Vocal development in captive harbor seal pups, *Phoca vitulina richardii*: Age, sex, and individual differences a)

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The goal of this research was to determine when harbor seal pup vocalizations become sufficiently distinctive to allow individual recognition. A total of 4593 calls were analyzed from 15 captive pups. Nineteen were harsh, broadband, staccato calls used in an aggressive context. The rest were tonal “mother attraction calls,” having an inverted “v”- or “u”-shaped spectrogram with harmonics and a fundamental frequency around 200–600 Hz. Calls were individually distinctive even in pups less than 2 weeks old, suggesting that mothers may be able to recognize pup vocalizations at this early age. Classification rates from discriminant function analysis were generally comparable to those of other phocids and less than in otariids, supporting the theory that recognition is more highly developed in otariids. Significant differences were found between male and female pup calls, and there were significant interactions between pup sex and age. The results of this study should be interpreted with caution until the findings are verified in wild harbor seal pups. © 2006 Acoustical Society of America [DOI: 10.1121/1.2226530]

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I. INTRODUCTION

Parent-offspring vocal recognition is common in many birds and mammals, and increases reproductive success by restricting parental care to genetically related offspring. Among pinnipeds, vocal recognition is widespread, although it is considered better developed in otariids (fur seals and sea lions) than in phocids (true seals) (see Insley et al., 2003 for a review). An important factor driving the evolution of recognition in pinnipeds may be the maternal strategy, with long periods of dependence and maternal separations correlated with mutual recognition (Insley, 1992; Insley et al., 2003). Otariids have a “foraging cycle strategy” marked by a long period of offspring dependence during which the mother alternates foraging trips to sea with time on land to nurse her pup (Bonner, 1984; Ofstedal et al., 1987). In contrast, many phocids have a “fasting strategy” in which mothers remain close to their pups for a short and intense lactation period (Bonner, 1984; Ofstedal et al., 1987). The finding that harbor seals forage during lactation challenged the traditional dichotomy of the otariid foraging cycle strategy and the phocid fasting strategy (Bowen et al., 1992). This begs the question of whether harbor seals have faced greater selective pressure on mother-pup recognition than have other phocids.

Female harbor seals give birth to a single pup annually, and the unusually precocial pups follow their mothers both on land and in the water within minutes. Unlike most pinnipeds, female harbor seals do not emit a “pup attraction call.” The pups, however, are quite vocal and begin to emit “mother attraction calls” several hours after birth (Lawson and Renouf, 1985). These calls presumably function to aid the mother and pup in maintaining contact and reuniting once separated (Renouf, 1984). Preliminary research found that pup calls appeared to be individually distinctive (Perry and Renouf, 1988; Renouf, 1984), and a captive adult was able to distinguish between playbacks recorded from different pups (Renouf, 1985).

Parents typically begin to recognize offspring calls just after they become individually distinctive and before offspring intermingle with conspecifics (bank swallow: Beecher et al., 1981a; McArthur, 1979; razorbill: Insley et al., 2003; McArthur, 1982; goat: Lenhardt, 1977). In pinnipeds, the ability to recognize pup calls immediately postpartum has not been tested, and factors affecting the ontogeny of recognition are unknown. Insley (2001) suggested that the critical time for otariids is 1–2 weeks postpartum when the mother leaves on her first foraging trip. Subantarctic fur seal mothers that were tested 7 months after parturition recognized playbacks from 1–2-day-old pups (Charrier et al., 2003a), suggesting that pup calls were distinctive at this early age.

Harbor seals are faced with the challenge of maintaining contact with mobile pups on land and in the water immediately after birth. Female harbor seals make diving bouts accompanied by their pups as early as 0–3 days postpartum (Bowen et al., 1999), and a mechanism for long-distance

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recognition should be in place by this time. Breeding rookeries are often in areas with low visibility, strong currents, and high ambient noise. Under these circumstances, the ability to discriminate among pups is important immediately after parturition.

Long-distance pup recognition using acoustic cues is only possible after pups begin to produce individually distinctive vocalizations. The primary goal of this research was to determine when harbor seal pup calls become sufficiently distinctive to allow individual recognition using acoustic cues. Additionally, we expected sex differences in the vocalizations, as well as changes in call structure due to physiological maturity. Therefore, a secondary goal of this research was to explore age and sex information in the calls. The present study is the first quantitative research on vocal development in harbor seal pups.

