Ethology

Observational Evidences of Vocal Learning in Southern Elephant Seals: a Longitudinal Study

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Abstract

Vocal learning in mammals is sparsely documented, and there are few reports of vocal learning by wild mammals. In particular, no information based on longitudinal data for identified individuals exists, even for well-studied highly social species in which vocal communication is an important aspect of social life. We present such information for the southern elephant seal (*Mirounga leonina*). We studied a small breeding population in the Falkland Islands over 8 yr (1995–2002). We recorded approx. 2400 agonistic vocalizations from approx. 285 different males, including many recorded over more than one breeding season (55 males were recorded for >2 yr and 29 were recorded throughout vocal development). Vocalizations are a key element of male agonistic behaviour in this species, the world's most polygynous vertebrate. For male agonistic vocalizations, we show that: (1) a limited number of discrete vocal types exists; (2) proportions of vocal types change over time; (3) observed trends of increase or decrease of vocal types are well explained by a process of vocal learning, in which younger peripheral males imitate vocal types of older more successful breeders.

Introduction

Vocal-production learning, i.e. the modification of the structure of vocalizations as a result of imitation of other individuals, is widespread and well known in birds (Janik & Slater 2000; Boughman & Moss 2003). It occurs in different ways and for different adaptive reasons, including recognition at different levels (individual, family, group, population, species), selection of social (often sexual) partners, and habitat matching (Janik & Slater 1997). On the contrary, evidence for vocal learning in mammals is scanty. The capacity to imitate natural and artificial sounds has been demonstrated for various captive and semi-wild mammals (Eaton 1979; Ralls et al. 1985; Boughman 1998; Poole et al. 2005), but documentation of intraspecific copying of natural, socially relevant sounds by specific individuals is very scarce for wild populations (Crockford et al. 2004).

Vocal-production learning may be particularly important in marine mammals because of their longevity and social complexity. Group-specific vocalizations of some cetacean species (in particular within matrilineal groups), have been explained by vocal learning and cultural transmission (Whitehead 1998; Deecke et al. 2000; Noad et al. 2000). However, such inferences are based on indirect evidence, not on longitudinal data for individually identified animals. In this paper, we provide the first evidence of vocal-production learning in a marine mammal, the southern elephant seal (*Mirounga leonina*), using a longitudinal data set.

Northern (*M. angustirostris*) and southern elephant seals are the most polygynous of all mammals, with a mating system based on harems (i.e. femaledefence polygyny) and strong competition among males for access to females (Galimberti et al. 2002). Male elephant seal agonistic vocalizations are one of the most important components of inter-male competition, and likely function to communicate information about the resource-holding potential of the emitter (Bartholomew & Collias 1962; Shipley et al. 1981, 1986; Sanvito & Galimberti 2003). In both species, agonistic vocalizations of mature males are structurally complex, stereotyped, and individually distinctive, and each male emits only one kind of vocalization, as identified by the specific arrangement of syllables and syllable parts (Shipley et al. 1981; Sanvito & Galimberti 2000b).

Some structural aspects of vocalizations may be learned because (1) young elephant seals have plastic vocalizations that become increasingly structured with age, and (2) vocalizations seem to vary geographically (Le Boeuf & Petrinovich 1974a; Sanvito & Galimberti 2000b). The presence of dialects in different breeding colonies is consistent with vocal-production learning but does not demonstrate its existence (Egnor & Hauser 2004). Data on geographic variation are cross-sectional in nature and could by themselves be explained by founder effects or sampling bias without vocal-production learning (Le Boeuf & Peterson 1969; Le Boeuf & Petrinovich 1974a; Sanvito & Galimberti 2000b).

