

Chapter 10

Acoustic Coding of Information in a Complex Social Network: Identity Signaling in Northern Elephant Seals



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Abstract The process of learning plays a pivotal role when an animal must correctly identify individuals within a dynamic social group. In male–male competition for access to reproductive success, a male’s ability to learn the calls that are associated with one’s rival can help to maintain structured dominance relationships and reduce the costs associated with fighting. Male northern elephant seals operate in one of the most competitive breeding systems among mammals, and selection pressures for accurate rival assessment are extreme. Through a long-term field effort that has tracked individual males over multiple breeding seasons, we have found that male elephant seals are operating in a large, spatially dynamic social network, which is conducive to the emergence of individual acoustic recognition and associative learning. Given their accessibility during the breeding season, the northern elephant seal provides an excellent comparative framework for studies of the relationship between signal function and an individual’s social environment.

10.1 Introduction

10.1.1 *Learning and Communication*

Communication is a fundamental feature of all animal social systems, and serves to support significant life history functions such as navigation, breeding, foraging, and parental care. While there are many ways to define communication, most agree that it involves the general process of information exchange between signalers and receivers, during which the receiver can extract biologically important information and potentially exhibit some kind of behavioral response. The potential information contained in animal vocalizations may range from motivational state to individual

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identity to competitive ability. While some responses to signal characteristics seem to be reflexive, learning often plays an important role in how animals interpret and respond to signal features associated with a caller. Individuals possess flexibility in their decision-making, and acquire valuable information as a consequence of their own behavior and the behavior of others. Imagine for a moment a male great tit defending his territory during the breeding season. While perched atop a branch, he hears the song of a nearby rival. The song may be produced by a male with whom he has already interacted, during which he successfully defended his territory, or alternatively, was defeated. How the listening male chooses to respond to his competitor (either by attacking or retreating from the invader) may be influenced by the male's previous experience with this individual. In this way, combined with inherent tendencies and direct assessments about size or strength, previous experiences and their consequences can alter the choices that animals make within communicative contexts.

While some behaviors are innate, such as an individual's reflexive fear of predators, many others are influenced by the process of learning. Learning can be defined as a behavioral change that arises from experience that is not attributed to maturation or development (Domjan 1998). Within the world of an animal, a particular action may be followed by an event that is positive, negative, or neutral. The type and magnitude of the consequence alters the probability of whether an emitted response is likely to be repeated in the future. The laws of associative learning have been well established through a long history of laboratory studies that carefully measured the conditions under which behavior changes over time for many species. These behavioral laws also apply in the natural world, where animals must make decisions within their environment based on what they have learned through prior experience. In the case of the great tit, the call of his neighbor is associated with an experience (being beaten by or beating the bird who is producing the call), and he must recall this event, and decide whether to attack or retreat in response.

10.1.2 The Role of Associative Learning During Individual Recognition

While individuals may be genetically predisposed to respond to various species-specific signals (e.g., through phenotype or allele matching), learning can play a pivotal role when a receiver must correctly identify individuals within a dynamic social group based on familiarity (Bradbury and Vehrencamp 1998). This process is referred to as individual recognition, and is commonly established through the process of associative learning. Individual recognition is accomplished when a receiver is able to discriminate between familiar conspecifics based on previous experience and memory of distinct features associated with that individual (Bradbury and Vehrencamp 1998; Hauser 1996). The information value of a signal is dependent

on the extent to which it is associated with, and therefore accurately represents, the individual (Seyfarth and Cheney 2003).

Communication strategies based on recognition are likely to evolve in social systems where the risks associated with misclassifying individuals are high. Under these conditions, recognition is dependent on both signal design and a receiver's perceptual tuning to key elements of the signal. In order to be meaningful for individual recognition, the identity signal, or individual signature, must be detectable amongst other features (both biotic and abiotic) within the environment, and must be memorable to the receiver. To be memorable, the signature should be stable across motivational contexts and time, and should exhibit very little within-individual variation. When being different from other individuals is advantageous, individually distinctive signals will spread via negative frequency-dependent selection, such that individuals who look, sound, or smell unique within social groups will be favored (Tibbets and Dale 2007; Sheehan and Tibbets 2009; Dale et al. 2001).

10.1.3 Selection Pressures that Drive the Emergence of Individual Recognition

The complexity of a signal's design is directly related to the number of classes that an individual must distinguish between. The more individuals within a social system, the more difficult the perceptual task becomes, and the higher the degree of "uniqueness" that an effective signal must exhibit (Bradbury and Vehrencamp 1998; Krams et al. 2012; Freeberg et al. 2012). This becomes even more imperative if individuals are highly mobile within the environment, thereby making the task of recognition more difficult due to the lack of reliable spatial cues. The relationship between signal complexity and an animal's social and ecological conditions has been explored across a variety of different colonial systems (Charrier et al. 2001; Aubin and Jouventin 2002; Mathevon et al. 2003), including species of cliff swallows. Medvin et al. (1993) evaluated two different species of swallow (the cliff swallow, *Hirundo pyrrhonota*, and the barn swallow, *H. rustica*) which are both colonial nesters. However, cliff swallows build nests that are more dispersed where there are fewer chicks for a mother to distinguish between. Barn swallows live in tightly packed, larger groups in which a mother has to distinguish her young amongst several hundred other chicks. Medvin et al. measured a number of call features from chicks in each environmental condition, and found that calls produced by chicks living in denser nesting environments exhibit far more variation in both the temporal and spectral domains (Medvin et al. 1993) than do chicks raised in more dispersed groups where the risk of misidentification is low.