II. METHODS

A. Subjects and study site

Aerial vocalizations were recorded from 15 captive harbor seal pups, Phoca vitulina richardii, at The Marine Mammal Center in Sausalito, California from March 13th until May 18th of 2002. The pups were born in the wild and brought in for rehabilitation at the age of 1–7 days postpartum; they were in acoustic and physical contact with other harbor seal pups (as they are under natural conditions). The Director of Veterinary Science, Dr. Frances Gulland, assigned an estimated date of birth to each pup based on the presence and condition of umbilicus, teeth, and white blood cell counts.

B. Recording vocalizations

Recordings were made with an Audio-technica 835b condenser microphone (frequency response of 40–20,000 Hz) and a Sony TCD-D8 DAT recorder at sampling rates of 44.1 and 48 kHz, allowing for an analysis range of at least 0–20 kHz. Flipper tags allowed individual pups to be easily identified, and recordings were immediately followed by a voice announcement to ensure that calls were assigned to the correct individual. All recordings produced during this study are archived by the Macaulay Library of Natural Sounds at the Cornell Laboratory of Ornithology in Ithaca, New York (www.animalbehaviorarchive.org).

C. Acoustical analysis

Recordings were digitized with a Roland UA-30 USB audio interface with DAT ACS digital connection cord using the software COOL EDIT PRO 1.2 (Syntrillium Software Corp., Phoenix, AZ) and an ESS Maestro sound card at a sampling rate of 44.1 or 48 kHz and 16-bit resolution. Spectrograms were generated using a 1024-point FFT with a Hamming filter. Vocalizations with high signal-to-noise ratio and unambiguous identity were selected and cued for subsequent digital analysis. Background noise was removed in COOL EDIT PRO with a Butterworth bandpass filter using cutoffs of 100 Hz and 15 kHz. Vocalizations were measured using a modified version of the Contour Similarity Technique (for detailed descriptions of this technique, see McCowan, 1995, and McCowan and Reiss, 2001). Sixty time and frequency points were extracted across the duration of each call by following the dominant frequency (the frequency of highest amplitude). Nineteen summary acoustic variables were calculated from these measurements (Table I).

D. Statistical analysis

1. Individual differences

Stepwise, cross-validation discriminant function analysis was performed to classify vocalizations based on the identity of the calling pup using SPSS 10.0 (SPSS Inc., Chicago, IL). To meet the assumptions of this test, continuous variables were tested for normality and log transformed as necessary. When sample sizes were unequal, percent correct expected...
by chance was calculated separately for each individual; the overall percent correct expected by chance was determined by adding the number of correctly classified calls expected for each individual and then dividing this sum by the total number of calls analyzed (Tabachnick and Fidell, 2001). Chi-square was then used to test whether correct classification was significantly greater than expected by chance. Holm’s sequential Bonferroni method was used to adjust alpha levels for multiple comparisons (Rice, 1989).

Since the fundamental frequency has been implicated as an individually distinctive feature in the vocalizations of harbor seal pups (Renouf, 1984; Perry and Renouf, 1988), cross-validation discriminant function analysis was also run on a subset of the data for which calls were filtered and measured from the fundamental frequency only. The 19 summary acoustic variables were calculated from 60 time and frequency points extracted from the fundamental frequency (Table I). Six pups with large sample sizes were chosen for this analysis, and 40 calls were randomly selected from each pup during each of three age groups (n=240 calls per age group). This analysis enabled a comparison of individuality as a function of age.

The Potential for Individuality Coding was calculated from the ratio of the between-individual coefficient of variation (CV_b) and the mean value of the within-individual coefficients of variation (CV_i) (Robisson et al., 1993; Lengagne et al., 1997). Coefficients of variation were calculated by dividing the standard deviation by the mean.

