appeared at the Año Nuevo study site during the 2010-2011 reproductive season. Red dots = "alpha" males that controlled female harems over the season; blue dots = "betas" males that reliably held harem flanking positions with opportunistic access to females; green dots = "peripheral" males that typically lacked access to harems (the "peripheral" males shown on the upper layer of the network were never observed interacting with alphas). Each arrow represents a directed interaction, drawn from a winner to a loser. The thickness of the arrows is proportional to the number of observed competitive events between two males (mean ± SD = 1.95 ± 2.02 events; range 1-19; 1170 competitive events; see Methods for details on data collection). Each Alpha male interacted with 37.6 ± 3.7 individuals (range 33-43). The number of interactants for Beta males was 26.1 ± 10.5 (range 10-39). More than 97% of relationships between males were fully asymmetric (*i.e.*, the interactions within a given dyad of males was always won by the same individual). The dyad is thus characterized by a well-established "dominant-subordinate" relationship, illustrating the stability of the hierarchy between males along the reproductive season. (**d**) Aerial schematic of a harem. Red, blue, and green dots represent "alpha", "beta", and "peripheral" males respectively; pink dots represent females.

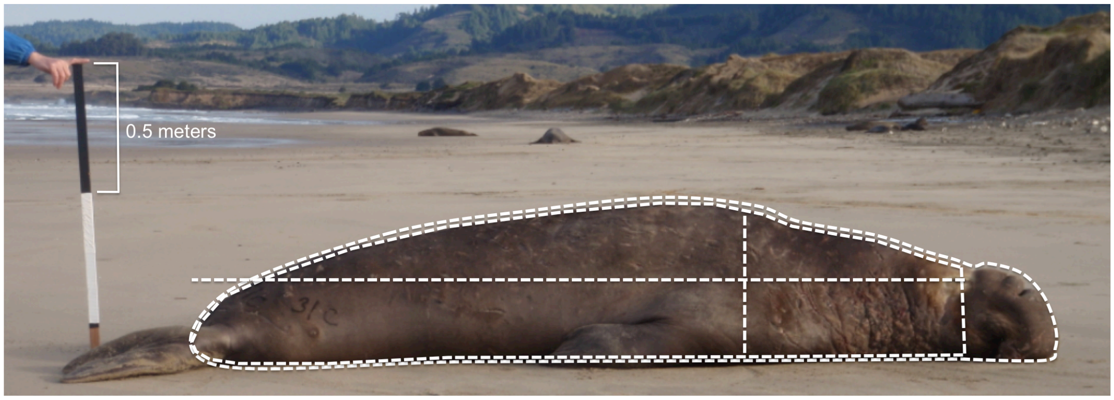


FIG 2. Assessment of morphological features. Photographs were taken with a calibrated scale to determine four parameters of body size: length (from front of eye to base of tail), vertical height (at axilla), total body perimeter, and head perimeter.

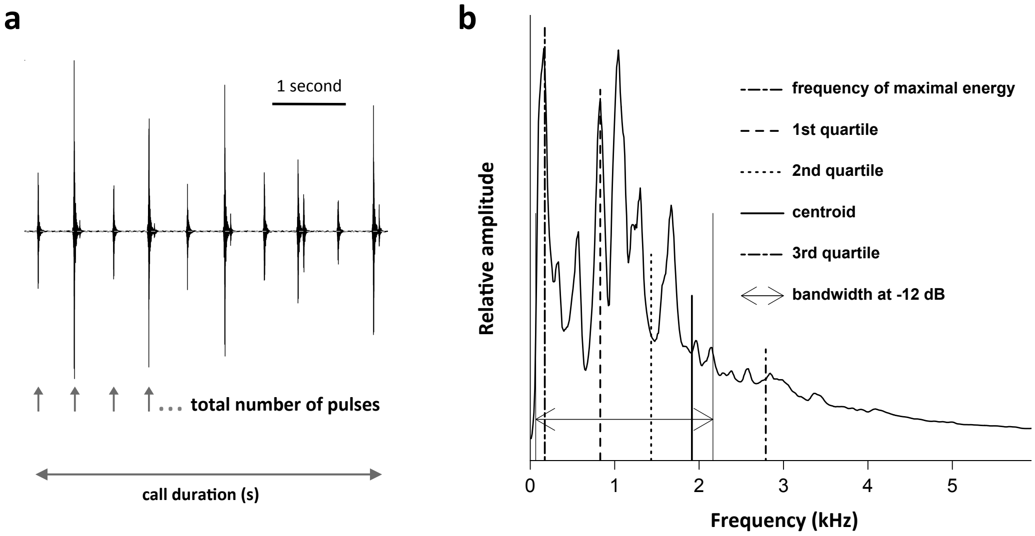
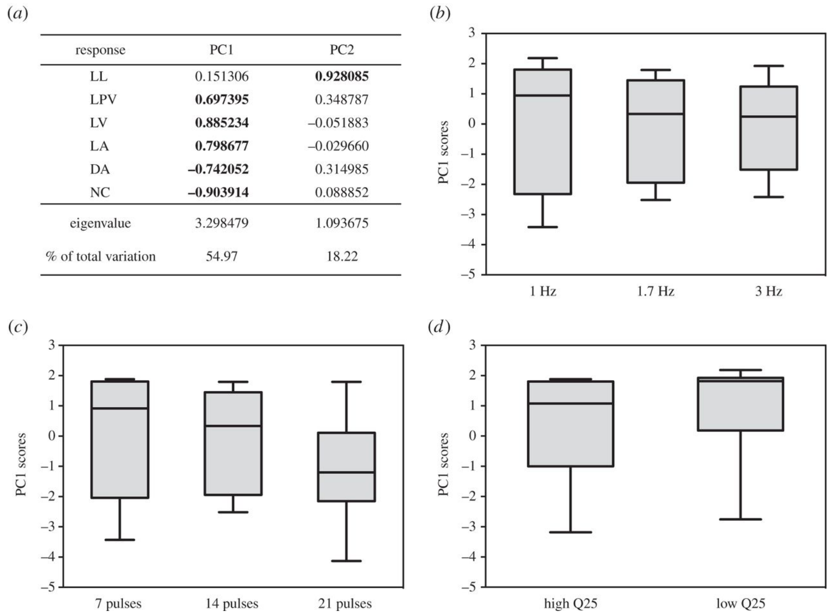


FIG 3. Measurement of temporal and spectral acoustic parameters. (**a**) Sample call waveform. We measured the total number of pulses over the call, the call duration, and calculated the number of pulses/second to get the pulse rate. (**b**) Call frequency spectrum. To characterize the call frequency content, we measured the frequency of maximal energy, the frequencies at each quartile of total energy (Q25 at 25%, Q50 at 50% and Q75 at 75%), the spectrum centroid and the -12 dB bandwidth.



(*a*)

response	PC1	PC2
LL	0.151306	**0.928085**
LPV	**0.697395**	0.348787
LV	**0.885234**	−0.051883
LA	**0.798677**	−0.029660
DA	**−0.742052**	0.314985
NC	**−0.903914**	0.088852
eigenvalue	3.298479	1.093675
% of total variation	54.97	18.22

FIG 4. Behavioral responses to modified calls. (**a**) Results of the PCA performed on the different behavioral measurements (latencies to look LL, for posture change LPC, to vocalize LV, and to approach LA; distance of approach DA; number of calls NC). (**b**) Responses to signals with modified pulse rate. (**c**) Responses to signals with different number of pulses. (**d**) Responses to lower- and higher-pitched calls. None of these signal variations produced significant differential responses in the males that were tested (n = 10).

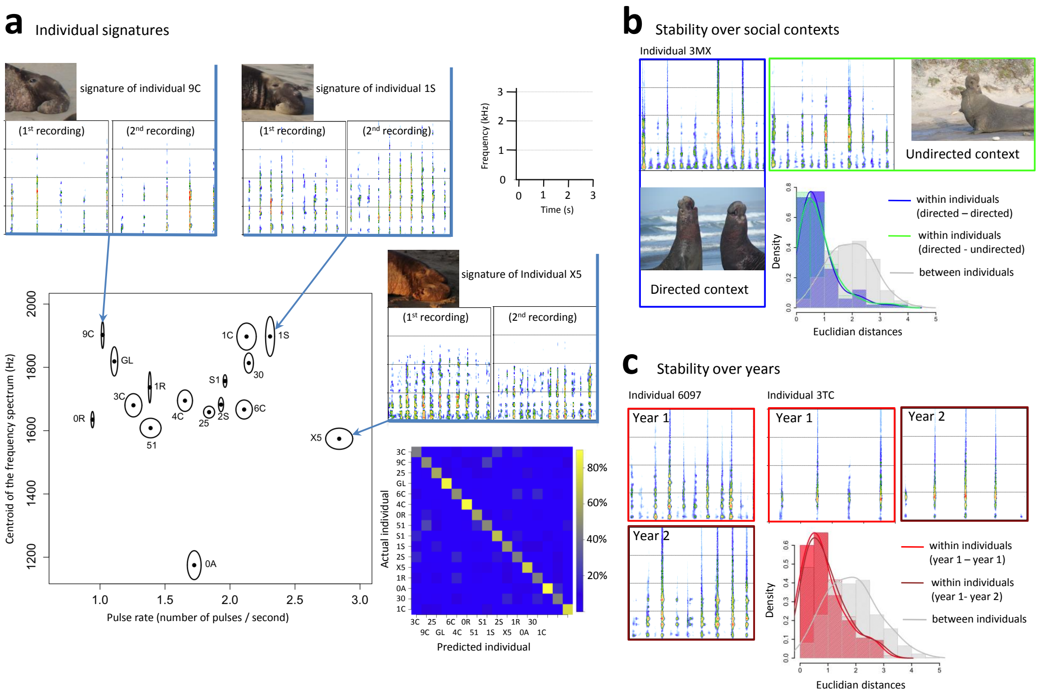


FIG 5. Individual signatures of the acoustic displays of male northern elephant seals. (**a**) As shown by the central graph and accompanying spectrograms on the sides, calls can be reliably assigned to individuals using two acoustic parameters (mean ± SE): the centroid of the frequency spectrum and the number of pulses per call (the two main factors that separate individuals on the first discriminant function of the cross-validated DFA). The confusion matrix provided is obtained from the cross-validated DFA. It shows by coloring cell (i, j) the conditional probability of guessing that the test call came from individual j when in fact it was emitted by i. The yellow diagonal of the matrix underscores the high probability of correct classification (average = 61.3% vs. chance = 6.3%, see text for details), highlighting the strength of the individual signatures. (**b**) Both spectrograms illustrate the consistency of an individual's calls in two different social contexts (calling alone and calling to a rival). The distribution of the Euclidian distances (density curves) underscores the similarity of calls within and between contexts (in the 2D space defined by the calls' frequency centroid and the pulse rate; n = 8 individuals, 2-6 calls/individual, see Methods). (**c**) Both pairs of spectrograms illustrate the consistency of an individual's calls over successive years. The distribution of Euclidian distances (density curves) shows the remarkable proximity of calls within and between years (n = 10 individuals, 5-6 calls/individual/year).

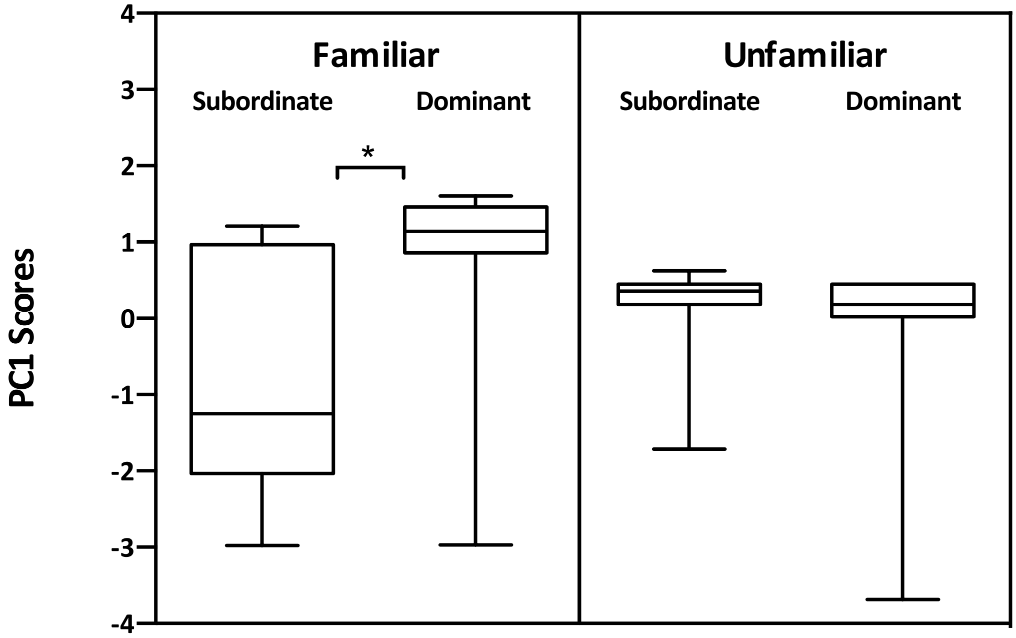


FIG 6. The conditional strategies of beta males. Panels show the behavioral responses exhibited by beta males when challenged with playbacks of lower ranking males (subordinate, S) or higher-ranking males (dominant, D). The behavioral responses are expressed by composite scores (PC1 scores) that integrate the assessment of several us (see text for details): lower PC scores indicate a stronger aggressive reaction (shorter latencies, calls produced during the playback and an approach to the loudspeaker), while positive scores indicate a retreat. The target males showed strong differential movements towards or away from the speaker when the calls of familiar subordinate or dominant individuals were presented (left panel, Wilcoxon test, n = 10, z = 2.547, P = 0.011). Conversely, the playback of calls from stranger individuals hardly elicited a behavioral reaction (right panel, Wilcoxon test, n = 10, z = 1.069 P = 0.285).

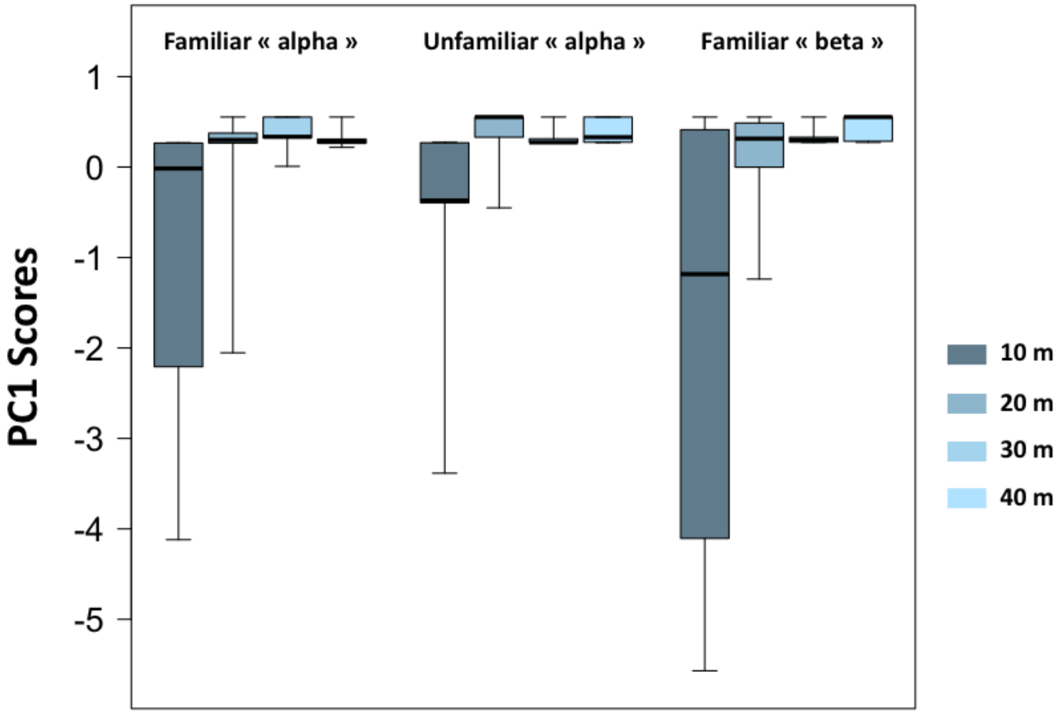


FIG 7. Behavioral response of alpha males to playbacks of calls from different male categories (familiar alpha, unfamiliar alpha, familiar beta) at different distances to illustrate the approach of an intrusive male. A negative PC score indicates a strong reaction (shorter latencies, calls produced during the playback and an approach to the speaker). Alpha males (n=5) showed a strong reaction only when the speaker was placed at 10 m (closest distance), regardless of familiarity (familiar/stranger) or social status (alpha/beta) of the caller.

