

Lifelong Patterns of Sound Production in Two Seals

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Abstract

Despite the important role that vocal communication plays in the social lives of nearly all mammals, few studies have documented the emergence and development of acoustic behavior within individuals throughout their lifetimes. It is even less common to examine learned vs innate aspects of vocal development in long-lived mammals. In this study, we routinely monitored spontaneous vocalizations produced by a male Pacific harbor seal (*Phoca vitulina*) and a female northern elephant seal (*Mirounga angustirostris*) raised in human care without conspecific individuals for more than 18 years. We used these unique longitudinal datasets to assess whether the call characteristics of captive individuals resembled those of wild conspecific seals. Additionally, we marked the developmental onset and seasonal timing of vocal activity to determine whether initial vocal expression coincided with reproductive maturity and to evaluate whether temporal patterns in vocal activity were similar across years. We found that resemblance of vocal behavior to that of wild individuals varied between subjects. Both seals showed appropriate maturational timing of vocal behavior associated with reproductive status. The male harbor seal showed a species-typical template for vocal production, whereas the female northern elephant seal produced calls with structure that differed considerably from those of wild individuals. These two case studies provide information relevant to ongoing studies on the ontogeny of sound production and the role that learning plays in vocal behavior.

Key Words: acoustic ontogeny, breeding behavior, vocal learning, vocal development, pinniped

Introduction

Vocal communication is central to the social lives of many animals, and the study of vocal behavior informs our understanding of breeding, foraging,

and parental care, as well as other important aspects of life history. In non-human mammals whose vocal behavior is well documented, juvenile exposure to varying environmental conditions has been shown to influence acoustic signaling during adulthood in some cases (McCowan & Reiss, 1995; Vergara & Barrett-Lennard, 2008; Snowdon & Elowson, 2011; Prat et al., 2015). However, the ways in which individuals attain the repertoire of sounds they produce and the extent to which learning influences vocal ontogeny have remained difficult to evaluate in long-lived species.

Among mammals that rely on acoustic communication, phocids (true seals) offer a promising yet understudied model to investigate vocal repertoire acquisition (Schusterman, 2008; Reichmuth & Casey, 2014; Ravnigani, 2018). Seals emit a variety of sounds in air and under water, with several vocalizations known to have specialized functions related to individual recognition or reproductive displays (Insley et al., 2003; Schusterman & Van Parijs, 2003; Reichmuth & Casey, 2014). In captive settings, some individuals have shown plasticity in their capacity to modify vocal behavior and sound production, learning to emit and inhibit species-typical vocalizations in response to conditioned cues (e.g., hand signals) and to produce novel variants of calls or call sequences (see Reichmuth & Casey, 2014; Stansbury & Janik, 2019). In one rare instance, a captive seal was shown to imitate components of human speech (Ralls et al., 1985). In the wild, some seal species exhibit geographic variation in vocal behavior, which is suggestive of acquired regional dialects (Le Boeuf & Peterson, 1969; Thomas & Stirling, 1983; Morrice et al., 1994; Terhune, 1994; Risch et al., 2007). Taken together, these observations support the notion that some seals may be capable of modifying their sound production as a result of social experience.

Although vocal behavior is important in the lives of seals, few studies have evaluated sound production throughout development and

maturation. Assessing the ontogeny of vocal behavior in wild seals is challenging as logistical and technical constraints make it difficult or impossible to track free-ranging individuals over large areas for long periods of time. A promising opportunity to determine how the vocalizations of individuals change throughout development is to document vocal behavior in captive animals reared in relatively controlled social environments. Such efforts have been productive in bioacoustic research with long-lived marine mammals (e.g., Bowles et al., 1988; McCowan & Reiss, 1995; Davies et al., 2006).

The emergence, annual patterning, and reliability of individuals' acoustic signals can be monitored within stable zoological environments with known social exposure. If the expression and development of species-typical vocalizations depend on input from one's social and auditory environment (i.e., an acoustic template), then the absence of conspecifics should result in the production of atypical calls (Janik & Slater, 1997; Tyack, 2016). Alternatively, if changes in the vocal behavior of an individual are due simply to maturational processes, then acoustic isolation from species-typical calls should have little influence on lifelong vocal expression (Janik & Slater, 1997; Boughman & Moss, 2003; Egnor & Hauser, 2004).

Here, we describe vocal development in two phocid seals: (1) a male Pacific harbor seal (*Phoca vitulina*) and (2) a female northern elephant seal (*Mirounga angustirostris*). Both individuals were reared in controlled settings with limited exposure to other captive pinnipeds and without significant exposure to conspecifics. Their acoustic behavior was monitored and recorded from early development (< 1 y old) throughout adulthood, over periods spanning 29 and 18 y, respectively. Our primary aim with this unique longitudinal dataset was to document the emergence, seasonal patterning, and long-term expression of vocal behavior in these individuals. Additionally, given growing interest in evaluating how vocal parameters relate to body size (e.g., Reby & McComb, 2003; Fischer et al., 2004), we assessed whether specific acoustic parameters changed with increasing age and mass. Finally, we sought to determine the extent to which sound production in these captive individuals resembled that of wild seals given the absence of social interaction with members of their own species.

Case Study 1 – Pacific Harbor Seal

Species Background

Harbor seals are one of the most widely distributed pinniped species and occur throughout temperate to Arctic coastal regions of the Northern Hemisphere. Pups are born in spring, and the period of maternal

dependency lasts for approximately 1 mo before weaning (Teilmann & Galatius, 2018). Dependent pups produce airborne calls to elicit attention from their mothers (Renouf, 1984)—these calls are individually distinctive based on frequency modulation (Renouf, 1984; Perry & Renouf, 1988; Khan et al., 2006). Although mature females do not emit attraction calls (Insley et al., 2003), it appears that mothers can recognize the calls of their filial pups (Renouf, 1985; Sauve et al., 2015). After weaning, young harbor seals remain relatively silent except for guttural threats produced on terrestrial haulouts. Adults breed annually following birthing and prior to molting in summer. During the breeding season, males establish hierarchies and defend aquatic territories through the use of fighting, chasing, and repetitive underwater acoustic displays (Sullivan, 1981; Van Parijs et al., 1999; Hayes et al., 2004). While it is difficult to confirm the role that vocalizations play in reproductive behavior—since both breeding and territory defense take place beneath the water's surface—these calls are believed to function in male-male competition during the mating season (Hanggi & Schusterman, 1994; Coltman et al., 1997; Hayes et al., 2004).

The most common underwater vocalization produced by mature male harbor seals is the *roar*, a predominantly low-frequency, broadband growl with peak frequency between 400 and 800 Hz and a duration of 2 to 8 s (Hanggi & Schusterman, 1994). Roars have been described as having little tonal quality and consist of at least two distinct phases: (1) a relatively quiet and gradually building pre-roar and (2) a louder, harsher pulsed component. While the exact developmental timing of the male roar is unknown, its emergence likely coincides with the onset of sexual maturity which occurs at 5 to 7 y of age (Bjørge, 1992). Roars appear to be highly stereotyped within an individual but show variation in structure, duration, and amplitude between different seals (Hanggi & Schusterman, 1994) and breeding populations (Van Parijs et al., 1999). During the breeding season, male harbor seals emit roars at highly regular rates in a submerged vertical body posture, surfacing only briefly to breathe before submerging again to resume their repetitive calling (Van Parijs et al., 1997, 2003).

