

DEVELOPMENT OF DISPLAY BEHAVIOR IN YOUNG CAPTIVE BEARDED SEALS

CAROLINE E. DAVIES
KIT M. KOVACS
CHRISTIAN LYDERSEN
Norwegian Polar Institute,
Polar Environment Center, 9296 Tromsø, Norway

SOFIE M. VAN PARIJS¹
Norwegian College of Fisheries Science,
University of Tromsø, N-9037 Tromsø, Norway
and
Bioacoustics Research Program,
Cornell Laboratory of Ornithology,
159 Sapsucker Woods Road, Ithaca,
New York 14850, U.S.A.
E-mail: sofie.vanparijs@noaa.gov

ABSTRACT

In this study of the ontogeny of vocal behavior in captive bearded seals, *Erignathus barbatus*, (three males and three females), only males exhibited vocal displays. The onset of display behavior coincided with sexual maturity. Males exhibited three types of dive displays associated with the performance of vocalizations. Vocalizing individuals were frequently attended by another male that maintained passive muzzle contact with the vocalizing male. These interactions were non-aggressive and might play a role in the establishment of a social hierarchy or they might allow the attendee to obtain “near-field” vocal information from the displaying male. Captive males’ vocalizations resembled those of males in the wild. However, display dives were shorter, and fewer vocalization types were documented among the captive males compared to bearded seals in the wild. The capacity of the captive males for producing well-formed, long calls with large frequency changes was also significantly less than for wild males. These capacities will likely develop further as the males grow older. Individual capacity for vocal production appears to develop gradually, showing plasticity in form development over time.

Key words: vocalization, dive displays, mating behavior, ontogeny, trills, bearded seals, *Erignathus barbatus*.

¹Address for correspondence: Northeast Fisheries Science Center, 166 Water Street Woods Hole, Massachusetts 02543-1026, U.S.A.

Courtship displays by males function for species identification and male–male competition as well as providing a basis in some species for female choice of potential mates (Bradbury and Vehrencamp 1998). In most species fighting between males is rare; assessment of male fitness usually occurs through a variety of sensory modalities, such as olfactory, acoustic, chemical, and visual displays (*e.g.*, Voigt and von Helversen 1999, Sacchi *et al.* 2003, Cooper and Goller 2004).

Pinnipeds use courtship displays during the breeding season. In most instances male displays are either vocal or visual in nature (see reviews in Insley *et al.* 2003, Rogers 2003, Stirling and Thomas 2003, Van Parijs 2003), although olfaction likely also plays a role within some species (*e.g.*, Hardy *et al.* 1991). In land-breeding species, a male's physical characteristics (*e.g.*, body size, tusk length) and vocal traits reflect male fitness and to a large extent determine reproductive success (see reviews in Boness 1991, Le Boeuf 1991). Little is still known about the characteristics that influence male fitness and reproductive success in aquatic-mating species. To date, acoustic and telemetry studies of wild animals or studies of captive animals have provided most information on aquatic male mating behavior (see Van Parijs 2003).

In aquatic-mating pinnipeds, the males of some species produce underwater vocalizations during the mating season, which serve in male competition and mate attraction (Van Parijs 2003; Hayes *et al.* 2004*a, b*). Dive displays are frequently associated with vocal display behavior (Van Parijs 2003). Females forage at sea when they are in oestrus (*e.g.*, Bowen *et al.* 1992, Boness *et al.* 1994, Lydersen *et al.* 1994, Thompson *et al.* 1994), which renders it impossible for males to monopolize large groups of females. In some species males hold discrete aquatic territories where they perform vocal and dive displays (Van Parijs *et al.* 1997, 2003*a*; Hayes *et al.* 2004*a, b*) targeting female travel routes, major foraging areas, or haul-out sites (Van Parijs *et al.* 1997, 2001). Male strategies differ between species. For example, harbor seal, *Phoca vitulina*, males exhibit a type of lek mating system (Van Parijs *et al.* 1997; Hayes *et al.* 2004*a, b*) while bearded seals, *Erignathus barbatus*, exhibit alternative mating strategies with males displaying either in small discrete territories or roaming over larger areas (Van Parijs *et al.* 2003*a*). Vocal characteristics of male displays show clear individual variation (Van Parijs *et al.* 2000, Rogers and Cato 2002, Van Parijs *et al.* 2003*b*, Hayes *et al.* 2004*a*) although stereotyped forms of vocalizations characterize breeding displays. In bearded seals, vocalizations differ significantly between males using the two different mating tactics with roaming males exhibiting calls that are shorter in duration than territorial males, a trait that may reflect male quality (Van Parijs *et al.* 2003*a*).

The ontogeny of display behavior has been studied in a variety of species (*e.g.*, Wilkinson and Huxley 1978, Tenthoren and Bergmann 1987, Henglmüller and Ladich 1991, Lovern and Jenssen 2001). Juveniles frequently display primitive forms of future adult mating-display behavior (*e.g.*, Goth and Jones 2003). For example pygmy marmosets, *Cebuella pygmaea*, produce babbling bouts that reduce in occurrence but are still observed in adults, and their vocalizations increase in diversity and structural formation with age (*e.g.*, Elowson *et al.* 1992, Snowdon and Elowson 2001). Juvenile exposure to varying environmental conditions can shape development and influence future adult display capabilities (*e.g.*, Redondo 1991, Groothuis 1992, Nicoletto 1996). In many bird species, juvenile vocalizations change gradually showing plasticity in development (*e.g.*, Ballintijn and Ten Cate 1997, Radford 2004).

Very little is known about the ontogeny of display behavior in pinnipeds. Studies of pup vocalizations have shown that call development is related to the need for

mother–pup recognition; although, the degree to which effective reunions are achieved varies widely (*e.g.*, Insley 2000, McCulloch and Boness 2000, Phillips and Stirling 2000, Insley 2001, Charrier *et al.* 2001, van Opzeeland and Van Parijs 2004). Unlike many other animal groups, the juvenile calls of pinnipeds do not seem to develop into part of the adult repertoire (*e.g.*, walrus, *Odobenus rosmarus*, Verboom and Kastelein 1995). Instead male vocal display behavior is thought to emerge around the onset of sexual maturity. This study examines the vocal and dive display activity in captive bearded seals from weaning to 6 yr of age. The aims were to (1) determine whether both sexes displayed and (2) pinpoint onset and development of this behavior in each individual.