We hypothesized that imitation of the syllable patterns of older males is a major factor in vocal development of young male elephant seals. If this is true, we expected vocal development in young males to be influenced mainly by those males that have the highest probability of being heard by young males before their adult vocal pattern is established. Elephant seals spend most of their lives at sea, where they are solitary and silent (Fletcher et al. 1996). When on land during the period of moult (about three weeks, Jan. to May, depending on age class), elephant seals rarely interact overtly or vocalize, aside from play-fighting between juveniles (pers. obs.; Laws 1956; Rasa 1971). Therefore, the only good opportunity for young males to learn vocalizations is during the breeding season (about 3 mo, late Aug. to late Nov., at our study site). Harem holders are usually the oldest males, and vocalize frequently to keep peripheral males away from females (McCann 1981). These vocalizations are the dominant component of the acoustic habitat of young males. Large harems have the greatest number of associated peripheral males (Galimberti et al. 2000), so our second hypothesis was that males holding large harems will influence vocal learning disproportionately. As a result, vocal types of the most successful holders should spread in the population. In contrast, if vocal imitation is not a main factor in vocal development, the spread of vocal types should be independent of the acoustic habitat of subadult seals. In this case, we expected no systematic trends over time in the distribution of vocal types, and no relationship between a vocal type's presence in successful males and its spread over time.

In this paper, we show that agonistic vocalizations of southern elephant seals, as recognized from visual inspection of waveforms, are a real phenomenon, and can be reliably classified based on their acoustic structure. We focused on temporal macrostructure of vocalizations because elephant seal males emit pulse trains with little frequency modulation (Sanvito & Galimberti 2000a), and because frequency attributes are strongly influenced by individual attributes of males such as body size, so are not good candidates for vocal learning (unpubl. data, Sanvito and Galimberti; Fitch & Hauser 2002; Reby & McComb 2003). We demonstrate that the relative frequencies of vocal types in the population change over years, and that this change likely results from the propagation of new types through imitative learning by younger peripheral males of older, more reproductively successful breeders.

Methods

Data were collected during eight breeding seasons (Sep. to Nov., 1995–2002) at Sea Lion Island, Falkland Islands (52°26′S, 59°05′W), which shelters a small and localized population of about 550 breeding females and 60 breeding males (Galimberti et al. 2001). All males were individually marked with tags and dye marks (Galimberti & Boitani 1999). Details of the research protocol and a report on the ethics of the research are available on-line (http://www.eleseal.it/es_lit.htm). We observed 15 694 agonistic interactions between males. Observations were carried out by 2–4 observers during observation periods of 2-h duration, randomly distributed across hours of the day, tidal phases, breeding beaches, and harems. Data were recorded using all-occurrences sampling (Altmann 1974). This method was chosen because it provides a full record of agonistic interactions and copulations during the observation period, so enables good estimates of dominance ranks, competitive success, and mating success. The information recorded ranged from basic data (identity and status of males; outcome of interaction; behaviour that settled the contest) to a full description and quantification of the behavioural sequence; therefore, different analyses are based on different samples of interactions (Galimberti et al. 2003).

Audio recordings of male aggressive vocalizations were obtained by a standard procedure in which a person approached the animal, eliciting the typical stereotyped aggression pattern that elephant seals use during natural encounters with other males, including aggressive vocalizations. Vocalizations emitted in response to standard stimulation were identical to vocalizations emitted during natural encounters (Sanvito & Galimberti 2000a). We recorded 103 h of vocalizations from males of all age classes (we considered juveniles as 3–5 yr old, subadults as 6–9 yr old, and adults as 10–16 yr old; Clinton, 1994), with 1–64 vocalizations recorded per male per year (total = 7405 vocalizations). To obtain balanced samples, we randomly selected five recordings per male per year, for a total of 2380 vocalizations from 284 different males, with some males present in more than one breeding season [range 1–6 seasons; $\bar{x} = 1.7 \pm 1.1$ (SD)]. Fifty-five males were recorded over three or more years, and 29 were followed throughout their entire vocal development, beginning from when they exhibited plastic, non-structured vocalizations to fully structured adult calls. Males were defined as *holders* (males with nearly exclusive access to females of their harem during the breeding season) or *peripherals* (males present in the breeding areas near harems, and frequently but usually unsuccessfully attempting to get access to females) (Galimberti et al. 2000).