Limited observations found that younger males may produce shorter, higher-frequency roars, which become longer in duration and lower in frequency with maturation (Nicholson, 2000). On this basis, Nicholson (2000) suggested that acoustic parameters of male harbor seal calls could serve as honest signals to convey a male's physical quality such as age, size, or health. Field experiments conducted by Hayes et al. (2004) have generally supported this idea.

Subject

The subject of the first case study was a male Pacific harbor seal identified as “Sprouts” (NOA0001707), who was born in captivity at SeaWorld San Diego in April 1988. He remained with his biological mother in an enclosure with other harbor seals for the first 9 mo of his life. His potential exposure to conspecific vocalizations during this time is unknown. Sprouts was subsequently transferred to Long Marine Laboratory at the University of California Santa Cruz when he was less than a year old. He lived at this facility in outdoor saltwater pools with available haulout space from his arrival in 1989 until his death at age 32 in 2020. Sprouts lived with female California sea lions (*Zalophus californianus*) but had no exposure to conspecifics. He was fed a daily diet of freshly thawed fish, and his body mass was determined weekly by weighing on a calibrated platform scale (± 0.1 kg).

Sprouts produced both spontaneous and conditioned vocalizations during his lifetime. At age 5, he was trained to emit an airborne *growl* vocalization through selective reinforcement. This growl was placed under stimulus control and became part of his training repertoire. When he was 17 y old, Sprouts was further conditioned to emit variations of this airborne vocalization to explore the degree of flexibility in his vocal behavior (for a review of this work, see Schusterman, 2008). His vocal training occurred only in air and did not appear to influence his natural underwater sound production. Description of his lifelong spontaneous underwater vocal behavior is the focus of this article.

Methods

Observations—From ages 1 to 6, qualitative behavioral records were maintained that included notations of vocalizations and associated breeding behavior. The timing, duration, and intensity of the harbor seal’s spontaneous underwater vocalizations were recorded daily by trained observers using all occurrence sampling from 6 to 29 y of age (Altmann, 1974). Underwater vocalizations were noted as either being “present” or “absent” for each day. If present, they were categorized as “mild” (~5 calls), “moderate” (~5 to 30 calls), or “intense” (~30+ calls during both day and night). Throughout his lifetime, husbandry records included descriptions of behaviors and postures associated with spontaneous underwater vocalizations.

Recordings—Representative acoustic recordings of this seal’s spontaneous underwater vocalizations were obtained for most years between late March and early July, coinciding with the peak breeding season for wild harbor seals in northern California (Temte et al., 1991). These recordings were collected

opportunistically at close range (< 5 m) with a stationary hydrophone mounted in a circular, partially in-ground pool (1.8 m deep; 7.6 m diameter). Nine different recording configurations were used throughout the 19-y study period (for equipment details, see Supplementary Table 1A; supplemental tables and audio files for this article are available in the “Supplemental Material” section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). Efforts were made to minimize background noise by reducing water flow and ensuring that no other individuals were present in the pool during recordings. While recording distance and orientation varied depending on the seal’s location within the pool, the subject’s position relative to the hydrophone was noted for each call.

Analysis—Recordings obtained during 1998 to 2001, 2004, and 2007 to 2017 were analyzed for this individual (ages 10 to 13, 16, and 19 to 29, respectively), and calls were qualitatively compared to published acoustic parameters for wild harbor seals (summarized in Supplementary Table 2A). Only complete vocalizations where all parameters of the spectral contour could be identified were selected for subsequent analysis. Recordings were analyzed using *Raven Pro*, Version 1.4 (Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY, USA). Eight vocal parameters were measured in the spectral and temporal domains: (1) 90% call duration (s), (2) duration of the pulsed portion of the call (s), (3) number of pulses, (4) dominant frequency over the 90% call duration (Hz), (5) Q1 frequency over the 90% call duration (Hz), (6) center frequency over the 90% call duration (Hz), (7) Q3 frequency over the 90% call duration (Hz), and (8) dominant frequency over the pulsed portion of the call. The 90% call duration was selected for this analysis because it is less susceptible to measurement error when compared to total duration. Temporal parameters were always measured from the waveform, and spectral parameters were measured from the spectrum or spectrogram. While the mode may provide a more representative estimate of these measurements for such broadband calls, we report the mean for each variable for each year to enable comparison with published data. For those metrics where mean values were published for wild harbor seals, we evaluated whether Sprouts’ call parameters fell within the reported range. For details pertaining to acoustic analysis parameters, see Supplementary Table 1A.

To evaluate whether this individual exhibited species-typical maturational timing and annual seasonal patterns of acoustic signaling throughout his lifetime, age at initial emergence of spontaneous underwater vocalizations was determined, as

was the seasonal timing of vocal activity. To evaluate whether spectral and/or temporal acoustic features were linked to this subject's body mass or age, we performed a simple linear regression analysis ('lm function' in *R* statistical package; RStudio Team, 2020). Additionally, an analysis of variance (one-way ANOVA) was used to assess the stability of measured call variables of the roar vocalization across years (*GraphPad Prism*, Version 9.0.0).

Results

Description of Roar Vocalizations—The spontaneous underwater calls produced by this harbor seal were predominantly low-frequency, broadband roars with average 90% duration of 3.6 s and 90% frequency bandwidth from 121 to 1,664 Hz (Table 1; Figure 1A-C). These calls ascended in amplitude over their duration, evoking the impression that the vocalizing animal was approaching the listener (i.e., a looming effect). The highest amplitude component of the call occurred in the terminal, pulsed portion (0.9 s) in which Sprouts emitted three to eight brief pulses in rapid succession (Figure 1A-C). While the mean value for all call features measured varied significantly across years ($p < 0.0001$ for all comparisons), the overall duration and structure of Sprouts' call—an ascending roar with multiple terminal pulses—remained stable over time (Figure 1A-C). His vocalizations were qualitatively similar to the underwater roars described for wild harbor seals (Figure 1D-E; Supplementary Table 2A & Supplementary Audio 1); and when compared to published values available for similar call parameters, the mean values obtained from Sprouts' calls fell within the reported range (Supplementary Table 2A). Furthermore, Sprouts demonstrated the characteristic display behavior exhibited by his wild counterparts (Sullivan, 1981; Hanggi & Schusterman, 1994). He would submerge his body in a vertical position with his head arched back and protracted while vocalizing and blowing bubbles.

Temporal Patterning—This seal began to produce stereotyped underwater vocalizations at age 6, the timing of which coincides with the onset of sexual maturity in wild male harbor seals (Bjørge, 1992). Subsequently, he emitted these acoustic displays seasonally throughout the duration of this study. Across all years, Sprouts generally began producing underwater vocalizations between December and April (moderate and intense calling behavior; Figure 2), with calls becoming more frequent in the spring and early summer, similar to the timing of the breeding for harbor seals in California (Bigg, 1981). Peak calling behavior typically occurred in May. Calling ceased abruptly each year at the onset of the annual molt in late July-early August. Sprouts' vocal behavior appeared to be consistent both with regard to the

structure of his acoustic signals and the timing between successive calls (Figure 1F).

The seasonal period over which this seal was routinely vocally active increased in duration as he got older and larger (Figure 2). Display periods were roughly three times longer between the ages of 16 and 22 than in early adulthood (ages 6 to 12). However, from ages 23 to 29, his vocal behavior again became abridged. The seasonal production of vocalizations coincided with an annual period of weight loss.