METHODS

Three male and two female bearded seal pups were captured when they were between 3 and 5 wk of age (post-weaning, minimum weight of 80 kg) in Kongsfjorden, Svalbard, Norway ($78^{\circ}55'N$, $12^{\circ}30'E$) in May 1998 using a small motor boat and a hoop net (see Gjertz *et al.* 2000 for details on pup capture). They were then placed in wooden holding cages ($3\text{ m} \times 3\text{ m}$) containing snow on the research vessel F/F *Jan Mayen* where they were cared for by a qualified animal trainer during their passage back to the Norwegian mainland. They were transported to “Polaria” (<http://www.polaria.no/>), an aquarium facility located in Tromsø, Norway ($69^{\circ}40'N$, $18^{\circ}55'E$) where they were housed in a ($16\text{ m} \times 9\text{ m} \times 3.5\text{ m}$) pool containing 450,000 liters of seawater (Fig. 1). The two females died at the ages of 2 and 5 yr (the first in mid-2001 and the second in early 2003). The first female became lethargic and a postmortem showed that she had a bad heart. The other female developed a shoulder abscess and a veterinarian deemed it necessary to operate on her after having tried antibiotic treatments. She died while under anaesthesia. Three new female pups were captured

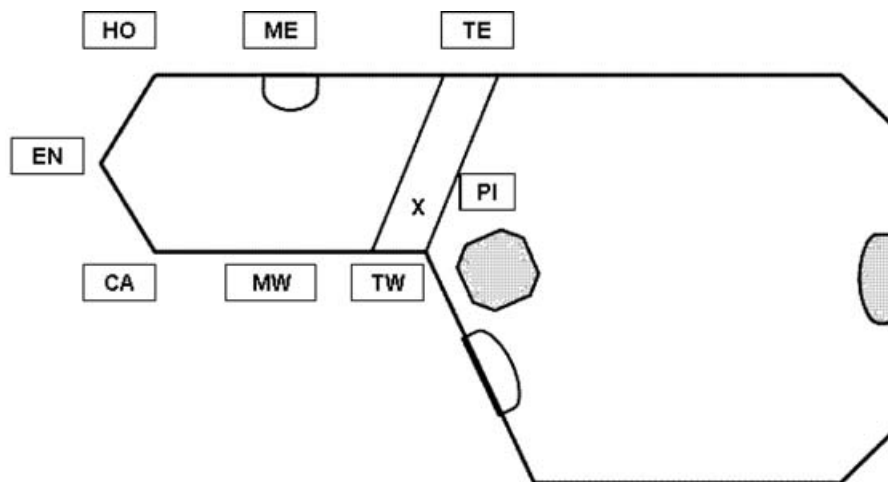


Figure 1. Aerial schematic of the pool ($16\text{ m} \times 9\text{ m} \times 3.5\text{ m}$) indicating the eight display locations used by the bearded seals: (1) PI, pillar, (2) TW, tunnel west, (3) MW mid-side west, (4) CA, cave, (5) EN, pool end, (6) HO, hosepipe, (7) ME, mid-side east, and (8) TE, tunnel east. Video recordings and visual observations were made at location “X.” The semicircles represent viewing windows and shaded areas represent solid pillars.

in May 2003 and introduced to the facility. All seals were caught and brought into captivity with permission from the Governor of Svalbard and the National Animal Care Committee.

All the seals were fed a diet of herring supplemented by vitamins. Individuals were easily identified by differences in pelage markings, but they also had varying vibrissae lengths and the animals also had individually numbered hind flipper tags, which differed in color depending on the sex of the animal. The seals were trained by the staff at "Polaria" for twice-daily shows and were, therefore, habituated to the presence of their trainers and to the public. A captive enrichment program was carried out with these animals so as to habituate them to their environment and to keep them active and interested. This study was carried out with permission and under supervision of the staff at the aquarium facility "Polaria." No bearded seal vocalizations were ever played to these seals. The dominance ranking of each individual was scored during all interactions related to food acquisition, with those obtaining access first being ranked higher than those obtaining food second, third, *etc.* All work was carried out in such a manner as to minimize disturbance to the seals. The seals used for this study remain in captivity.

Underwater vocalizations were recorded using a hydrophone (model HTI-96-MIN, High Tech Inc., Gulfport, MS; frequency response: 0.005–30 kHz \pm 1.0 dB; -165 dB re 1 V/ \pm Pa) fixed in position within a cavity in the edge of the seal tank at location HO (see Fig. 1) and a Sony TCD-D8 digital audio tape recorder (response: 0.005–22 kHz 1.0 dB). Staff at Polaria assisted this study by noting when vocalizations commenced and ceased, throughout the duration that they were in the facility (8+ h per day, every day of the week). No display vocalizations were heard during the first three springs in captivity. Vocal behavior when it occurred was clearly audible throughout the entire aquarium facility, including the offices, therefore, it is unlikely that the presence of vocalizations was missed during opening hours but it is possible that they occurred during the night. Vocalizing individuals were identified by the presence of an inflated throat and in some cases the presence of bubbles.

In February and March 2002 (5 d) and 2003 (4 d), opportunistic acoustic recordings of vocalizing individuals were made by S. Van Parijs. Vocalizing individuals were identified by their posture, the inflation of their vocal tract, and in some cases the presence of bubbles related to call production. Similar vocal display behavior has been well documented in the wild for harbor seals (Nicolson 2001). From late March to early June 2004 (71 d), daily observations of the bearded seals were made between 0800 and 1200 from an underwater viewing tunnel situated beneath a section of the pool (Fig. 1). The presence or absence of vocal behavior in each of the individuals was monitored by the aquarium staff until April 2006.