The design of signature signals is also dependent on the ecological constraints of the environment itself. With regard to acoustic signaling in noisy environments, the risk of misidentification of target individuals is high. The range over which signature information is still perceptible to the receiver, or the active communication space of the signal depends (among other things) on the specific features within the call that

are responsible for encoding individual identity. Among the various kinds of signaling strategies, signature information is most often exhibited in the acoustic domain (e.g., Aubin and Jouventin 2002; Charrier et al. 2002; Searby and Jouventin 2003; Mathevon et al. 2003). For example, the territorial call of the male corncrake (*Crex crex*) encodes individual identity through temporal features of their vocalization, and this information can be transmitted up to 100 m through dense vegetation without degradation (Rek and Osiejuk 2011). Alternatively, if identity information is encoded in frequency-related features of the call (specifically higher frequencies), then signature information may disappear faster due to the susceptibility of high frequencies to be lost with increasing distance (Mathevon et al. 2008). Detectability may be improved by possessing a loud signal (Brumm 2004), having a signal that exhibits a frequency range well matched to penetrate the environment, or having a signal that is highly repetitive (Brumm and Slater 2006).

10.1.4 Intra-sexual, Mate, and Kin Individual Recognition

Interactions between individuals range from antagonistic (e.g., exchange of information between individuals competing for resources) to affiliative (e.g., exchange of information between parents and offspring), and the potential costs of misidentification have a large effect on signal design. The degree to which individual recognition facilitates coordination between individuals varies depending on the nature of the interaction. However, any system that relies on individual recognition likely involves frequent interactions between group members under social conditions where a receiver has to distinguish between multiple individuals. In these circumstances, the receiver has the opportunity to learn the unique qualities of an individual of interest, and can associate these cues with information that assists the receiver in navigating his/her social environment (e.g., finding offspring, mates, or identifying rivals).

The ability to accurately assess and respond to other individuals is paramount when the consequences associated with misidentification have a detrimental effect on fitness. This can be demonstrated clearly during conflict resolution between individuals, during which the optimal outcome for one individual is different than that of the other. In some cases, the suboptimal outcome can be energy expenditure, injury, or even death. Under these circumstances where the cost of misidentification is high, it becomes increasingly important that individuals correctly identify their rivals. As females are typically the resource of interest, this effect is most pronounced during male–male competition, during which males compete for access to breeding opportunities. Males may produce signals that contain information about the relative fighting ability or threat level of the sender, and receivers may have the opportunity to extract information from those signals and make appropriate decisions about whether to attack or flee (Searcy and Nowicki 2005). Under these consequences, misidentification of rivals can have detrimental social effects, as males may accidentally challenge more dominant individuals and lose, or alternatively, allow a subordinate male to displace his position within the social hierarchy.

10.1.5 Honest Signaling Versus Individual Signatures

Depending on the social system within which information exchange occurs, males competing for resources may rely on acoustic signals that communicate phenotypically linked acoustic cues that indicate the size or strength of the sender, or alternatively, that convey individual identity. In the former system, information about an individual's size, age, or level of arousal is encoded within specific features in the call, thereby giving the receiver an honest indication of the signaler's fighting ability. Variation among callers allows receivers to distinguish between males that possess varying levels of resource holding potential (e.g., Kitchen et al. 2003). This kind of signaling approach is likely more common in unstable social systems in which repeated social interactions between individuals are infrequent, and animals must acquire information about their competitor's level of threat quickly. In this scenario, receivers can gain important information about a signaler even without prior experience with that individual. For example, male American bison (*Bison bison*) utilize call amplitude to assess the physical condition and motivation of potential competitors (Wyman et al. 2012). Conversely, in more stable social groups in which males have the opportunity for repeated interactions, individuals competing for resources may be more likely to rely on acoustic signals that convey individual identity (Tibbetts and Dale 2007). These signals are often consistent within a given individual but variable between group members, and require association with competitors and consequences become meaningful. In this case, learning the identity and relative fighting ability of one's rivals allows a male to assess the strength and/or stamina of his familiar competitors (Tibbetts and Dale 2007). Such associative learning can lead to improved rival assessment over time.

Although both types of signaling strategies are useful in assessing one's opponents, they can be distinguished by observing the responses of individuals to the calls of unfamiliar rivals. Signals conveying individual identity are only useful in informing listeners about the fighting ability of familiar rivals with whom they have had previous experience. Alternatively, honest signals can inform listeners about the impending threat of both familiar and unfamiliar senders. Recognition of one's previous opponent can 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 an alternative means for rival assessment (such as individual recognition) may be necessary.

10.1.6 Male–Male Competition Among Northern Elephant Seals

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 breeding males. Because

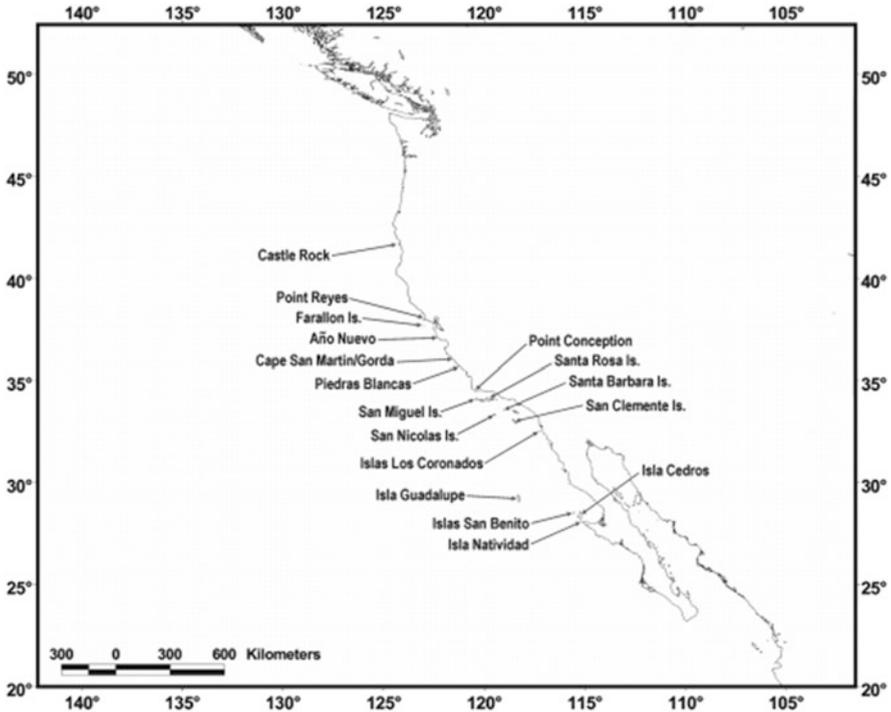


Fig. 10.1 Present locations of known northern elephant seal breeding colonies along the coasts of California and Mexico. Primary rookeries are located at San Miguel Island, San Nicolás Island, Año Nuevo, Point Reyes, the Farallon Islands, and Piedras Blancas (in California), and Isla Guadalupe and Islas San Benito (in Mexico) (from Lowry et al. 2014)