CHAPTER 2

THE RISE AND FALL OF DIALECTS IN NORTHERN ELEPHANT SEALS

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Casey C, Reichmuth C, Costa C, Le Boeuf B. 2018 The rise and fall of dialects in northern elephant seals. *Proc. R. Soc. Lond. B.* **285**, 20182176.

ABSTRACT

Vocal dialects are fundamental to our understanding of the transmission of social behaviors 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 geographic 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, geographic differences in vocal behavior 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—due 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.

INTRODUCTION

Understanding how animals acquire information from other individuals and identifying the mechanisms that support the transmission of social behaviors are fundamental themes in behavioral ecology and evolutionary biology (Reader and Laland, 2002; Laland and Janik, 2006; Mundinger, 1980). The topic of vocal dialects among animals has particular significance, due to its importance in studies of both human language and animal communication. Dialects represent similarities in vocal behavior that are specific to geographic 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 Podos, 2007; Lameria *et al.,* 2010). The examination of vocal dialects enables a consideration of the social, environmental, and demographic conditions that promote and maintain behavioral variation among animals (Podos, 2007).

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.,* Green, 1975; Prat *et al.,* 2017; Nevo *et al.,* 1987). However, dialects can be dynamic (Payne, 1996; Baker and Jenkins, 1987; Trainer, 1983). Like other behavioral 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 (Henry *et al.,* 2015). 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 behavior over time (Green and Marler, 1979).

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 (Podos, 2007). In some cases, geographic variation is maintained by assortative mating through female choice, which contributes to reduced gene flow between different populations (Henry *et al.,* 2015; Rothstein and Fleischer, 1987; Lipshutz *et al.,* 2016) and eventually leads to speciation (Podos, 2007; Lachlan and Servedio, 2004). In other instances, dialects may be adaptive to varying social or ecological landscapes, and continue to diverge between populations over time (Ruegg *et al.,* 2006; Wright and Dahlin, 2018). Alternatively, dialects may arise as epiphenomena of other evolutionary processes (*e.g.,* learning or patterns of dispersal) (Podos, 2007; Henry *et al.,* 2015; Andrew, 1962; Holland *et al.,* 1996), and may change over successive generations due to cultural drift or frequency-dependent selection (Mundinger, 1980; Slater, 1989). Few studies have documented the persistence of dialects in mammals (Deecke *et al.,* 2000; Payne and Payne, 1985; Rendell and Whitehead, 2005). This is likely due to the logistical difficulties of collecting longitudinal recordings from free-ranging animals with extended life spans, which are required to document changes in vocal behavior 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 (Hoelzel *et al.,* 1993). Northern elephant seals recovered following protection in 1922, eventually recolonizing most of their historic range along the west coast of North America (Stewart *et al.,* 1994). There are now more than 210,000 individuals, and their population continues to increase by 3 to 4% per year (Lowry *et al.,* 2014). It is notable that all living individuals of the species are descendants of the remnant population from only a century ago (Anthony, 1924).

Northern elephant seals presently breed at twelve sites along the coasts of Mexico and California (Lowry *et al.,* 2014). Operating within a system of extreme polygyny, adult males battle to establish dominance hierarchies that determine access to large harems of breeding females (Le Boeuf, 1974). 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 (Sandegren, 1976). The exchange of these displays serves to mitigate otherwise costly physical fights between rival males during periods of extended fasting (Bartholomew and Collias, 1962). 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 (Le Boeuf and Petrinovich, 1972; Casey *et al.,* 2015).

Fortuitously, the calls of northern elephant seals were recorded when the recovering population was less than a third of its present size. Le Boeuf and Peterson

(Le Boeuf and Peterson, 1969) 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 geographic dialects were demonstrated by common temporal patterns in the vocalizations specific to each breeding colony—providing the first evidence of vocal dialects for any non-human mammal (Le Boeuf and Peterson, 1969). With the exception of the Isla de Guadalupe source population, these historical recordings were obtained within one generation[1] 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 (Hoelzel, 1999), Le Boeuf and Peterson suggested it was unlikely that the observed geographic variation in vocal patterns were related to genetic differences between regions (Le Boeuf and Peterson, 1969). Le Boeuf and Petrinovich 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 (Le Boeuf and Petrinovich, 1974). 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.

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[1] As 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 (Le Boeuf and Laws, 1994).

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 provides 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 due to inbreeding in this species (Hoelzel, 1999; Adabia-Cardosa *et al.,* 2017; Bonnell and Selander 1974; Sanvito *et al.,* 2013) compounded by extreme polygyny (Le Boeuf, 1972), enables consideration of the non-genetic factors that contribute to both geographic and individual variation in acoustic communication.

METHODS

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 (Le Boeuf and Peterson, 1969). 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).

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) (Fig. 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) 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) with a Brüel & Kjær 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 (Le Boeuf, 1972; Le Boeuf and Laws, 1994). Additionally, photographs were taken of each marked and recorded individual, and an independent observer later confirmed the age-class of males.

Acoustic analysis

Previous research confirmed the stability of an adult male's display vocalization across motivational contexts, within seasons, and across years (Casey *et al.,* 2015; Le Boeuf and Petrinovich, 1974). Therefore, only adult calls were analyzed, 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 (Casey *et al.,* 2015) 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 (Le Boeuf and Peterson, 1969; Casey *et al.,* 2015; Shipley *et al.,* 1981; Mathevon *et al.,* 2017). 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 (Fig. 2a). We identified the rhythmic portion of the vocalization as the bout component that had a defined pattern, which often consisted of repeating intervals (Fig. 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 (Fig. 2c). Each unit contained individual elements, which were defined as perceptually discrete sonic components (Fig. 2d). Elements were divided into two types based on duration: elements < 200 ms were considered pulses, whereas elements > 200 ms were considered bursts. This duration criterion was selected based on perceptual differences between the sounds evident to human listeners.

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/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.

Analysis of acoustic variation

We conducted a multivariate Discriminant Function Analysis (DFA) with all measured call features (R studio 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 produced canonical discriminant functions representing the combinations of the acoustic variables that provide the maximum separation among groups in multidimensional acoustic space (Bee *et al.,* 2001). Percent correct classification, obtained from the classification matrix, served as a metric of how well the measured variables separated between sites. Site-specific percent-correct scores were compared with a N-1 Chi-squared test to determine whether calls from males at historical sites had different percent-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 geographic 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 (Anderson, 2006). We then applied a one-way ANOVA to these scores to confirm the increase in variation at each site over time.

RESULTS

Call description

The calls from 105 historical adult males from the four breeding sites (Fig. 1a; Año Nuevo Island, n = 24; San Miguel Island, n = 14, San Nicolas Island, n = 9, Isla de Guadalupe, n = 58) were reanalyzed. 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 (Table I, Fig. 3a). 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.

In contrast, calls from 171 contemporary males recorded at the same four sites 47 years later (Fig. 1a; Año Nuevo Island, n = 42; San Miguel Island, n = 38; San Nicolas 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 (Fig. 3b). Modern-day males displayed substantial between-individual call variation within each site (Table I, Fig. 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 (Table I, Fig. 3b).

Call analysis

The DFA analysis revealed that males from the historic data set 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%). In 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 to 55%). Percent correct classification declined significantly for Año Nuevo, San Nicolas, and San Miguel (N-1 Chi-squared X^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 percent correct classification (N-1 Chi-squared X^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 (Table II, III). Vocal displays from the historic data set were well separated in acoustic space according to location, as seen by the clustered distribution of calls within each site (Fig. 4a, colored points) and confirmed by the results of the DFA. Furthermore, there was more overlap among males from different contemporary colonies (Fig. 4b, colored 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 (Fig. 4a,b), corresponding to an increase in acoustic variation between the two sampling periods (Fig. 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 data sets occurred along with substantial changes in population size at each breeding colony (Fig. 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: $F(1, 46) = 63$, $p < .0001$, San Miguel = $F(1,15) = 8$, $p < .001$, Isla de Guadalupe: $F(1, 24) = 27$, $p < .001$), based on the analysis of homogeneity of multivariate dispersions.

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 behavior. There is likely 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 (Henry *et al.,* 2015; Lynch, 1996). 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 (Laland and Janik, 2006; Lynch, 1996). it is usually not possible to exclude genetic contributions to such differences in vocal behavior. In this case, there are several notable factors that suggest the rapid rise in vocal diversity cannot have 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 (Hoelzel, 1999; Bonnell and Selander, 1974; Sanvito *et al.,* 2013), with the lowest levels of microsatellite variability reported for any mammalian species (Abadia-Cardosa, 2017). Thus, learning appears to be a likely 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 (Shipley *et al.,* 1986). 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 (Marler and Peters, 1982). This crystallization process, at least in passerine birds, is a proximal phenomenon based on learning through auditory experience (Marler and Peters, 1982; Kroodsma and Baylis, 1982; Slater, 1989; Nelson, 1997). While there is some anecdotal evidence to suggest that learning is also important to the formation of elephant seal acoustic displays (see Reichmuth and Casey, 2014 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*., Jenkins 1978; Slater and Ince, 1979; Lemon, 1975; Lachlan *et al.,* 2018) . Studies tracking the acoustic behavior 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 (Le Boeuf and Petrinovich, 1974). Following the population bottleneck, the displays of northern elephant seals were preserved within the few surviving individuals (< 20) on Isla de Guadalupe, with very few males likely present in that remnant population (Stewart *et al.,* 1994; Townsend, 1885). 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 (Townsend, 1885). 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 (Le Boeuf and Peterson, 1969).

With an initially low level of movement between sites, the historical dialects present in the 1960's 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 1960's (Stewart *et al.,* 1994). Concurrent with the arrival of new immigrants, novel calls were likely 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 likely 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 (Casey *et al.,* 2015; Mathevon *et al.,* 2017). 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 (Mathevon *et al.,* 2017). Thus, in this system of extreme polygyny, powerful selection pressures for avoiding harm and conserving energy favor 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.,* Aubin and Jouventin, 1998; Mathevon *et al.,* 2003; Medvin *et al.,* 1993), fewer studies consider how interactions among males competing for resources influence signal design and increased signal complexity (*e.g.,* Ord *et al.,* 2001; Tibbets, 2004). 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 (Ord *et al.,* 2001). Thus, as the number of rivals each male elephant seal encounters during the breeding season increases (due to population growth), small structural differences between the calls of familiar opponents likely 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.

AKNOWLEDGEMENTS

Animal research was conducted with authorization from the Institutional Animal Care and Use Committee at UCSC, and U.S. NMFS permits 14636 and 19108. Data collection at Guadalupe Island, Mexico was conducted in collaboration with Fernando Elorriaga-Verplanken under authorization of permits issued by Dirección General de Vida Silvestre (DGVS-SEMARNAT): SGPA/DGVS/00195/15 and SGPA/DGVS/05782/15, as well as the authorization of Comisión Nacional de Áreas Naturales Protegidas-Reserva de la Biosfera Isla Guadalupe (CONANP). U.S. site-specific permissions were granted by Año Nuevo State Reserve (Año Nuevo), Channel Islands National Park (San Miguel Island), and NAVAIR Point Mugu, Naval Base Ventura (San Nicolas Island). Research was supported by National Geographic Explorers Award 944-14. We gratefully acknowledge C. Nasr, P. Forman, B. Funari, E. McHuron, L. Huckstadt, D. Flores, J. Romero, B. Southall, B. Wakefield, and volunteers from the Pinniped Cognition and Sensory Systems Laboratory for data collection assistance. We thank D. Crocker for coordinating research activities, and J. Ugoretz, P. Robinson, P. Morris, R. Holser, G. Oliver, I. Williams, and community members from Isla de Guadalupe for logistical support. In particular, we thank Dr. F. Elorriaga-Verplancken from the Departamento de Biologia Marina y Pesquirias CICIMAR-IPN in Mexico for enabling and contributing to all data collection at Isla de Guadalupe. We thank I. Charrier, N. Mathevon, J. Linossier, and M.T. Tinker for statistical advice, and J. Sills, B. Lyon, P. Tyack, A. Friedlaender and J. Estes for editorial comments. Two anonymous reviewers provided insightful and helpful comments that greatly improved the quality of the manuscript.

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	n	Number of elements in unit (mode, range)	Number of different elements in unit (mode, range)	Unit duration, ms (mean ± SD)	Duration of sonic portion of unit, ms (mean ± SD)	Duration of silent portion of unit, ms (mean ± SD)	Degree of isochronic ity (mean ± SD)	Unit repetition rate, Hz (mean ± SD)
Historic Data (1968, 1969)								
Año Nuevo	24	1 (0)	1 (0)	1.22 ± 0.11	0.5 ± 0.11	0.72 ± 0.12	0.06 ± 0.03	0.82 ± 0.06
San Miguel	14	1 (0)	1 (0)	0.57 ± 0.1	0.05 ± 0.05	0.51 ± 0.08	0.06 ± 0.05	1.86 ± 0.25
San Nicolas	9	1 (0)	1 (0)	0.6 ± 0.3	0.15 ± 0.16	0.44 ± 0.2	0.09 ± 0.06	2.17 ± 0.69
Isla de Guadalupe	58	2 (1-2)	1 (0)	0.72 ± 0.11	0.12 ± 0.03	0.65 ± 0.1	0.03 ± 0.03	1.52 ± 0.33
Contemporary Data (2014, 2015)								
Año Nuevo	42	1 (1-4)	1(1-2)	0.83 ± 0.32	0.27 ± 0.19	0.57 ± 0.32	0.11 ± 0.13	1.42 ± 0.58
San Miguel	59	1 (1-2)	1(1-2)	0.86 ± 0.26	0.25 ± 0.26	0.63 ± 0.3	0.07 ± 0.06	1.26 ± 0.35
San Nicolas	38	1 (1-13)	1(1-2)	0.81 ± 0.38	0.29 ± 0.43	0.5 ±0.29	0.11 ± 0.21	1.46 ± 0.75
Isla de Guadalupe	32	1 (1-2)	1 (1-2)	0.89 ± 0.31	0.31 ± 0.13	0.63 ± 0.23	0.09 ± 0.05	1.13 ± 0.28

TABLE I. Summary of acoustic parameters measured for males with sample size (n) from the historic and contemporary breeding sites. For continuous parameters we report the mean and standard deviation of each variable, and for discrete data we report the mode and range. For a complete explanation of these variables, see Fig. 2.