During the study hours the facility was closed to the public, allowing undisturbed observations to be made. To minimize disturbance to the seals and ensure constant observation conditions, a routine was followed each day, taking observations from the same position within the tunnel and remaining quiet. The focus of this study was on vocalizing individuals and their behavior. Focal sampling began when an individual started to vocalize; we called this the start of a "display bout." A display bout ended when an individual surfaced to breathe. The following behavioral data were collected on the vocalizing individual during each display bout: (1) identity and sex, (2) location within the pool, (3) behavior while vocalizing, (4) the number of vocalizations within a bout, (5) dive duration (s), (6) whether the individual vocalized alone or with an attending individual, (7) sex and behavior of the attending individual, and (8) interactions between non-vocal individuals or attending individuals during or directly after the vocalization bout. Collection of behavioral data lasted throughout

the duration of a display bout. Video footage was made for illustrative purposes using a digital video camera (Sony Handycam DCR-TRV950 Mini DV Digital Camcorder). Based on preliminary observations of pool usage, the pool area was divided into eight locations used by individuals for display purposes: (1) PI, pillar; (2) TW, tunnel west; (3) MW mid-side west; (4) CA, cave; (5) EN, pool end; (6) HO, hosepipe; (7) ME, mid-side east; and (8) TE, tunnel east (Fig. 1). The tunnel was covered by a transparent dome.

All acoustic recordings where more than one individual vocalized or where the individual was unknown were discarded. This ensured that recordings came only from known individuals. Acoustic recordings were transformed into spectrograms using Gram Version 4.1.2 (Fast Fourier Transform: dt: 12 ms, df: 102 Hz, FFT size: 1,024). All calls were separated on the basis of their spectrogram quality into poor, fair, or good calls (see Van Parijs *et al.* 2004). Only good-quality calls were selected for further analysis. Forty calls were analyzed for each individual per recording day. Seven vocal parameters were measured for each vocalization: (1) total duration (s), (2) start frequency, startF (kHz) (3) end frequency, endF (kHz), (4) minimum frequency, minF (kHz), (5) maximum frequency, maxF (kHz), (6) frequency change, FCH (maximum–minimum frequency) (kHz), and (7) number of steps (inflections) within a call (see Van Parijs *et al.* 2001 for more details regarding these measurements). Parameter measurements were made directly from the spectrograms on screen (cursor error: ± 6 ms; ± 22 Hz). In addition, sounds that introduced or followed a call, short ascents and descents, were noted when present. An ascent was defined as a rapid rise in frequency, which could occur either prior to the call (ascS) or at the end of the call (ascE). A descent was defined as a rapid fall in frequency at the end of the call. The overall form of each call was noted as to whether the call descended in frequency, remained at a constant frequency or ascended in frequency. Based on this information vocalizations were classed into call types (based on call types identified in Van Parijs *et al.* 2001).

Variation within and between individuals was explored using classification trees (CARTS). Tree-based methods offer a useful approach to exploring complex data (for mathematical details see Chapter 10 in Venables and Ripley [1999] and D'eath and Fabricius [2000]). CARTS are generated by repeated binary splitting of a data set, so that each split minimizes the probability of misclassification of the classifying variable (in this instance, individual). Splits sequentially generate the most homogenous possible groups. With noisy data, trees can become overly large, and pruning is used to achieve an optimal tree. CARTS are an analytical tool that is now widely used (for more details and examples see, *e.g.*, Van Parijs and Corkeron 2002, Oswald *et al.* 2003, Van Parijs *et al.* 2003, van Opzeeland and Van Parijs 2004). Analyses were carried out in R, version 1.9.1 (Ithaka and Gentleman 1996), using the RPART library version 3.1-5 for CARTS, and the MASS library version 6.3-2 for other analyses.

RESULTS

Display Behavior

Display behavior was composed of both display dives and underwater vocalizations. It was only ever observed in males in this study. Females never vocalized or carried out stereotypic dive displays. The females rarely came into the area of the pool where the males preferred to display and when they did they showed no interest in the males, *i.e.*, they did not approach or interact with them and remained at a distance. Male A

Table 1. The percentage of time the three captive male bearded seals (A, B, C) exhibited each of the three dive display behaviors (1 = static, 2 = tail dive, 3 = head dive) and the percentage of time spent displaying at the eight locations within the aquarium. *n* indicates the number of observed display bouts.

Male	Display behavior %			Pool location %								<i>n</i>
	1	2	3	PI	TW	MW	CA	EN	HO	ME	TE	
A	47	31	22	1	18	11	32	17	9	11	1	401
B	79	7	14	0	9	9	63	6	6	7	0	282
C	85	15	0	15	2	1	76	3	1	1	1	156
Total	65	20	15	3	12	9	49	11	7	8	1	839

began to display sporadically in March 2002 at the age 4 yr, while males B and C began to display in late March 2003 at the age 5 yr. All three males displayed during most days in the 2004 study period. From their introduction to the aquarium until the end of this study the difference in the weight of the three males was negligible. Male A was the dominant individual within the group, with B being dominant over C. From a total of 904 min of recordings a total of 3,522 good-quality calls were measured in 2002 ($n = 213$), 2003 ($n = 173$), and 2004 ($n = 3,136$).

All three males were primarily observed vocalizing in one half of the pool. Within this area, the individual males showed somewhat different spatial preferences for display locations (Table 1). Once at a display location, an individual would remain there for the duration of the display bout. All three males spent the majority of their display time at location CA (49%). Male A divided his display time between all eight locations, spending 32% of his time at location CA. Male B displayed at location CA for 63% and male C for 76% of the observations.

At the start of a display bout a male would establish himself at a given location in the pool and assume a characteristic posture with his body in a rigid posture, neck retracted with the throat enlarged and head back (Fig. 2a). He would then begin to vocalize. During each display bout, an individual would maintain one of three possible display behaviors throughout the bout. Dive displays were not correlated with pool location. The three dive displays were—type 1: static, the individual vocalized while their body remained rigid in a set position, either vertical midway within the water column or horizontal at the surface (Fig. 2a), type 2: tail dive, the individual had their body in a vertical position, actively descending tail first in the water column and then passively floating back up to the surface vocalizing during both the descent and ascent phases (Fig. 2b), and type 3: head dive, the individual performed a head-first dive to the pool floor and then passively floated up to the surface vocalizing only during the ascent phase (Fig. 2c, d). Eighty-two percent of the time type 2 displays were followed by a type 3 display as the individual came to the surface and pushed back down into the water. All three males performed type 1 and type 2 displays, with type 1 being the dominant display behavior observed (Table 1). Only males A and B performed the third display type.