Relationship Between Acoustic Characteristics and Body Size—Sprouts achieved his highest mass of 122 kg at ages 23, 25, and 26 (Figure 2). Notably, while his age was positively correlated with his mass across the duration of this study ($R^2 = 0.81$, $F(1, 13) = 56.76$, $p \leq 0.0001$), there were no spectral features of his vocalizations that showed a positive correlation with either mass or age. Only one temporal feature—the number of pulses produced in the terminal portion of his call—showed a weak but significant positive relationship with both age ($R^2 = 0.22$, $F(1, 13) = 5$, $p = 0.04$) and weight ($R^2 = 0.19$, $F(1, 13) = 4.35$, $p = 0.05$).

Summary

Although this harbor seal was housed without acoustic exposure to conspecific males during reproductive development, he produced seasonal vocal displays that were similar to the breeding vocalizations of wild male harbor seals. He began emitting stereotyped vocalizations at the onset of sexual maturity at age 6, and he continued to exhibit acoustic displays and characteristic posture reliably over the course of his lifetime. Additionally, the annual timing of his vocal behavior coincided with the breeding season of wild harbor seals along the California coast. Even without conspecific individuals (competitors or potential mates) and with food readily available each day, Sprouts lost up to 39% of his body mass during each reproductive season following sexual maturity; this weight loss likely reflected the combined energetic costs associated with displaying, which included sustained physical effort, altered behavioral patterns, and presumed changes in hormonal status (Coltman et al., 1997).

The duration of this vocally active period generally increased as the seal got older. Larger body size in adulthood was related to earlier onset of reproductive behavior each year, with cessation of calling behavior occurring in mid-summer regardless of his age or size. Interestingly, only one feature of his call showed a significant correlation with body mass over his lifetime, despite a previous finding that spectral call features scale predictably with body size among wild seals

Table 1. Spectral and temporal acoustic measurements (mean \pm standard deviation [SD]) of spontaneous underwater vocalizations produced by a captive male Pacific harbor seal (*Phoca vitulina*). Note that representative acoustic data were collected for 16 y within the 29-y study period. Values are reported over the 90% call duration except where noted. Also provided are this seal's age, maximum annual mass, and number of vocalizations analyzed per year. On average across years, 90% of the energy of these vocalizations fell between 121 and 1,664 Hz. Refer to Supplementary Table 1A for recording and analysis details.

| Year | Age (y) | Maximum annual mass (kg) | Sample size (number of calls) | Spectral parameters | | | | | Temporal parameters | | | |
|-----------|---------|--------------------------|-------------------------------|-------------------------|---|-------------------|-----------------------|-------------------|---|------------------|--|------------------|
| | | | | Dominant frequency (Hz) | 90% bandwidth lower and upper bounds (Hz) | Q1 frequency (Hz) | Center frequency (Hz) | Q3 frequency (Hz) | Dominant frequency over pulsed portion of call (Hz) | 90% duration (s) | Duration of pulsed portion of call (s) | Number of pulses |
| 1998 | 10 | 85 | 10 | 59 \pm 0 | 47-517 | 59 \pm 0 | 162 \pm 133 | 337 \pm 88 | 333 \pm 137 | 3.6 \pm 0.3 | 0.7 \pm 0.2 | 3 \pm 0 |
| 1999 | 11 | 88 | 5 | 286 \pm 213 | 84-960 | 334 \pm 159 | 381 \pm 172 | 603 \pm 195 | 383 \pm 174 | 4.4 \pm 0.7 | 1.3 \pm 0.6 | 5 \pm 2 |
| 2000 | 12 | 91 | 10 | 328 \pm 166 | 126-1,064 | 394 \pm 25 | 461 \pm 44 | 650 \pm 167 | 443 \pm 28 | 4.1 \pm 0.3 | 0.8 \pm 0.2 | 4 \pm 1 |
| 2001 | 13 | 96 | 6 | 379 \pm 4 | 90-1,129 | 370 \pm 11 | 420 \pm 39 | 508 \pm 42 | 418 \pm 48 | 4.3 \pm 0.3 | 1.2 \pm 0.2 | 5 \pm 1 |
| 2004 | 16 | 116 | 10 | 665 \pm 243 | 387-3,788 | 595 \pm 168 | 823 \pm 192 | 1,239 \pm 464 | 712 \pm 244 | 3.2 \pm 0.8 | 1.1 \pm 0.4 | 5 \pm 2 |
| 2007 | 19 | 116 | 9 | 429 \pm 102 | 317-2,037 | 410 \pm 52 | 487 \pm 86 | 884 \pm 146 | 450 \pm 105 | 3.5 \pm 0.6 | 0.8 \pm 0.3 | 5 \pm 2 |
| 2008 | 20 | 112 | 10 | 108 \pm 105 | 61-1,365 | 177 \pm 141 | 348 \pm 166 | 735 \pm 211 | 469 \pm 372 | 2.1 \pm 0.5 | 0.8 \pm 0.3 | 4 \pm 1 |
| 2009 | 21 | 113 | 10 | 87 \pm 24 | 55-887 | 95 \pm 32 | 197 \pm 137 | 432 \pm 105 | 272 \pm 228 | 3.7 \pm 0.5 | 0.7 \pm 0.3 | 4 \pm 2 |
| 2010 | 22 | 117 | 10 | 61 \pm 12 | 48-845 | 72 \pm 23 | 212 \pm 150 | 361 \pm 172 | 142 \pm 128 | 3.6 \pm 0.5 | 0.8 \pm 0.3 | 5 \pm 2 |
| 2011 | 23 | 122 | 7 | 705 \pm 307 | 410-8,762 | 688 \pm 153 | 1,328 \pm 160 | 2,540 \pm 220 | 784 \pm 278 | 4.0 \pm 0.7 | 0.8 \pm 0.2 | 5 \pm 1 |
| 2012 | 24 | 120 | 8 | 79 \pm 29 | 43-1,018 | 72 \pm 22 | 168 \pm 130 | 463 \pm 107 | 207 \pm 223 | 4.5 \pm 0.8 | 0.8 \pm 0.2 | 5 \pm 1 |
| 2013 | 25 | 122 | 6 | 441 \pm 388 | 80-1,176 | 447 \pm 72 | 711 \pm 57 | 842 \pm 31 | 762 \pm 65 | 3.3 \pm 0.3 | 0.9 \pm 0.1 | 6 \pm 1 |
| 2014 | 26 | 122 | 10 | 137 \pm 205 | 52-1,170 | 141 \pm 179 | 442 \pm 297 | 730 \pm 239 | 606 \pm 303 | 3.7 \pm 0.6 | 1.1 \pm 0.2 | 6 \pm 2 |
| 2015 | 27 | 118 | 6 | 346 \pm 418 | 61-1,082 | 340 \pm 195 | 643 \pm 265 | 846 \pm 101 | 801 \pm 113 | 3.8 \pm 0.2 | 1.1 \pm 0.0 | 8 \pm 1 |
| 2016 | 28 | 118 | 10 | 73 \pm 23 | 54-734 | 127 \pm 136 | 236 \pm 267 | 400 \pm 355 | 373 \pm 369 | 3.0 \pm 0.5 | 0.7 \pm 0.1 | 4 \pm 0 |
| 2017 | 29 | 116 | 10 | 53 \pm 6 | 39-1,140 | 52 \pm 6 | 329 \pm 278 | 608 \pm 370 | 400 \pm 375 | 3.2 \pm 0.7 | 0.9 \pm 0.3 | 5 \pm 1 |
| All years | | | 137 | 245 \pm 270 | 121-1,664 | 254 \pm 221 | 435 \pm 331 | 734 \pm 533 | 456 \pm 297 | 3.6 \pm 0.8 | 0.9 \pm 0.3 | 5 \pm 2 |

