Individual variation in the pup attraction call produced by female Australian fur seals during early lactation

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Otarid seals (fur seals and sea lions) are colonial breeders with large numbers of females giving birth on land during a synchronous breeding period. Once pups are born, females alternate between feeding their young ashore and foraging at sea. Upon return, both mother and pup must relocate each other and it is thought to be primarily facilitated by vocal recognition. Vocalizations of thirteen female Australian fur seals (Arctocephalus pusillus doriferus) were recorded during the breeding seasons of December 2000 and 2001, when pups are aged from newborns to one month. The pup attraction call was examined to determine whether females produce individually distinct calls which could be used by pups as a basis for vocal recognition. Potential for individual coding, discriminant function analysis (DFA), and classification and regression tree analysis were used to determine which call features were important in separating individuals. Using the results from all three analyses: $F_0$, MIN F and DUR were considered important in separating individuals. In 76% of cases, the PAC was classified to the correct caller, using DFA, suggesting that there is sufficient stereotypy within individual calls, and sufficient variation between them, to enable vocal recognition by pups of this species. © 2006 Acoustical Society of America. [DOI: 10.1121/1.2202864]

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I. INTRODUCTION

Recognition between parents and their offspring has been studied extensively in colonial species, e.g., Californian sea lions, Zalophus californianus (Schusterman et al., 1992); Mexican free-tailed bats, Tadarida brasiliensis mexicana (Balcombe and McCracken 1992); razorbills, Alca torda (In-sley et al., 2003b), and king penguins, Aptenodytes patagonicus (Jouventin et al., 1999). In some colonial species, offspring are usually mobile at a young age and consequently able to socialize with similar-aged conspecifics and parents must be able to recognize them when they return from foraging trips (Scherrrer and Wilkinson, 1993). As parental care promotes the survival of young, thus enhancing the parents’ own reproductive success, selection should favor a parent-offspring recognition system (Gubernick, 1981).

In pinnipeds, maternal-offspring recognition appears to be widespread, with most exhibiting some degree of recognition. However, there are some exceptions, for example a lack of maternal recognition exhibited by Hawaiian monk seals (Job et al., 1995). Various sensory modalities such as spatial, vocal, and olfactory cues are also considered important in the reunion process between a mother and her pup (Riedman, 1990). However, in a crowded breeding colony, acoustic signaling is thought to be more effective for long-range communication (Trillium, 1981).

Breeding and maternal care strategies among the Otariidae (fur seals and sea lions) are generally similar, with mothers giving birth at a natal colony and providing exclusive care to their own young. A few days after birth, females depart on foraging trips offshore and upon their return must relocate their own young within the colony (Riedman, 1990). This process continues until weaning. Once pups are born, there is an initial period of bonding where nuzzling and vocalizing occurs between a mother and her newborn (Ried-
man, 1990). Mothers call to pups using the call termed the pup attraction call (PAC) and pups counter call using the female attraction call. This period of intense vocalizing aids imprinting between a mother and her newborn pup (Riedman, 1990), and occurs within a few days of birth (Charrier et al., 2001).

For vocalizations to be used in individual recognition they must display stereotypy within individuals and significant variation between them (Falls, 1982). Although the presence of individual variation is insufficient evidence that recognition occurs, it is the important initial stage in demonstrating a potential for the recognition process. Individuality of the PAC has been described in several otariid species (Insley et al., 2003a) with the overall structure of the PAC showing general similarities, although slight differences were evident between the species (Page et al., 2002; Stirling and Warneke, 1971).

Preliminary analysis of the PAC produced by female Australian fur seals suggested it was of a lower frequency than that produced by other Arctocephalines (Stirling and Warneke, 1971). Detailed information on the structure of the Australian fur seal PAC, however, is lacking such that it is not possible to discern whether it is distinct from, or displays a different degree of individuality than, that of other Arctocephalines.

The aims of this study, therefore, were to: (1) establish detailed acoustic parameters that describe the PAC produced by female Australian fur seals; (2) determine the degree of individual variation; and (3) determine the acoustic features that contribute to the individuality of calls.