During a display bout, males produced an average of $4 \text{ s} \pm 2.4 \text{ SD}$ ($n = 390$) vocalizations, with each display bout lasting an average of $42.5 \text{ s} \pm 17.4 \text{ SD}$ ($n = 382$). Individuals would occasionally release bubbles while vocalizing. Bubbles did not indicate that the individual was about to surface as all the males continued to vocalize during a display bout regardless of whether they produced bubbles or not.

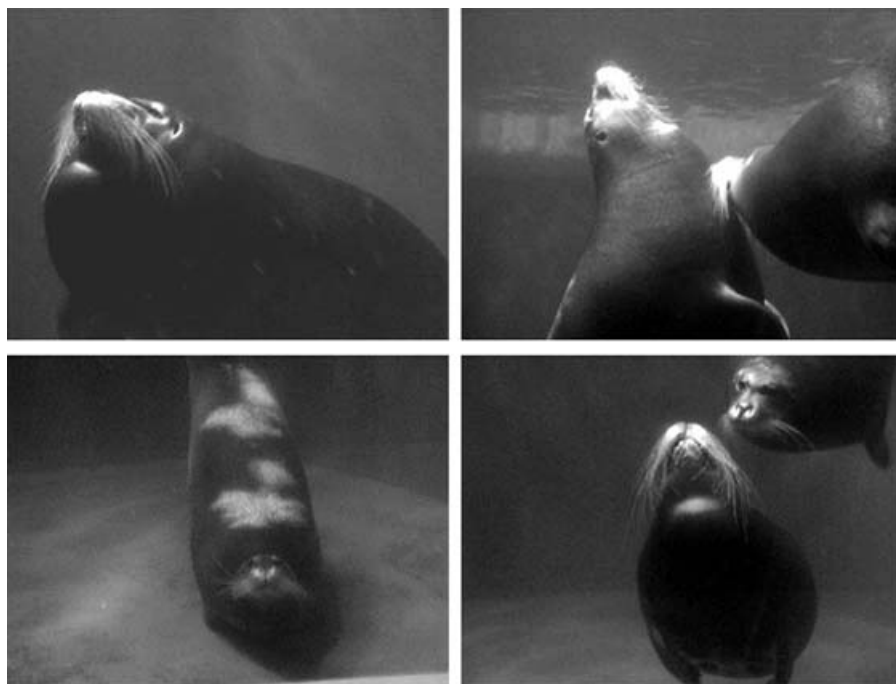


Figure 2. Underwater images of captive male bearded seal display behavior while vocalizing: (a) the characteristic type 1 display posture with the body in a rigid position, neck retracted, throat enlarged, and head tipped back, (b) a type 2 display with a male in attendance maintaining passive muzzle contact, (c) the descent phase of a type 3 display, and (d) vocalizing during the ascent phase of a type 3 display.

Individuals were not seen to produce bubbles when not engaged in display behavior. During a display bout a male either vocalized alone or with one or two attending males that maintained passive muzzle contact with the throat of the vocalizing individual (Fig. 3b, Table 1). Attending individuals were always other males; females were never seen approaching a vocalizing individual. The attending individual maintained muzzle contact until the display bout was completed and often remained in close proximity to the vocalizing individual for a few minutes thereafter. Males A and B spent most of their time either alone or with one attending male, and were only rarely seen vocalizing with two attending males (Table 2). Male C predominately displayed alone and was never seen with two attending males.

Display bout durations of the captive individuals were compared to 22 individuals that were followed with focal animal sampling in the wild (details can be found in Van Parijs *et al.* 2003). Mean (\pm SD) display dive duration of wild males ($113.0 \text{ s} \pm 65.2$) was significantly longer than that of captive males ($42.5 \text{ s} \pm 17.4$) (ANOVA: $F_{1,1,200} = 101.2$, $SS = 5,003$, $P < 0.001$).

Vocal Development

The vocalization types used by the three captive males fell into two categories, the trill and the moan (Fig. 3). Moans were low-frequency flat tonal calls while trills