Variable	**PC1**	**PC2**
Number of Elements	0.230	**0.477**
Unit Duration	**-0.581**	0.107
Sonic Portion of Unit	**-0.574**	0.0170
Terminal Silent Gap	0.0112	**- 0.530**
Degree of Isochroniscity	-0.128	**-0.655**
Primary Beat Rate	**0.513**	-0.225

TABLE II. Results of the principal components analysis preformed on the calls from the historic data set. Variables contributing the most to differentiating between calls are shown in bold. Given the heterogeneity of the historic data with respect to the number of different elements (all sites only had calls with one element type), this variable was excluded from the historic analysis.

Variable	**PC1**	**PC2**
Number of Elements	0.329	-0.381
Number of Different Elements	0.330	-0.378
Unit Duration	-0.446	-0.453
Sonic Portion of Unit	0.0950	**-0.599**
Terminal Silent Gap	**-0.557**	0.124
Degree of Isochroniscity	-0.093	0.077
Primary Beat Rate	**0.507**	0.357

TABLE III. Results of the principal components analysis preformed on the calls from the contemporary data set. Variables contributing the most to differentiating between calls are shown in bold.

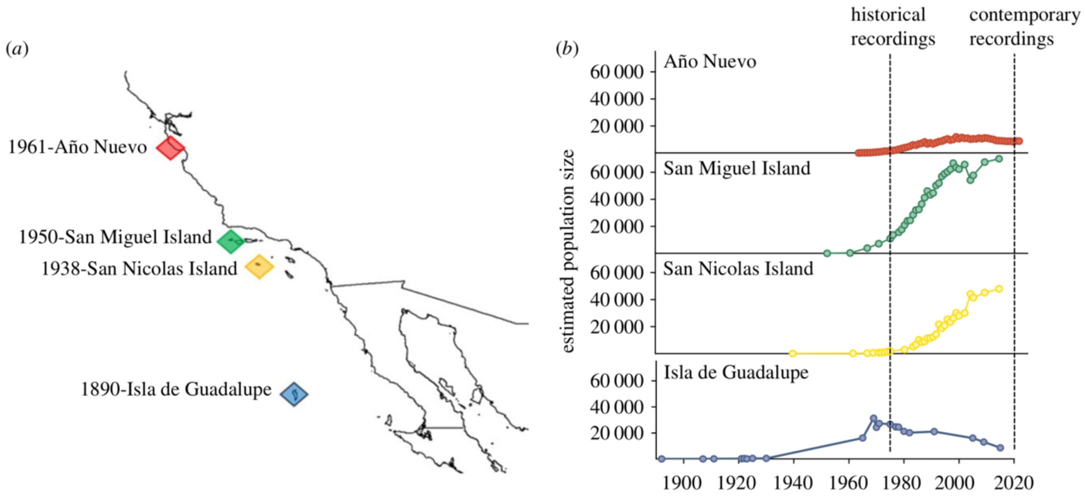

FIG 1. Study locations and associated populations trends at each breeding location. Panel (**a**) illustrates the four breeding sites (and corresponding colonization dates) along the United States and Mexican coasts sampled during 1968-69 and 2014-2015. Panel (**b**) presents the population trends at each location following exploitation. Dotted vertical lines indicate when recordings were obtained for the historic and contemporary data sets: Año Nuevo, San Miguel, San Nicolas (Lowery *et al.,* 2014), and Isla de Guadalupe (Anthony, 1924, Townsend 1885, Reichmuth and Casey, unpublished data).

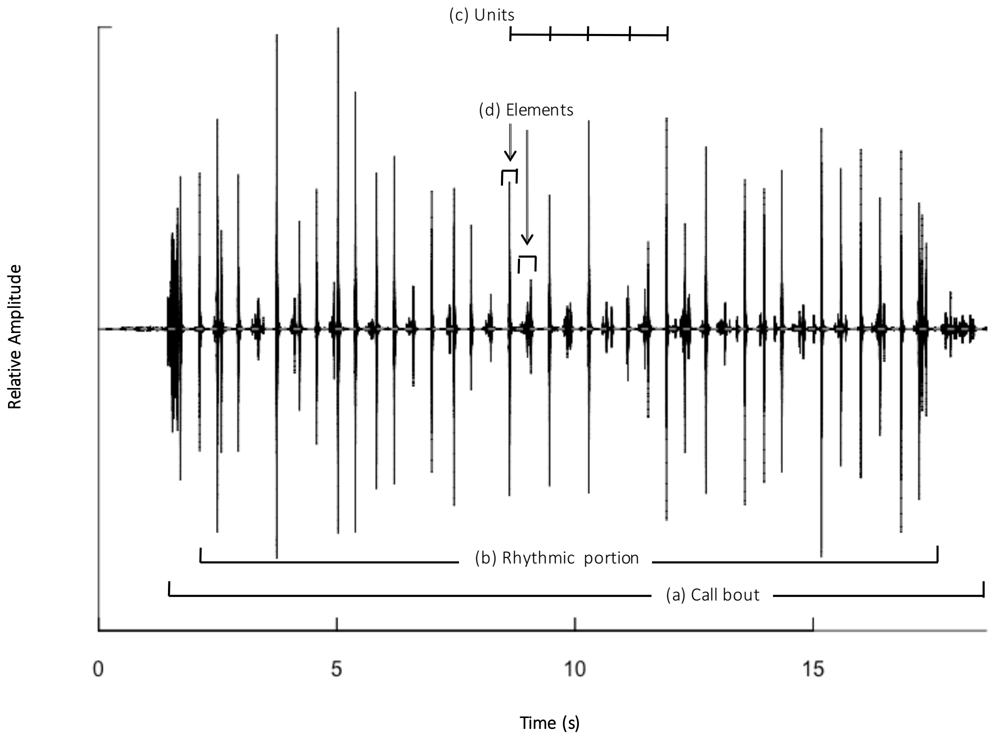

FIG 2. Waveform of a representative adult male northern elephant seal call, and terminology used for temporal analysis of call substructure. Variables measured include (**a**) the call bout, (**b**) rhythmic portion of call, (**c**) call unit, and (**d**) call elements (see text for details).

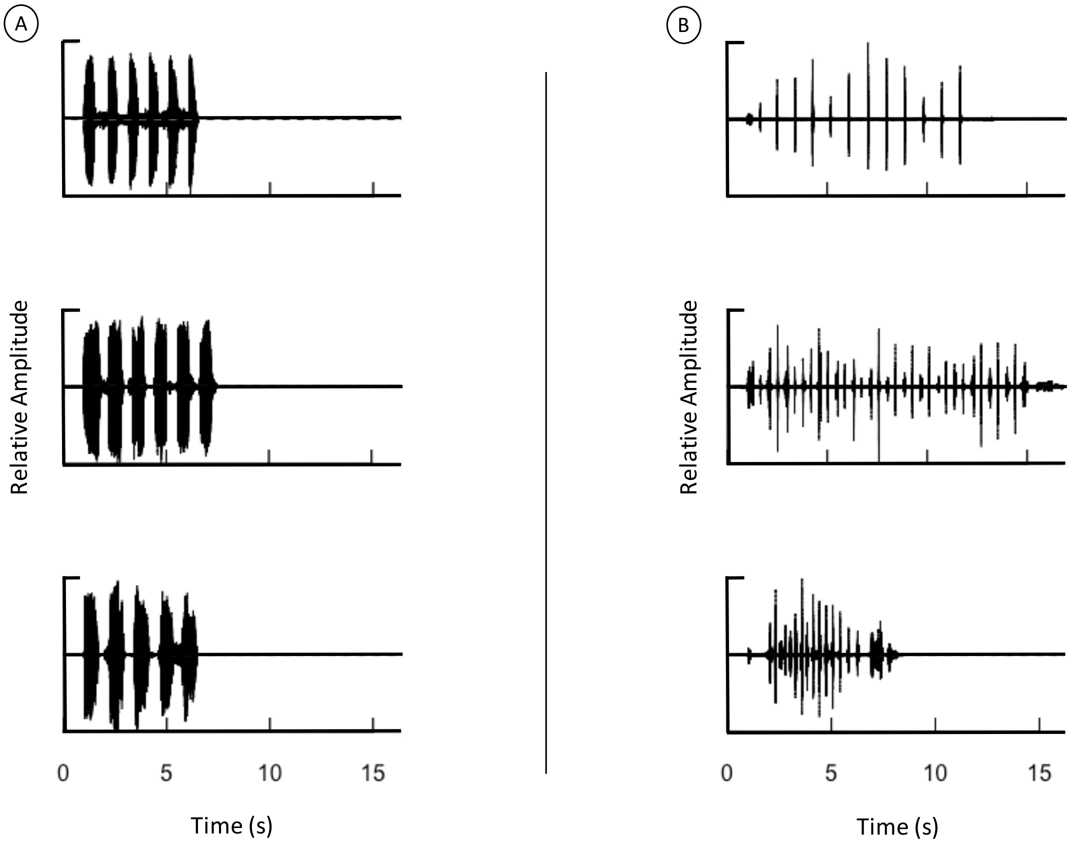

FIG 3. Waveform comparison of representative signature calls produced by three adult male elephant seals in 1968 (**a**), and three adult males in 2014 (**b**) at the Año Nuevo breeding colony. Time (s) is shown on the X-axis, and relative amplitude is shown on the Y-axis.

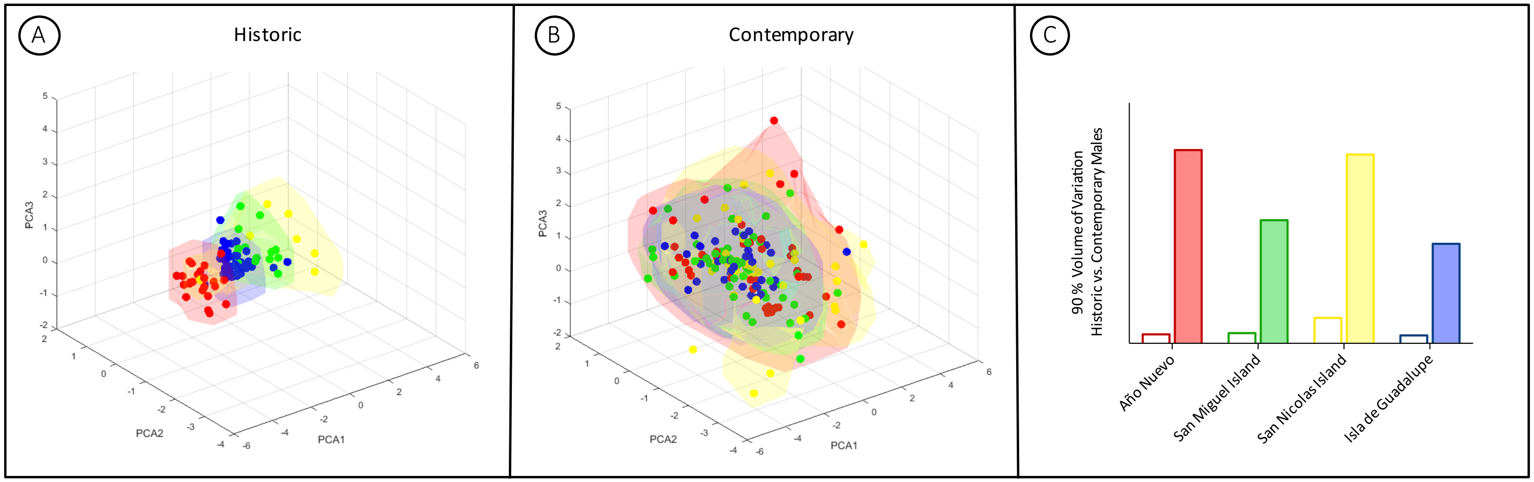

FIG 4. Comparison of between-individual call variation between historical and contemporary sampling periods**.** Panels illustrate the results of the PCA of the measured call variables plotted using the three principle components that captured 90% of the variance observed in the data. Panel (**a**) represents 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.

CHAPTER 3

THE GENESIS OF A GIANT: BEHAVIORAL, SOCIAL, AND VOCAL ONTOGENY OF THE MALE NORTHERN ELEPHANT SEAL

ABSTRACT

Social knowledge acquired early in life likely relates to an individual's subsequent position within structured dominance hierarchies. As animal social groups are characterized by both affiliative and agonistic interactions between individuals, the mechanisms that sustain dominance relationships supported solely by competitive relationships are less well understood. To identify the conditions that facilitate social learning and support the development of stable hierarchical relationships within groups of familiar rivals, we explored the ontogeny of spatial, social, and communicative behavior among male northern elephant seals (*Mirounga angustirostris)*. We find that as males seals grow up, restriction of their fine-scale movement patterns on the breeding colony creates a predictable social environment in which repeated interactions promote greater connectivity between individuals. Moreover, as males become physically and behaviorally mature, their ritualized vocal displays transition from highly variable and unstructured calls to stable and unique individual acoustic signatures, which supports recognition between familiar rivals. The developmental onset of reliable signature calls along with concurrent changes in space occupancy coincide with the establishment of a stable, structured, interaction network between mature males. These results suggest that ontogenetic changes in male behavior can be important determinants of adult social networks.

INTRODUCTION

In many animal societies, individuals interact with one another and develop complex relationships that create social structure. The establishment of these relationships require a series of exchanges between two familiar individuals (Hinde, 1976), and the nature of these associations range from cooperative to antagonistic (Alexander, 1974). Dominance hierarchies are common among animal social groups when individuals compete for access to limited resources, and can be found in most taxa including insects, birds, and mammals (*e.g.,* Kolmer and Heinze, 2000; Grasso *et al.,* 1002; Freeman *et al.,* 1992). Importantly, an individual's position within a hierarchy can influence reproductive success, physiology, and health (*e.g.,* Côté and Festa-Bianchet, 2001; Sapolsky, 2005; McDonald, 2008), and ultimately has a substantial effect on overall fitness. Understanding the development, structure, and persistence of dominance relationships therefore has broad implications for the ecology and evolution of populations and species (Croft *et al.,* 2009).

Dominance status is commonly influenced by intrinsic factors such as individual size, strength, or fighting ability (*e.g*., Issa *et al.,* 1999; Hammerstein, 1981; Blanchard *et al.,* 1988). However, non-phenotypic factors such as social experience and winner/loser effects play an equally important role in hierarchy formation (Archie *et al.,* 2014; Chase *et al.,* 2002), especially in species with repeated interactions between individuals (Silk, 2003; Bernstein, 1981). In stable hierarchies where competitive rivals interact frequently, dominance relationships and/or territorial defense are often maintained through individual recognition of rivals (Tibbets and Dale, 2007). Here, assessment based on prior experience reduces costly aggressive interactions by allowing animals to avoid escalated contests with opponents with whom they have previously fought. To correctly identify opponents, each individual must produce a reliable individual-specific cue using one or several sensory modalities that receivers can perceive and decode (Tibbets and Dale, 2007; Sheehan and Tibbetts, 2009). Rivals can then recognize competitors according to these distinctive characteristics, and associate that individual (and their relative fighting ability) with those features. In this kind of social system based on learning and experience, animals must have opportunity to not only learn the unique characteristics of their familiar competitors, but also have sufficient experience with individuals for these cues to become meaningful.

Given that that social knowledge may be as significant as physical attributes with respect to hierarchy position (Chase *et al.,* 2002), the developmental process by which individuals provide and acquire information within their social environment is imperative to their fitness (Zhiji *et al.,* 2017, Turner *et al.,* 2018). However social development is challenging to evaluate among long-lived gregarious mammals. As familiarity is necessary to the formation of dominance relationships among adults, the behavior of individuals during maturation should provide ample experience to fine-tune their recognition abilities. In stable social systems, juveniles gain social knowledge by learning general evaluation skills through low-stakes interactions with other individuals, as well as acquiring their own unique signals that others within their network can come to recognize them by.