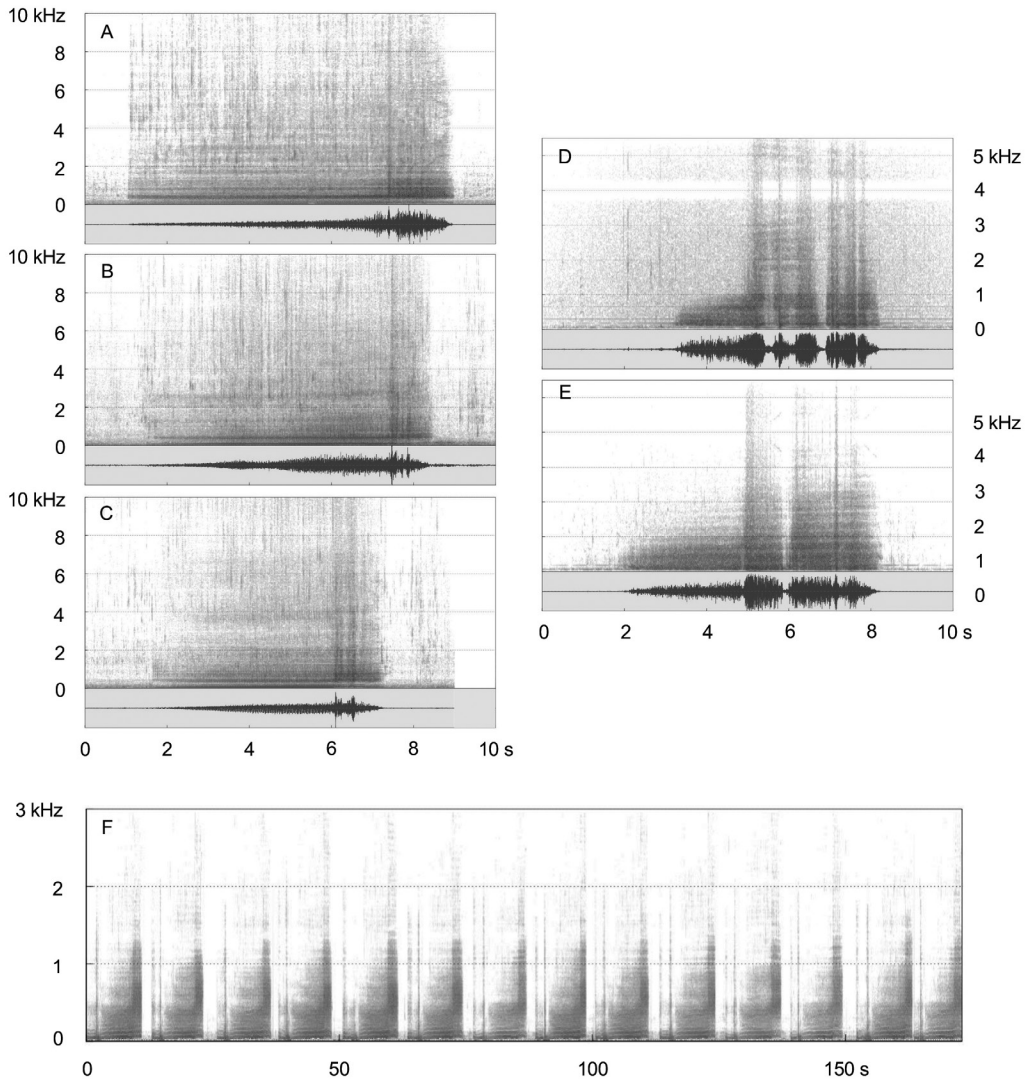


Figure 1. Within-individual comparison of vocalizations produced by Sprouts, a captive male Pacific harbor seal (*Phoca vitulina*), across multiple years. Spectrograms and associated normalized waveforms are provided for Sprouts' underwater roar vocalizations recorded at age 12 in 2000 ([A] sampling rate: 22,050 Hz, FFT size: 1,024, 3-dB bandwidth: 31 Hz), age 21 in 2009 ([B] sampling rate: 96,000 Hz, FFT size: 4,096 samples, 3-dB bandwidth: 33.7 Hz), and age 28 in 2016 ([C] sampling rate: 48,000 Hz, FFT size: 2,048, 3-dB bandwidth: 33.7 Hz). Below, Panel F depicts a portion of a calling bout recorded in 1999 at age 11 showing the regular patterning of calls (sampling rate: 22,050 Hz, FFT size: 2,048, 3-dB bandwidth: 15.5 Hz). While there is some variation in terms of spectral characteristics (e.g., dominant frequency; frequency bandwidth), the overall duration and structure of Sprouts' call—an ascending roar with multiple terminal pulses—is stable over time. For comparison, representative calls obtained from wild male harbor seals are shown in panels D and E (sampling rate: 11,025 Hz, FFT size: 512, 3-dB bandwidth: 31 Hz; note the different frequency axis for these two panels). These recordings were obtained at unknown distances from vocalizing individuals, while the recordings of Sprouts were obtained at close range (< 5 m). Since Sprouts' calls did not propagate far from their source and were generally recorded at higher sampling rates, relatively more high-frequency components are apparent than in recordings obtained from wild seals. A Hanning window with 90% overlap was used for all spectrograms. Calls from wild harbor seals (D & E) were provided courtesy of S. Hayes; these vocalizations were recorded in Moss Landing, California, as described in Hayes et al., 2004. The .wav files associated with this figure are provided as supplementary material (Supplementary Audio 1).