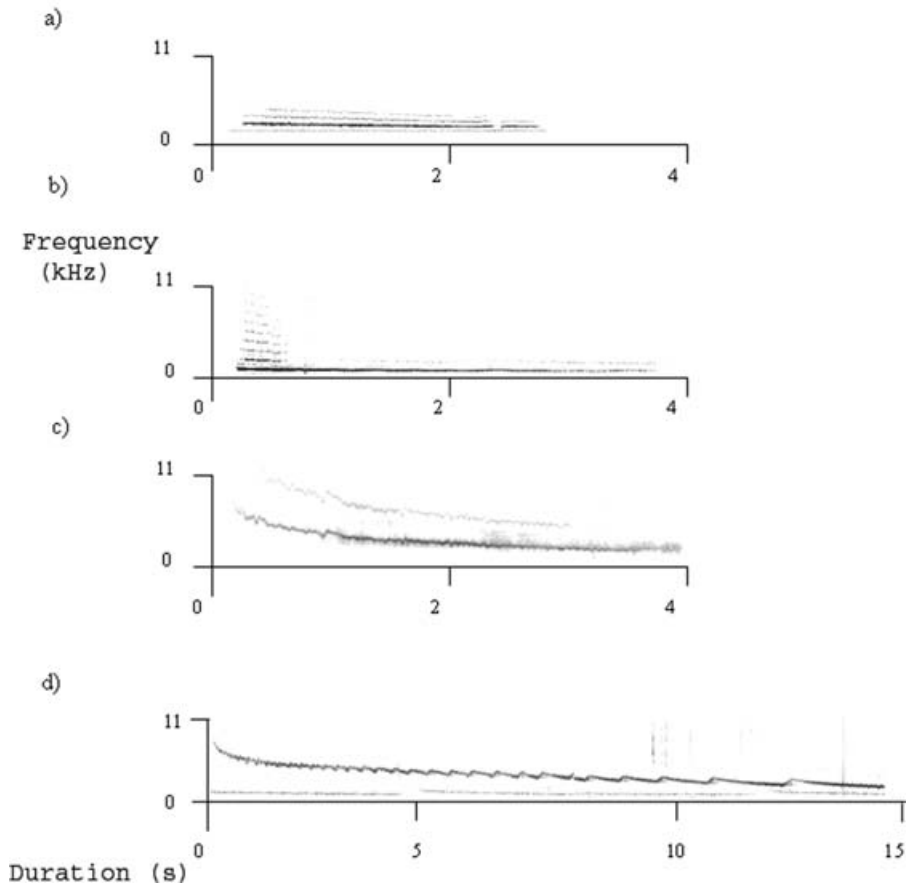


Figure 3. Spectrograms of the two call types used by the three captive male bearded seals, the (a) moan and (c) trill. Alongside them are examples of spectrograms of the (b) moan and (d) trill from male bearded seals in the wild, recorded in Svalbard, Norway.

cascade down in frequency increments called “steps” starting at higher frequencies than moans. CART analyses showed clear individual variation between males. Both call types, the trill and the moan, split according to the individual based on the duration of the calls. Male A had considerably longer calls than either males B and C, while B’s calls were longer than C’s. Overall, 4% of calls were misclassified for the trills ($n = 113$ of 2,831) and 12% of moans were misclassified ($n = 28$ of 691).

Temporal changes in vocal behavior were also apparent. Data were only available over a 3-yr period for male A. For this individual duration determined the split in the first node, splitting 2002 and 2003 from 2004 for both call types. Frequency change split both call types during the first 2 yr. Therefore, changes in frequency range within an individual changed most in the first years of vocalizing; while lengthening of the call duration became more predominant later on (Fig. 4 shows a visual representation of these changes for the trill call type). For trills 3.7% of calls were misclassified for

Table 2. The attendance patterns of the three captive displaying male bearded seals (A, B, C). A male either displayed (Caller) on his own (0 Attender's) or with one (1A) or two (2A) males in attendance. *n* indicates the number of observed display bouts.

Male	Caller:Attender %			<i>n</i>
	1C:0A	1C:1A	1C:2A	
A	64	33	3	401
B	54	38	8	282
C	94	6	0	156
Total	67	29	4	839

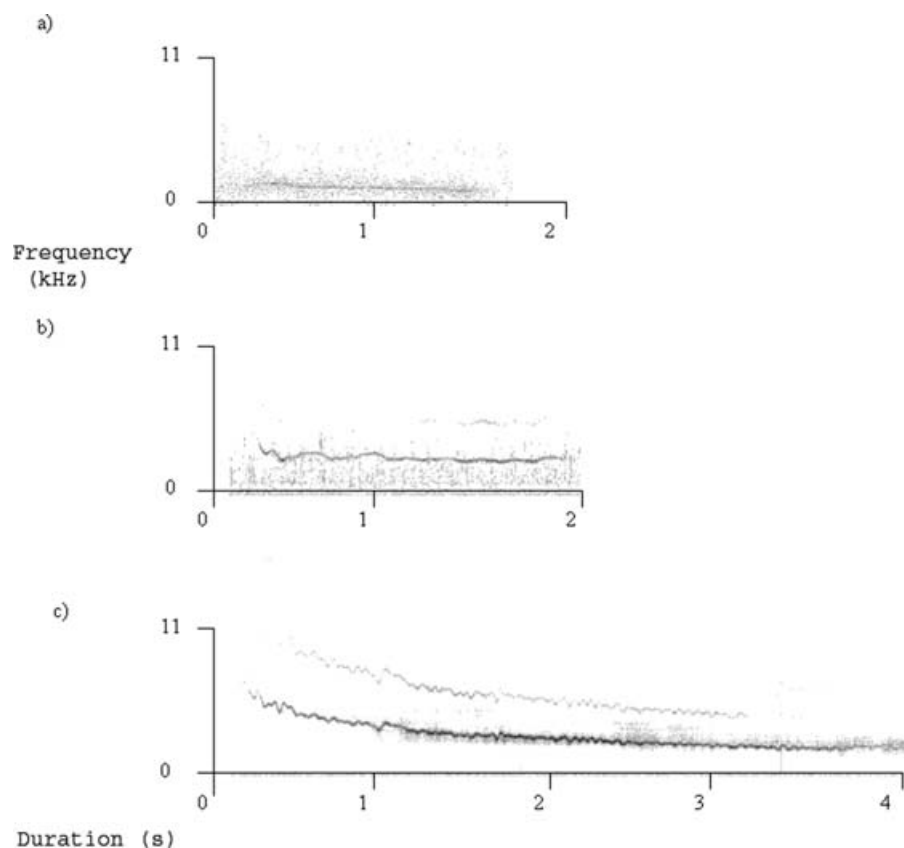


Figure 4. Example spectrograms for the trill vocalization type of Male A in (a) 2002 (at 4 yr of age), (b) 2003 (at 5 yr), and (c) 2004 (at 6 yr).

the first node and 4.2% in the second. While for the moan the numbers were slightly higher with 9.6% and 6.1% of calls being misclassified at the first and second nodes, respectively.

The vocalizations produced by the captive males were compared with the same call types used by wild males. Vocalizations from wild males were taken from 14 male

Table 3. Descriptive statistics (mean \pm SD) for the trill ($n = 2,831$) and moan ($n = 691$) call types produced by three captive male bearded seals during display behavior. Similar data for the trill ($n = 2,855$) and the moan ($n = 351$) from 14 wild male bearded seals for comparison from Van Parijs *et al.* (2001).