elephant seals congregate in predictable breeding locations each year, they enable the direct observation and close-range recording of acoustic displays emitted during competitive interactions, a detailed assessment of male dominance relationships, as well as the ability to experimentally test the significance of these calls to listening individuals. Additionally, the behavior of northern elephant seals has been studied extensively over the past several decades, providing the opportunity to ask both proximate and ultimate questions about communication and learning in this species.

Historic populations of northern elephant seals were rapidly and systematically extirpated along the coastline and offshore islands of North America beginning in the early 1800s to satisfy demand for rendered oil. More than 200,000 seals had been killed by the turn of the century, and the species was considered extinct by 1884. A small remnant population, rediscovered in 1911 on Isla de Guadalupe (150 miles from mainland Mexico), likely consisted of less than 20 individuals. Following the collapse of the sealing industry and subsequent protection by the Mexican government, these survivors enabled the population to recover to more than 210,000 animals, which can be observed each winter (December–March) at eight main island or mainland rookeries along the coasts of California and Mexico during the annual breeding season (Lowry et al. 2014; see Fig. 10.1).

The northern elephant seal is the largest seal in the northern hemisphere, with males weighing between 1500 and 2300 kg, and females reaching approximately one-third the size of males at 400–900 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. Mature males arrive at these annual breeding sites early in the season to establish their dominance status prior to the arrival of adult females. The status of males within this social network has previously been divided into descriptive ranks based on each individual's proximity to female harems throughout the breeding season: alpha males hold stable positions within female harems, beta males hold flanking positions relative to harems, and younger, peripheral males are totally excluded from access to females (Le Boeuf 1974; Casey et al. 2015). It is worth noting that there is no evidence that females exhibit selection with regards to competing males. Their behavior is driven more by suitable haul-out space than by proximity to dominant individuals (Le Boeuf and Laws 1994).

Subadult 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.

10.1.7 Acoustic Signaling in Male Northern Elephant Seals

While the position of males within the dominance hierarchy is initially established through physical confrontations on breeding rookeries (Le Boeuf 1974; Haley 1994), the majority of agonistic encounters between males are resolved through the use of ritualized threat displays (Le Boeuf 1974). These displays are composed of multimodal components including visual posturing that emphasizes body size; incredibly 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). These vocalizations are among some of the loudest recorded among any mammal in air, and can reach up to 131 dB re: 20 μ Pa (peak) (Southall et al. 2019). The vocalizations produced by males during their displays, traditionally called “clap threats,” contain 3–20 broadband units emitted at high levels with repetition rates of a few pulses per second (Le Boeuf and Peterson 1969). Individuals show reliable substructure within the repeatable units comprising the rhythmic portion of each call, which enables even a human listener to easily discriminate between individuals. These acoustic displays appear to

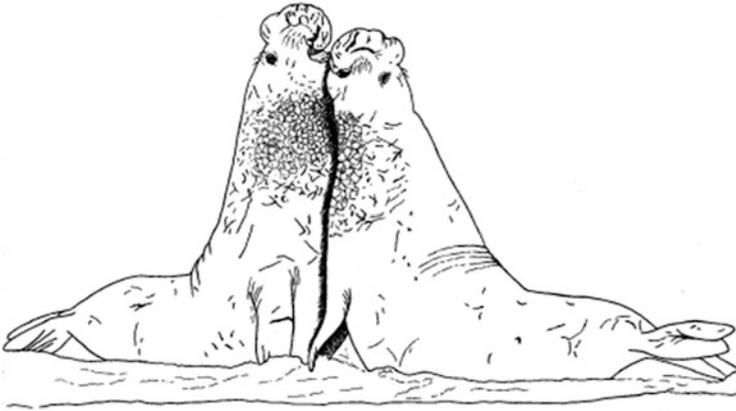


Fig. 10.2 Two equally matched adult male northern elephant seals engaged in battle at the beginning of the breeding season. Drawing by E. Levy

be of particular importance to male northern elephant seal, as calling males are often able to control the movement of rivals over large distances (Bartholomew and Collias 1962; Sandegren 1976), even under circumstances where visual cues are limited (Shipley and Strecker 1986). In over 8000 observations of competing males during multiple breeding seasons, over 80% of interactions involved vocalizations on the part of at least one of the males (Casey et al. 2015).

Throughout the breeding period, dominant individuals closely monitor the behavior of subordinate males who retreat from the vocal displays of their dominant rivals. Fighting is rare during most of the season (Cox 1981), presumably because of the effectiveness of communicative exchanges, the extreme energetic cost of engaging in battle during a prolonged fasting period, and the risk of serious injury or death (Le Boeuf and Laws 1994). Less than 6% of competitive interactions that occur between males involve physical contact (Casey et al. 2015). Battles only occur when repeated vocal exchanges are insufficient to end an escalating conflict, and neither individual retreats—typically between males who have not fought previously (Casey et al. 2015; see Fig. 10.2) and whose relative dominance status is uncertain (Bartholomew and Collias 1962).