II. METHODS

A. Study species

Australian fur seals (Arctocephalus pusillus doriferus) come ashore between late October and early December giving birth 1 to 2 days later (Warneke and Shaughnessy, 1985; Shaughnessy and Warneke, 1987). Females then alternate between suckling their young ashore and foraging out at sea, with maternal attendance patterns lasting approximately 1.7 days, and foraging trips increasing in duration as lactation progresses (Arnould and Hindell, 2001). Female Australian fur seals suckle pups until they are 10 to 11 months of age (Arnould and Hindell, 2001); with lactation generally varying from 9 to 12 months in the Otariidae (see exceptions Bowen, 1991).

B. Data collection and acoustic analyses

The study was conducted at a breeding colony on Kanowna Island (39°10'S, 146°18'E), Bass Strait, Australia (Fig. 1) This colony has an annual production of ca2300 pups (Kirkwood et al., 2005), and the peak pupping date is 1 December (Warneke and Shaughnessy, 1985). This island has two main colonies: East and Main Colony (Fig. 1). Recordings were made over a one week period during two consecutive breeding seasons (10–16 December 2000 and 6–13 December 2001). Pups during this recording period were aged from newborn to one month of age.

In-air vocalizations of 13 adult female Australian fur seals were recorded using a Sony digital tape recorder (TCD-D8) with a directional K6/ME66 Sennheiser microphone (frequency response 50–20 000 Hz±2.5 dB). Recordings were made at a distance of 5–25 m from the vocalizing
<table>
<thead>
<tr>
<th>Pup attraction call</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fundamental frequency (F0)</td>
<td>As all calls analyzed were harmonically rich, the distance between each harmonic band should be equal. Therefore, the fundamental frequency also equals the distance between two harmonics. To keep measurements uniform, we took all readings of this feature from the center of the call (Hz).</td>
</tr>
<tr>
<td>Duration (DUR)</td>
<td>Duration of the first harmonic band (ms)</td>
</tr>
<tr>
<td>Initial frequency (IN F)</td>
<td>The start frequency of the first harmonic band (Hz)</td>
</tr>
<tr>
<td>END frequency (END F)</td>
<td>Explains the frequency of the last point of the harmonic band (Hz)</td>
</tr>
<tr>
<td>Minimum frequency (MIN F)</td>
<td>Minimum frequency of the first harmonic band (Hz)</td>
</tr>
<tr>
<td>Maximum frequency (MAX F)</td>
<td>Maximum frequency of the first harmonic band (Hz)</td>
</tr>
<tr>
<td>Peak frequency (PEAK F1)</td>
<td>This was measured from the center of the call. It describes the location of the energy band or harmonic that has the most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak.</td>
</tr>
<tr>
<td>Peak frequency (PEAK F2)</td>
<td>This was measured from the center of the call. It describes the location of the energy band or harmonic that has the second most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak.</td>
</tr>
<tr>
<td>Peak frequency (PEAK F3)</td>
<td>This was measured from the center of the call. It describes the location of the energy band or harmonic that has the third most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak.</td>
</tr>
<tr>
<td>Peak frequency (PEAK F4)</td>
<td>This was measured from the center of the call. It describes the location of the energy band or harmonic that has the fourth most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak.</td>
</tr>
<tr>
<td>Mean frequency (MEAN F)</td>
<td>This was calculated by dividing the call into 15 intervals (i.e., 16 points). The frequency at each of these points was measured and then averaged (Hz).</td>
</tr>
<tr>
<td>Coefficient of frequency modulation (CoPM)</td>
<td>CoPM is as a measure of frequency modulation between consecutive intervals (Harrington, 1989). In this study, 16 data points across H1 were measured and the absolute differences in frequency between these consecutive intervals were summed and then averaged. These averages were then standardized by dividing by the mean fundamental frequency of the PAC and then multiplying by 100 (%).</td>
</tr>
<tr>
<td>Peak energy band</td>
<td>The energy band number is given to describe the location of the energy band or harmonic that has the most energy distributed in it (Hz). This was measured from the center of the call. When there were multiple peaks of equal energy we only reported the frequency of the first peak.</td>
</tr>
</tbody>
</table>

1Log transformations (log 2) were conducted to normalize variables.