Vocal type	Vocal parameters	Captive males	Wild males
Trill	Duration (s)	6.3 \pm 2.4	29.2 \pm 15.3
	Start frequency (kHz)	4.3 \pm 1.2	3.9 \pm 1.9
	End frequency (kHz)	2.4 \pm 1.2	0.3 \pm 0.4
	Minimum frequency (kHz)	2.2 \pm 1.4	0.2 \pm 0.1
	Maximum frequency (kHz)	4.4 \pm 2.1	5.6 \pm 1.3
	Frequency change (kHz)	1.9 \pm 1.1	5.4 \pm 2.4
	Frequency range (kHz)	0.8 to 5.8	0.1 to 6.2
	No. of steps	3 to 17	2 to 53
Moan	Duration (s)	5.6 \pm 3.3	7.4 \pm 5.1
	Start frequency (kHz)	1.2 \pm 0.9	1.4 \pm 0.2
	End frequency (kHz)	0.8 \pm 0.4	0.6 \pm 0.4
	Minimum frequency (kHz)	0.7 \pm 0.1	0.5 \pm 0.3
	Maximum frequency (kHz)	1.2 \pm 0.7	9.1 \pm 4.5
	Frequency change (kHz)	0.5 \pm 0.3	6.3 \pm 3.9
	Frequency range (kHz)	0.3 to 9	0.1 to 13.5
	No. of steps	0	0

bearded seals recorded during April and May 1999 within Kongsfjorden, Svalbard (Van Parijs *et al.* 2001). For each individual, a minimum of 15 vocalizations were used for the moan and 200 for the trill. Given that the trill is the most predominant call type in this species' repertoire, it was possible to use a much larger sample size in these analyses. All three captive males produced both the trill and the moan. The trills of captive males were significantly shorter in duration (ANOVA: $F_{1,5,685} = 73.4$, $SS = 3,308$, $P < 0.001$), the frequency change was smaller (ANOVA: $F_{1,5,685} = 112$, $SS = 6,012$, $P < 0.001$) and the end frequency was higher (ANOVA: $F_{1,5,685} = 56.3$, $SS = 1,021$, $P < 0.001$) compared with wild males (Table 3). The number of steps in trills of the captive males was significantly fewer (ANOVA: $F_{1,5,685} = 54.1$, $SS = 1,799$, $P < 0.001$) and each step was less consistent in shape compared with wild males (see Fig. 3c, d for a visual comparisons). The moan vocalization was also shorter in duration and the frequency change was smaller in captive males compared with wild males (ANOVA: $F_{1,1,041} = 60.4$, $SS = 1,203$, $P < 0.001$). Furthermore the maximum frequency in wild males was higher than for captive males (ANOVA: $F_{1,1,041} = 53.8$, $SS = 1,006$, $P < 0.001$).

DISCUSSION

Studies of bearded seals in the wild have shown that males perform stereotypic vocal and dive displays during the mating season (Van Parijs *et al.* 2001). However, these studies lacked conclusive evidence to support the hypothesis that only males vocalized during the mating season (Van Parijs 2003), although all circumstantial evidence certainly suggests that this is the case. This study provides further information to suggest that male bearded seals vocalize underwater while females remain silent.

However, given that only one female reached the age of 5 yr, further observation is needed to determine whether this statement can be upheld.

Detailed behavioral data are difficult to obtain for aquatic-mating pinnipeds given the logistical difficulties involved in studying these species in the wild. A study of this nature was only possible with captive animals. Nonetheless it is important to recognize that captivity can influence individuals in markedly different ways from wild animals. Underwater display behavior such as vocalizing, and bubble blowing have been described for male harbor seals (*e.g.*, Allen 1985). These behaviors have been shown to be linked to the dominance rank of an individual with adult males exhibiting significantly more of these activities than subadult males (Nicolson 2001). Our study showed that male bearded seals use at least three different dive display behaviors, with individual males showing preferences for a particular display type. Male attendance behavior associated with the displays consisted of passive muzzle contact with a vocalizing male. There are no known reports of similar behavior in animals other than pinnipeds, but similar attendance behavior has been observed in wild male harbor seals, where it was hypothesized that this behavior may be linked to the establishment of a social hierarchy (Nicolson 2001). The vocalizing individual may use this behavior as a method for conveying information on dominance ranking. Our study provides supports this theory. For example, male C was the subordinate individual and correspondingly he was attended the least of the three males and displayed the least. Male A, the most dominant individual, began vocalizing a year before the other two. Another factor separating the three individuals is call duration with calls being longer for the most dominant individual, male A, shorter for B, and shortest for C, the least dominant male. Call duration has already been shown to be linked to alternative mating strategies for males in the wild, with territorial males exhibiting the longer calls compared to roaming males in Svalbard (Van Parijs *et al.* 2003). The possible link between increased call duration and male mating success and/or lung capacity was also made.

An additional or alternative hypothesis to that of "dominance rank" may be that attending males are gaining near-field acoustic information that is not available by listening in the far field (Bradbury and Vehrencamp 1998). Pinnipeds have exceptionally sensitive vibrissae, which have been shown to be capable of detecting minute water movements, which should allow seals to gain hydrodynamic information resulting from movements of other aquatic animals (Denhardt *et al.* 1998). Therefore, the potential sound information available to individuals in the near field as opposed to the far field requires further investigation.

The exposure of the captive males under study in this investigation to other bearded seals in the wild was short, as they were captured just after weaning (between 3 and 5 wk of age). Bearded seal pups swim at birth (*e.g.*, Lydersen *et al.* 2002) and it is, therefore, likely that they were exposed to underwater vocalizations and potentially may have observed displaying males during the time they were with their mothers. The impact of such early exposure to mating behavior is hard to evaluate. The captive males in this study began to vocalize when they were either 4 or 5 yr of age. Wild bearded seals males reach sexual maturity at around 6 yr of age when males weigh approximately 240 kg (Andersen *et al.* 1999). The captive males began displaying when their body weight ranged between 230 and 250 kg (Fig. 2) demonstrating that this behavior is linked to the onset of sexual maturity, which the captives reached at an early age.