We used portable digital recorders (Sony DAT TCD-D100; Sony Corporation, Tokyo, Japan) and dynamic cardioid microphones (Sennheiser MD 441 (Sennheiser Electronic GmbH & Co. KG, Wedemark, Deutschland), frequency response = 30–20 000 Hz, sensitivity, free field, no load, at 1 kHz = 1.8 mV/Pa ± 2 dB). Sounds were recorded at 48 kHz sampling frequency with 16-bit resolution. Sounds were then digitally transferred to a computer, and analysed with Canary software (v. 1.2; Macaulay Library, Cornell Laboratory of Ornithology, Ithaca, NY, USA). We used the following settings for spectral analyses (Charif et al. 1995; Sanvito & Galimberti 2000a): hamming window function with frame length of 21.33 ms (1024 pts) and corresponding filter bandwidth of 190.31 Hz; frame overlap of 50% with time-grid resolution of 10.67 ms; and frequency-grid resolution of 11.72 Hz (FFT = 4096 pts).

Male aggressive vocalizations are composed of a series of pulsed bouts ('bouts' hereafter) that are repeated in sequence several times. Each bout is subdivided further into: (1) 'syllables', single acoustic events with a continuous time representation as spectrograms; and (2) 'syllable parts', portions of syllables that differ from one another in pulse rate (Sanvito & Galimberti 2000a). Each vocalization was classified as a vocal type by visual inspection of waveforms, using features of bout duration, plus overall diversity and temporal patterning of syllables and 'syllable parts'. Frequency features and spectrograms of the sounds were not used to classify them in vocal types. The main vocal types recognized in this study are shown in Fig. 1.

We measured 15 variables for each vocalization (Sanvito & Galimberti 2000a,b): number of bouts per vocalization; bout duration; total vocalization duration; relative peak time (=ratio between absolute peak time, i.e. the time from the beginning of the bout at which the highest amplitude in the bout occurs, and bout duration); duration of syllable part with maximal peak pressure; relative peak intensity (=ratio between peak intensity per hertz, i.e. the maximal intensity/Hz in the bout, calculated from the spectrogram, and peak pressure, i.e. the pressure in the selected bout with the maximal absolute value, calculated from waveform); peak frequency; fundamental frequency; dominant frequency; first formant; 12-dB bandwidth; minimal frequency at −6 dB; number of syllables per bout; syllable rate; and number of syllable types per bout. We calculated eight more variables from power spectra: 12-dB bandwidth proportion occupied by signal (proportion of frequency bandwidth in which spectrum exceeded threshold amplitude of −12 dB); dominance of peak intensity (ratio of relative average intensity of whole bout to peak pressure); energy below 1 kHz (area of power spectrum below 1 kHz, as percentage of total spectrum); power spectrum total slope (slope of regression line fitted through whole spectrum, from 0 to 24 kHz); power spectrum ascending slope (slope of regression line fitted through spectrum, from beginning to peak), and its coefficient of determination (the proportion of variance explained by the relationship, R^2); power spectrum maximal amplitude to 4 kHz slope (slope of regression line fitted through spectrum, from peak to 4 kHz) and its coefficient of determination.

To compare acoustic structure among vocal types we used a non-parametric MANOVA with Bray–Curtis distance and Monte Carlo test (Anderson 2001). To test observed vs. expected variation in proportions of different vocal types among years (see Results), we used non-parametric exact tests. When we expected