Several investigators have noted individual differences in call characteristics between males within specific breeding sites (Bartholomew and Collias 1962; Shipley et al. 1981). This variation has been attributed to phenotypic traits and/or social dominance rank (Bartholomew and Collias 1962), as well as maturational effects (Schusterman 1978). Alternatively, it has been suggested that these signals function to convey individual identity and that males relate distinctive features of a threat call to a specific male through learned associations (Sandegren 1976; Shipley et al. 1981). Regardless of the potential function of male threat displays, several independent researchers have commented on the apparent stability of a male's vocalization both within seasons and across multiple years (Le Boeuf and Petrinovich 1974). Until recently, it was still unclear 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.

10.2 The Case for Identity Signaling in Male Northern Elephant Seals

Our research team has spent nearly a decade attempting to decode the signals of these giants at our field site at the Año Nuevo breeding colony in central California. During this time, we carefully monitored adult male elephant seals while ashore during the annual breeding season. Information about individual phenotype, fine-scale spatial use patterns, and pairwise competitive interactions was collected, cataloged, and combined with detailed analyses of their specialized acoustic displays. In essence, we determined who these individuals were, where they went during the breeding season, what they sounded like, and how successful they were at operating in their dynamic social network.

We took a comprehensive approach to this work, and individually identified subadult and adult males (using small plastic flipper tags and black hair dye) reliably seen at the Año Nuevo breeding colony study site (for details see Casey et al. 2015). We closely monitored their movements throughout the season, and observed male–male interactions to characterize where each male fell within the overall dominance hierarchy. With regard to vocal displays, we were interested in first determining the distinctiveness of each male’s call and which features of the vocalization were most stable within an individual. From our own experience, we found that a practiced human observer could accurately identify a male based solely on the temporal characteristics of his call. At the beginning of each breeding season, we were delighted when we heard the vocalizations of our favorite males (even before reading their identification tags) when they emerged from the water, as it meant they had survived another year at sea. For a subset of individuals that we were able to track both within and across seasons, we also assessed the reliability of these vocalizations across years and social contexts. We wanted to examine, for example, whether a male’s call would change in response to varying levels of perceived threat. Data pertaining to the size and dominance status of callers was then compared to the vocalizations produced by these males, to determine whether specific call parameters may be correlated with a male’s resource holding potential.

After an analysis of the calls recorded from multiple adult males within and between years, we found that the vocal displays produced by adult male elephant seals were individually unique (Fig. 10.3), with one temporal and one spectral call component sufficient to allow for accurate differentiation of individuals (Fig. 10.4). This analysis confirmed previous observations that there are notable and consistent differences in the calls of adult males, and these signals remain the same, even when emitted during different behavioral states (e.g., calling alone versus during a fight).

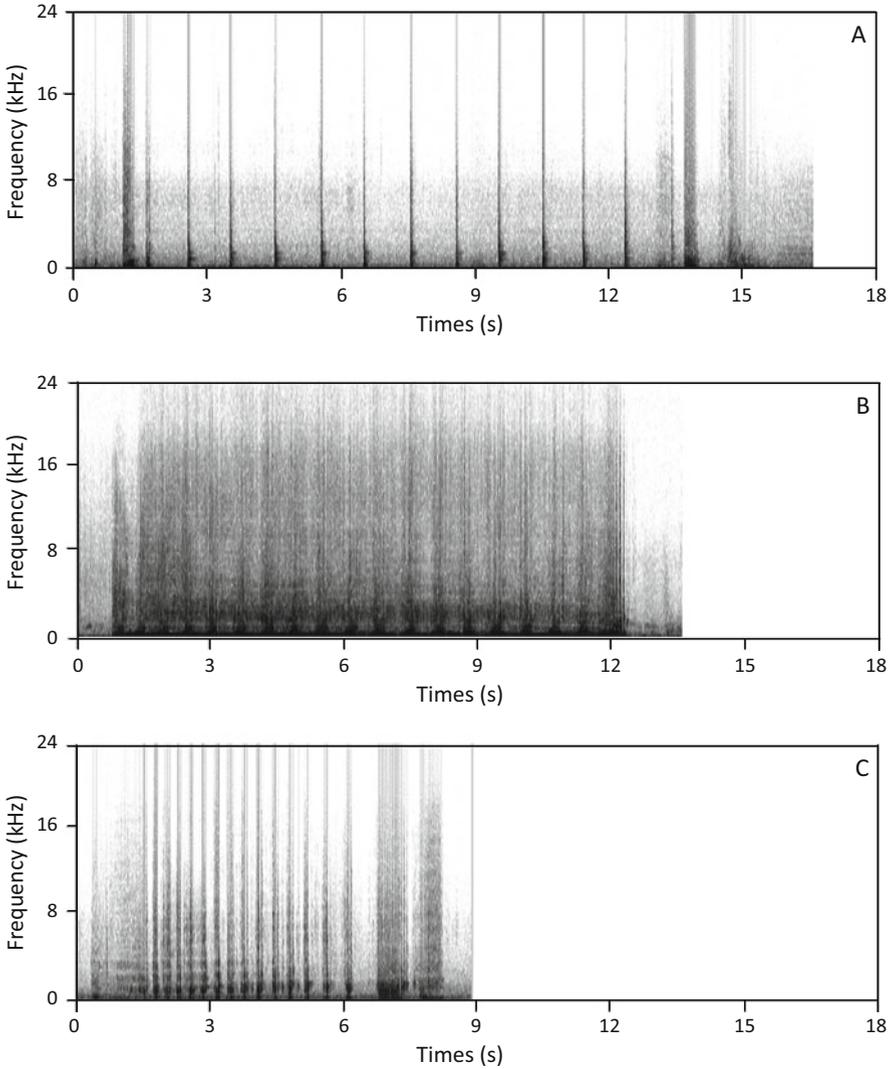
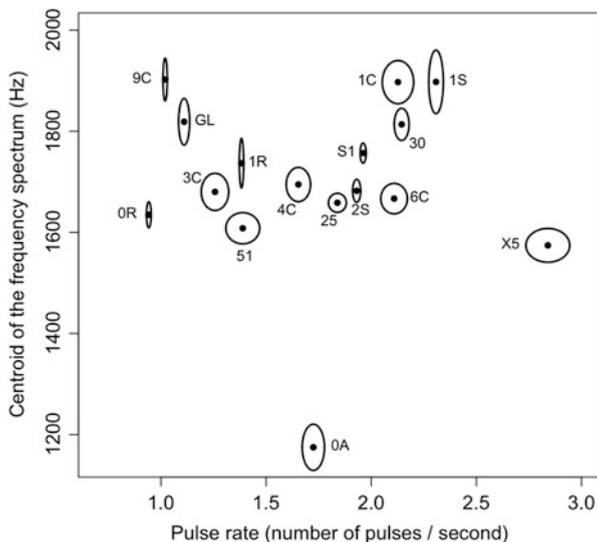