The naive display behavior of the captive males strongly resembled that of wild males (Van Parijs *et al.* 2003). However, there were clear differences in vocal behavior

with the young captive males exhibiting only two of the four known mating-display vocalization types documented in wild seals (Van Parijs *et al.* 2001). Furthermore, vocalizations were shorter in duration, they occurred within a smaller frequency range and they were less well formed in structure compared to wild males. This suggests that young males acquire the capacity for better vocal control through practice. The capacity for control over frequency change is important during the initial phase of vocal development while the capacity to produce longer calls seems to emerge with time. The length of the display bouts in captive males was considerably shorter than those of wild males. It seems unlikely that sufficient information for producing both vocal and dive displays would have been gained during their brief exposure to wild bearded seals in order for this to have influenced the development of their display behavior 4 or 5 yr later at sexual maturity. Individual capacity for vocal production appears to develop gradually, showing plasticity in form development over time.

ACKNOWLEDGMENTS

We thank the staff at Polaria for their help throughout the duration of this project. Thanks also go to the R Core Development team for producing and releasing their powerful program for open source use. SVP was funded by a postdoctoral fellowship from the University of Tromsø, Norway. All other financial support for this study was provided by the Norwegian Polar Institute. Thanks also go to Steve Insley, Nicolas Mathevon, and an anonymous reviewer for their constructive comments on this manuscript.

LITERATURE CITED

- ALLEN, S. G. 1985. Mating behavior in the harbor seal. *Marine Mammal Science* 1:84–87.
- ANDERSEN, M., A. M. HJELSET, I. GJERTZ, C. LYDERSEN AND B. GULLIKSEN. 1999. Growth, age at sexual maturity and condition in bearded seals (*Erignathus barbatus*) from Svalbard, Norway. *Polar Biology* 21:179–185.
- BALLINTIJN, M. R., AND C. TEN CATE. 1997. Vocal development and its differentiation in a non-songbird: The collared dove (*Streptopelia decaocto*). *Behaviour* 134:595–621.
- BONESS, D. J. 1991. Determinants of mating systems in the *Otariidae* (*Pinnipedia*). Pages 1–44 in D. Renouf, ed. *Behavior of pinnipeds*. Chapman and Hall, London, U.K.
- BONESS, D. J., W. D. BOWEN AND O. T. OFTEDAL. 1994. Evidence of a maternal foraging cycle resembling that of Otariid seals in a small phocid, the harbor seal. *Behavioural Ecology and Sociobiology* 34:95–104.
- BOWEN, W. D., O. T. OFTEDAL AND D. J. BONESS. 1992. Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). *Physiological Zoology* 65:844–866.
- BRADBURY, J. W., AND S. L. VEHRENCAMP. 1998. Mating games and signalling. Pages 743–982 in *Principles of animal communication*. Sinauer Associates, Inc., Sunderland, MA.
- CHARRIER, I., N. MATHEVON AND P. JOUVENTIN. 2001. Mother's voice recognition by seal pups. *Nature* 412:873.
- COOPER, B. G., AND F. GOLLER. 2004. Enhancement and constraint of song motor patterns by visual display. *Science* 303:544–546.
- D'EATH, G., AND K. E. FABRICIUS. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192.
- DEHNHARDT, G., B. MAUCK AND H. BLECKMANN. 1998. Seal whiskers detect water movements. *Nature* 394:235–236.
- ELOWSON, A. M., C. T. SNOWDON AND C. J. SWEET. 1992. Ontogeny of trill and J-call vocalizations in the pygmy marmoset, *Cebuella pygmaea*. *Behaviour* 43:703–715.

- GJERTZ, I., K. M. KOVACS, C. LYDERSEN AND Ø. WIIG. 2000. Movements and diving of bearded seal (*Erignathus barbatus*) mother and pups during lactation and post-weaning. *Polar Biology* 23:559–566.
- GROOTHUIS, T. 1992. The influence of social experience on the development and fixation of the form of displays in the black headed gull. *Animal Behaviour* 43:1–14.
- GOTH, A., AND D. N. JONES. 2003. Ontogeny of social behavior in the megapode Australian brush-turkey (*Alectura lathami*). *Journal of Comparative Psychology* 117:36–43.
- HARDY, M. H., E. ROFF, T. G. SMITH AND M. RYG. 1991. Facial skin glands of ringed and gray seals, and their possible function as odoriferous organs. *Canadian Journal of Zoology* 69:189–200.
- HAYES, S. A., D. P. COSTA, J. T. HARVEY AND B. J. LE BOEUF 2004a. Aquatic mating strategies of the male Pacific harbor seal (*Phoca vitulina richardii*): Are males defending the hotspot? *Marine Mammal Science* 20:639–656.
- HAYES, S. A., A. KUMAR, D. P. COSTA, D. K. MELLINGER, J. T. HARVEY, B. L. SOUTHALL AND B. J. LE BOEUF. 2004b. Evaluating the function of the male harbour seal, *Phoca vitulina*, roar through playback experiments. *Animal Behaviour* 67:1133–1139.
- HENGLMÜLLER, S. M., AND F. LADICH 1999. Development of agonistic behaviour and vocalization in croaking gouramis. *Journal of Fish Biology* 54:380–395.
- INSLEY, S. J. 2000. Long term vocal recognition in the northern fur seal. *Nature* 406:404–405.
- INSLEY, S. J. 2001. Mother-offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Animal Behaviour* 61:129–137.
- INSLEY, S. J., A. V. PHILLIPS AND I. CHARRIER. 2003. A review of social recognition in pinnipeds. *Aquatic Mammals* 29:181–201.
- IHAKA, R., AND R. GENTLEMAN 1996. R: A language for data analysis and graphics. *Journal of Computer and Graphical Statistics* 5:299–314.
- LE BOEUF, B. J. 1991. Pinniped mating systems on land, ice and in the water: Emphasis on the Phocidae. Pages 45–64 in D. Renouf, ed. *Behavior of pinnipeds*. Chapman and Hall, London, U.K.
- LOVERN, M. B., AND T. A. JENSSSEN. 2001. The effects of context, sex, and body size on staged social interactions in juvenile male and female green anoles (*Anolis carolinensis*). *Behaviour* 138:1117–1135.
- LYDERSEN, C., M. O. HAMMILL AND K. M. KOVACS. 1994. Diving activity in nursing bearded seal (*Erignathus barbatus*) pups. *Canadian Journal of Zoology* 72:86–103.
- LYDERSEN, C., K. M. KOVACS, S. RIES AND M. KNAUTH. 2002. Precocial diving and patent foramen ovale in bearded seal (*Erignathus barbatus*) pups. *Journal of Comparative Physiology B* 172:713–717.
- MCCULLOCH, S., AND D. J. BONESS 2000. Mother-pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada. *Journal of Zoology* 251:449–455.
- NICOLETTO, P. F. 1996. The influence of water velocity on the display behavior of male guppies, *Poecilia reticulata*. *Behavioral Ecology* 3:272–278.
- NICHOLSEN, T. 2001. Underwater behaviour and social structure of harbor seals (*Phoca vitulina*) off Monterey, California. M.Sc. thesis, San Francisco State University, San Francisco, CA. 98 pp.
- OSWALD, J. N., J. BARLOW AND T. F. NORRIS. 2003. Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. *Marine Mammal Science* 19:20–37.
- PHILLIPS, A. V., AND I. STIRLING. 2000. Vocal individuality in mother and pup South American fur seals, *Arctocephalus australis*. *Marine Mammal Science* 16:592–616.
- RADFORD, A. N. 2004. Voice breaking in males results in sexual dimorphism of green wood-hoopoe calls. *Behaviour* 141:555–569.
- REDONDO, T. 1991. Early stages of vocal ontogeny in the magpie (*Pica pica*). *Journal fur Ornithologie* 132:145–163.
- ROGERS, T. L. 2003. Factors influencing the acoustic behaviour of male phocid seals. *Aquatic Mammals* 29:247–260.