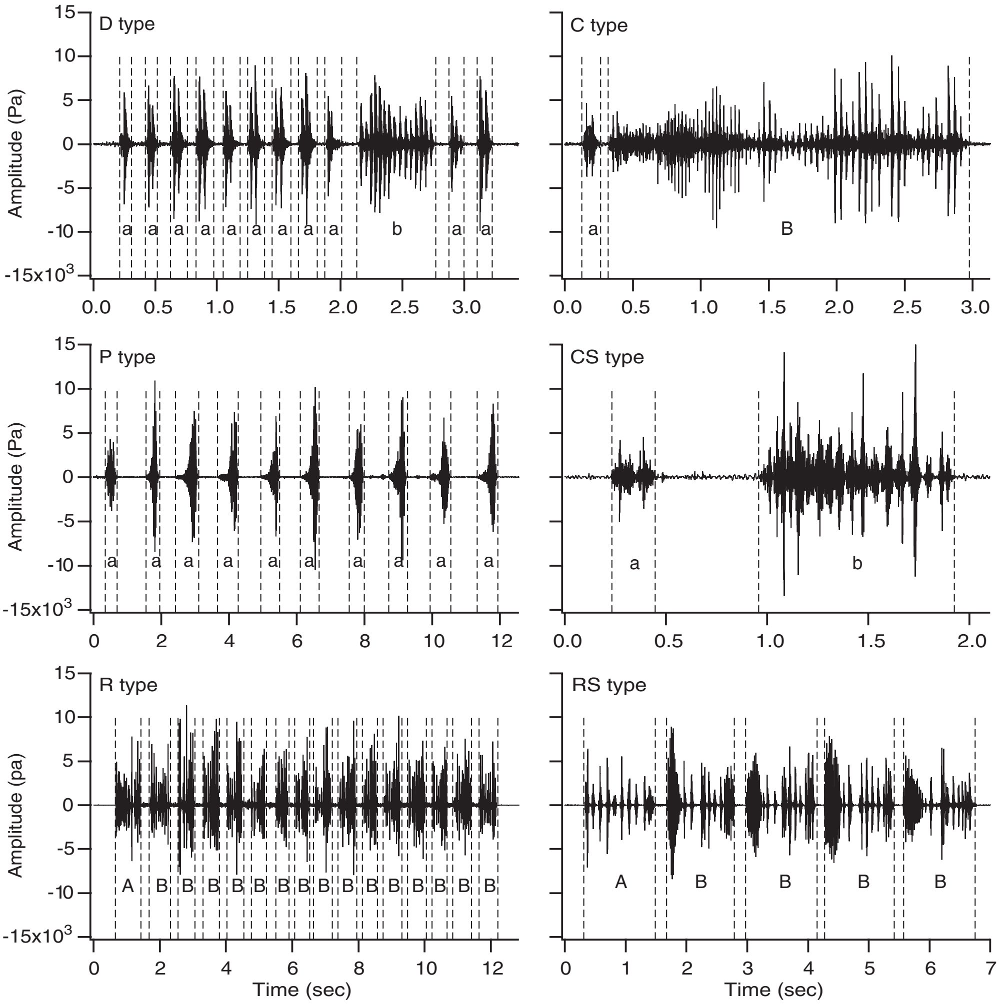

Fig. 1: Vocal types differed greatly in temporal attributes, syllable diversity and syllable organization. Waveforms of a typical bout of each of the six main vocal types are shown: D = drumming; C = continuous; CS = continuous simplified; R = repetitive; RS = repetitive slow; P = pulsing. Note the different time scales for different vocal types. Each bout is divided into its syllables. Small letters indicate syllables in which the pulse rate is constant (i.e. fundamental frequency is constant), while capital letters indicate syllables in which the pulse rate changes (i.e. they are made of more than one syllable part). Equal letters indicate the same syllable type within each bout (i.e. an 'A' syllable of the R type is not the same as an 'A' syllable of the RS type)

a decreasing or increasing trend we used a Cochran–Armitage trend test (Armitage 1955). When we expected a bell-shaped trend, with a gradual increase, a plateau, and then a gradual decrease, we used a permutation test with arbitrary scores (Good 1994). The scores were devised as follows: monotonic increasing scores for the first 3 yr of the study, equal scores for the two middle years, and monotonic decreasing scores for the last 3 yr.

When the calculation of exact probability was not feasible, we calculated a Monte Carlo approximation (Manly 1997). Data exploration, basic statistics, and discriminant analysis were run in SPSS (version 11, SPSS Inc., http://www.spss.com). Exact and Monte Carlo tests were run in STATXACT (version 4, Cytel Corporation Inc., http://www.cytel.com).