Owing to extreme selection pressures for rival assessment, the northern elephant seal (*Mirounga angustirostris*) provides a compelling system in which to explore the ontogeny of social behavior, as structured dominance hierarchies among adult males have been extensively described (Le Boeuf and Peterson, 1969; Le Boeuf 1974; Haley *et al.,* 1994; Casey *et al.,* 2015) and can provide the basis for comparison with juvenile behavior. This migratory species breeds on islands and mainland rookeries in Mexico and California in winter each year. Both males and females fast during this time, living off of blubber reserves and losing more than a third of their body mass during the breeding season (Deutsch *et al.,* 1994). The males in residence include adults (8-14 years old) and sexually mature but physically (and socially) immature subadults (4-7 years old) (Haley *et al.,* 1994). The breeding behavior of males ins extremely competitive, where less than 10% of males reach adulthood, and less than 1% ever gain access to breeding opportunities (Clinton and Le Boeuf, 1993). Reproductively mature males compete for status within dominance hierarchies at the beginning of each season prior to the arrival of females (Le Boeuf, 1974; Haley *et al.,* 1994). Once established, dominance relationships between males are fairly stable within each season, and the majority of agonistic encounters between males are resolved through the use of ritualized threat displays (Le Boeuf, 1974; Bartholomew and Collias, 1962). These displays are comprised of multi-modal components including visual posturing that emphasizes body size; extremely loud, pulsed vocalizations directed at opponents; and occasional seismic cues that are produced by slamming their heavy chests against the ground (Bartholomew and Collias, 1962; Sandegren, 1976).

The acoustic features of these ritualized signals are essential in mediating male-male competition—each adult male possesses a unique acoustic signature, and vocal variation among males supports individual recognition through the process of associative learning (Casey *et al.,* 2015). Both timbre and the rhythmic features of these calls are of particular importance, and males can remember subtle differences in call structure, allowing them to use these call features to discern between familiar competitors (Mathevon *et al.,* 2017). The extreme costs of conflict during fasting appear to sustain this social system, and a male's knowledge of their social network (including the reliable vocal signatures of their rivals) likely contributes to their reproductive success within and between breeding seasons.

In this study, we aim to provide a comprehensive view of the development of the social behavior of male elephant seals. To explore the factors that support individual recognition between rivals, we describe the ontogeny of spatial, social, and communicative behavior among males. As predictability in time and space influences the potential for repeated social interactions among competitors, we evaluate fine-scale movement patterns of males during reproductive development and determine whether space utilization changes as a function of age. We also assess social relationships of males across different age classes to characterize the development of the male social network. Finally, given that adult vocalizations are highly individually stereotyped, we examine the development of male vocal signatures, and identify the timing during maturation that the calls become individually unique and recognizable to others.

GENERAL METHODS

Study site

Research occurred at Año Nuevo State Reserve in San Mateo County, California, USA which includes mainland and island coastal beach haul-outs where northern elephant seals congregate each winter to breed. Approximately 2000 seals are distributed over a 3 km^2 span of mainland beaches. About 430 of these individuals are subadult and adult males, 12% (~52) of which are fully mature adults. The site includes at least 20 harems annually, each with up to 150 adult females and their pups.

Identification of individuals

As part of a long-term population monitoring effort at the study site (Lowery *et al.,* 2014), 300 weaned pups are tagged annually each with two serially numbered tags placed in the interdigital webbing of their hind-flippers (Jumbo@ Rototags, Dalton Supplies Ltd, Henley-on-Thames, UK). As a result, natal history and age are known for a subset of individuals in this colony. Additionally, some males are flipper-tagged as subadults or adults without a known birth record.

Between 2010 and 2018, we identified subadult and adult males upon their annual return to the Año Nuevo mainland for the breeding season (December-March) by placing unique dye marks on their dorsal flanks (as in Casey *et al.,* 2015). These marks were referenced to flipper tags when present. Once marked, all males were photographed to document physical features including secondary sexual characteristics. Between 81 and 350 males were identified in this manner each season. Over the course of the study, 110 males were monitored for at least two or more reproductive seasons by their tag numbers.

Estimation of age

The age class of non-tagged males whose wean date was unknown was based on overall body size, the development of the proboscis, and scarring of the chest shield (Le Boeuf and Peterson, 1969; Clinton and Le Boeuf, 1993). Due to the importance of identifying developmental stages in this work, we used photographs of a subset of known-age males that were tagged at weaning to augment these physical criteria used to determine age classes. Sub-adult 1 (SA1), subadult 2 (SA2), subadult 3 (SA3), subadult 4 (SA4) and adult males were 4, 5, 6, 7 and 8+ years old, respectively (see Fig. 1 for detailed description of characteristics used to define each age class). These physical criteria were used to estimate the age class of each male when marked in the field. At the end of each season, three observers reviewed photographs of each male to confirm age designations.

Assessment of dominance status

Each male within our study was assigned a qualitative descriptive rank at the end of the season, based on his repeatedly-sampled spatial proximity to female harems. Alpha males held stable positions within female harems, beta males held flanking positions relative to harems, and peripheral males were excluded from access to harems (Le Boeuf, 1974; Norris *et al.,* 2010).

Study 1: Ontogeny of space utilization and residency patterns

Fine-scale site fidelity represents a significant structural component of animal societies by setting boundaries to an individual's potential social interactions. Studies of site fidelity have mainly focused on an individual's loyalty to natal breeding sites or familiar breeding grounds (Papi, 1992; Switzer, 1993), with less attention directed towards understanding fine-scale use of those environments, and how such use space patterns influence an individual's social network (*e.g.,* Wolf and Trillmich, 2007). In some colonial breeding systems, fine-scale fidelity to specific locations creates stable social environments that provide individuals with the opportunity to form long-term associations with familiar conspecifics during and between reproductive seasons (*e.g.* Wolf and Trillmich, 2007; Insley, 2000).

Despite several decades of research on northern elephant seals, detailed descriptions of space utilization among male elephant seals while on shore remains sparse. Juvenile seals of both sexes show a strong homing instinct to return to their natal colony (Oliver *et al.,* 1998). Both male and female adult seals return to the same colony each year between foraging migrations to breed and molt as adults (Le Boeuf *et al.,* 2000). While ~ 70% of females return to their birth site each year (Reiter *et al.,* 1981), the percentage of males that return annually is not known. Male tenure on the colony within a breeding season increases with age and size (Le Boeuf and Laws, 1994), but movement and residency patterns while on shore at fine scales are unknown. While observations suggest that some exceptional bulls dominate breeding opportunities at the same harem location (*i.e.,* a small sub-area spanning < 100 m) over successive seasons (Le Boeuf, 1974; Reichmuth, personal communication) there is little information available regarding how space utilization or time spent ashore within the breeding colony changes as males mature.

Here, we characterize within-colony residency and movement patterns of male northern elephant seals during the breeding season, and describe how male presence on the colony and home range change with maturation.

Methods

Data collection

Data were collected during four breeding seasons concluding in 2013, 2014, 2017, and 2018. Observations at the rookery began each season in November prior to the arrival of males and extended through the end of the breeding season and male departure (mid-March). During each season, an average of 55 daily surveys of animal distribution (range 34-71) were conducted. Experienced observers monitored the colony and recorded whether marked and/or tagged individuals were present. Marks and tags were read directly or with the assistance of binoculars, spotting scopes, or cameras. The GPS position of each identified male was recorded once per survey day with a Bad Elf Pro+ GPS (site accuracy of +/- 1.5 m). GPS measurements were obtained within 3 elephant seal body lengths (maximum distance 12 m) of target individuals to minimize disturbance. Re-sight data were archived in a long-term life-history database maintained at UC Santa Cruz. Sampling effort was directed towards adult males in the 2013 and 2014 seasons, and then expanded to include younger males during the 2017 and 2018 seasons.

To evaluate male seals' total time spent ashore and whether it varies as a function of age, a subset of tagged individuals from each age class were tracked during the 2018 breeding season (n=10 for each age class). To determine whether a male's time spent ashore changed as a function of age, we compared the time males spent on the colony (number of days from the first sighting to the last sighting) across all age classes using a one-way ANOVA. We then used a Tukey-Kramer HSD post-hoc test to evaluate which age-classes were significantly different from one another. Among adult males, we compared the residency time of alphas and non-alphas using a Student's T-test (n=5 alphas, 5 non-alphas). This comparison was made within one season to avoid potential confounds of environmental conditions and other seasonal factors.

Analysis

Location data were used to estimate the home range for each focal male that was observed at the colony for at least 10 or more days throughout the season. The occurrence probability distribution—or home range—for each male was calculated using the kernel density tool in the geospatial modeling environment module of ArcGIS (version 10.6.1) and QGIS (version 3.2.2). A polygon was created to encompass sighting locations within a 95% and 50% home range boundary, using a grid cell size of 1m^2. To restrict these home range estimates to only include haul-out space suitable for seals, we applied a boundary layer of available habitat to this grid that removed water and inland areas not considered suitable habitat. We used the 95% kernel density estimate (95% KDE) to quantify each male's overall distribution, and the 50% KDE to represent the core area of space use, as this measure is typically considered an accurate representation of an animal's home range as it removes outliers (Burt, 1943; Bekoff and Mech, 1984). Home range data were calculated for each individual and then averaged by age class. We compared the mean 50% and 95% home range sizes between age classes using one-way ANOVAs for each measured parameter between each age class. We then used a Tukey-Kramer HSD post-hoc test to evaluate which specific age classes were significantly different from one another with respect to home range. Among adults, we also evaluated whether alpha males occupied smaller home ranges than other mature males (alpha = 5, non-alpha = 5) using an unpaired student's T-test. All statistical analyses were performed in GraphPad Prism (version 6.0) and JMP Pro (version 14.0).

Results

Focal male elephant seals observed were present at the Año Nuevo breeding rookery from late November to early March. In the subset of males for which time spent on the colony was measured in 2018, residency varied significantly among age classes (F (4, 45) = 12.93, $p < 0.0001$) (Fig 2.; TABLE I, II). SA1s were the first to arrive and depart, coming ashore on average by 27 November and departing by 3 January, prior to the arrival of most females. The average time ashore for SA1s was 37 ± 11 days (mean, SD), and males of this age class remained ashore for significantly shorter than all other age classes. The average arrival date for SA2s was nearly a month later than SA1s, with a 49 ± 12 day residency ashore. Males of this age class stayed much longer than SA1s, and but less time than all other older age classes. While arriving at the same time as SA2s, SA3s were ashore for an average of 64 ± 7 days, departing around 1 March. SA4 and adult males displayed the longest time spent ashore during the breeding season, arriving in mid-December and departing at the end of February, for an average of 71 ± 4 and 68 ± 10 days, respectively (TABLE I). Adults, SA4s, and SA3s did not vary significantly with respect to amount of time spent at the colony. Among adults, there was no significant difference in male presence on the colony between alphas and non-alphas.

We collected > 10 re-sights for each of the 208 individuals over the six-year sampling effort (SA1 = 9, SA2 = 27, SA3 = 40, SA4 = 56, AD = 76) which showed that within-season home ranges varied considerably between age classes (F(4, 201) = 14.21, $p < 0.0001$) (Fig. 2, 3; Table II, III). SA2 males occupied the largest home range (50% KDE = 0.07 km^2) which differed in size when compared to all other age classes. SA3s (50% KDE = 0.04 km^2) and SA4s (50% KDE = 0.04 km^2) had larger home ranges than SA1s (50% KDE = 0.01 km^2) and adults (50% KDE = 0.02 km^2), whose home ranges are statistically similar to one another. Among adults, the 50% home ranges of alpha males were much smaller than all other males (n= 21 alphas, 50% KDE = 0.01 km^2; n = 54 non-alphas, 50% KDE = 0.03 km^2 $p < .0001$).

Summary

Our assessment of fine-scale space utilization patterns of male northern elephant seals indicates that as individuals mature, their terrestrial home ranges decrease in size. SA2s had the largest home ranges of any age class, while adults occupied the smallest area within the colony during the breeding season. Among adults, more dominant alpha males occupied a smaller home range than less dominant males. The long-term trend of transitioning from more variable space-use (as exhibited by younger age classes at the onset of puberty) to increased stability (exhibited by adults) likely has a significant influence on the social associations between males at this breeding site. As males mature, their movement patterns on the colony become more constrained, creating a more predictable social environment where males are likely to re-encounter individual competitors. Additionally, our findings that males increase time spent on the breeding colony with age suggests that older males have increased energy reserves and are able to fast longer than younger subadult males. Longer tenure on the colony also provides older individuals with more opportunities to engage in competitive interactions. In dominance hierarchies or territorial systems that have extensive overlap between males with respect to both space and time, knowledge of familiar competitors is likely an efficient way to save energy and reduce risk, and thus may confer direct benefits to individuals.

Study 2: The development of social relationships

Social interactions between familiar individuals are fundamental to communication systems, as patterns of sociality influence both the evolution of animal signaling (Bradbury and Vehrencamp, 1998) and cognition (Whiten, 2000). Within dominance hierarchies based on individual recognition of one's competitor, learning is critical to the formation of stable social relationships, as the outcome of interactions between two individuals is inherently influenced by the consequences associated with their previous encounters. Within dominance hierarchies where individuals compete for reproductive opportunities, a male's success depends on his ability to accurately navigate these social relationships (Chase *et al.,* 2002). The developmental process by which young males interact with and acquire social knowledge of their competitors is therefore likely imperative to his eventual fitness as an adult (McDonald, 2007).

Given the extremely polygynous mating system of elephant seals, considerable attention has focused on their how dominance hierarchies are formed. Several studies found a strong correlation between dominance position and estimated reproductive success (Haley *et al.,* 1994). Dominance position among adult males is established and maintained through the use of ritualized vocal displays (Le Boeuf, 1974; Sandegren, 1976), and adult males are capable of linking the calls of individuals with the outcome of previous interaction through associative learning (Casey *et al.,* 2015).

Despite substantial research with this species, very few studies have evaluated the strength of associations between rivals and characterized the complexity of a male's social network. Additionally, while sub-adult males are present on the breeding rookery each season, little is known about the degree of familiarity among these young competitors within this competitive social system. The goals of this work were to describe the social network of male northern elephant seals, and determine how patterns of interactions between males change as a function of age. Specifically, we aimed to 1) determine the average number of rivals that sub-adult and adult males interact with during the breeding season, 2) evaluate whether the degree of familiarity between individuals changes with maturation.

Methods

Behavioral observations and sampling effort

Dyadic interactions involving marked and/or tagged subadult and adult male elephant seals were observed during the 2018 breeding season using similar sampling methods described by Casey *et al.* (2015). Observations were typically conducted with binoculars from the vantage point of a raised sand dune above the colony. We defined an interaction between two individuals when we observed the agonistic behavior of one individual (visual posturing, vocalizing, or forward movement) directed towards or affecting the behavior of another male. The victor in each pairwise interaction was defined by his displacement of another male, evidenced by the loser moving away with either a slight change in body position (e.g. head turn away from dominant animal) or an obvious change in phonotaxis (negative = retreat). For each interaction, we recorded the identity of the apparent winner, whether he had vocalized during the interaction, and how far he had moved. The same information was recorded for the loser. We also recorded whether males engaged in physical contact, and if so, scored the intensity of that contact (from a single bite or chest slap to sustained combat). In cases where the outcome of these interactions was unclear, the exchange was noted as a draw and excluded from further analysis. In the majority of observations, there was a clear dominant and subordinate outcome. *Ad libitum* behavioral sampling was conducted by 1-2 experienced observers for at least 3 hours each day, between four-five days per week, from late December to early March. Observers were stationed at different areas of the breeding colony and were in communication with one another via radios to prevent repeated sampling of the same events by different observers. While monitoring the behavior of males, effort was made to observe all interactions regardless of the age-class of the animals involved.