Fig. 10.3 Comparison of representative vocalizations produced by three adult male northern elephant seals of equal dominance status within the hierarchy at the Año Nuevo breeding colony. All three calls were recorded at 0-degree orientation and within 10 m of the vocalizing animal. Spectrograms using a Hamming window and 90% overlap are provided for Male 3C (Panel A) Male 10A (Panel B) and Male X579 (Panel C); sampling rate 24 kHz, FFT size 256

Each call appears to be composed of a series of repeating units, which is perceived by human listeners as the tempo of the vocalization. Within these repeating units, some males exhibited substructural components that help to acoustically differentiate individuals. In agreement with previous observations of this species, we also

Fig. 10.4 Calls can be reliably assigned to individuals using two acoustic parameters (mean \pm 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). Adapted from Casey et al. (2015)



discovered that the calls (including call amplitude) produced by adult males are stable across multiple seasons. The repetitive nature of these high-amplitude calls may potentially aid in signal detection in high density social environments. One of our study males produced a call with a peak sound pressure level reliably measured to be 140 at 1 m, which is one of the loudest sounds ever recorded among mammals (Suer et al. 2011). Interestingly, despite his call amplitude, this individual was not particularly dominant within the hierarchy and spent the majority of his time on the outskirts of a harem held by another adult male.

While we observed a great deal of variation between the calls of adult males, and a range of social ranks among breeding individuals, we found no correlation between the kind of call a male exhibits and his dominance status. For example, the calls illustrated in Fig. 10.3 were all produced by alpha males from different harems recorded at the Año Nuevo breeding colony in 2011.

The variation in call structure between individuals and the stability of calls within males over time supported the hypothesis that these calls function as identity signals that males must learn and subsequently remember throughout the breeding season (Fig. 10.3). The presence of vocal signatures by itself, however, was not sufficient to illustrate that social recognition does indeed occur within this complex social system (Insley et al. 2003). The role that learning plays in the social lives of males can only be investigated with a clear experimental approach during which the level of an individual's experience with the caller is systematically assessed. To address this, the results of our vocal analysis were then applied to two field playback experiments that tested predictions about whether these unique signals effectively function to convey individual identity.

In the first set of playback experiments we targeted 10 beta males reliably present at the Año Nuevo study site. We first sought to determine whether the acoustic



Fig. 10.5 Playback configuration in the field testing each male’s responsiveness to the calls of familiar rivals. The focal animal receiving the playback is circled, and the playback speaker is positioned ~7 m away from, and on axis with, the target animal. Researchers are positioned outside of the direct line of view of the male of interest, and are able to initiate the playback remotely

portion of this multimodal display was enough to elicit a behavioral response from the receiver, as suggested by observations of males retreating from or challenging rivals when visual cues are limited. In other words, we asked “can vocalizations alone substitute for callers themselves?” We also wished to explore whether the calls of known rivals would prompt differential responses depending on relative dominance status between the caller and receiver. For these experiments, each of the 10 target males received the playback of their most familiar dominant and subordinate rival, and their behavioral response was recorded and compared to observations of these interactions under natural conditions (Fig. 10.5). These subordinate and dominant treatments were selected based on our own observations in the field. The results of these experiments confirmed our observations that males would respond differentially to the calls of their familiar subordinate and dominant rivals. In these experiments, 75% of the animals exhibited a behavioral response to the playback condition, and of those that responded, 86% did so in the predicted direction—i.e., males exposed to their most familiar dominant rival retreated from the speaker, and those exposed to their most familiar subordinate rival attacked the speaker.

In a second set of playback experiments performed at a distant breeding location, we examined whether previous experience with the caller was necessary to elicit a behavioral response from the animal that was listening. In these experiments, we traveled to the Piedras Blancas breeding colony located 480 km south of the Año Nuevo breeding location. We observed the social interactions of competing males at this site, and selected 10 beta males to receive the same subordinate and dominant treatments given to individuals at the Año Nuevo colony. The only difference between these two conditions is that males from the Piedras Blancas breeding colony

had never interacted with the individuals whose call they were being presented. In these experiments, only 15% resulted in the male responding to the playback stimuli at all, and only two in the “predicted” direction. In the majority of cases the males attended to the sounds being produced by the playback speaker, but did not exhibit a retreat or approach response, but instead opted to stay put where they were with no measurable change in body position relative to the playback speaker.

The results of these experiments demonstrated that the vocal component of male multimodal displays is enough to elicit a behavioral response from the receiver, suggesting that the calls themselves can functionally substitute for the individual during agonistic interactions. Furthermore, when presented with the playbacks of familiar dominant and subordinate associates, males were able to discriminate between the vocalizations of known individuals and respond appropriately based on the relative dominance status of the caller. In order for the playback to encourage a significant response from the animal being tested, however, it appeared that each male must have had prior experience with the individual whose call he was receiving. Males with no prior experience with a caller exhibited little response to playbacks, confirming that males do not respond to phenotypically linked information within the construct of the call, but rather associate variation in call structure with the consequences of previous challenges with familiar rivals. This does not mean that the males exposed to unfamiliar calls were indifferent; rather, their responses could 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. In these cases, males may require additional information about their opponent before deciding to attack or retreat.