Results

Acoustic Habitat of Subadult Males

Holders were the dominant feature of both social and acoustic habitats. They represented only 22.2% of the males present in the breeding colony (mean of the eight breeding season of the study) but were involved in 65.3% of all (n = 15 694) agonistic interactions and initiated 64.3% of interactions. Holders initiated and peripherals reacted in 64.2% of interactions. Vocalizations were the single most important component of male agonistic behaviour: males also used optical displays, chases, and fights when interacting, but vocalizations alone settled 50.8% of contests (n = 15 694). Furthermore, vocalizations were uttered by one or both males in 69.7% of interactions (n = 8824). Holders emitted at least one vocalization in 54.5% of interactions with peripherals (n = 8824).

Classification of Vocal Types

We recognized six main vocal types shared by two or more males over 8 yr of study (Fig. 1). Bouts of the pulsing (P), repetitive (R), and repetitive slow (RS) vocalizations were generally longer than bouts of other types. Bouts of the drumming (D), P, and R vocalizations were characterized by many syllables, whereas continuous (C) and continuous simplified (CS) bouts generally had only 2–3 syllables; RS bouts were intermediate. C and CS vocal types were similar to each another in macrostructure (i.e. the arrangement of syllables and syllable parts within the bout). CS was the simplest vocal type and was a simplified version of C, with the same number and pattern of syllables (1 brief syllable followed by 1 or 2 longer ones), but a less variable pulse rate (longer syllables had only one part in CS and three or more in C). Of the vocal types with many syllables, D was characterized by the repetition of 1–2 brief uniform syllables plus a single longer one towards the end of the bout, all with uniform pulse rates (i.e. consisting only of one syllable part). P consisted only of a series of one kind of brief syllable with constant pulse rate, repeated slowly many times at a uniform rate (approx. 1.1 syllables per second). R and RS types were similar to one another, with one initial syllable (that might differ among males) followed by the repetition of a complex syllable made of different syllable parts. The repeated syllables were briefer, more numerous, and repeated more rapidly in R than in RS, imparting a slower rhythm to the latter. Some males had a unique (UNQ) structured vocalizations (i.e. not shared with any of the other males), with varied patterns of syllables and syllable parts. Finally, some males (mostly juveniles) had no fixed structured vocal pattern (non-structured vocalizations or NSVs hereafter), and their bouts had variable patterns of syllabic structure. Variations on vocal types were present, but the patterns were distinct enough to allow unequivocal and repeatable classification of types by visual inspection.

Reality of Vocal Types

To validate the reality of vocal types we: (1) verified the internal reliability of the types with a blind recognition trial; (2) analysed acoustic differences among types using non-parametric multivariate analysis; and (3) classified vocal types using acoustic features by discriminant analysis. Reliability of vocal-type classification was high. In a blind recognition trial, in which the operator was asked to classify the same sound of a set of 20 (including all vocal types) three times with randomized presentation, classification was correct in 100% of cases.

Vocal types differed greatly, based on non-parametric MANOVA with 23 variables (10 000 resamplings; $p = 0.0001$). Each variable, except vocalization duration, differed significantly among types [univariate ANOVAS with randomization test, 10 000 resamplings, sequential Bonferroni correction with Holm (1979) method; $p < 0.05$ in each case]. Variables that differed most among vocal types were related to bout macrostructure (syllable rate, number of syllables, and number of syllable types) and simple temporal attributes of bouts (bout duration; duration of syllable part with maximal peak pressure). Finally, frequency, intensity, and power spectra 'shape' variables differed among vocal types, indicating that differences in macrostructure also were related to differences in the frequency domain.