2. Sex differences

Stepwise cross-validation discriminant function analysis was conducted on a subset of the data containing 1500 calls to classify vocalizations based on the sex of the calling pup using SPSS 10.0. Five pups of each sex with large sample sizes were chosen for this analysis, and 150 calls were randomly selected from each pup. Continuous variables were tested for normality and log transformed as necessary. Chi-square was used to test whether correct classification was significantly greater than expected by chance. Mixed-effects linear regression, which is discussed further in the next subsection, was used to identify which variables were significantly different between males and females.

3. Age differences

Differences in vocalizations attributable to age were examined using mixed-effects linear regression with the nested repeated measure (or random grouped effect) of “recording session within id,” in S-PLUS 2000 statistical software (Data Analysis Products Division., MathSoft, Seattle, WA; Pinheiro and Bates, 2000). Regression diagnostics confirmed that the variables followed normality and variance assumptions. The covariates or fixed effects included sex and age (in weeks) of the vocalizing pup. The nested repeated measure of recording session within id accounted for any clustering due to individuals or recording session, and was based on the assumption that there would be more variability in call characteristics of the individuals across recording sessions than there would be in recording sessions across individuals.

3. Age differences

FIG. 1. Spectrogram of typical harbor seal pup vocalizations with inverted “v” or “u” shape.

III. RESULTS

A. General call characteristics

The total data set included 4593 vocalizations recorded from 15 harbor seal pups. Most (n=4574) calls were relatively tonal, having an inverted “v”- or “u”-shaped spectrogram with the fundamental frequency around 200–600 Hz and harmonics (Fig. 1). See Table II for descriptive statistics on measured call characteristics made by following the dominant frequency of the call.

B. Aggressive vocalizations

The remaining 19 calls were harsh, broadband, staccato calls used in an aggressive context toward another seal pup or human (Fig. 2). Most of these aggressive calls (n=15) were recorded from one individual. Aggressive vocalizations were recorded in a sequence of one to three calls and were produced by both male and female pups. The major energy in these vocalizations was from 200–2000 Hz, and duration ranged from 0.12 to 1.07 s (mean=0.57 s).

C. Individual differences

1. Discriminant function analysis

The 19 calls identified as aggressive vocalizations were excluded from the analysis, resulting in a sample size of 4574 calls. With all age groups combined, stepwise cross-validation discriminant function analysis classified 29.3% of calls correctly, which is significantly more than the 11.5% correct expected by chance ($X^2, P<0.0001$). See Table III. Classification scores for individuals ranged from 3.6% to 53.0% correct, and were significantly greater than expected by chance in 11 of the 15 harbor seals ($X^2, P<0.0001$).

The discriminant function analysis generated ten significant canonical discriminant functions representing the linear combinations of the variables that maximally separate groups in multidimensional space. The first canonical discriminant function accounted for 52.5% of the variation between individuals and loaded most heavily with duration and jitter factor. The second discriminant function, which accounted for 19.3% of the variation, loaded most heavily with mean frequency, the mean frequency divided by the minimum frequency, and call duration.
2. Fundamental frequency discriminant function analysis

Cross-validation discriminant function analysis was also run on a subset of the data containing 40 calls each from six pups during three different age groups \( n=240 \) per age group for which calls were filtered and measured from the fundamental frequency only. Overall percent-correct classification scores were significantly greater than expected by chance for each of the three age groups as well as all ages combined \( \chi^2, P<0.0001 \), Table IV. Classification scores using measurements made from just the fundamental frequency were higher than classification scores using measurements made by following the dominant frequency of the call.

The fundamental frequency analysis for all age groups combined generated five significant canonical discriminant functions. The first function accounted for 45.7% of the variation between individuals and loaded most heavily with mean frequency and finish frequency. The second discriminant function, which accounted for 29.6% of the variation, loaded most heavily with maximum frequency and the coefficient of frequency modulation. The third function accounted for an additional 16.2% of the variation between individuals and loaded most heavily with duration and coefficient of variation.

3. Potential for individuality coding

Measured call characteristics from the vocalizations of harbor seal pups recorded in this study had Potential of Individuality Coding values ranging from 0.98 to 1.18 (Table V).