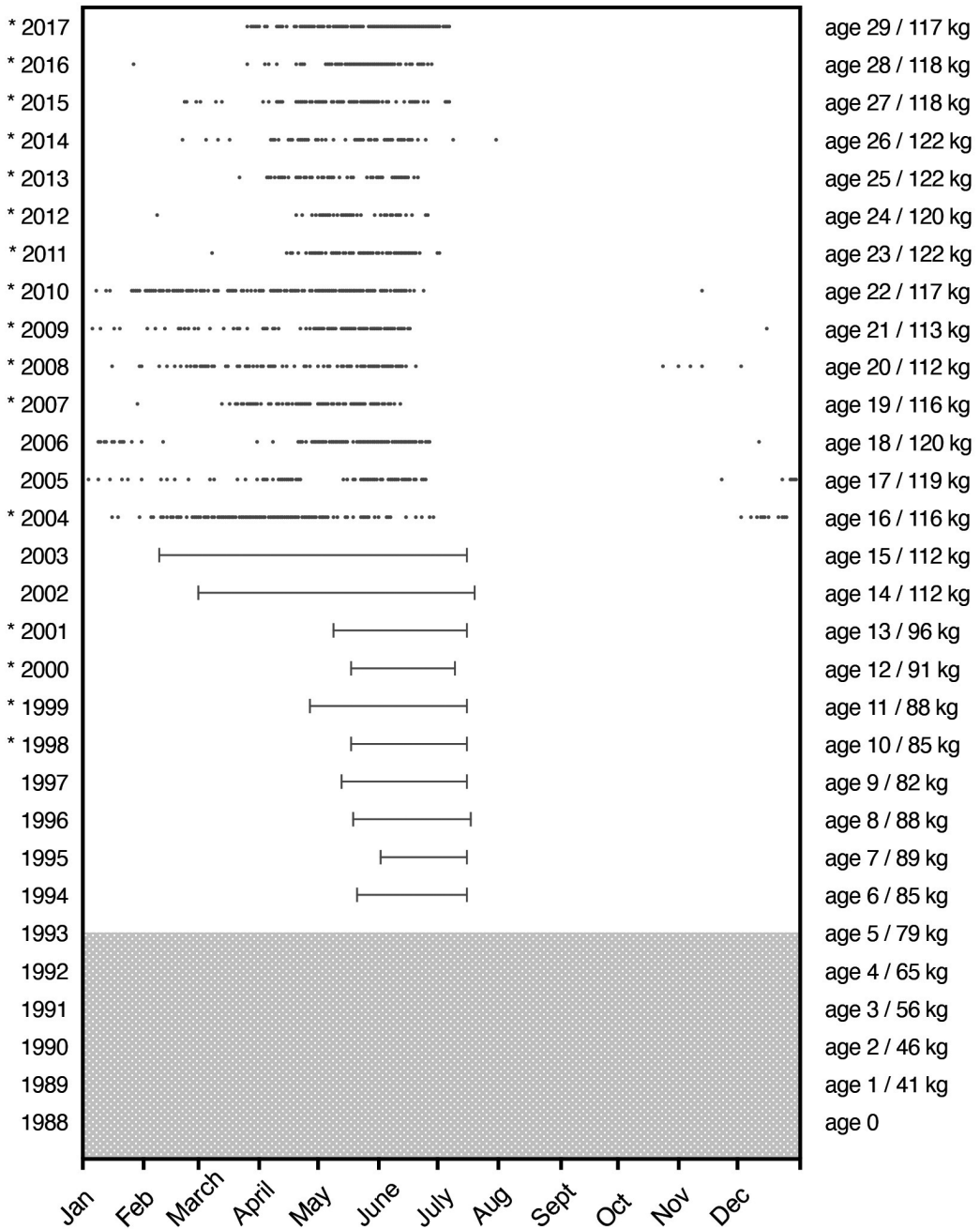


Figure 2. Lifelong temporal pattern of spontaneous underwater vocalizations produced by a captive Pacific male harbor seal. Onset of vocal behavior occurred in 1994 at age 6. Solid horizontal lines (years 1994 to 2003) denote periods of vocal activity estimated from husbandry summaries, weight records, and daily observations. The dots shown for years 2004 to 2017 indicate days for which moderate or intense vocal behavior was scored. Vocal recordings were analyzed for the 16 y marked with an asterisk. The seal's age and maximum annual mass are also provided for each year. From 2004 to 2017, cessation of acoustic behavior corresponded to the start of the annual molt, which began on July 7 (SD = 7.6 d).

(Nicholson, 2000). The number of pulses produced in the terminal portion of his roar vocalizations reliably signaled body size in this individual.

Case Study 2 – Northern Elephant Seal

Species Background

Female northern elephant seals primarily vocalize during the winter breeding season (December to March) which occurs annually on islands and mainland rookeries along the coasts of California and Mexico after long foraging migrations at sea (Le Boeuf & Laws, 1994). Reproductive maturity occurs between 3 to 8 y of age, and a typical female lifespan is 16 y (Condit et al., 2014). Elephant seals are not known to routinely produce calls under water. Females on shore produce two primary airborne calls: (1) a generalized threat call emitted during disturbance and (2) a pup attraction call that is directed toward their offspring during the period of dependence (Bartholomew & Collias, 1962; Le Boeuf, 1972). While the developmental emergence of acoustic reproductive displays has been documented for male northern elephant seals (Casey et al., 2020), the ontogeny of vocal behavior has not been studied in females.

The female *threat* vocalization has been described as a loud, deep, belching roar which “resembles the sound made by a human vomiting violently” (Bartholomew & Collias, 1962, p. 10). Emitted during agonistic encounters or when defending their pups, threat calls are pulsed, broadband vocalizations that contain steady harmonics, with maximum energy typically falling below 700 Hz (Supplementary Table 2B). The duration and amplitude of the threat call will often vary depending on the female’s motivation (Southall et al., 2003).

Female northern elephant seals bear their first young between 2 to 6 y of age (Reiter & Le Boeuf, 1991). During the reproductive season, *pup attraction* calls are produced by a female as soon as her pup is born and throughout the ~27-d lactation period (Bartholomew & Collias, 1962; Reidman, 1990). These vocalizations differ in structure, tonality, and function from threat calls and serve to maintain contact with the dependent pup (Bartholomew & Collias, 1962; Petrinovich, 1974; Reiter et al., 1981; Southall et al., 2003). Female pup attraction calls consist of several similar individual segments, each approximately 0.2 s in duration and with a fundamental frequency that rises and then falls between approximately 500 and 1,000 Hz (Supplementary Table 2B). These calls are frequency-modulated, graded signals with several well-marked harmonics, and individual segments may be repeated four to six times per second. The calls are relatively short in duration, and the

rate of emission is influenced by the distance of separation between the mother and her offspring (Bartholomew & Collias, 1962). Pups are the only conspecifics observed to attend to the pup attraction call, and responsiveness to these signals has been demonstrated to be imperative to pup survival (Reiter et al., 1981).

Subject

The subject of this case study was “Burnyce” (NOA0004829), a female northern elephant seal housed at Long Marine Laboratory (LML) for 18 y. After stranding as a weanling in 1993, she was brought into rehabilitation at SeaWorld San Diego for 4 mo prior to her transfer to LML when she was less than 1 y old. Similar to Sprouts, she lived outdoors in flow-through seawater pools with available haulout space for the duration of the study and was periodically housed with two female California sea lions. During the first year of her life, Burnyce was housed with one other juvenile female northern elephant seal for approximately 10 mo, after which she had no further direct contact with conspecifics. Throughout her life, her mass was obtained weekly (± 0.1 kg).

Methods

Observations—The timing, duration, and intensity of this subject’s vocal behavior were scored daily by trained observers using all occurrence sampling. These behavioral data were obtained every day from her arrival at LML in 1993 to her death at age 18 in 2011. Beginning in 1999 (age 6), vocalizations were noted as either being “present” or “absent” each day. If present, they were categorized as “mild” (~5 calls), “moderate” (~5 to 30 calls), or “intense” (~30+ calls during both day and night). Prior to 1999, qualitative behavioral records were maintained.

Recordings—To examine the ontogeny of Burnyce’s vocal behavior, her spontaneous calls were opportunistically recorded between 2000 and 2011 (ages 7 to 18). As only airborne calls were emitted, her vocalizations were recorded in air on axis (< 5 m distance) during spontaneous calling events using one of three configurations (for equipment details, see Supplementary Table 1B).