Discriminant analysis with cross-validation achieved good classification success, with a mean of 82.1% of the vocalizations classified correctly (57.9–93.3% for different vocal types). D and B types were classified best (85.9% and 93.3% respectively); these had a distinctive and simple macrostructure, with brief syllables and constant pulse rate (Fig. 1). The worst performance was for the C and RS types (57.9% and 58.9% respectively), which have complex long syllables and variable pulse rate (Fig. 1). Types C and CS partially overlapped because, as noted above, CS was a simplified version of C, with the same number and pattern of syllables, but less variable pulse rate. However, classification by visual inspection of waveforms of C and CS types was 100%.

Vocal Learning

Mature males had structured vocalizations and retained their vocal types over successive years, whereas young males had NSVs (Sanvito & Galimberti 2000b). The proportion of males with NSVs decreased with age, from 100% at age 3 to 1% at age 10 (Fig. 2; Exact Cochran-Armitage test for trends in proportions: trend parameter = −0.8654, 95% exact confidence interval = −1.073, −0.6742; p = 0.0001).

We tested the hypothesis of imitation of harem holders by comparing the observed frequencies of vocal types in the 8 yr of study with frequencies expected from the appearance and disappearance of successful males with particular vocal types. We hypothesized that new vocal types should arise in the population, and their spread would depend on the competitive success of males using these types, because males holding large harems would be imitated by many young males. The process could be amplified if any of the young imitators became holders, whereas the vocal type would disappear from the population through natural mortality of males with that vocal type if it is not imitated or is imitated only by young males that later fail to hold a harem. Hence, we expected: (1) frequencies of vocal types to change over years; (2) the oldest vocal types (types C and D, already present in the population at the beginning of our study) to be at some point of the increasing/decreasing trend of vocal types' appearance, showing either a bell-shaped or a decreasing trend in their frequencies; and (3) new vocal types to appear in the population and spread if they belonged to reproductively successful males.

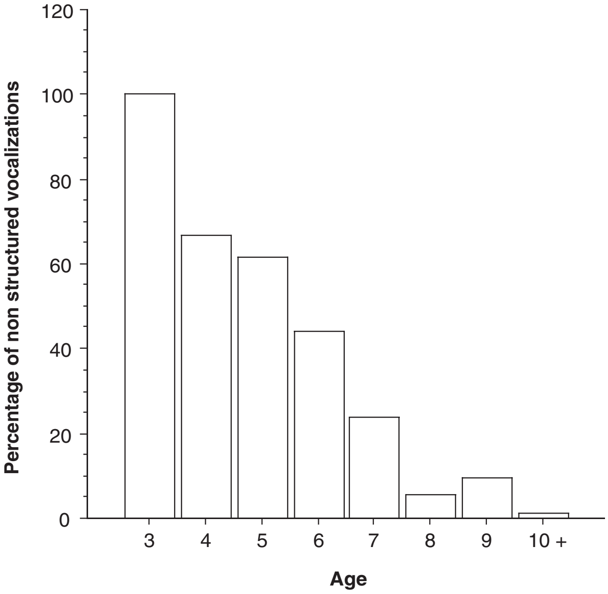

Fig. 2: Vocalizations changed from non-structured and variable to structured and stereotyped over development. Bar diagram shows percentage of males with non-structured vocal types for each age (year) class

Frequencies of vocal types were not homogeneous among years (chi-square test for independence, with randomization: $\chi^2 = 184.2$; $p_{10k} = 0.0001$). Observed proportions of males with different vocal types, expected variation, and corresponding statistical results, are shown in Table 1. All observed trends in proportions of different vocal types were statistically different from zero, and in accordance with our predictions. Vocal type D was the most common of the old vocal types and showed a bell-shaped trend; it was still present in the population, although at low frequency, 2 yr after the end of this study. The other old vocal type, C, was decreasing when we started

Table 1: Changes in the percentages of vocal types over the 8-year study. The last column indicates the number of males with structured vocalizations in each breeding season. Initially only vocal types C and D were present, but these declined in frequency and nearly disappeared as new vocal types appeared and spread. We used exact permutation tests with scores increasing then decreasing to test the bell-shaped trend for vocal type D, and Cochran-Armitage exact-trend test for increasing or decreasing trends for other vocal types (observed trend parameters and exact p values for each test are shown)