D. Sex differences

1. Discriminant function analysis

Cross-validation discriminant function analysis was conducted on a subset of the data containing 1500 calls \( (150 \text{ from each of five male and five female pups}) \) to classify vocalization based on the sex of the calling pup. With all age groups combined, 66.1% of calls were classified correctly, which is significantly more than the 50% correct expected by chance \( \chi^2, P<0.0001 \). The analysis generated one significant canonical discriminant function that accounted for all of the variation between sexes, and loaded most heavily with duration, inflection factor, and mean frequency.

2. Mixed-effects linear regression

When the sex of the vocalizing pup was the only fixed effect considered, only one of the summary acoustic variables was significantly different between males and females: the coefficient of frequency modulation (Table VI). Male harbor seal pup calls had higher coefficients of frequency modulation than did those of female pups.

However, when the interaction between the sex and age of the vocalizing pup was considered, several other variables revealed significant differences: mean frequency, frequency at peak amplitude, duration, location of maximum frequency,

![Image](image_url)

FIG. 2. Spectrogram of three harsh, broadband, staccato calls used in an aggressive context by harbor seal pups (compare with Fig. 1).

<table>
<thead>
<tr>
<th>Acoustic Variable</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>SD</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start frequency</td>
<td>102.63</td>
<td>8067.20</td>
<td>435.44</td>
<td>371.52</td>
<td>0.85</td>
</tr>
<tr>
<td>Finish frequency</td>
<td>103.44</td>
<td>7315.00</td>
<td>457.63</td>
<td>304.93</td>
<td>0.67</td>
</tr>
<tr>
<td>Minimum frequency</td>
<td>102.63</td>
<td>1145.10</td>
<td>237.47</td>
<td>80.36</td>
<td>0.34</td>
</tr>
<tr>
<td>Maximum frequency</td>
<td>343.27</td>
<td>8595.80</td>
<td>1224.88</td>
<td>572.72</td>
<td>0.47</td>
</tr>
<tr>
<td>Mean frequency</td>
<td>255.05</td>
<td>1845.95</td>
<td>661.32</td>
<td>208.58</td>
<td>0.32</td>
</tr>
<tr>
<td>Frequency at Peak Amplitude</td>
<td>180.73</td>
<td>3106.10</td>
<td>805.39</td>
<td>348.76</td>
<td>0.43</td>
</tr>
<tr>
<td>Frequency range</td>
<td>33.71</td>
<td>8411.50</td>
<td>987.41</td>
<td>574.19</td>
<td>0.58</td>
</tr>
<tr>
<td>Maximum frequency / mean freq</td>
<td>1.04</td>
<td>10.51</td>
<td>1.89</td>
<td>0.71</td>
<td>0.38</td>
</tr>
<tr>
<td>Mean frequency / minimum freq</td>
<td>1.05</td>
<td>11.80</td>
<td>3.04</td>
<td>1.31</td>
<td>0.43</td>
</tr>
<tr>
<td>Duration</td>
<td>117.19</td>
<td>2444.04</td>
<td>610.73</td>
<td>203.70</td>
<td>0.33</td>
</tr>
<tr>
<td>Location of minimum frequency</td>
<td>0.00</td>
<td>1.00</td>
<td>0.47</td>
<td>0.44</td>
<td>0.95</td>
</tr>
<tr>
<td>Location of maximum frequency</td>
<td>0.00</td>
<td>1.00</td>
<td>0.47</td>
<td>0.24</td>
<td>0.52</td>
</tr>
<tr>
<td>Start frequency slope</td>
<td>-6.42</td>
<td>3.48</td>
<td>0.17</td>
<td>0.30</td>
<td>—</td>
</tr>
<tr>
<td>Middle frequency slope</td>
<td>-3.48</td>
<td>1.49</td>
<td>-0.01</td>
<td>0.22</td>
<td>—</td>
</tr>
<tr>
<td>Finish frequency slope</td>
<td>-2.33</td>
<td>7.39</td>
<td>-0.16</td>
<td>0.27</td>
<td>—</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>0.57</td>
<td>3836.37</td>
<td>177.30</td>
<td>174.87</td>
<td>0.99</td>
</tr>
<tr>
<td>Jitter factor</td>
<td>2.08</td>
<td>67.50</td>
<td>15.31</td>
<td>7.57</td>
<td>0.49</td>
</tr>
<tr>
<td>Coefficient of frequency modulation</td>
<td>0.04</td>
<td>3.60</td>
<td>0.59</td>
<td>0.35</td>
<td>0.59</td>
</tr>
</tbody>
</table>
### TABLE III. Results of cross-validation discriminant function analysis to classify individual harbor seal pups based on call characteristics measured by following the dominant frequency. Bold numbers are correctly classified calls; others are incorrectly classified (overall 29.3% correct, n=4574). Chi-square tested significance. Asterisk indicates significance using Holm’s sequential Bonferroni method to adjust alpha levels for multiple comparisons (Rice, 1989).