Calculation of network statistics

Social network analysis has recently emerged as a quantitative framework for understanding patterns of social structure among individuals within a population or social group (Shizuka and McDonald, 2012). Using observational data of direct interactions between members of a group, this approach evaluates social ties between individuals, and can help to identify potential individual qualities (*e.g.*, age, dominance status) that may influence the structure of social groups (Wey *et al.,* 2008). A social network is composed of individuals (represented by nodes) that are connected by their interactions (represented by lines; Whitehead, 2008). In each network, the weight of connecting edges is determined by summing the number of interactions for each dyad. In addition to these relational data, attributes of individuals can also be incorporated into the network (*i.e.* age).

We used a network analysis approach to assess the number of social partners and the strength of association between male seals from different age classes. We constructed weighted social networks based on the dominance interactions scored in the field using the 'igraph' package in R for network analysis (Csardi and Nepusz, 2006). To investigate differences among individuals with respect to their social relationships, we compared degree centrality (total number of social partners), and average nodal strength (total number of times pairs of males interacted) between males of different age classes. We then evaluated the significance of these relationships using one-way ANOVAs for each parameter, and used a Tukey-Kramer HSD post-hoc test to evaluate which specific age classes were significantly different from one another. All statistical analyses were performed in GraphPad Prism (version 6.0) and JMP Pro (version 14.0).

Results

Sampling effort

Observations began on 29 November 2017 and extended through 8 March 2018, resulting in 71 days of sampling effort (including ~ 215 hours of behavioral recording) that spanned the entire breeding season. A total of 1,352 interactions were observed between 207 identified competing individuals. Of these males, 40 were adults, 46 were SA4s, 66 were SA3s, 38 were SA2s, and 17 were SA1s.

Description of social relationships across age-classes

An assessment of social relationships among males across age classes demonstrate that both nodal strength ($F_{4, 190} = 10.31$, $p < 0.0001$) and degree centrality change as a function of increasing age ($F_{F4, 190} = 14.28$, $p<0.0001$) (TABLE IV; Fig. 4, see Fig 5. for description of results). In general, young males (SA1s and SA2s) participated in lower-intensity interactions with fewer individuals within their same-age or adjacent cohort throughout the season. SA1 males were frequently observed interacting in low-stakes encounters (characterized by low physical intensity scores) with other SA1s (58% of all total interactions). SA2 males encountered a greater diversity of age classes than SA1s, and interacted most frequently with SA3s (30% of all interactions). The majority of an SA2's interactions with SA3s, SA4s, and adults resulted in the SA2 male loosing (98%). These encounters rarely resulted in physical contact, as most SA2s were moved by older individuals with calling or visual posturing. Similar to SA2s, SA3s interacted with males of all age classes, however 85% of these interactions occurred with males that were the same age or older.

Adult and SA4 males had a significantly higher degree of centrality than other age classes, indicating that they have more social partners than SA1s-SA3s ($p<0.002$ for all comparisons, TABLE IV, Fig. 4,5). Additionally, adults and SA4s had stronger nodal strength with their social partners than younger (SA1-SA3) individuals ($p<0.001$ for all comparisons, figure S2b), suggesting that older males have stronger associations with these familiar competitors. SA4 and adult males preferentially interacted with other SA4 or adult males (67% and 73% for each age class, respectively). The majority of these interactions did not involve physical contact between individuals, as calling was sufficient in settling exchanges between males. However, a higher proportion of the fights that did occur resulted in sustained combat. These fights typically occurred between two individuals who had not previously interacted, or whose dominance status was uncertain.

Summary

The results of this analysis demonstrate that the nature of social relationships changes between competing rivals as males mature—young individuals have fewer social partners with whom they are less familiar, whereas older males compete with a greater number of rivals, and the strength of those associations is much stronger throughout the breeding season. The number of competitors that a given male encounters is tied to his home-range patterns on the colony, as fine-scale space utilization sets the limits to an individual's social environment (Wolf and Trillmich, 2007). For example, SA1 males arrive earlier than other age-classes during the breeding season, exhibit a small home range, and stay for a short period of time. Consequently, there are fewer opportunities for them to interact with other males, explaining their low degree centrality, nodal strength, and their propensity to interact with other SA1s. SA2 males have much larger home ranges than any other age classes, and thus have fewer repeated interactions with the same individuals over the course of the breeding season. This pattern is captured by their low nodal strength with others within their network. Once males reach social maturity and are able to compete with other sexually mature males, their home ranges decrease substantially in size, and their time ashore increases. The threshold for this transition appears to be taking place within the SA4 age class, which likely coincides with a substantial increase in size which allows them to fast for longer periods of time successfully compete for access to females. This restriction in space utilization and increase in time spent ashore sets the stage for all elite males that survive to social maturity to operate within a relatively large—yet familiar—social network.

Study 3: The ontogeny of male vocal displays

Changes in vocal behavior that occur over an individual's lifetime may be influenced by both maturation and experience (Bolhuis and Giraldeu, 2005). Despite the important role that vocal communication plays in the social lives of nearly all animals, detailed descriptions of acoustic development in mammals are sparse. This is likely due to inherent difficulties in obtaining longitudinal data (*e.g.,* acoustic recordings) from wild animals with extended life spans under natural conditions. Among adult male northern elephant seals, calling is a critical component of male agonistic interactions as the majority of competitive encounters are resolved through the exchange of ritualized vocal displays, ultimately reducing unnecessary aggression during periods of extended fasting on land (Sandegren, 1976). Adult males produce a unique call that enables individual recognition among familiar rivals within the male dominance hierarchy (Casey *et al.,* 2015). These loud, pulsatile vocalizations exhibit substantial variation in temporal pattern among individuals, with differences in pulse rate and spectral features supporting individual recognition (Mathevon *et al.,* 2017). Additionally, the acoustic displays produced by adult males are highly stable within individuals, across social contexts, and over successive reproductive seasons (Casey *et al.,* 2015).

The ontogeny of individual vocal displays in northern elephant seals is unresolved. It is known that the calls of juvenile males are more variable than those of adults, particularly with respect to call structure and pulse rate, suggesting that males undergo a transitional period during development in which their calls lack the characteristic structure of adult males (Shipley *et al.,* 1986). A previous assessment of vocal development in this species demonstrated that young males exhibit extensive variability with respect to both call structure and the rate at which sonic elements are emitted (Shipley *et al.,* 1986). Notably, the authors concluded that while males are capable of generating basic call components that are similar to those used by adults, they do not produce the stereotyped displayed that characterize older animals (Shipley *et al.,* 1986). To date, no study has tracked individual animals throughout the season to assess the stability of call features within individuals over time.

Here, we provide a comprehensive analysis of the acoustic displays of young male northern elephant seals, and evaluate how both temporal and spectral features change with maturation. To assess whether call stability changes as a function of age-class, we track focal individuals throughout the season and characterize the intra- and inter-individual variation of their vocalizations. This information enables a more precise consideration of the timing during maturation at which point the calls of male elephant seals become sufficiently recognizable to others.

Methods

Data collection

The vocal displays produced by males of all age classes were opportunistically recorded over six breeding seasons (2011, 2012, 2013, 2014, 2017, and 2018). We recorded calls using a Neumann KMR 82I Condenser Shotgun Microphone linked to a Fostex FR-2 Field Memory Recorder (24-bit/48 kHz), or with a calibrated Brüel and Kjær 4189 condenser microphone (with UA-1650 windscreen) connected to a Brüel and Kjær 2250 sound-level meter (24-bit/48 kHz). Acoustic recordings were collected at distances of 1-10 m and between 0 and 90 degrees orientation from calling males. Recordings were obtained without disruption of normal behavior by remaining below the seals' response threshold to human presence (*i.e.,* Holt *et al.,* 2010; Southall *et al.,* 2003; Casey *et al.,* 2015). Annotations appended to each recording included age and id microphone orientation, and distance to the calling animal.

Acoustic analysis

We analyzed acoustic displays of each age class (SA1-adults) using high quality recordings where all parameters of the spectral contour could be identified. Based on these criteria, we described the calls of 47 individuals in both the temporal and spectral domains (7-10 males per age class, 5-10 calls per individual, 443 calls total).

Because adult males show reliable substructure within the repeating units comprising the rhythmic portion of their vocal display (Casey *et al.,* 2015, Mathevon *et al.,* 2017), we conducted a thorough analysis of the temporal features of each male's acoustic display. We defined a call bout as the entire vocalization, including any introductory and terminal snorts and rumbles. We identified the rhythmic portion of the vocalization as the bout component that had a defined pattern, which often consisted of repeating intervals. 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. Each unit contained individual elements, which were defined as perceptually discrete sonic components. Elements were divided into two types based on duration: those < 200 ms were considered pulses, whereas those > 200 ms were considered bursts. This duration criterion was selected based on perceptual differences between the sounds evident to human listeners.

Calls were analyzed using the acoustic sound analysis program Raven Pro 1.5. Eight temporal variables were manually measured from the waveform: rhythmic portion duration (s), unit duration (s), duration of the sonic portion of each unit (s), duration of the silent portion of each unit (s), 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/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. Additionally, we noted whether introductory or terminal snorts and rumbles were associated with each vocalization. For discrete parameters, we report the range, mean, and standard deviation of each variable; for continuous data, we report the mode and range.

Five spectral characteristics were measured from the average spectrum: the 25%, 50% and 75% frequency quartiles (1st quartile: 'Q25', 2nd quartile: 'Q50' and 3rd quartile: 'Q75', in Hz), peak frequency (Peak Freq.), and the 90% frequency bandwidth. Additionally, we noted whether each call shows a harmonic structure, and if so, we measured the fundamental frequency (f_0). All measurements were obtained from the spectrum with the following settings: sampling rate 48 kHz; Hamming window; FFT size 2048 (filter bandwidth 7 Hz); overlap 90%. To assess whether specific call features varied significantly as a function of age, we performed a series of one-way ANOVAs for each measured parameter between each age class. used a Tukey-Kramer HSD post-hoc test to evaluate which specific age classes were significantly different from one another. All statistical analyses were performed in GraphPad Prism (version 6.0) and JMP Pro (version 14.0).

Our previous work demonstrated that the frequency centroid and unit repetition rate are the most significant variables contributing to individual signatures of adult males (Casey *et al.,* 2015), however the exhaustive temporal analysis conducted here provides new metrics that may be important to conveying individual identity. An acoustic feature's potential for individual coding (PIC) was determined as the ratio of between-male to within-male coefficients of variation (PIC = $\frac{CVb}{CVw}$). Within-male coefficients of variation ($CVw = \left[\frac{SD}{x}\right]\ x\ 100$) was calculated based on the means and standard deviations from individual calls for each male. Between male coefficients of variation $CVb = \left[\frac{SD}{x}\right]\ x\ 100$) were based on the grand mean and standard deviation of all calls. A PIC value greater than 1.0 indicates that a given acoustic feature is more variable among individuals than within individuals and can potentially function to convey individual identity. This analysis was applied to all call parameters for the adult vocalization except for the number of elements in each unit, and the number of different elements in each unit.

To determine whether the consistency of a male's display call changes with age, we conducted a standard multivariate Discriminant Function Analysis (DFA) using five call features (R, version 3.3.0). We selected the five call variables showing the highest PIC values in adult males, excluding any call variables that were highly correlated (features with an R^2 value > 0.5). Within each age class, we classified calls by individual, with male identity as the group identifier and acoustic measures as discriminant variables. Percent correct classification obtained from the classification matrix (generated by the DFA) provided a metric of how well the measured variables separated the individuals within each age-class. To determine the effect of age on the likelihood that calls could be correctly assigned to an individual, percent-correct scores for each age-class were compared with a N-1 Chi-squared test.

Results

Description of calls

SA1s—SA1s produced calls that were relatively short in duration (2.9 s ± 1.3), and were comprised of repeating units that were highly variable within each individual and significantly shorter in duration (mean = 0.4 ± 0.1) than those of older males ($p < 0.05$ for all comparisons). Additionally, their calls had a faster unit repetition rates (2.5 Hz ± 0.4) in comparison to all other age classes ($p < 0.01$ for all comparisons). Each repeating unit (with associated sonic elements) had variable duration, such that it was difficult for a human listener to detect a consistent tempo within each call (TABLE V, Fig. 6). SA1s did not exhibit consistent sub-structural components in their calls, however males often switched between different elements within one calling bout. SA1s produced calls that were more tonal and less broadband in comparison to SA4s and adult males, and were the only age class to produce calls with harmonic structure; the average fundamental frequency of these calls was 75 Hz ± 74 (TABLE V). Within one recording session, males of this age class often oscillated between attempted primitive version of the pulsed male vocal display, and calls that more closely resembled more continuous female threat vocalizations (Bartholomew and Collias, 1962). While there was high variability within the calls produced by each male, all SA1s emitted calls that were relatively similar to one another (Fig. 6). Despite the structural and temporal consistencies between the calls of SA1s, call duration, unit duration, unit repetition rate, and duration of the silent portion of each unit generated PIC values above 1.0, indicating that these call features are more variable between than within individuals.

SA2s—While SA2s produced calls that had an average unit repetition rate slower than SA1s (1.7 s ± 0.5, $p < 0.01$), all other acoustic features did not vary significantly between these two age classes. Similar to SA1s, SA2s produced highly unstructured calls that often alternated between longer and shorter elements within each repeating unit. SA2 males did not produce calls with any harmonic structure; however, similar to SA1s, portions of calls emitted by SA2s often resembled the belching characteristics of female threat vocalizations. With respect to PIC scores, Q1 frequency, center frequency, peak frequency, unit duration, unit repetition rate, and the silent portion of each unit all had values greater than 1.0.

SA3s—Notable among SA3s was their significantly longer call duration than both SA2s and SA1s (8.0 s ± 3.1, $p < 0.01$ for both comparisons), and their increase in stability of unit structure across the duration of each call (Fig. 6). SA3s were reliable in their usage of each sonic element, and did not alternate between element types within or between calls (TABLE V). Despite the consistencies in call features within individuals, it was difficult for human listeners to ascribe a particular call to an individual given the similarity of calls between males. SA3s did not produce vocal displays with harmonic structure, and possessed a Q3 frequency that was significantly higher than SA2s (915 Hz ± 265, $p<0.05$), indicating that the calls were more broadband than those of younger individuals. Additionally, the peak frequency of their calls was lower than that of SA1s (276 Hz ± 73, $p<0.05$). All measured call features had a PIC score greater than 1.0, with Q3 Frequency, unit duration, the duration of the sonic portion of each unit showing PIC values greater than 2.0, indicated increased within-individual stereotypy relative to younger males.

SA4s—The calls of SA4s were noticeably variable among individuals, yet very consistent within individuals (FIG. 6). It is within this age class that sub-structural components begin to emerge, with individual males reliably producing one or more elements and different element types within each repeating unit of their vocalization. SA4 males also begin to consistently use introductory and/or terminal flourishes surrounding the repeating rhythmic portion of their vocalization (Fig. 6, TABLE V). Interestingly, two of the ten SA4 males sampled alternated between two different stereotypic vocalizations within and between recording sessions. With respect to spectral characteristics, SA4s exhibited higher peak frequencies than SA2s and SA3s (627 Hz ± 265, $p<0.005$ for both comparisons) that suggested their calls were more broadband ($p<0.0001$ for 90% frequency bandwidth comparison to both

SA1s and SA2s). SA4s never emitted calls with harmonic structure (TABLE V). Additionally, they demonstrated higher Q1 and center frequencies than younger males (544 Hz ± 247, $p<0.05$ for all comparisons). All measured call parameters displayed a PIC value greater than 1.0, with unit duration and unit repletion rate exhibiting PIC scores greater than 4.