Clearly, there is important information contained within the calls of individuals, but are males truly capable of discriminating slight differences in two main parameters that acoustically separate these signature calls—pitch and rhythm? We explored this question through a follow-up set of playback experiments, during which we experimentally modified the most distinctive characteristics of the vocalizations of familiar dominant rivals and then tested how this influenced a male’s responsiveness to playbacks of these signals (Mathevon et al. 2017). We tested 10 beta males with a range of calls that had been altered with respect to both tempo and pitch, the two acoustic features of the vocalizations that were most reliable within individuals (Casey et al. 2015, Fig. 10.4). Some of these alterations were within the normal range of intraindividual variation, while others fell outside of this range. The playbacks revealed that both the natural calls and the experimental calls from dominant individuals that were modified within the range of typical intraindividual variation elicited expected retreat behavior from tested males, indicating that they were still able to recognize these familiar contestants. Conversely, the experimental calls with alterations outside of this range (but within the range of the population) were ignored by the tested males (Mathevon et al. 2017). This finding is consistent with previous observations of the natural behavior of males in

response to calls from familiar dominant versus unknown rivals. While the use of spectral features for individual discrimination has been found in a number of mammals including pinnipeds (Aubin et al. 2015; Charrier et al. 2003), the northern elephant seal is the first mammal species shown to learn, remember, and use sound metrical patterns across a wide range of tempi in a biologically representative context (Mathevon et al. 2017).

10.3 The Social Conditions that Support Individual Recognition in Northern Elephant Seals

Clearly associative learning plays an important role in this system, and males must learn the calls of their rivals in order to optimize energy conservation. What specific social conditions might encourage this kind of signaling strategy? During male–male competition over access to mating opportunities, the use of individually distinct vocalizations should occur in a system where individual recognition is more informative and less costly than a system based on vocalizations conveying only information about one’s size or fighting ability. Male northern elephant seals must therefore have the opportunity to not only learn the distinctive call characteristics of their most familiar competitors, but also have sufficient experience with their rivals for these cues to become meaningful. These behavioral patterns should be influenced by ecological conditions at the breeding site, including availability of suitable haul-out space, which in turn influences the distribution of seals within the colony. A communication system based on a competitor’s ability to learn and remember these identity signals should be expected to exhibit the following social and environmental conditions: (1) males returning to the same general location on the breeding beaches each year (fine-scale site fidelity), (2) a strong degree of familiarity between rivals, and (3) the use of reliable acoustic signatures during competitive interactions that have predictable outcomes.

10.4 Fine-Scale Site Fidelity of Male Northern Elephant Seals

Fine-scale site fidelity constitutes an important structural component in animal social networks, as it sets limits to the space over which social interactions can occur and provides the opportunity for repeated interactions between group members (Wolf et al. 2007). While loyalty to a particular breeding colony has been broadly considered for both sexes, details pertaining to fine-scale site fidelity within the colony (both within a season and throughout an animal’s lifetime) among male elephant seals remain sparse. Male tenure within a breeding season has been broadly considered, and roughly 20% of the males within one colony remain until all the females

have departed (Le Boeuf 1974). Additionally, dominant males have been reported to be successful breeders for up to three consecutive years (Le Boeuf 1974) at the Año Nuevo breeding colony, indicating some level of fidelity to a specific breeding location.

While there has historically been less of an emphasis on tagging males within the Año Nuevo population, recent improvements in our ability to track individual males have enabled us to follow focal individuals across multiple years. As a consequence, we now know that the majority of our study males return to the same breeding colonies between seasons. This development offers an incredible opportunity to explore the behavioral strategies that males exhibit across different age classes during breeding events, which may ultimately lead to their reproductive success later in life. Of the 11 alpha males we observed during the 2016 breeding season for example, 10 had been observed at the Año Nuevo breeding rookery in prior years. Additionally, all of them arrived early in the breeding season relative to other males, and stayed until every last female departed to sea. We often witnessed successful males return after their foraging trips to within 5 m of the location where they had been seen during the previous year, even before any females arrived at these breeding beaches. Once individuals have reached sexual maturity (between 4–6 years of age), males may avoid moving to new breeding sites, as they may need to fight to establish a new position within an unfamiliar dominance hierarchy.

One of our most well-studied individuals at Año Nuevo provides an example of the level of insight these kinds of detailed observations can provide. Timmy (tag number U46) was born during the 2008 breeding season and was immediately abandoned by his mother. He was subsequently nursed by another female, and was successfully weaned at the end of the season although he was below the average weaning weight. Since 2008, Timmy has been sighted at the breeding colony each season. As a subadult he was observed drifting between locations around the colony and was always seen on the perimeter of groups of females. During the 2015–2016 season (at the age of 7), he began to compete more directly with older, more dominant individuals, and was consistently observed near a single harem interacting with an established group of adult males. Although he lost nearly every fight he instigated in the winter of 2016, he was noted as being a very motivated and energetic individual, often getting chased out of the harem by a more dominant male only to turn around and try his luck again. During the 2017 breeding season, Timmy returned to the same area he was in the previous year, and quickly asserted his dominance and controlled access to a small group of females for approximately one month. He was later displaced by a larger individual, and yielded to holding a beta position within the hierarchy for the remainder of the season. We hope that Timmy will return to Año Nuevo next year, and perhaps finally attain his alpha status on the rookery. Ultimately his success in becoming dominant may be related to prior knowledge and ability to navigate the complex social network of male northern elephant seals. Although anecdotal, Timmy's story provides some insight into the different behavioral strategies that enable a male to one day achieve breeding opportunities as an adult, and has motivated our

research team to continue to track focal individuals throughout their lifetimes. These kinds of observations suggest that males are operating in a stable, complex social environment that is conducive to the emergence of individual recognition and associative learning.