<table>
<thead>
<tr>
<th>Acoustic variable</th>
<th>Mean±SD</th>
<th>CVb</th>
<th>Mean CVi</th>
<th>PIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start frequency</td>
<td>435.44±371.52</td>
<td>0.85</td>
<td>0.76</td>
<td>1.12</td>
</tr>
<tr>
<td>Finish frequency</td>
<td>457.63±304.93</td>
<td>0.67</td>
<td>0.61</td>
<td>1.10</td>
</tr>
<tr>
<td>Minimum frequency</td>
<td>237.47±80.36</td>
<td>0.34</td>
<td>0.33</td>
<td>1.03</td>
</tr>
<tr>
<td>Maximum frequency</td>
<td>1224.88±572.72</td>
<td>0.47</td>
<td>0.44</td>
<td>1.06</td>
</tr>
<tr>
<td>Mean frequency</td>
<td>661.32±208.58</td>
<td>0.32</td>
<td>0.29</td>
<td>1.12</td>
</tr>
<tr>
<td>Freq at peak amplitude</td>
<td>805.39±348.76</td>
<td>0.43</td>
<td>0.40</td>
<td>1.08</td>
</tr>
<tr>
<td>Frequency range</td>
<td>987.41±574.19</td>
<td>0.58</td>
<td>0.55</td>
<td>1.05</td>
</tr>
<tr>
<td>Maximum freq / mean freq</td>
<td>1.89±0.71</td>
<td>0.38</td>
<td>0.36</td>
<td>1.04</td>
</tr>
<tr>
<td>Mean freq / minimum freq</td>
<td>3.04±1.31</td>
<td>0.43</td>
<td>0.41</td>
<td>1.04</td>
</tr>
<tr>
<td>Duration</td>
<td>610.73±203.70</td>
<td>0.33</td>
<td>0.29</td>
<td>1.15</td>
</tr>
<tr>
<td>Location of minimum frequency</td>
<td>0.47±0.44</td>
<td>0.95</td>
<td>0.97</td>
<td>0.98</td>
</tr>
<tr>
<td>Location of maximum frequency</td>
<td>0.47±0.24</td>
<td>0.52</td>
<td>0.51</td>
<td>1.02</td>
</tr>
<tr>
<td>Coefficient of freq modulation</td>
<td>0.59±0.35</td>
<td>0.59</td>
<td>0.58</td>
<td>1.01</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>177.30±174.87</td>
<td>0.99</td>
<td>0.84</td>
<td>1.18</td>
</tr>
<tr>
<td>Jitter factor</td>
<td>15.31±7.57</td>
<td>0.49</td>
<td>0.49</td>
<td>0.99</td>
</tr>
</tbody>
</table>

**TABLE IV.** Results of cross-validation discriminant function analysis using a subset of the data containing 40 calls each from six pups during three different age groups (n=240 per age group) measured from the fundamental frequency alone. The “% Correct” column contains percentages of calls classified correctly. Chi-square tested whether correct classification was significantly greater than the 16.67% expected by chance. Asterisk indicates significance using Holm’s sequential Bonferroni method to adjust alpha levels for multiple comparisons (Rice, 1989).

**TABLE V.** Potential for individuality coding (PIC) of harbor seal pup calls. The potential for individuality coding is the ratio of the between-individual coefficient of variation (CVb) and the mean value of the within-individual coefficients of variation (CVi).
E. Age differences

In addition to maturational changes in male and female pup calls (See Sec. III D above), there were also significant age differences in pup calls regardless of sex. When the age of the pup was the only fixed effect considered in the repeated measures linear regression, the following summary acoustic variables remained significant: location of the maximum frequency, coefficient of variation, and jitter factor (Table VI). In addition, the following variables decreased significantly with age in pups of both sexes: minimum frequency, maximum frequency, frequency range, location of the minimum frequency, and coefficient of frequency modulation (Table VI). See Fig. 4 for graphs generated from the linear mixed-effects models demonstrating the effect of age.