Adults—Similar to the vocalizations produced by SA4s, adult males produced calls that were highly individually stereotyped, with temporal patterns that varied considerably between individuals (Fig. 6). Individual adult males exhibited calls that contained between 1 and 3 elements within each repeating unit, with some males consistently utilizing different element types in the repeating rhythmic portion of their vocalization (TABLE V). Additionally, some individuals produced calls with consistent introductory/terminal flourishes. Adults had a higher Q3 frequency than all other age classes (1332 Hz ± 481, $p < 0.05$ for all comparisons), highlighting the broadband nature of the impulsive adult vocalizations. With respect to PIC values, all call features were associated with PIC values greater than 1.0. The duration of the sonic portion of each unit had an associated PIC value of 3.2, and unit duration, the terminal silent portion of each unit, and unit repetition rate had extremely high PIC values of 4.3, 4.6, and 5.7, respectively, highlighting these temporal features as strong indicators of individual identity in adult males. Central frequency and Q3 frequency also had PIC values > 1.0. Qualitatively, human listeners could easily ascribe the vocal displays of SA4s and adults to the correct individual based on the temporal characteristics of his call.

Discrimination among individuals as a function of age

The five highest, uncorrelated PIC scores for adult males were used to inform the DFA analysis for males of all age classes. These spectral and temporal variables included the unit repetition rate, the silent portion of each unit, the sonic portion of each unit, the central frequency, and the Q3 frequency. The classification matrix generated by the DFA analysis revealed that call stereotypy increased with increasing age (Fig. 6). The calls of SA1 males were correctly assigned to individuals with an average classification rate of 39% (chance classification = 5.2-14.3%). SA2 calls were correctly assigned to the correct individual with a classification rate of 48% (chance = 5.3-10.5%), SA3 calls exhibited a 54% correct classification rate (chance = 5.4-10.8%), and SA4s and adults produced calls that could accurately be assigned to the correct male with an average classification rate of 83% (chance = 6.0-12.0%) and 84% (chance = 14.3%), respectively (Fig. 6). Among SA1s-SA2s and SA4s-adults, duration of the silent portion of each unit and unit repetition rate were strongly correlated with the first and second discrimination roots of the DFA. Among SA3 males, duration of the sonic portion of each unit and Q3 were correlated with the first and second root. While the percent correct classification scores did not differ between SA1s and SA2s, the accuracy of call classification did increase significantly for SA3s relative to SA1s (N-1 Chi-squared X^2 (1) = 28.2, $p<0.05$), and for SA4-Adults relative to SA3s (N-1 Chi-squared X^2 (1) = 40.8, 41.39, $p < 0.0001$ for both comparisons).

Summary

We found that the consistency of a male's vocal display increases with age from SA1 to SA3 (approximately 4-6 years old) and begins to stabilize once males reach the SA4 age class (approximately 7 years of age). As adults, males possess a reliable acoustic signature that remains unaltered over successive years (Casey *et al.,* 2015). This progression of vocal behavior represents significant changes in both the spectral and temporal domain of each male's call. The SA1-SA2 age classes (4-5 years old) lack consistency in call structure with respect to both unit repetition rate and the use of reliable elements within the repeating portion of their call, making it difficult to acoustically differentiate between individuals. While the calls of SA3 males (6 years old) exhibit stronger consistency with respect to both rhythm and structure, they show surprisingly low between-individual variation. Across the SA1-SA3 age classes, several frequency characteristics decrease with maturation, supporting the notion that some call parameters may be constrained by vocal tract length, and could serve as honest information about an individual's body size to listeners. However, the impulsive, broadband nature of the calls of both SA4s and adults may make it difficult to acquire reliable size information from individuals of these age classes. Consistent differences between individual males emerge at approximately 7 years of age (SA4), coinciding with the timing at which males develop more stable associations with others within the dominance hierarchy. These differences are mainly supported by variation in the temporal features of each male's call, and support our previous findings that subtle structural differences in the vocal displays of males enable recognition of familiar competitors among mature individuals.

DISCUSSION

Over the course of a male elephant seal's lifetime, individuals transition from high variability towards increased stability with respect to social behavior. Among older animals, restriction of fine-scale movement patterns creates a predictable social environment in which repeated interactions between group members can occur. As they mature, males transition from producing calls that are highly variable to highly stereotyped acoustic displays that differ substantially between animals. This enables older males to associate the outcome of social interactions with their familiar competitors with reliable acoustic cues. Across all three measures of behavior (space utilization, social relationships, and vocalizations), it appears that the transition from the SA3 to SA4 age class (approximately 6-7 years of age) is an important period during male social development. While it is tempting to interpret the behavior of juveniles as a "less-developed" form of the adult repertoire, young animals must solve a suite of social problems that are much different than those experienced by older animals, including avoiding harm on a breeding rookery dominated by large and powerful adult males. It is therefore not surprising that sub-adult juveniles exhibit alternate behavioral strategies in comparison to their older counterparts in response to these contrasting social pressures.

The goal for any male elephant seal is to gain access to and mate with multiple females. Given the aggregation patterns and synchrony of haul-out behavior of estrous females, a small portion of elite males are able to monopolize access to most breeding opportunities, which has led to a system of extreme harem-defense polygyny (Le Boeuf, 1972). Only older and larger individuals that possess increased energy reserves and stamina are capable of competing for and defending females while fasting throughout the annual breeding season, which may span more than two months. SA1s cluster in areas not used by competing adults, and leave the colony well before peak breeding in February, while SA2s move extensively to avoid conflicts with older, larger and more aggressive males. As these individuals reach physical and behavioral maturation, they exhibit greater connectivity with other top contenders in their social network.

Our results demonstrate that older males remain in individually specific and predictable locations throughout the breeding season, and participate in a stable dominance hierarchy with dozens of familiar individuals all jockeying for a prime position relative to females. However only a few individuals reach alpha status; this begs the question of why most subordinate SA4 and adult males also exhibit fine-scale site fidelity, as opposed to shifting their positions to explore different harems around the colony. In this highly competitive and high-risk system, rival familiarity (within and potentially between seasons) is likely an important determinant of future reproductive success. For example, social knowledge and early connectivity within a social network have been show to predict male success in an avian lek system characterized by a strong mating skew (McDonald, 2007). Although the majority of non-alpha individuals rarely mate with females (Le Boeuf, 1974), these males may be "climbing the social ladder," and gaining important information about their present and future competitors. While this hypothesis has not yet been explicitly explored in elephant seals, research with other species has demonstrated clear fitness benefits to individuals exhibiting greater sociality (defined by the number and types of social bonds) early in life (Stanton and Mann, 2012; McDonald 2007). Long-term studies tracking the social encounters of individuals as they progress through developmental stages would elucidate whether early social patterns and relationships influence later reproductive success in this species.

Given potential fitness benefits of social knowledge among adult male elephant seals, early social interactions between subadults appears to be essential to normal behavioral development. Our results demonstrate that young SA1 and SA2 males return to the colony prior to peak breeding activity, during which time they participate in fluid social exchanges that include mock fighting, chasing, and exchange of calls with other young individuals. These interactions typically do not have clear "winners" and "losers." Previous work in other social species has found that basic communicative skills are acquired during this kind of low-stakes "play" behavior, which becomes essential to later adult interactions (Bekoff, 1972). During these encounters, a male's responsiveness to a competitor's vocalization may improve with experience through social conditioning. Additionally, given the ritualized nature of the fully-formed SA4 and adult male elephant seal display, low-stakes interactions during early development likely allow males to gradually increase the conspicuousness of various elements of these multi-modal signals (*i.e.,* visual posturing and vocalizations).

Documenting developmental changes in acoustic behavior is the first step in assessing the influences that physical maturation and learning have on the adult vocal displays of male seals. Young males appear to have a plastic calling phase, characterized by the production of various element types used in different combinations. This is similar to the vocal development of southern elephant seals (*Mirounga leonina),* which also transition from possessing non-structured, variable calls to fixed vocalizations as adults (Sanvito *et al.,* 2007). Longitudinal recordings of young southern elephant seals showed that an adult's vocalization was most similar to that of the dominant male present during the sub-adult period of development, and suggest that vocal learning as a result of auditory exposure may influence sound production in this species. Interestingly, the shift from high plasticity to high specificity in the individual vocalizations of both northern and southern male elephant seals during ontogeny can be compared to that of songbirds, the phylogenetic group that has most convincingly demonstrated advanced vocal learning capabilities (Wilbrecht and Nottebohm, 2003).

It is unclear whether male northern elephant seals require auditory input from their environment in order to develop their acoustic displays. While it is inherently difficult to parse environmental and genetic influences shaping sound production in wild animals, the northern elephant seal presents a particularly intriguing model.

These seals exhibit an extreme deficit in genetic variability due to human-induced population decline and subsequent inbreeding (Abadia-Cardosa *et al.,* 2017), which could allow for potential isolation of genetic factors contributing to vocal ontogeny. Given the transition from high variability to increased consistency in tempo as animals mature, young males may require substantial practice in order to control their pulse production. In this case, males may not learn by imitating others (as is the case with song birds), but be conditioned to produce more stable vocalizations by successfully inducing predictable responses from their competitors.

Interestingly, our analysis indicates that specific spectral characteristics (namely the first frequency quartile and peak frequency) decrease as males transition from the SA1 to SA3 age class. These findings are consistent with predictions of source filter theory, which suggest that call characteristics are influenced by both the larynx (sound producing mechanism) and vocal tract length (Taylor and Reby, 2010). Peak growth among males occurs between three and five years of age, with relative growth rates of approximately 10% per year (Clinton and Le Boeuf, 1993). Additionally, the standard length of males increases each year of life until physical maturity (8 years of age), after which point males apparently stop growing (Clinton and Le Boeuf, 1993). Given the strong relationship between vocal tract length and body size in mammals (Riede and Fitch, 1999; Fitch, 1997), the frequency content of vocalizations have the potential to provide honest information about the phenotype of callers (e.g., Fitch and Reby, 2001; Fitch 1997; Reby and McComb, 2003). This may be advantageous to younger males that lack vocal signatures and stable social relationships, and so may rely on size-related information during rival assessment. While our previous work with his species has demonstrated that certain call features are correlated with morphological traits among older animals, a male's size does not predict his dominance status within the colony (Casey *et al.,* 2015). Furthermore, playback experiments with adult males demonstrate that males do not attend to the available honest information during competitive encounters (Casey *et al.,* 2015). In a system where large size and physical strength are ubiquitous among the relatively few males that survive to adulthood, hierarchy structure appears to be influenced by individual strategy and the dynamics of social interactions rather than small differences in physical attributes among these elite contenders.

We have shown that young males transition towards smaller, more predictable home-ranges as they mature. Among older animals, restriction of fine-scale movement patterns creates a stable social environment in which repeated interactions between group members occur. As a result, while young males have fewer social partners with whom they are less familiar, older animals interact with more individuals within their dominance network, and their familiarly with those animals increases with age. To facilitate individual recognition among competitors, the calls of male seals transition from being highly variable within individuals, to highly stereotyped signature calls that differ substantially between animals. This enables older males to associate the outcome of social interactions with their familiar competitors with reliable acoustic cues, which in turn mediates energy expenditure during periods of extended fasting in this species. Thus, the mere acoustic display of a dominant rival, even from some distance, is usually sufficient to control the behavior of subordinate individuals (Casey *et al.,* 2015).

Taken together, these findings provide an enriched perspective of the ontogeny of social behavior among male northern elephant seals, which in turn help to explain the developmental process by which individuals provide and acquire information within a social environment that is supported by individual recognition of one's competitors.

AKNOWLEDGEMENTS

Research was conducted under authorization of National Marine Fisheries marine mammal research permits 14636 and 19108, with oversight from the Institutional Animal Care and Use Committee of the University of California Santa Cruz. Permission to work at the field site was provided by Año Nuevo State Park.

Drs. Colleen Reichmuth, Nicolas Mathevon, and Isabelle Charrier, and Claire Nasr and Parker Forman provided fundamental collaboration that enabled this study. Support for this work was provided by the Chateaubriand Fellowship, and the UC Santa Cruz Chancellor's Dissertation Fellowship (include Chateaubriand fellowship and others).

We gratefully acknowledge the contributions made by Emma Levy, who assisted in several aspects of data collection during this study. We thank Teng Veng, Brandon Southall, Ari Friedlaender and volunteers from the Pinniped Cognition and

Sensory Systems Laboratory for their contribution to data collection and analysis. We are grateful to Dan Crocker and Dan Costa for coordinating research authorizations and activities, and Dan Costa, Patrick Robinson, Rachel Holser, and Guy Oliver for logistical and other support. Finally, we thank Juliette Linossier, Bruce Lyon, Peter Tyack, and Jim Estes for statistical advice and editorial comments on this manuscript

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Age class	Mean Number of Resights	Range	Mean Arrival Date	SD (day)	Mean Departure Date	SD (days)	Mean Time Ashore (days)	SD (days)
SA1	15	10-23	11/27/17	10	1/3/18	11	37	10
SA2	16	12-22	12/23/17	13	2/9/18	12	49	8
SA3	18	11-24	12/27/17	7	3/1/18	7	64	7
SA4	26	12-36	12/17/17	11	2/26/18	4	71	13
AD	30	11-47	12/19/17	21	2/26/18	10	68	21

TABLE I. Summary of attendance patterns exhibited by male seals (n=10 per age class) observed during the breeding season ending in 2018, including mean time spent ashore of each age class. Observations indicate that the duration of a male's stay at the colony increases with age.

Age	Age	Time Ashore	95% HR	50% HR
AD	SA1	<.0001*	0.92	0.97
AD	SA2	<.01*	<.0001*	<.0001*
AD	SA3	0.96	<.01*	<.05*
AD	SA4	0.99	<.01*	<.001*
SA4	SA1	<.0001*	0.12	0.16
SA4	SA2	<.01*	<.05*	<.001*
SA4	SA3	0.76	0.99	0.99
SA3	SA2	0.06	0.21	<.01*
SA3	SA1	<.001*	0.06	0.14
SA2	SA1	<.05*	<.001*	<.0001*

TABLE II. Resulting p-values from Tukey-Kramer HSD post-hoc tests between each age class with respect to male time spent ashore, 95% home range, and 50% home range. Significant values are indicated by *.

	GPS re-sights used for home-range analysis			Home range size (Kernal Density Estimates)						
Age Class	**Number of seals**	**GPS resights (average)**	**GPS resight range**	**95% area (km^2)**	**Range**	**SD**	**50% area (km^2)**	**Range**	**SD**	**Seasons included**
SA1	9	15	10-24	0.054	0.0002 - 0.16	0.06	0.01	0.00002 -0. 03	0.01	2018
SA2	27	16	10-32	0.18	0.02 - 0.17	0.1	0.07	0.006- 0.17	0.05	2012, 2014, 2016, 2017, 2018
SA3	40	18	10-39	0.14	0.02 -0 .28	0.07	0.04	0.042 - 0.1	0.03	2012, 2014, 2016, 2017, 2018
SA4	56	20	10-52	0.13	0.005 - 0.35	0.09	0.04	0.002 - 0.14	0.04	2012, 2014, 2016, 2017, 2018
AD	76	27	11-60	0.08	0.008 - 0.35	0.08	0.02	0.0007 - 0.1	0.02	2012, 2014, 2016, 2017, 2018

TABLE III. Spatial patterns exhibited by male seals (n = 208) during five annual breeding seasons. Home ranges are expressed as both 95% and 50% mean KDE areas (km^2) for each age class.