Analysis—Recordings obtained during 2000 to 2002, 2005, 2009, and 2011 (ages 7 to 9, 12, 16, and 18, respectively) were analyzed for this northern elephant seal. Vocalizations were organized by descriptive type and qualitatively compared to available data from wild females (Supplementary Table 2B). Methods used with Sprouts’ data were similarly utilized in this analysis. Seven vocal parameters were measured in the spectral and temporal domains for the elephant seal: (1) 90% call duration (s), (2) dominant frequency over the 90%

call duration (Hz), (3) the 90% frequency bandwidth (Hz) over the 90% call duration, (4) Q1 frequency over the 90% call duration (Hz), (5) center frequency over the 90% call duration (Hz), (6) Q3 frequency over the 90% call duration (Hz), and (7) number of amplitude inflections over the total call duration. For details pertaining to analysis parameters, see Supplementary Table 1B. For those metrics where mean values were published for wild female northern elephant seals, we evaluated whether Burnyce's call parameters fell within the reported range for this species.

To determine whether this subject exhibited species-typical seasonality of acoustic signaling throughout her lifetime, the initial onset of vocal behavior and its timing during the year were qualitatively compared to published data pertaining to the vocal behavior of wild female northern elephant seals (Table 2B). We performed a linear regression ('lm function' in *R* statistical package) to evaluate whether spectral and/or temporal acoustic features were linked to this seal's mass or age (RStudio Team, 2020), and a one-way ANOVA to assess the stability of measured call variables in Burnyce's vocalizations across years (*GraphPad Prism*, Version 9.0.0).

Results

Description of Vocalization—The calls produced by this captive female northern elephant seal were qualitatively dissimilar to previously reported vocalizations (threat calls and pup attraction calls) emitted by wild female northern elephant seals (Figure 3; Supplementary Audio 2). In addition, her unusual calls were produced in air in a stereotyped manner and in an atypical posture for female elephant seals, with her head elevated to its maximum height in a rigid posture. Burnyce's vocalizations, which we termed *bellows*, were broadband, frequency-modulated, high-amplitude calls with a strong harmonic structure and an overall average 90% duration of 7.1 s (Figure 3A-C). Roughly 90% of their energy fell between 321 and 667 Hz; and on average, Burnyce produced six distinct amplitude modulations over the total duration of each call (Table 2). While the dominant frequency of Burnyce's calls falls within the reported range of both the threat call and the pup attraction call (Supplementary Table 2B), her calls have several obvious structural differences (Figure 3). To the human listener, Burnyce's bellows have a rich tonal quality and oscillate in pitch, similar to the call produced by the television character Tarzan (Figure 3A-C; Supplementary Table 2B & Supplementary Audio 2). While the mean values for each measured call feature varied significantly across years ($p < 0.0001$ for all comparisons), the overall structure of Burnyce's call—multiple

frequency modulations with strong harmonics—remained stable over time (Figure 3A-C).

Temporal Patterning—This female northern elephant seal first began producing regular vocalizations at 4 y of age, the timing of which coincides with the average onset of sexual maturity in wild female northern elephant seals (Le Boeuf & Laws, 1994; Condit et al., 2014). She continued to produce these bellowing calls seasonally over similar intervals throughout the duration of this study; however, she notably produced fewer vocalizations during the final years of her life. Within each year, Burnyce reliably began to exhibit moderate and intense calling behavior in February, which coincided with the beginning of her expected annual estrous (Figure 4). During this annual period of vocal activity, Burnyce was observed to produce several call bouts sequentially throughout the day. Notably, although she generally became less vocal toward the end of March, the seasonal offset of her vocal behavior was not consistent (Figure 4).

Relationship Between Acoustic Characteristics and Body Size—As the subject progressed through developmental stages, she accordingly increased in size and mass. Over the course of her lifetime, Burnyce achieved her highest mass of 515 kg at 16 y of age (Figure 4). While age was positively correlated with her mass across the years of this study ($R^2 = 0.68$, $F(1, 4) = 8.33$, $p < 0.05$), the measured spectral features of her vocalizations did not show a strong correlation with changes in her mass or age. Additionally, while the mean value for all call features varied significantly across years ($p < 0.0001$ for all comparisons), the overall structure of Burnyce's call—several frequency modulations with strong harmonics—remained stable over time.

Summary

This captive female northern elephant seal—who was primarily raised without access to conspecifics—produced an aberrant call that has not been previously described, in combination with an atypical posture display while vocalizing. While there is some overlap between the frequency content of her vocalizations and published values for those of wild female northern elephant seals, her calls differed considerably with respect to their structure. Specifically, her bellow vocalizations were much longer, contained multiple frequency modulations, and showed structural stereotypy within and across seasons. Despite these obvious differences, the initial onset of her vocal behavior (at age 4) and its timing during the season (primarily surrounding presumed estrous) were both similar to the timing of vocal activity for wild, reproductively mature female northern elephant seals. While her age and

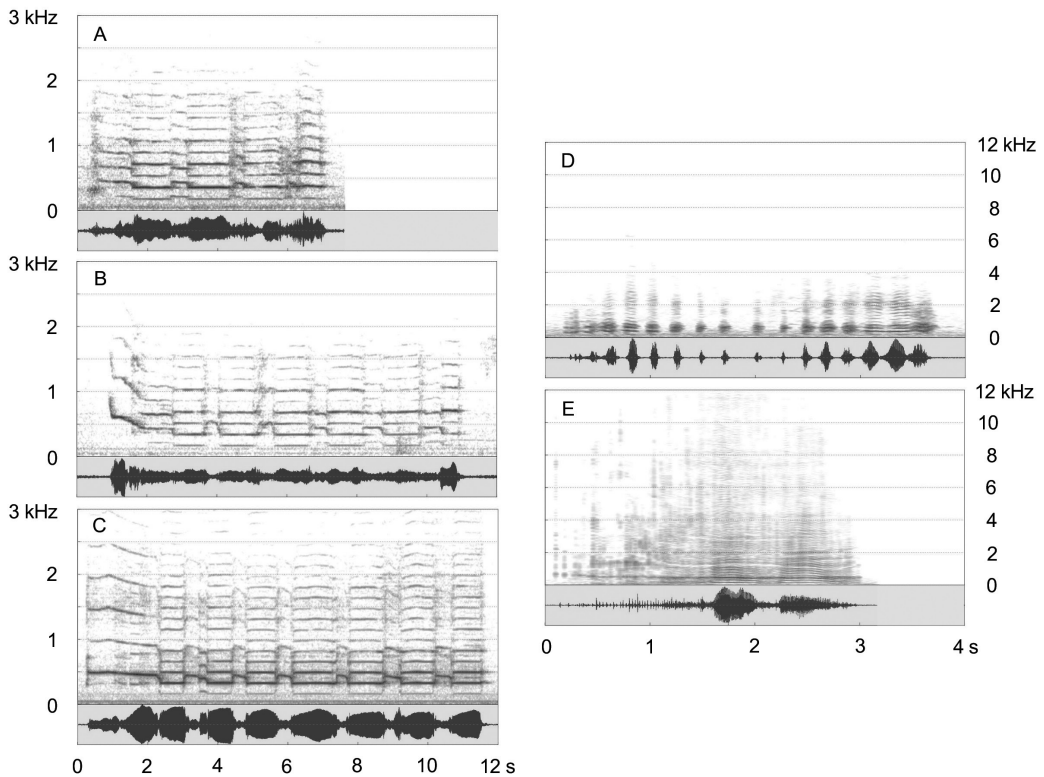


Figure 3. Within-individual comparison of vocalizations produced by a captive female northern elephant seal (*Mirounga angustirostris*) across multiple years. Spectrograms and associated normalized waveforms are provided for this seal's stereotypical in-air *bellow* vocalization recorded at age 8 in 2001 (A), age 12 in 2005 (B), and age 18 in 2011 (C). Representative calls obtained from wild female northern elephant seals—a pup attraction call (D) and a threat vocalization (E)—are shown for comparison. Note the different time and frequency axes for these panels. The sampling rate for all recordings was 48,000 Hz, and spectrogram parameters were Hanning window, 90% overlap, FFT size: 4,096, 3 dB bandwidth: 16.9 Hz. Calls from wild seals were provided courtesy of C. Casey. These vocalizations were recorded at Año Nuevo State Reserve in San Mateo, California, in 2015 with a Neumann KMR 82i Condenser Shotgun Microphone connected to a Fostex FR-2 Field Memory Recorder. The audio files associated with this figure are provided as supplementary material (Supplementary Audio 2).

mass were strongly correlated, none of the spectral features of this seal's call showed an obvious relationship with increasing body size.