IV. DISCUSSION

A. General call characteristics

Most calls produced by harbor seal pups during this study were relatively tonal, having an inverted “v-” or “u”-shaped spectrogram with the fundamental frequency around 200–600 Hz and harmonics. These calls had acoustic features similar to those commonly described in the literature and presumed to function as “mother attraction calls” (Schef-fer and Slipp, 1944; Bishop, 1967; Newby, 1973; Renouf, 1984; Ralls et al., 1985; Perry and Renouf, 1988). Pup vocalizations of the western Atlantic harbor seal, Phoca vitu- lina concolor, have a fundamental frequency at about 350 Hz and harmonics (Ralls et al., 1985). The mean (±SD) duration of calls in this study (0.57±0.30 s) falls between the reported values for the Atlantic subspecies of 0.31±0.14 s (Perry and Renouf, 1988), 0.81±0.19 s (Ralls et al., 1985), and 1.1±0.7 s (Van Parijs and Kovacs, 2002).

B. Aggressive vocalizations

Nineteen of the calls recorded in this study were harsh, broadband, staccato calls used in an aggressive context towards another seal pup or human. These calls resemble “growls” or “hisses” reported in previous studies (Bishop, 1967; Sullivan, 1982; Van Parijs and Kovacs, 2002), although no quantitative data was provided. The earliest age at which a pup was recorded vocalizing aggressively in this study was 16 days postpartum. Further research is needed to explore the development of aggressive behavior in harbor seal pups.

C. Individual differences

The results of this study indicate that harbor seal pup calls are individually distinctive, confirming preliminary re- search (Perry and Renouf, 1988; Renouf, 1984). Classifica-
tion scores from discriminant function analysis were 29% correct overall. For effective maternal recognition under natural conditions, female harbor seals need to discriminate between pups at a much higher rate of success; several factors may contribute to this discrepancy. Classification scores from discriminant function analysis are based solely on the information contained in a single vocalization, whereas harbor seal mothers have an entire calling bout available to them as well as geographic, visual, and olfactory cues.

Individually distinctive contact calls have been found in all pinnipeds studied to date (for a review, see Insley et al., 2003). Discriminant function analysis has resulted in a wide range of percent-correct classification scores (see Table VII), but whether this reflects species differences in stereotypy or is an artifact of sample size differences is unknown. Percent-correct classification scores have been shown to increase corresponding to a decrease in the number of individuals and the number of signals per individual (Bee et al., 2001). Despite these limitations, the range of classification scores does conform to current ideas regarding recognition abilities in pinnipeds. Percent-correct classification scores tend to be higher for otariids than phocids (see Table VII), supporting the theory that recognition is more highly developed in otariids. Harbor seals are phylogenetically and behaviorally similar to grey seals, with females of both species making regular separations from their pups, and the two species have similar percent-correct classification scores in discriminant function analysis (Table VII). The ability of females to recognize pup calls has been studied in two different populations of grey seals with differing results. Grey seal females on Sable Island in Canada were able to recognize the calls of their own pups, whereas on the Isle of May in Scotland females failed to recognize pups (McCulloch et al., 1999; McCulloch and Boness, 2000). The only test of recognition in harbor seals was with a single captive female who was able to discriminate between recordings of two different pups (Renouf, 1985). Based on what we have learned about grey seals, recognition abilities in harbor seals should be studied in several populations. It is also interesting to note that Hawaiian monk seals, the only other pinniped in which mothers were found not to recognize their pups, had the lowest classification scores reported for any species at 14% correct (Job et al., 1995).