10.5 The Social Network of Male Northern Elephant Seals

The stability of male seals in time and space will influence the number of social partners that an individual interacts with within and across breeding seasons, and the strength of association and familiarity between rival males. Paired with associative learning capabilities that allow individuals to link acoustic signatures to predictable social consequences, the use of reputation signals may produce an evolutionary stable strategy within the context of dominance interactions in familiar social groups. Additionally, signal design is likely influenced by the number of individuals a male must discriminate between. In our study, individual male elephant seals were observed to engage with as many as 43 opponents over the course of a single breeding season. While the relationship between signal and social complexity still remains to be investigated in this species, small differences between individuals in call substructure likely aid in this process. Through close observation of males within and between breeding seasons, we have been able to characterize important details of this dynamic social network.

A male's success within this social system depends on managing knowledge of his relative dominance status compared to others within the hierarchy. While the Año Nuevo colony in California has approximately 400 breeding males that may be present across an ~ 3 km² breeding area, the site is divided into 11 evenly distributed stable harems, each with anywhere between 50 and 150 adult females and their pups. One alpha adult male (age 8–11 years old) controls access to a single harem throughout the season, while beta males (most of whom are 7 and older) sit on the outskirts of these groups awaiting the perfect time to attempt to breed with one of the females while the alpha is not looking (Fig. 10.6). Over the course of one breeding season, we observed alpha males maintaining stable relationships with an average of 38 other individuals (Casey et al. 2015—Fig. 10.7). Alpha males must learn to balance their time between vigorously defending their harems and also breeding with females, while minimizing energy and water loss during periods of extended fasting. The defensibility of the alpha male's harem varies with the density of females, as larger harems become increasingly more vulnerable to infiltration by other individuals (Le Boeuf and Laws 1994).

The costs of overexertion are evident in observations of males ascending to the peak of the social hierarchy early in the season, only to be overthrown by their close competitors after engaging in excessive chasing and fighting. However, this is not to say that these individuals are incapable of returning in subsequent seasons to resume their position as top males within the hierarchy; we observed one male who was ousted half-way through the breeding season by two beta males, only to come back the following year to reign again as alpha at the same harem. It is important to note

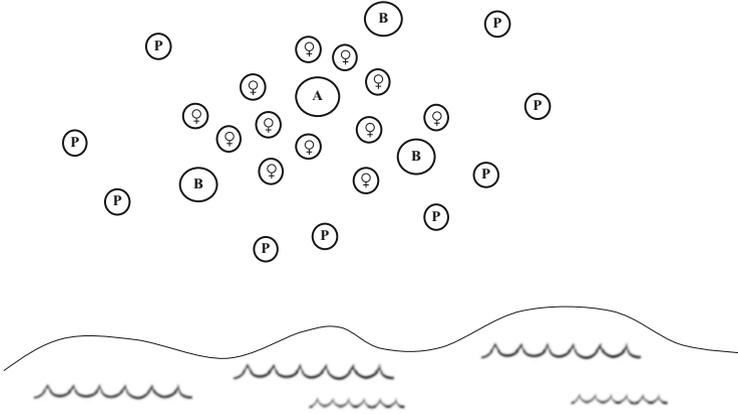


Fig. 10.6 Aerial schematic of a typical harem. The “A” dot represents the alpha male, who is positioned in the center of a group of females, and is surrounded by several “B” dots, representing beta males. Peripheral males (P dots) remain on the outskirts of the harem without access to females



Fig. 10.7 An example of the social network of northern elephant seal males. Bottom row of larger dots = alpha males and corresponding names that controlled female harems over the season; second from bottom dots = beta males that reliably held harem flanking positions with opportunistic access to females; top two rows of lighter dots = peripheral males that typically lacked access to harems. Each arrow represents an 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. Adapted from Casey et al. (2015)

that in this case we observed no change in the call characteristics emitted by this individual—further indicating that the calls of adults do not change relative to their fighting ability. Substituting fighting and chasing with calling may represent the most efficient strategy for avoiding harm and conserving energy in a system where the costs associated with excessive activity may have unfavorable consequences for individual reproductive success.

Beta males display a number of different strategies in pursuit of breeding opportunities throughout the season. Some individuals attempt to tire the alpha through continual harassment, while others tuck their noses under and slink across the sand and into the harem to mate with females while the alpha is asleep or distracted. We have even seen beta males sleep through the first half of the season in a nearby sand dune, and then attempt to overthrow the nearest alpha who had already exhausted much of his energy reserves. An alpha's harem is most susceptible to beta males toward the end of the season when females begin to depart to sea. As females are leaving the harem and approaching the shoreline, they must somehow evade dozens of subordinate males that are eagerly waiting for their opportunity to finally mate. This process is incredibly dangerous for females, as hormonally crazed beta and peripheral males will fight relentlessly around her as she attempts to run this dangerous male gauntlet. Indeed, we have witnessed females who are crushed to death as multiple males attempt to mate with her during this process. Some alpha males will escort females to the waterline to prevent subordinate males from copulating with her during her departure, which leaves his harem vulnerable to lurking betas. This is often the period where we witness beta males attain the most breeding success during the season, as alpha males are already exhausted and cannot escort females and guard their harem at the same time. There is obvious variation in the behavioral tactics of males, and this topic warrants further investigation in relationship to reproductive success.

What is clear from these observations is the level of familiarity between alpha and beta males, which provides individuals with the opportunity to learn the distinctive features of their closest competitor's calls during agonistic interactions. These relationships are stable both in association and the space over which they occur. In addition to constantly jockeying with one another for prime positions relative to female groups, beta males also spend a great deal of time chasing away peripheral males (ages 4–7 years old) from the harem. A smart alpha male may have a few familiar beta rivals he tolerates near his harem, and in turn those beta males indirectly assist in keeping away peripheral individuals (Fig. 10.6). Over a single season, we observed beta males maintain stable relationships with an average of 26 other individuals (Casey et al. 2015—Fig. 10.7).