	D	C	CS	P	R	RS	n
Breeding season							
1995	67.7	32.3	0.0	0.0	0	0	31
1996	53.8	41.0	2.6	0.0	0	2.6	39
1997	65.1	25.6	2.3	4.7	0	2.3	43
1998	75.5	12.2	2.0	4.1	0	6.1	49
1999	62.0	16.0	6.0	4.0	2	10	50
2000	65.5	1.8	7.3	7.3	1.8	16.4	55
2001	52.2	0.0	13.0	13.0	4.3	17.4	23
2002	19.4	3.2	19.4	16.1	29	12.9	31
Expected pattern	Bell-shaped	Decreasing	Increasing	Increasing	Increasing	Increasing	
Observed trend parameter		−0.499	0.481	0.443	1.340	0.366	
Exact p	0.0027	0.0000	0.0002	0.0007	0.0007	0.0005	

the study and has since disappeared from the population. New vocal types appeared and some have spread in the population. For example, type R had a particularly clear pattern of spread in the population. It was noted first in a male named APRIM; during the 1999 and 2000 breeding seasons it was a subadult (6 and 7 yr old respectively), peripheral with low breeding success, and was the only male with vocal type R. In 2001 it was an 8-yr-old subadult, and became a holder briefly and in 2002 became holder of the main harem, with six to eight peripheral males in attendance on different days. During that breeding season, vocal type R was uttered by several subadult males that had NSVs in the previous year, and one of them held a small harem later that season, furthering the process of spread (Table 1). Vocal types CS and RS followed a similar pattern: initially they were unique, then they spread after the males that used them became main breeders. Seven (12.5%) of the 56 males with UNQ vocal types in our study were holders in one or more seasons. Four of them became holders of main harems with many peripheral males, and in all cases their vocal types spread subsequently. Each of the other three males was present for only one season with a marginal small harem, and their vocal types were not imitated by any other male, hence disappeared from the population with them. None of the males with UNQ vocalizations that died before becoming a harem holder was imitated by other males.

In a sample of 21 young males previously recorded with NSVs, and that showed a stable association with a specific holder during the breeding season (based on individual daily records), 57.1% adopted the vocal type of the holder (exact binomial test, with expected proportion $= 1/7 = 0.1429$: $p = 0.0000$; 95% exact confidence limits for the proportion: 0.3402–0.7818). It should be noted that the one-seventh expected proportion is conservative, because all males adopting a specific vocal type, not shared by anybody else, are pooled in the UNQ vocal type. Therefore, in the calculation of the expected proportion, a male that adopted an UNQ vocal type, and which harem holder also had a UNQ vocal type, is counted as adopting the same vocal type of his harem holder, which is not the case as UNQ types are different from one another by definition.

Discussion

Vocal learning and imitation of the macrostructure of conspecific vocalizations explain our observations on temporal changes in male elephant seal vocal types best. Other explanations are possible but unlikely, due to the constraints of the breeding biology and social system of our study population. In particular, the pattern of vocal types that we observed could not have been due to inheritance of vocal types. For six males, we determined: (1) the genetic father at 95% probability using microsatellite markers (Fabiani et al. 2004); and (2) the vocal type of the genetic father. None of these males showed the father's vocal type. Additional evidence against a genetic basis for vocal types regards vocal type C. This vocal type was emitted by the most successful male in our population at the beginning of the study (lifetime number of estimated pups sired >350), but it disappeared completely by 10 yr later, when the sons of this male reached maturity (own data).

Another hypothetical mechanism for the spread of new vocal types is repeated immigration from other populations that differ vocally (Le Boeuf & Petrinovich 1974b). However, immigration of breeding individuals is extremely rare at Sea Lion Island (Galimberti & Boitani 1999; Fabiani et al. 2003). In addition, our results are based on individuals with well-documented breeding histories, so any undetected immigration must have been very small. In conclusion, vocal learning by imitation of the most successful breeding males (i.e. those holding the largest harems) is the most reasonable and parsimonious explanation for our observations.