Harbor seal contact calls were individually distinctive even in pups less than 2 weeks old. Classification scores were higher using measurements from the fundamental fre-
frequency than from the dominant frequency of the call. This result is consistent with previous findings that the fundamental frequency is a reliable indicator of identity in harbor seals (Renouf, 1984; Perry and Renouf, 1988) and other pinnipeds (South American fur seals: Phillips and Stirling, 2000; subantarctic fur seals: Charrier et al., 2002; northern fur seals: Insley, 1992; grey seals: McCulloch et al., 1999; northern elephant seals: Insley, 1992; Hawaiian monk seals: Job et al., 1995).

### TABLE VII. Empirical studies of “mother attraction calls” in pinnipeds demonstrating distinctive calls and/or maternal recognition. (%“Correct,” “Seals,” “Calls” refers to the results of discriminant function analysis; Y=yes, N=no).

<table>
<thead>
<tr>
<th>Species</th>
<th>%Correct</th>
<th>#Seals</th>
<th>#Calls</th>
<th>Are pup calls individually distinctive?</th>
<th>Do mothers recognize pup calls?</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Otariids</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Southern sea lions</td>
<td>89%</td>
<td>33</td>
<td>99</td>
<td>Y Fernandez-Juricic et al., 1999</td>
<td></td>
</tr>
<tr>
<td>Subantarctic fur seals</td>
<td>83%</td>
<td>10</td>
<td>100</td>
<td>Y Page et al., 2002; Charrier et al., 2002; Roux and Jouventin, 1987</td>
<td></td>
</tr>
<tr>
<td>New Zealand fur seals</td>
<td>79%</td>
<td>10</td>
<td>100</td>
<td>Y Page et al., 2002</td>
<td></td>
</tr>
<tr>
<td>Northern fur seals</td>
<td>79%</td>
<td>8</td>
<td>160</td>
<td>Y Insley, 1992</td>
<td>Y Insley, 2000, 2001</td>
</tr>
<tr>
<td>Antarctic fur seals</td>
<td>52%</td>
<td>9</td>
<td>90</td>
<td>Y Page et al., 2002</td>
<td></td>
</tr>
<tr>
<td>S. American fur seals</td>
<td>51%</td>
<td>13</td>
<td>260</td>
<td>Y Phillips and Stirling, 2000</td>
<td></td>
</tr>
<tr>
<td><strong>Phocids</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern elephant seals</td>
<td>64%</td>
<td>8</td>
<td>126</td>
<td>Y Insley, 1992</td>
<td>Y Petrovich, 1974</td>
</tr>
<tr>
<td>Grey seals</td>
<td>32%</td>
<td>20</td>
<td>216</td>
<td>Y McCulloch et al., 1999; Caudron et al., 1998</td>
<td>Y McCulloch and Boness, 2000</td>
</tr>
<tr>
<td>Harbor seals</td>
<td>29%</td>
<td>15</td>
<td>4574</td>
<td>Y Present study; Perry and Renouf, 1988; Renouf, 1984</td>
<td>Y Renouf, 1985</td>
</tr>
<tr>
<td>Harp seals</td>
<td>…</td>
<td>…</td>
<td>…</td>
<td>Y Van Opzeeland and Van Parijs, 2004</td>
<td></td>
</tr>
<tr>
<td>Hawaiian monk seals</td>
<td>14%</td>
<td>15</td>
<td>428</td>
<td>Y Job et al., 1995</td>
<td>N Job et al., 1995</td>
</tr>
</tbody>
</table>

aBased on the ability of one captive female to discriminate between recordings of two different pups.

FIG. 4. Graphs generated from repeated measures linear regression demonstrating the fixed effect of “age” for variables describing harbor seal pup, *Phoca vitulina richardii*, vocalizations that were significant (α<0.05) with the random effect of “recording session within id.” Squares represent males, and triangles represent females.
D. Sex differences

Significant differences were found between male and female pup calls. Male pup calls had higher coefficients of frequency modulation than calls of female pups. Young pups of both sexes had similar values for mean frequency, but as they matured, female calls became higher in mean frequency while male calls became lower. Likewise, young animals of both sexes had similar values for frequency at peak amplitude, but as they matured, females became higher while males became lower. The mean duration of female vocalizations remained relatively constant throughout the study period, but the mean duration of male calls increased as they matured. The location of maximum frequency, coefficient of variation, and jitter factor values were all higher in female pup calls during the first few weeks of age, becoming gradually lower in females and higher in males so that male values were highest in pups over 5 weeks of age.