Age	**Age**	**Degree Centrality**	**Nodal Strength**
AD	SA1	<.0001*	<.001*
AD	SA2	<.0001*	<.0001*
AD	SA3	<.0001*	<.0001*
AD	SA4	0.61	0.77
SA4	SA1	<.001*	<.01*
SA4	SA2	<.0001*	<.01*
SA4	SA3	<.01*	<.01*
SA3	SA2	0.45	0.9
SA3	SA1	0.35	0.84
SA2	SA1	0.99	0.99

TABLE IV. Results Tukey-Kramer HSD post-hoc test between each age class with respect to male degree centrality and male nodal strength. Significant values are indicated by *.

SA1s

	Range	Mean	Std. Dev.
Spectral Parameters			
Quartile 1 frequency (Hz)	273-506	378	87
Center frequency (Hz)	367-661	539	107
Quartile 3 frequency	539-823	700	109
90% frequency bandwidth (Hz)	612-841	720	81
Peak frequency (Hz)	335-691	496	123
Temporal Parameters			
Call duration (s)	1.6-5.7	2.9	1.3
Unit duration (s)	0.33-0.5	0.41	0.06
Duration of sonic portion in each unit (s)	0.15-0.28	0.2	0.04
Duration of silent portion of each unit (s)	0.17-0.27	0.2	0.04
Unit repetition rate (Hz)	2.06-3.18	2.54	0.37
Degree of isochronicity	0.08-0.24	0.41	0.06
Descriptive Characteristics			
Number of elements in each unit	1	1	
Number of different elements in each unit	1-2	1	
Percentage of calls that contain introductory snorts/rumbles	0-30%	6%	5%
Percentage of calls that contain terminal snorts/rumbles	10-80%	53%	52%
Percentage of calls that contain harmonics	10-70%	29%	28%
Fundamental frequency (Hz)	59-86	75	74

SA2s

	Range	Mean	Std. Dev.
Spectral Parameters			
Quartile 1 frequency (Hz)	183-640	305	130

Center frequency (Hz)	302-841	455	164
Quartile 3 frequency	502-938	654	129
90% frequency bandwidth (Hz)	677-1109	818	140
Peak frequency (Hz)	185-823	367	178
Temporal Parameters			
Call duration (s)	3.0-8.68	4.9	1.7
Unit duration (s)	0.42-1.12	0.68	0.24
Duration of sonic portion in each unit (s)	0.14-0.35	0.24	0.07
Duration of silent portion of each unit (s)	0.21-0.78	0.44	0.19
Unit repetition rate (Hz)	0.89-2.49	1.67	0.54
Degree of isochronicity	0.05-0.25	0.16	0.05
Descriptive Characteristics			
Number of elements in each unit	1	1	
Number of different elements in each unit	1-2	1	
Percentage of calls that contain introductory snorts/rumbles	0-30%	3%	10%
Percentage of calls that contain terminal snorts/rumbles	0-100%	57%	46%
Percentage of calls that contain harmonics	0%	0%	*n/a*
Fundamental frequency (Hz)	*n/a*	*n/a*	*n/a*

SA3s

	Range	**Mean**	**Std. Dev.**
Spectral Parameters			
Quartile 1 frequency (Hz)	155-347	258	78
Center frequency (Hz)	314-894	586	206
Quartile 3 frequency	476-1274	915	256
90% frequency bandwidth (Hz)	935-1895	1419	265
Peak frequency (Hz)	164-403	276	73

Temporal Parameters			
Call duration (s)	4.76-12.11	8.04	3.07
Unit duration (s)	0.55-1.14	0.88	0.2
Duration of sonic portion in each unit (s)	0.08-0.34	0.24	0.08
Duration of silent portion of each unit (s)	0.41-0.86	0.65	0.13
Unit repetition rate (Hz)	0.88-1.81	1.22	0.33
Degree of isochronicity	0.06-0.24	0.1	0.05
Descriptive Characteristics			
Number of elements in each unit	1	1	
Number of different elements in each unit	1	1	
Percentage of calls that contain introductory snorts/rumbles	0-40%	10%	10%
Percentage of calls that contain terminal snorts/rumbles	0-80%	20%	30%
Percentage of calls that contain harmonics	0%	*n/a*	*n/a*
Fundamental frequency (Hz)	*n/a*	*n/a*	*n/a*

SA4s

	Range	**Mean**	**Std. Dev.**
Spectral Parameters			
Quartile 1 frequency (Hz)	117-783	544	247
Center frequency (Hz)	466-1069	819	208
Quartile 3 frequency	766-1292	1089	167
90% frequency bandwidth (Hz)	1024-1781	1544	225
Peak frequency (Hz)	122-921	627	265
Temporal Parameters			
Call duration (s)	6.44-14.17	9.21	2.27
Unit duration (s)	0.4-1.41	0.86	0.32
Duration of sonic portion in each unit (s)	0.08-0.62	0.3	0.19

Duration of silent portion of each unit (s)	0.16-1.13	0.57	0.29
Unit repetition rate (Hz)	0.71-2.51	1.36	0.58
Degree of isochronicity	0.04-0.31	0.11	0.09
Descriptive Characteristics			
Number of elements in each unit	1-2	1	
Number of different elements in each unit	1-2	1	
Percentage of calls that contain snorts/rumbles	0-100%	46%	46%
Percentage of calls that contain snorts/rumbles	0-100%	11%	31%
Percentage of calls that contain harmonics	0%	*n/a*	*n/a*
Fundamental frequency (Hz)	*n/a*	*n/a*	*n/a*

Adults

	Range	**Mean**	**Std. Dev.**
Spectral Parameters			
Quartile 1 frequency (Hz)	192-766	575	167
Center frequency (Hz)	220-1253	924	278
Quartile 3 frequency	328-1971	1332	481
90% frequency bandwidth (Hz)	523-1603	1197	371
Peak frequency (Hz)	211-914	579	238
Temporal Parameters			
Call duration (s)	5.02-13.98	7.68	2.56
Unit duration (s)	0.38-1.06	0.75	0.26
Duration of sonic portion in each unit (s)	0.15-0.28	0.2	0.04
Duration of silent portion of each unit (s)	0.01-0.62	0.35	0.22
Unit repetition rate (Hz)	0.95-2.84	1.55	0.62
Degree of isochronicity	0.04-0.18	0.09	0.04
Descriptive Characteristics			

Number of elements in each unit	1-3	1	
Number of different elements in each unit	1-2	2	
Percentage of calls that contain snorts/rumbles	0-100%	79%	42%
Percentage of calls that contain snorts/rumbles	0-100%	28%	39%
Percentage of calls that contain harmonics	0%	*n/a*	*n/a*
Fundamental frequency (Hz)	*n/a*	*n/a*	*n/a*

TABLE V. Mean, range, and standard deviations of spectral and temporal measurements obtained from males representing each age class. For discrete parameters, we report the range, mean, and standard deviation of each variable; for continuous data, we report the mode and range. The sample sizes for each age class are as follows: SA1s—8 individuals, 75 calls total, SA2s—9 individuals, 94 calls total, SA3s—10 individuals, 10 calls total, SA4s—10 individuals, 82 calls total, and Adults—10 individuals, 100 calls total.

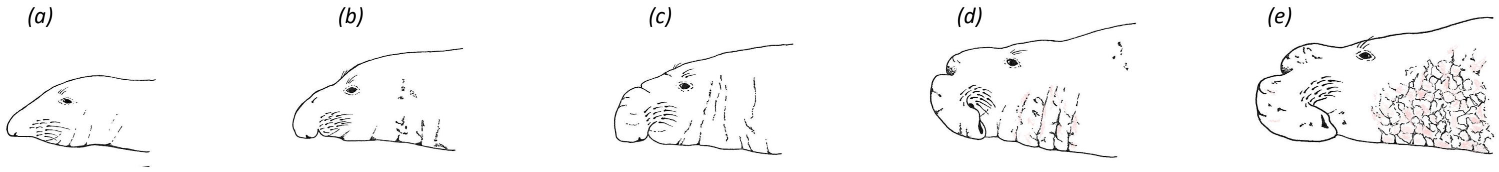

FIG 1. Illustration of secondary sexual characteristics associated with each age class. Males categorized as sub-adult 1 (SA1) were four years old. These individuals are approximately the size of adult females, with a wide nose that is not elongated and without a mid-nose indentation; while they possess some chest wrinkles, these males have no scarring on the chest (**a**). Males categorized as sub-adult 2 (SA2) were five years old and larger than adult females. These individuals have a proboscis that extends down to the mouth when the seal rests flat on the ground; they have no mid-nose indentation. Wrinkles are present along the chest-shield but there is no scarring (**b**). It is at this age that puberty apparently begins, with secondary sexual characteristics starting to emerge. Males categorized as sub-adult 3 (SA3) were six years old. Their proboscis extends down past the mouth while resting on the ground, and a mild mid-nose indentation is evident. Scarring of the chest-shield is noticeable, with thickened skin and some wrinkles but no pink tissue (**c**). Males categorized as sub-adult 4 (SA4) were approximately seven years old. These seals have a proboscis that folds onto the ground while resting, a significant mid-nose indentation, and scarring along the chest that has some pink coloration. The chest shield can extend proximally towards the eye while observed resting on the ground (**d**). Fully mature males were categorized as adults (8+ years old). Adults have a wide proboscis with a pronounced mid-nose indentation; while at rest, the nose extends to the ground and folds back under the mouth. Adults typically display a noticeable, calloused pink chest shield that extends proximally past the eyes and up along the dorsal side of the head (**e**). Drawings by E. Levy.

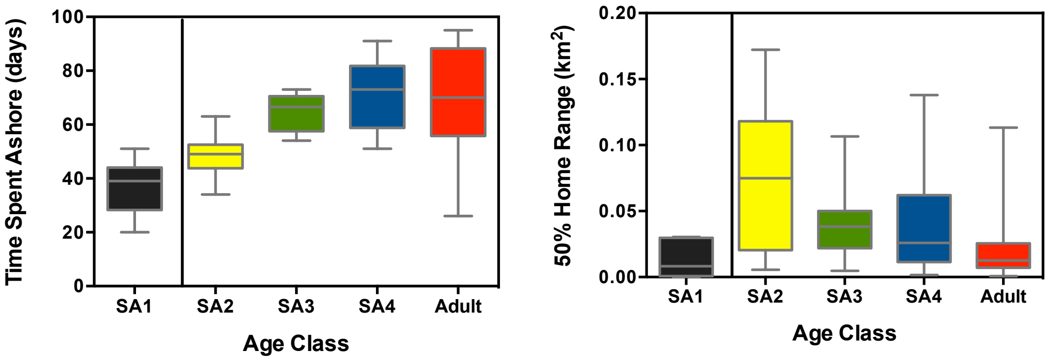

FIG 2. Male time spent ashore (left panel) and 50% home range size km^2 (right panel) for each age class. Sample sizes are provided in Tables 1 and 2. Boxes show quartile data while whiskers show total range. Black vertical lines after the SA1 age class indicate the onset of sexual maturity. Male presence on the colony increases with age, while 50% home range declines with maturation. Statistical comparisons are provided in TABLE II.

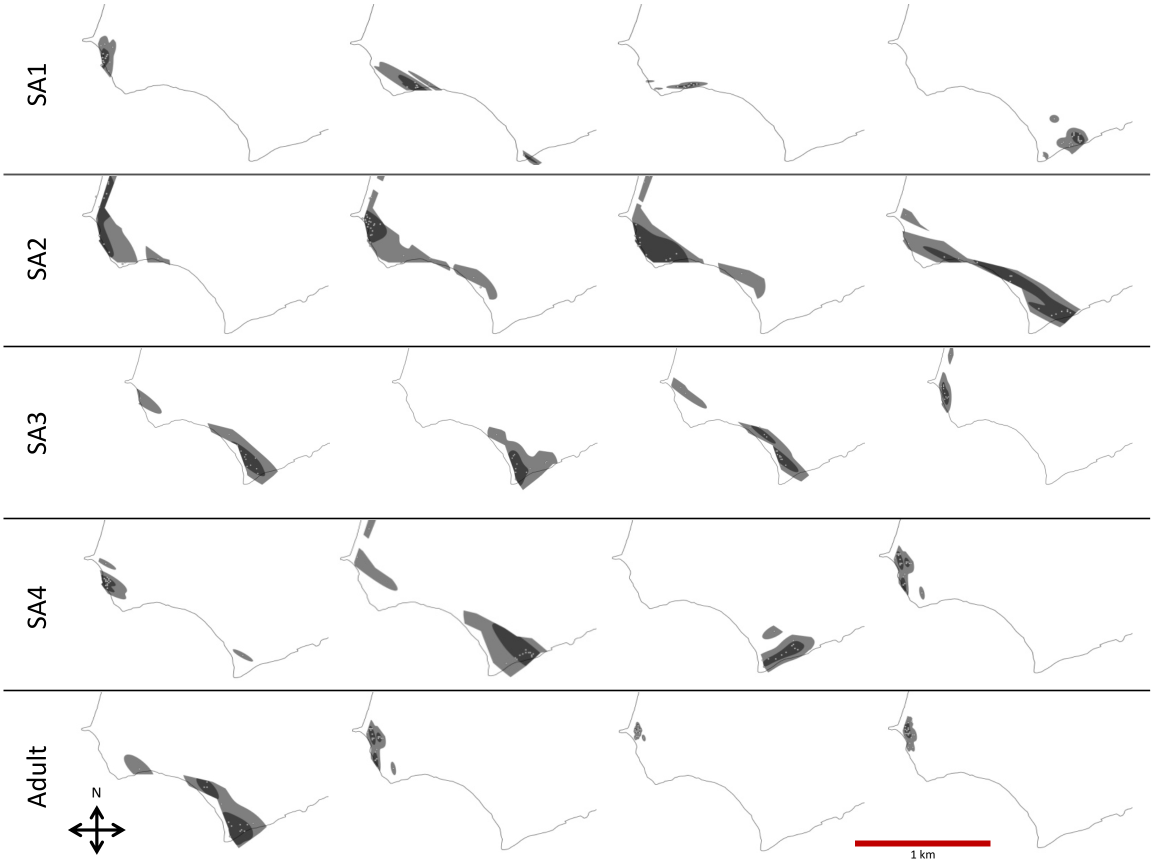

FIG 3. Home-range estimates for four individuals representative of each age class. The contour of the mainland coastal breeding area is shown by the think grey line; the 95% Kernel Density Area is shown by the lighter shaded area while the 50% Kernel Density Area is shown by the darker shaded area. The SA1 home range was captured over shorter period of time prior to the arrival of most females and older age-classes of males (November-January). Among the adult age class (AD), the first seal shown had a peripheral status, while seals in positions 2, 3, and 4 were Alpha males, which occupied considerably smaller home ranges than males of other descriptive ranks (see text for statistical results).