2Could not be normalized.

3Categorical data.

animal and were conducted during the early morning or afternoon of each day. Individuals were recorded at different locations and sampled during a single recording to avoid re-recording the same focal animal.

Thirteen PACs from thirteen females (N=156) with high signal-to-noise ratios were examined, with all calls having rich harmonic structure (Phillips and Stirling, 2001). Vocalizations were analyzed using SIGNAL 3.1 software package (Engineering Design, MA), at a sampling rate of 25 000 Hz, a frequency resolution of 1024-point fast Fourier transforms (FFT), and an analyzing bandwidth of 24.41 Hz (sampling rate/FFT). Monitor settings produced cursor error rates of ±5.36 ms in the time domain and ±25.97 Hz in the frequency domain. Call features analyzed from the PAC are described in Table 1 and displayed on sonograms [Figs. 2(a)–2(c)].

Measurements were made on the first harmonic since the fundamental frequency was not always entirely visible on the spectrogram.

C. Description of the PAC

The description of features and values characterizing the PAC are presented in Tables I and II. As frequency features were measured from the first harmonic band they were divided by two to represent the fundamental frequency. This ensures that results were comparable with other studies as it is more common to represent call features of the fundamental (Caudron et al., 1998; Collins et al., 2005). The features divided by two were: IN F, END F, MIN F, MAX F, and MEAN F.
TABLE II. Characterization, CVs and potential for individual coding (PIC) values of call variables of the pup attraction call produced by thirteen female Australian fur seals ($N=156$).

<table>
<thead>
<tr>
<th>Pup attraction call</th>
<th>Mean</th>
<th>s.d.</th>
<th>CVs</th>
<th>Mean CV</th>
<th>PIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>F0</td>
<td>262.1</td>
<td>34.6</td>
<td>13.5</td>
<td>4.6</td>
<td>2.9</td>
</tr>
<tr>
<td>DUR</td>
<td>1030.3</td>
<td>278.5</td>
<td>27.6</td>
<td>19.3</td>
<td>1.4</td>
</tr>
<tr>
<td>INF</td>
<td>226.2</td>
<td>50.6</td>
<td>22.8</td>
<td>15.2</td>
<td>1.5</td>
</tr>
<tr>
<td>END F</td>
<td>183.9</td>
<td>48.1</td>
<td>26.7</td>
<td>19.6</td>
<td>1.4</td>
</tr>
<tr>
<td>MIN F</td>
<td>178.8</td>
<td>44.4</td>
<td>25.3</td>
<td>18.2</td>
<td>1.4</td>
</tr>
<tr>
<td>MAX F</td>
<td>290.9</td>
<td>44.3</td>
<td>15.5</td>
<td>6.6</td>
<td>2.4</td>
</tr>
<tr>
<td>PEAK F1</td>
<td>827.7</td>
<td>374.5</td>
<td>46.1</td>
<td>27.1</td>
<td>1.7</td>
</tr>
<tr>
<td>PEAK F2</td>
<td>1055.2</td>
<td>546.0</td>
<td>52.7</td>
<td>43.6</td>
<td>1.2</td>
</tr>
<tr>
<td>PEAK F3</td>
<td>1258.7</td>
<td>581.0</td>
<td>47.0</td>
<td>44.1</td>
<td>1.1</td>
</tr>
<tr>
<td>PEAK F4</td>
<td>1299.5</td>
<td>608.8</td>
<td>47.8</td>
<td>45.3</td>
<td>1.1</td>
</tr>
<tr>
<td>MEAN F</td>
<td>251.7</td>
<td>34.9</td>
<td>14.1</td>
<td>5.2</td>
<td>2.7</td>
</tr>
<tr>
<td>CoFM</td>
<td>4.4</td>
<td>1.6</td>
<td>36.7</td>
<td>32.4</td>
<td>1.1</td>
</tr>
</tbody>
</table>

![Image](image.png)

FIG. 2. Sonogram of a pup attraction call (PAC) produced a female Australian fur seal. (b) Harmonic band with associated call features measured from the pup attraction call produced by a female Australian fur seal. Call features measured from sonograms are indicated on diagram. (c) Power spectra of a pup attraction call produced by a female Australian fur seal. Peak frequency indicated on diagram.