Peripheral males rarely ever infiltrate these female groups, and show far less spatial stability within the colony compared to both alphas and betas. While higher ranking individuals can be consistently seen in association with one harem throughout the season, these peripheral subadults tend to float around the colony, loosely associated with different social groups. Interestingly, studies of male development have noted that younger animals rarely vocalize on the rookery during the height of the breeding season, as their activities are closely monitored

by older individuals. Additionally, the calls of juveniles appear to be highly variable, and show particular instability with regard to call structure and pulse rate (Shiple et al. 1986). While it would be challenging for listeners to associate these unstable calls with known individuals, this may actually be advantageous for subadult males. If you are a loser, you may not want to be remembered! This could be advantageous to subadult males, who rarely win competitive contests and so might wish to remain acoustically inconspicuous until they have a fair chance at competing for reproductive access.

Notably, more than 97% of relationships observed between males over the course of a single breeding season were fully asymmetric (i.e., the interactions within a given dyad of males were always won by the same individual). These dyads are thus characterized by well-established “dominant–subordinate” relationships, illustrating the stability of the hierarchy between males (Casey et al. 2015). These observations support the existence of a communication system based on learning, in that the consequence associated with an individual’s call is predictable within a given season. As individual vocal signatures remain stable over successive years and the majority of males appear to return to the same breeding-beaches annually, 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. Alternatively, previous dominance status may have no bearing on these social relationships at the beginning of a new season, and one’s competitive ability may be based on a number of factors such as foraging success and/or individual motivation. Given the strong association between males within and across seasons, multiyear recognition of rivals warrants further investigation in this species.

10.6 Vocal Ontogeny of Male Acoustic Displays

Despite many years of study, little is known about the ontogeny of northern elephant seal male vocal displays within an individual, and whether they are genetically based or shaped by auditory experience. Early work noted that the calls of juvenile males are more variable than those of adults (Shiple et al. 1986), suggesting that males go through a transitional period during development in which their calls lack the characteristic structure of adult males. This draws certain parallels to the ontogeny of passerine bird songs, in which the vocalizations produced by juveniles are a highly variable version of the adult repertoire, and then undergo a crystallization period and become relatively fixed beyond a certain age (Marler and Peters 1982). Studies of song development in passerine birds have shown that a common feature of vocal development includes a stage of babbling—characterized by overproduction and variability in structure—that is regarded as a “training” and a motor phase during which individuals have the opportunity to develop their own calls in relationship to the acoustic signals of adults (Snowdon and Hausberger 1997). We often observe subadult male northern elephant seals producing calls in social isolation from the

harem and in a nondirected context, and that are highly variable in frequency, duration, and amplitude. The urge to produce these calling bouts appears to be hormonally driven, and can last for hours if uninterrupted. While it is difficult to tease apart the environmental and genetic influences shaping sound production, the northern elephant seal presents a particularly intriguing model. These seals exhibit a deficit in genetic variability due to human-induced population decline and subsequent inbreeding (Hoelzel 1999), which could allow for potential isolation of genetic factors contributing to vocal ontogeny. Further studies are required to determine the extent to which learning and the acoustic environment shape the development of these specialized acoustic displays, and the exact timing of call crystallization in this species.

10.7 Conclusions

The behavior of animals is best observed under natural social conditions; however, unraveling the information that is encoded within acoustic signals, and understanding how individuals use this information to adjust their behavior during social encounters, presents several challenges. Recent studies have correlated acoustic features with phenotypic traits and/or the ability to convey individual identity (Sanvito et al. 2007); however, few studies in mammals have confirmed the biological function of these signals through systematic experiments that evaluate the 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 test the capacity of an individual to discriminate between the calls of conspecifics (Sayigh et al. 1999). This type of work is often prohibitively difficult, as it requires the ability to follow target individuals over time, extensive knowledge of the social relationships between individuals within a breeding group, detailed analysis of acoustic displays, and the opportunity to conduct playback experiments with focal animals. Despite the logistical challenges, these combined approaches are critical to understanding the role that recognition and learning play in mediating competition between individuals, and may provide insight into the social conditions driving the development of communication strategies among different animal groups. Given the growing interest in status signaling and selective pressures influencing the structure of animal social networks (Bergman et al. 2003; Charlton et al. 2011; Taylor et al. 2010; Ilany et al. 2013; Arnott and Elwood 2009), future studies should combine both descriptive and experimental methods to gain a true understanding of the information gained by listeners during social exchanges.

From a comparative perspective, our most comprehensive understanding of vocal communication comes from studies of passerine birdsong. Detailed field observations have been paired with careful laboratory experiments to address questions of mechanism, ontogeny, function, and phylogeny of vocal signaling in several songbird species (Konishi 1989). This holistic approach has resulted in birdsong being

regarded as a model system for understanding the evolution of acoustic communication across several animal taxa, including those distantly related from birds. However, as these species operate in different social environments and display a wide diversity of acoustic signaling, it seems evident that we should continue to search for new models for cross-species comparisons, so that we may understand the relative importance of acoustic signaling across varying evolutionary landscapes.

The northern elephant seal has presented us with a remarkable opportunity to understand the role that sound plays in the reproductive behavior of mammals that rely on sound during important life history events. Calls can be easily recorded and attributed to known individuals and linked with specific behaviors; individuals can be followed throughout their vocal (and physical) development; and the function of different sound types can be experimentally tested and manipulated using playback experiments. Through this work, we have been able to decode the information contained within the specialized calls produced by males, and evaluate the role that learning plays during this process. What is notable about this system is the complexity of the social relationships between males, the ability of individuals to use this information, and the stability of these social relationships in time and space. As is usually the case, our findings have opened the door to several new questions pertaining to memory, development, and how these signals may have been influenced by this species' dramatic population decline and recovery from near-extinction. Future research focused on this species will continue to afford a detailed comparative framework for studies of acoustic communication in other mammalian species.

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