Discussion

The case studies presented herein include long-term acoustic and behavioral datasets for two seals raised in relative acoustic isolation from conspecifics. As such, they can be used to evaluate developmental outcomes in the absence of natural social and vocal experience. By assessing whether the structure and temporal expression of vocal behavior deviates from that of individuals raised in natural conditions, these findings allow us to consider inherent flexibility in vocal production

for these species and the potential role of learning in vocal behavior. We carefully evaluated the vocal behavior of two individuals over the course of their lifetimes and found that—despite being raised in similar auditory and social conditions—the resemblance of their vocal behavior to that of wild individuals differed between subjects.

The captive male Pacific harbor seal, Sprouts, produced a seasonal, stereotypical, guttural roar vocalization which qualitatively resembled the calls of free-ranging male harbor seals. Sprouts was raised in isolation from conspecifics aside from his first few months of life, the only period when he may have heard the underwater roars of adult male harbor seals. It is difficult to rule out whether a possible early exposure could have

Table 2. Spectral and temporal acoustic measurements (mean \pm SD) of spontaneous airborne vocalizations obtained from a captive female northern elephant seal (*Mirounga angustirostris*) over multiple years. Note that representative acoustic data were obtained for 6 y within the 18-y study period; sample size is 10 calls per year, with the exception of 2005, which had only two recorded calls. Acoustic values are reported over the 90% duration of the call. Also provided are this seal's age, maximum annual mass, and the number of vocalizations analyzed per year. On average across all years, 90% of the energy of these vocalizations fell between 321 to 667 Hz. Refer to Supplementary Table 1B for recording and analysis details.

| Year | Age (y) | Maximum annual mass (kg) | Sample size (number of calls) | Spectral parameters | | | | | Temporal parameters | | |
|-----------|---------|--------------------------|-------------------------------|-------------------------|---|-------------------|-----------------------|-------------------|---------------------|---------------------------------|--|
| | | | | Dominant frequency (Hz) | 90% bandwidth (Hz) lower and upper bounds | Q1 frequency (Hz) | Center frequency (Hz) | Q3 frequency (Hz) | 90% duration (s) | Number of amplitude modulations | |
| 2000 | 7 | 423 | 10 | 398 \pm 116 | 346-826 | 361 \pm 9 | 416 \pm 106 | 649 \pm 131 | 4.9 \pm 0.5 | 4 \pm 0 | |
| 2001 | 8 | 442 | 10 | 360 \pm 7 | 318-743 | 359 \pm 8 | 413 \pm 105 | 648 \pm 118 | 4.9 \pm 0.7 | 4 \pm 1 | |
| 2002 | 9 | 457 | 10 | 383 \pm 108 | 339-719 | 349 \pm 5 | 409 \pm 113 | 628 \pm 143 | 6.1 \pm 0.9 | 5 \pm 1 | |
| 2005 | 12 | 470 | 2 | 650 \pm 58 | 334-873 | 492 \pm 66 | 645 \pm 50 | 691 \pm 17 | 10.2 \pm 0.8 | 7 \pm 1 | |
| 2009 | 16 | 515 | 10 | 377 \pm 79 | 293-518 | 339 \pm 50 | 384 \pm 70 | 445 \pm 46 | 8.7 \pm 2.7 | 7 \pm 2 | |
| 2011 | 18 | 475 | 10 | 346 \pm 55 | 309-485 | 336 \pm 36 | 355 \pm 48 | 438 \pm 47 | 10.5 \pm 2.0 | 8 \pm 1 | |
| All years | | 463 | 52 | 384 \pm 97 | 321-667 | 354 \pm 41 | 405 \pm 102 | 567 \pm 141 | 7.1 \pm 2.7 | 6 \pm 2 | |

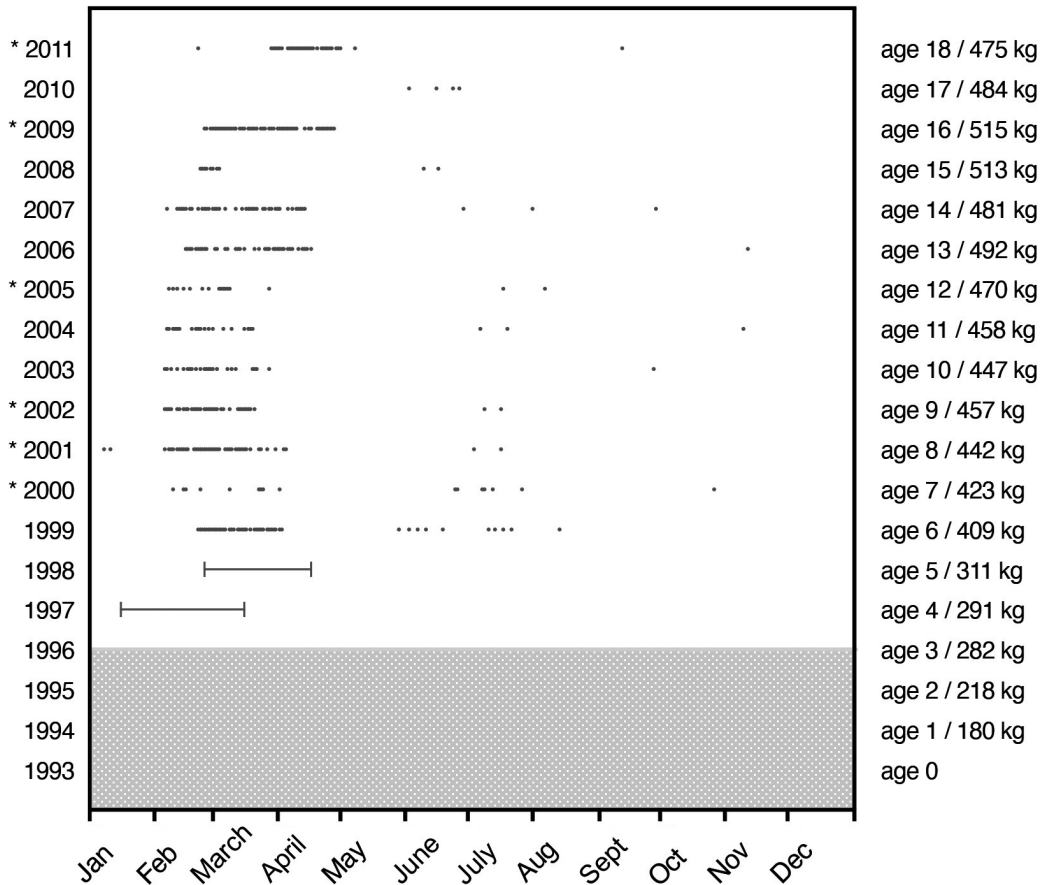


Figure 4. Lifelong temporal pattern of spontaneous airborne vocalizations produced by a captive female northern elephant seal. Onset of vocal behavior occurred in 1997 at age 4. Solid horizontal lines (years 1997 to 1998) denote periods of vocal activity estimated from husbandry summaries, weight records, and daily observations. The dots shown for years 1999 to 2011 indicate days for which moderate or intense vocal behavior was scored. Vocal recordings were analyzed for the 6 y marked with an asterisk. The seal's age and maximum annual mass are also provided for each year.