- ROGERS, T. L., AND D. H. CATO. 2002. Individual variation in the acoustic behaviour of the adult male leopard seal, *Hydrurga leptonyx*. *Behaviour* 139:1267–1286.
- SACCHI, R., P. GALEOTTI, M. FASOLA AND D. BALLASINA. 2003. Vocalizations and courtship intensity correlate with mounting success in marginated tortoises *Testudo marginata*. *Behavioral Ecology and Sociobiology* 55:95–102.
- SNOWDON, C. T., AND A. M. ELWSON. 2001. 'Babbling' in pygmy marmosets: Development after infancy. *Behaviour* 138:1235–1248.
- STIRLING, I., AND J. A. THOMAS. 2003. Relationships between underwater vocalizations and mating systems in phocid seals. *Aquatic Mammals* 29:227–246.
- TENTHOREN, B., AND H. H. BERGMANN. 1987. Changing and constancy of characteristics in young vocal development of Barnacle geese (*Branta leucopsis*). *Behaviour* 100:61–91.
- THOMPSON, P. M., D. MILLER, R. COOPER AND P. S. HAMMOND. 1994. Changes in the distribution of female harbor seals during the breeding season—implications for their lactation strategy and mating patterns. *Journal of Animal Ecology* 63:24–30.
- VAN OPZEELAND, I. C., AND S. M. VAN PARIJS. 2004. Individuality in harp seal (*Phoca groenlandica*) pup vocalizations. *Animal Behaviour* 68:1115–1123.
- VAN PARIJS, S. M. 2003. Aquatic mating in pinnipeds: A review. *Aquatic Mammals* 29:214–226.
- VAN PARIJS, S. M., AND P. J. CORKERON. 2002. Ontogeny of vocalisations in infant black flying foxes, *Pteropus alecto*. *Behaviour* 139:1111–1124.
- VAN PARIJS, S. M., P. M. THOMPSON, D. J. TOLLIT AND A. MACKAY. 1997. Distribution and activity of male harbour seals during the mating season. *Animal Behaviour* 54:35–43.
- VAN PARIJS, S. M., G. D. HASTIE AND P. M. THOMPSON. 2000. Individual and geographic variation in the vocal behaviour of the harbour seal. *Animal Behaviour* 59:559–568.
- VAN PARIJS, S. M., K. M. KOVACS AND C. LYDERSEN. 2001. Spatial and temporal distribution of vocalising male bearded seals—implications for male mating strategies. *Behaviour* 138:905–922.
- VAN PARIJS, S. M., C. LYDERSEN AND K. M. KOVACS. 2003a. Vocalisations and movements suggest alternative mating tactics in male bearded seals. *Animal Behaviour* 65:273–283.
- VAN PARIJS, S. M., P. J. CORKERON, J. HARVEY, S. A. HAYES, D. MELLINGER, P. ROUGET, P. M. THOMPSON, M. WAHLBERG AND K. M. KOVACS. 2003b. Regional patterns in vocalizations of male harbor seals. *The Journal of the Acoustical Society of America* 113:3403–3410.
- VAN PARIJS, S. M., C. LYDERSEN AND K. M. KOVACS. 2004. The effects of ice cover on the behavior of aquatic mating male bearded seals. *Animal Behaviour* 68:89–96.
- VENABLES, W. N., AND B. D. RIPLEY. 1999. *Modern applied statistics with S-PLUS*. 3rd Version. Springer-Verlag, New York, NY.
- VERBOOM, W. C. A., AND R. A. KASTELEIN. 1995. Rutting whistles of a male Pacific walrus (*Odobenus rosmarus divergens*). Pages 45–64 in R. A. Kastelein, J. A. Thomas and P. Nachtigall, eds. *Sensory systems of aquatic mammals*. De Spil Publishers, Woerden, The Netherlands.
- VOIGT, C. C., AND O. VON HELVERSEN. 1999. Storage and display of odour by male *Saccolpteryx bilineata* (Chiroptera, Emballonuridae). *Behavioral Ecology and Sociobiology* 47:29–40.
- WILKINSON, R., AND C. R. HUXLEY. 1978. Vocalizations of chicks and juveniles and development of adult calls in Aldabra white-throated rail, *Dryolimnas cuvieri aldabranus* (Aves Rallidae). *Journal of Zoology London* 186:487–505.

Received: 6 December 2005

Accepted: 10 April 2006

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:
Supplementary Movie