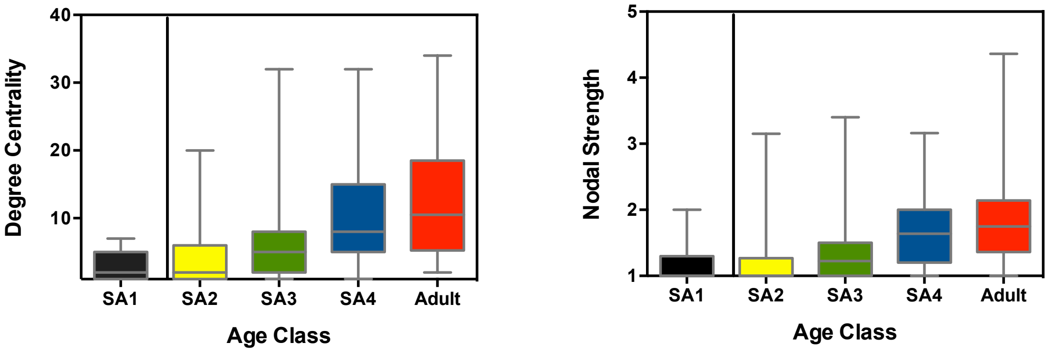

FIG 4. Male degree centrality (left panel) and nodal strength (right panel) for each age class. Boxes show quartile data while whiskers show total range. Black vertical lines after the SA1 age class indicate the onset of sexual maturity. Degree centrality (number of social partners) increases with age, as does nodal strength (degree of familiarity between social partners). Statistical comparisons are provided in TABLE IV.

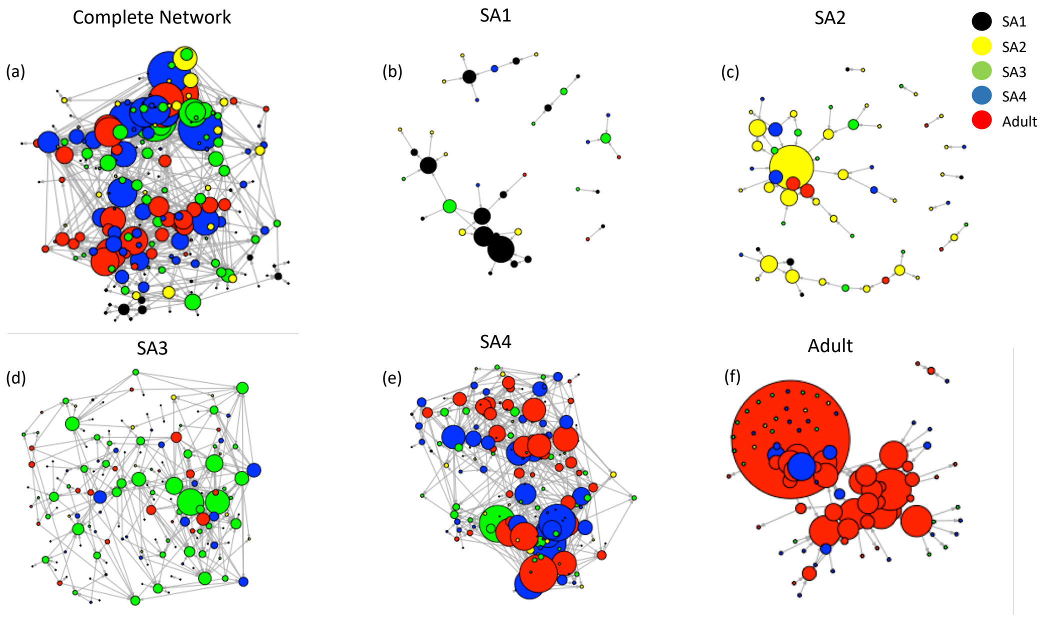

FIG 5. The social networks of male northern elephant seals. Data are from the 2018 breeding season (November to March). Circles are males and lines are dyadic competitive interactions. Age classes are separated by color (SA1: 4 years-old; SA2: 5 years-old; SA3: 6 years-old; SA4: 7 years-old; Adult: 8+ years-old). The size of circles corresponds to the males' degree centrality (males with larger circles have more social partners). **(a)** Complete network reporting all observed interactions between all males (n = 207 males). **(b-f)** Networks characterizing successive age classes illustrating interactions which show all SA1s (n = 17), all SA2s (n = 38), all SA3s (n = 66), all SA4s (n = 46), and all adults (n = 40). SA1 males interacted with an average of 2.8 different individuals within their social network (SD = 2.2, range = 1-7) and encountered each individual an average of 1.2 times (SD = 0.3, range = 1-2). SA2 males interacted with an average of 3.8 unique individuals (SD = 4.1, range = 1-20), with an average of 1.2 interactions with each individual (SD = 0.45, range = 1-3.2). SA3 males interacted with an average of 6.0 different individuals (SD = 5.4, range = 1-32), with an average of 1.3 interactions with each animal (SD = 0.45, range = 1-3.4). SA4s interacted with an average of 10.3 unique individuals (SD = 7.5, range = 1-32), with an average of 1.7 interactions with each individual (SD = 0.6, range = 1.32). Adult males interact with an average of 12 individuals over the breeding season (SD = 9.1, range = 2-34), and averaged 1.9 interactions with each individual (SD = 0.7, range = 1-4.2). Young males (SA1 and SA2) interact with only a few individuals, and avoid older males. As males mature they exhibit greater connectivity to competitors within the network. SA4 males preferentially interact with same-age or

older individuals, while most adults interact primarily with each other. Although each age class shows some individuals with higher degrees of centrality compared to others, it is only in adults that a few males monopolize most of the interactions.

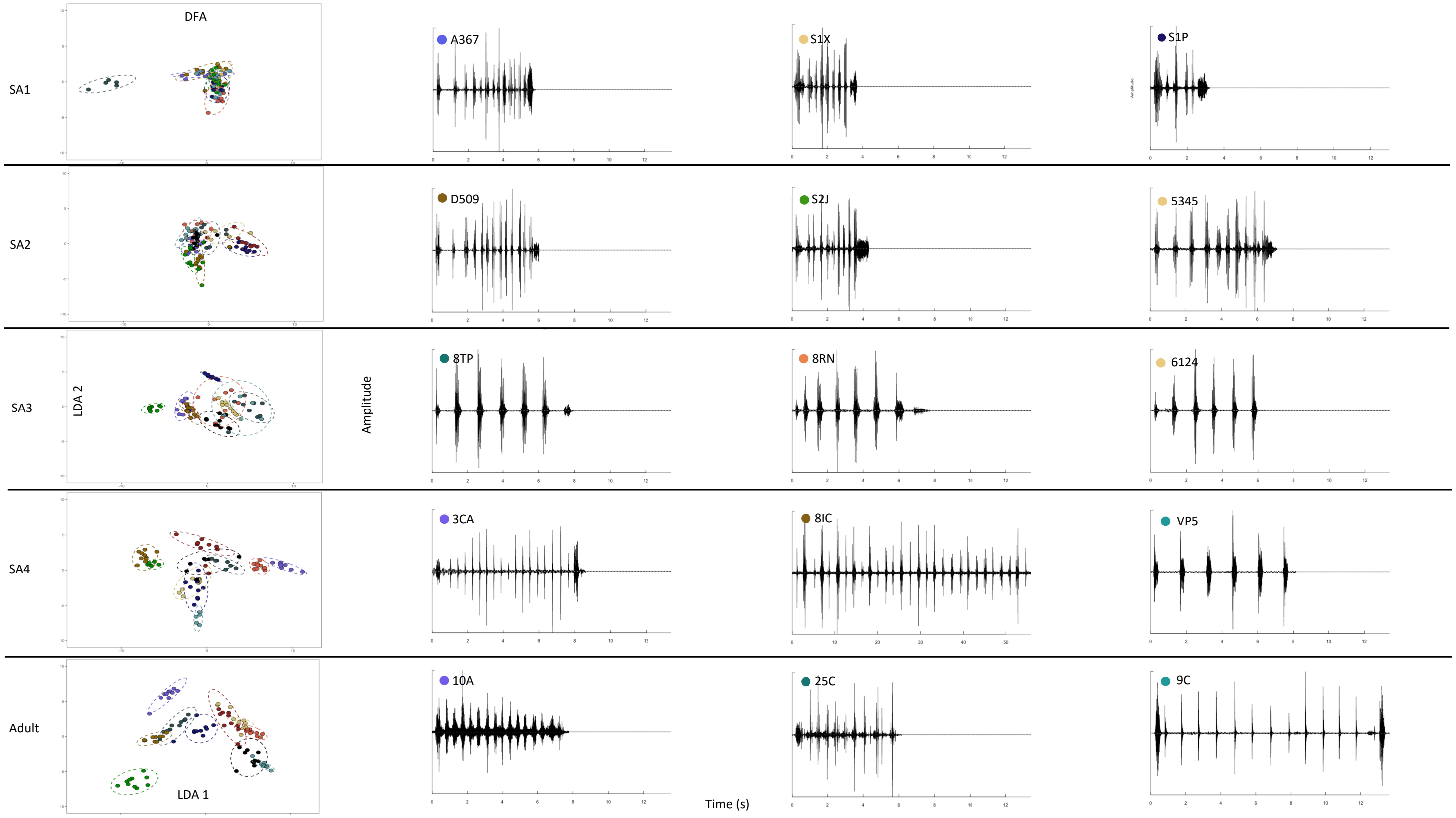

FIG 6. The results of the DFA analysis for each class and representative waveforms of males included in the analysis. Within the DFA results, colored points represent different males within each age class. The x and y-axes represent the maximum difference between groups based on a combination of predictor variables. The dotted ellipses illustrate a 95% confidence level for the data. If two groups differ significantly, the confidence ellipses tend not to intersect.

GENERAL CONCLUSIONS

Studies that follow individuals throughout their lifetimes contribute to our growing understanding of the evolution of behavioral traits in animals. Such longitudinal observations allow us to see complex yet subtle patterns unfold, and provide the basis for assessing fitness consequences of behavior under the selective conditions in which they naturally occur (Blumestein, 2010). When long-term studies can be conducted over multiple generations, it allows for a powerful opportunity to consider more ultimate questions by measuring the strength and direction of selection of a given behavior over time (Clutton-Brock and Sheldon, 2010).

Among animals that use sound to communicate with one another, discerning the information that is encoded within animal signals, and understanding how individuals exploit this information during social encounters, requires a detailed understanding of individual behavior. Bioacoustic studies often provide evidence that acoustic features may be correlated with phenotypic traits (*e,g.,* Sanvito *et al.,* 2007, Wyman *et al.,* 2008) and/or the ability to convey individual identity (*e.g.,* Soltis *et al.,* 2005); however, far fewer studies have confirmed the biological function of signals through systematic experiments that evaluate the spontaneous response of animals to the calls of individuals within their social network (*e.g.* Reby *et al.,* 2005, Charlton *et al.,* 2010). A complete understanding of signal form and function requires both analysis of call variables, as well as targeted experiments that evaluate how receivers assess and respond to these signals (Sayigh *et al.,*1998). Despite significant logistical challenges, these combined approaches are critical to understanding the role that assessment, recognition and learning may play in mediating interactions between individuals, and can provide insight into the social conditions that underpin these communication systems. Given the growing interest in signature signals (*e.g.,* Ord *et al.,* 2001*)* status signaling (*e.g.,* Taylor *et al.,* 2010; Wyman *et al.,* 2008) and the selective pressures influencing the structure of animal social networks (*e.g.,* Arnott and Elwood, 2009; Bergman *et al.,* 2003), synergistic efforts that combine both descriptive and experimental methods should contribute to a more complete understanding of the information gained by listeners during social exchanges.

The northern elephant seal provides the opportunity to examine both the structure and the function of vocalizations used to mediate social interactions between competing males. In this species, the stereotyped calls produced by males while ashore during the breeding season can be easily recorded and attributed to known individuals and linked with specific behaviors. Individuals can be followed with minimal disturbance throughout development, as these seals congregate at natal sites to breed at the same time each year. Finally, the function of different signals can be experimentally tested and manipulated using field playback experiments. These optimal conditions have allowed my collaborators and I to decode the information contained within the calls produced by males, and evaluate the role that learning plays in the social lives of male seals. Our findings demonstrate that mature males do not produce calls that convey an individual's size or willingness to fight, but rather males emit individually unique vocal signatures that rivals have learned to associate with the outcome of previous competitive interactions. By exploring the timing of the emergence of these specialized acoustic signals during development, we found that that the production of reliable signature vocalizations coincides with the stabilization of fine-scale space utilization and social relationships among males as they mature. The availability of historical research afforded me the unique opportunity to compare the vocal behavior of male northern elephant seals at the population level over four generations. I found that the vocal displays of breeding males changed dramatically during this period, as early patterns of vocal dialects were overtaken by the need for individual distinctiveness. This shift in vocal behavior was concurrent with significant changes in population structure, and new call characteristics were likely introduced into each breeding site through migration and cultural transmission.

These discoveries provide substantial fodder for new questions pertaining to the social lives of northern elephant seals. For example, while males are capable of recognizing their rivals within seasons, it is still unknown whether individuals possess long-term memory of their competitive rivals across years. Given the stereotypy of each males' vocal signature across multiple years, and the stability of male social relationships within each breeding season, there is an opportunity to explore the long-term dynamics of structured dominance hierarchies, and whether males possess persistent social memory of their familiar competitors. Such a question would be of general interest within the field of animal behavior, as it merges principles of both cognition and sociality (Bruck, 2013).

The work described in this dissertation builds upon several classic studies of male northern elephant seals (see Clinton and Le Boeuf, 1993; Deutsch *et al.,* 1990; Haley *et al.,* 1994; Le Boeuf, 1972; Shipley *et al.,* 1981). However, it only scratches the surface of the social dynamics of males and how they navigate a breeding system of such extreme competition. The results of Chapter 1 certainly suggest that a male's knowledge of his social network should influence his reproductive success, however this has not yet been clearly tested. Specifically, it is unknown whether early social interactions between young males predicts an individual's dominance trajectory later in life. Given that sexually mature males must often wait several years before reaching alpha status (if they ever do at all), beta males may gain direct but delayed benefits by learning about their competitors within and between seasons. Studies of long-tailed manakin (*Chiroxiphia lineris)*, for example, have demonstrated that network connectivity early in life predicts male success an average of 4.8 years later (McDonald, 2007). Continued research with elephant seals could evaluate how males move through the hierarchy during maturation to attain beta and alpha positions as adults, and whether specific behavioral characteristics exhibited by younger individuals predict the their eventual social status.

Finally, given that size is not a clear predictor of dominance status among adult males (Casey et al., 2015), individual strategy during the breeding season appears to be related to a male's reproductive opportunities. Several investigators have commented on the variety of behavioral strategies that adult males employ during the breeding season, yet no study has documented these differences, evaluated how they change with development and/or experience, and related them to an individual's ultimate dominance position within his social hierarchy. By tracking young individuals throughout their development, it may be possible to determine whether there is a relationship between specific behavioral strategies and subsequent reproductive success as an adult (as in Silk *et al.,* 2003; Silk *et al.,* 2010; Archie *et al.,* 2014). These individual strategies would not only consider time spent ashore, but also encompass a male's behavior while sea. As seasonal resource acquisition likely impacts a male's ability to fast throughout the annual breeding season, small differences in foraging success likely impact the duration of a male's breeding tenure, stamina, and perhaps his willingness to fight. Linking the at-sea foraging behavior of individuals with their behavior during the breeding season would provide a holistic view of the factors influencing male survival and reproductive success.

Collectively, the research presented in this dissertation explores both proximate and ultimate questions concerning communicative behavior of male northern elephant seals. Building upon of a strong foundation of behavioral and life history research with the northern elephant seal at UC Santa Cruz, the findings reported here improve our understanding of the important role that vocal signaling plays in the lives of this highly competitive mammalian species, and offers a detailed comparative framework for general studies of animal acoustic communication.

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