influenced his vocal behavior later in development; however, the results of this study suggest that male harbor seals possess a durable, species-typical template for the roar vocalization that does not require sustained auditory-vocal feedback from conspecifics. This observation from Sprouts can be paired with one of the most cited (and controversial) accounts of vocal learning in a non-human mammal, another captive male harbor seal named "Hoover."¹ After being fostered by human caretakers during early development, Hoover subsequently spontaneously and regularly emitted several recognizable words and phrases in an accent similar to that of his original caretaker's. These calls were produced year-round while his head was above the water's surface (Ralls et al., 1985). Hoover's behavior showed compelling

evidence of vocal flexibility as he imitated sounds that were entirely unique to this species' vocal repertoire. Intriguingly, Hoover also emitted species-typical underwater roars as a mature male during the breeding season, indicating that this individual produced both learned and innate vocalizations throughout his lifetime. Sprouts also demonstrated some vocal plasticity outside of the breeding season (Schusterman, 2008) in addition to producing typical roar vocalizations when in rut. Thus, it appears that some calls may be more susceptible to change than others.

In evaluating possible intrinsic factors influencing vocal production among harbor seals, we found that Sprouts expended significant effort producing underwater physical and acoustic displays during the annual reproductive season; this

effort was likely driven by an increase in testosterone production (Fedurek et al., 2016; Sills et al., 2020). As his age and mass increased, his period of vocal activity during the year generally became longer. Displaying over a longer seasonal period would presumably provide a reproductive advantage as there would be more opportunities to either attract mates or repel rivals. Thus, the calling behavior of male harbor seals may serve as honest indicators of individual quality. Studies evaluating breeding behavior of wild male harbor seals have demonstrated that larger males may have a mating advantage over smaller individuals since, with greater energy stores, they can afford to spend less time foraging and more time displaying during the breeding season (Coltman et al., 1997). Given these factors, and the results from this individual, the calling rate, duration of vocal activity, and perhaps the number of pulses could reasonably be reliable indicators of male quality for listeners since these metrics could reveal the physical attributes of the signaler. In fact, playback experiments with free-ranging male harbor seals have demonstrated heightened responses when the pulsed portion of roar vocalizations are manipulated (Hayes et al., 2004). If a male's quality is indeed assessed based on calling rate and/or duration of vocal activity in harbor seals, then this would serve as a potential explanation as to why Sprouts invested considerable time and energy into calling throughout the breeding season.

Unlike the harbor seal, the female northern elephant seal in this study produced an unusual, protracted, frequency-modulated bellow vocalization during the annual reproductive season that has not been described for this species. The context of her vocal behavior was also notably dissimilar to that of free-ranging female northern elephant seals' threat vocalization and pup attraction calls. When emitting her bellow vocalization, Burnyce would always sit upright in a stereotypical prone posture that was more similar to the vocal displays of adult male northern elephant seals than to the calls produced by females, while her long bellow call was not similar to that produced by either wild males or females. Interestingly, Burnyce's post-mortem pathology report indicated some unusual findings in her reproductive tract. These included fibrous material containing a small mass on each side of her uterus, which may have been residual (undeveloped) testes. It is unknown whether this feature is atypical relative to wild female northern elephant seals as the reproductive anatomy of mature individuals has not been well-studied. However, the presence of these tissues may be related to altered hormone levels in this individual, which, in turn, may have influenced her vocal behavior following sexual maturity.

From the perspective of learning, Burnyce's anomalous vocal behavior in adulthood demonstrates some flexibility in sound production and suggests that exposure to conspecifics via auditory feedback may be necessary for normal call development in this species. An abnormal underlying physiological condition may have also contributed to the unusual sounds she produced. Additionally, Burnyce never gave birth to or attended to a pup, which could be necessary to provide appropriate hormonal cues and/or to elicit species-typical vocal behavior. There is circumstantial evidence to suggest that male northern elephant seals acquire their adult calls on the basis of social experience (Sanvito et al., 2007; Casey et al., 2020). However, there has been no attempt to evaluate the vocal behavior of captive male northern elephant seals under controlled conditions, and very little consideration has been given to the vocal behavior of wild female northern elephant seals. Thus, the extent to which social exposure influences vocal behavior during development remains unknown.

Despite the differences observed between Burnyce's vocal behavior and that of wild female elephant seals, the seasonal timing of Burnyce's vocal behavior closely matched that of free-ranging individuals. This suggests that the onset of vocal behavior within each year may be driven by endogenous factors corresponding with the start of the annual reproductive season. Notably, during the last 2 y of this study (ages 17 and 18), the onset and duration of Burnyce's vocal behavior were delayed and shorter in comparison to previous years. While age-specific patterns of vocal activity have not been evaluated in females of this species, reproductive senescence has been reported in multiple female traits in other pinniped species (Beauplet et al., 2006; Bowen et al., 2006). The breeding behavior of female northern elephant seals in the wild has been tracked throughout their reproductive development, and individuals continue to successfully wean pups up through at least age 14 (Le Boeuf & Laws, 1994; Condit et al., 2014). As an individual near the limit of her species' natural lifespan, perhaps Burnyce exhibited a cessation in reproductive function later in life, which may have been reflected in the expression of her vocal activity. While the behavior of post-reproductive females has been considered in a handful of mammals both in captivity and in the wild (for review, see Croft et al., 2015), the relationship between reproductive senescence and the expression of acoustic behavior has not been systematically evaluated and warrants further investigation.

Animal communication in nature is complex and influenced by a multitude of interacting factors; however, there is considerable information to be gained through longitudinal studies of known

individuals living in zoological settings. Although interpretations of the behavior of animals in captivity as “representative” should be made cautiously, these detailed long-term case studies add to the limited knowledge available on the roles of development and learning in vocal production for two phocid species. Continued research exploring the motor, sensory, and physiological underpinnings of acoustic ontogeny are needed to understand the role that auditory feedback plays in vocal production among seals.

Endnote

¹The unique case of Hoover inspired other efforts to teach harbor seals to produce human speech-like sounds in captivity (for review, see Reichmuth & Casey, 2014). However, despite limited success, and many cases of young seals reared by human caretakers, no study has yet replicated Hoover’s command of human words and phrases (helgenorthsouthtv, 2016). Notably, Hoover’s postmortem pathology report indicated that there was unusual calcification within his cranium, which was associated with some degree of brain damage (Deacon, 1997). Perhaps his strange ability to mimic human sounds can be explained in part by abnormal brain development.

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Portions of this research were presented by CR at the 157th meeting of the Acoustical Society of America in 2009. Some findings were also included in KS’s Master’s thesis, *Ontogeny of Display Behaviours in a Captive Male Harbour Seal* (*Phoca vitulina*), submitted to the University of St Andrews in 2010.

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