Experimentation, including playback, often is used to study vocal learning (Janik & Slater 2000; Nelson, 2000; Schusterman 1978), but is not always feasible in many natural settings. For this reason, Rendell & Whitehead (2001) advocated an 'ethnographic' approach using observed vocal variation within and across social groups that cannot be explained by genetic or environmental factors. Application of this approach to marine mammals has uncovered vocal variation at different social and spatial levels (Noad et al. 2000; Rendell & Whitehead 2003; Van-Parijs et al. 2003). The indirect and suggestive evidence for vocal learning offered by this approach can be strengthened by longitudinal data on known individuals, including early stages of vocal ontogeny, as in our study. The evidence we provide is correlational, as in any observational study, but shows strong agreement between expected and observed patterns. This evidence might be strengthened by playback experiments, but this is not a realistic option for wild elephant seals because their aggressive vocalizations have exceptionally high sound levels (Sanvito & Galimberti 2003). In addition, it would be difficult to devise an experimental test of our proposal that vocal learning is due to imitation after a period of vocal plasticity, because seals could not be maintained in experimental conditions for such long periods of time, for practical and ethical reasons.

A problem that remains open is the origin of new vocal types. They could result from immigration of adult males from other populations, that may have different vocal patterns, but, as stated above, immigration is very rare. Alternatively, new vocal types may result from imperfect imitation of established types, for example through changes in the number or position of syllables, or variation in pulse rate or in syllable parts within syllables. The latter explanation has some support from the relationship between C and CS vocalizations, with the latter apparently being a simplified version of the former.

A puzzling aspect of elephant seal social behaviour is the presence of young subadult males on land during the breeding season. These males have little chance of reproducing but pay a high cost for attendance because they fast while on land and lose substantial body mass (own data). Fasting costs may be offset by gains in social experience, which improves competitive abilities in subsequent years (Deutsch et al. 1994). This hypothesis is suggestive, but has never been demonstrated before. At Sea Lion Island, vocal imitation by young individuals of reproductively successful males may be an important component of the development of social competence. The breeding ground is the only place where young elephant seals can learn and practise the vocalizations that are so important in later social life. As noted above, seals are solitary and silent when at sea, and interact and vocalize little during terrestrial moult (Fletcher et al. 1996). Moreover, the different age classes differ in the timing of moult, so young males have little exposure to structured vocalizations of older males outside the breeding season (Laws 1956; Carrick et al. 1962; Hindell & Burton 1988).

Male elephant seals differ greatly in reproductive success within and across breeding seasons and on a lifetime basis (Le Boeuf & Reiter 1988). At Sea Lion Island, variation in mating success across males is the highest ever recorded for a vertebrate (Galimberti et al. 2002), and is reflected in the distribution of true genetic paternities (Fabiani et al. 2004). Dominance hierarchies show strong linearity (Galimberti et al. 2003), and access to females is related strictly to competitive success and dominance rank. Therefore, traits related to male competition are likely under strong selection. Vocalizations have a key role in establishing and maintaining dominance relationships in elephant seals of both species (Sandegren 1976; McCann 1981). Specific features of vocalizations and vocal behaviour that are important in dominance relationships among males are little known. Vocalizations seem to transmit information about the resource-holding potential of the emitter (Sanvito & Galimberti 2003). Therefore copying the syllable structure of successful males may be a form of cheating. In contrast, other acoustic features (frequency and intensity) seem to encode information about phenotype (Sanvito & Galimberti 2003), making the spread of truly dishonest signals unlikely. In any case, vocal communication plays integral roles in the social biology of elephant seals, and vocal-production learning seems to be an important mechanism by which male vocal attributes are acquired. An adaptive basis to the phenomenon could be related to short-term advantages of dishonest signalling, or general long-term advantages of acquiring vocal types that are familiar to individuals in the population. At present however, it seems most parsimonious to explain the phenomenon as a non-adaptive by-product of the tendency of young males to copy vocalizations of those males that they hear most frequently.

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