Sex differences have also been found in the vocalizations of harp seal pups, *Phoca groenlandica*; males and females were separated on the first split of the classification tree, and female calls were classified correctly more often than male calls (Van Opzeeland and Van Parijs, 2004). Sex differences in vocalizations may function as a means for parents to allocate resources differentially based on offspring sex, and/or reflect early development of sexual dimorphism in vocal behavior (Saino et al., 2003). There is no evidence for differential resource allocation in harbor seals. The sex ratio is 1:1 both at birth and weaning (Ellis, 1998), and although male harbor seal pups do weigh more than females at weaning, this reflects greater birth mass of males rather than differential maternal investment during lactation (Ellis, 1998; Bowen et al., 2001). Sex differences in pup calls are also unlikely to reflect early development of sexual dimorphism in vocal behavior, since this call disappears from the vocal repertoire at weaning. However, sex differences in harbor seal pup vocalizations may reflect early development of the sexual size dimorphism characteristic of adults. This size dimorphism is already apparent at birth, with male pups weighing more than females (Ellis, 1998).

E. Age differences

Pups produced calls with well-defined acoustic features as young as 2 days postpartum. These mother attraction calls appear to encode identity information from a young age, although call structure does change throughout maturation. Discriminant function analysis classified calls correctly significantly more often than expected by chance even when pups were less than 2 weeks old. As discussed in the previous subsection, age-related changes in many call characteristics varied according to the sex of the pup. The following variables decreased significantly over time in pups of both sexes: location of the maximum frequency, coefficient of variation, jitter factor, minimum frequency, maximum frequency, frequency range, location of the minimum frequency, and coefficient of frequency modulation. These ontogenetic changes in frequency are similar to those reported in other mammals ( vervet monkey: Hauser, 1989; pigtail macaque: Gouzoules and Gouzoules, 1989), and likely reflect the gradual enlargement of the vocal tract.

There has not been much research on the ontogeny of pup calls in pinnipeds. California sea lions may recognize vocalizations from their 2-week old pups, suggesting that the calls are individually stereotyped at this time (Gisiner and Schusterman, 1991; Schusterman et al., 1992), although visual and olfactory cues could not be ruled out in these studies. Research on subantarctic fur seal pups showed significant age-related changes in the fundamental frequency and the percentage of quavering in pup calls (Charrier et al., 2003a). Calls of young pups emphasized some high frequencies, while the spectral energy in the calls of older pups was concentrated on the first harmonics (Charrier et al., 2003a).

F. Directions for future research

Further research is needed to confirm that harbor seal mothers recognize the calls of their pups under natural conditions in the wild. In addition to investigation of wild pup calls, observational studies of natural separations could determine whether vocal activity in pups facilitates successful reunions upon the return of the mother to the breeding rookery.

It is unknown which acoustic characteristics harbor seal mothers use to recognize the vocalizations of their own offspring; call characteristics measured in this study may not accurately reflect perceptually salient features. Playback studies using artificially manipulated signals such as those recently conducted by Charrier and colleagues on black-
headed gulls and subantarctic fur seals (Charrier et al., 2001, 2002, 2003b) could help to elucidate the cues used by harbor seals in voice discrimination.

The present study did not examine the effects of motivational state on characteristics of harbor seal pup vocalizations, although recordings were made under similar conditions in an attempt to minimize the possible influence of motivation. Preliminary observations suggest that distressed pups have a greater number of calls per calling bout, a faster rate of call emission, and more harmonics (Renouf, 1984; Perry and Renouf, 1988). Future research should take motivational state information into account.

The harbor seal and the closely related spotted seal provide a unique opportunity for comparative study of the effects of breeding density on the vocal recognition system. Spotted seals, which breed on isolated ice floes, are expected to have a less reliable system of mother-offspring recognition than harbor seals, which breed in rookeries where there is greater risk of confusion. The absence of mother-pup recognition in spotted seals is suggested by a pup-exchange experiment in which a female spotted seal accepted a strange pup (Burns et al., 1972). However, further research on wild populations of both harbor seals and spotted seals is needed to test these predictions.

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