**D. Statistical analysis of the PAC**

1. **Potential for individual coding**

Potential for individual coding (PIC) (Robinson et al., 1993; Charrier et al., 2002; Charrier et al., 2003a) analysis was used to obtain quantitative information about each variable, allowing the comparison of their potential as individuality markers in the recognition system (i.e., if they are likely or unlikely to be used in the individual recognition process) (Charrier et al., 2003a). This technique determines a ratio of the between-individual variation relative to the within-individual variation. The analysis first calculates the coefficient of variation (CV) for each call feature examined:

$$CV = \frac{s.d.}{Mean} \times 100$$

A corrected CV (CV*) was calculated following Sokal and Rohlf (1985)

$$CV^* = \left(1 + \frac{1}{4n}\right) \times (CV)$$

where $n =$ number of individuals.

Both between-individuals (CVb) and within-individuals (CVi) CV values were calculated. The (CVb) was calculated for each characteristic for all individuals. While the CV_{grand mean} was calculated for each individual for each characteristic, and a grand mean was generated. A PIC value was used generated using

$$PIC = \frac{CV_b}{CV_{i, grand mean}}$$

The higher the PIC value, the greater its contribution is to the individual coding process (Charrier et al., 2003a).

2. **Discriminant function analysis**

In addition to the PIC, discriminant function analysis (DFA) and classification and regression tree (CART) analysis were also used. The DFA compares variation among individuals across several variables at the same time. The analysis is useful as it is likely that combinations of variables are used in the recognition process. The DFA also calculates the percentage of correctly classified calls and therefore determines the ability of the chosen variables to discriminate among individuals (Klecka, 1980).

Following normal transformation, DFA was conducted on the variables identified in the PAC, to investigate inter-individual variation (Table I). Peak F1 and PEAK F2 could not be normalized and were excluded from the DFA. In addition, as part of the computations involved in the DFA, the analyses determined whether any of the call parameters were...
redundant. If there are any redundant variables, the analysis will not proceed until one of them is removed. In the current study there were no variables that were redundant and consequently all variables were included in the DFA (Table I).

To examine the stability of the discriminant function a cross-validation procedure was performed on the results. The data were split into two groups; one group (training data) contained half of the replicates for each individual and was used to determine the discriminate function, while the second group (test data) contained the remaining half of the data and was used to evaluate the stability of the classification. This process was repeated swapping the training and test data, ensuring that each call replicate was used in both the test data set and training data set at least once during the cross-validation procedure.

3. Classification and regression tree analysis

There are several assumptions and limitations that are associated with DFA including normality and homogeneity of variance and it is also sensitive to outliers and missing data. On the other hand, CART analysis is a nonparametric technique that does not assume any specific distribution of data (De’ath and Fabricius, 2000) and is therefore more flexible in the variables that can be incorporated in the analysis. Therefore all variables were considered in CART analysis to determine which were important in separating individual seals.

Classification and regression trees explain differences of a single response variable by repeatedly splitting the data into more homogeneous groups, using combinations of variables (De’ath and Fabricius, 2000). Each group is characterized by a value of the response variable, the number of observations, and the values of the variables that describe it (De’ath and Fabricius, 2000).

A subsample of 12 parameters from 7 individuals were used to determine which features were important in splitting individuals. In total, 10 variables were found to be important (all except PEAK F4 and COFM) and these were then used to analyze the complete data set.

4. Peak frequency distribution in the PAC

Preliminary analysis indicated the PACs produced by females were rich in harmonic structure but that the energy was not distributed evenly between the harmonic bands. In most individuals, the majority of energy appeared in only one band, with the occasional individual producing the majority of energy in two or three harmonic bands. Consequently, the peak distribution of energy in harmonic bands was examined in females to determine if this call feature could be used as a basis to separate them.

III. RESULTS

A. Description of PAC

Female Australian fur seals produce loud calls that are frequency modulated and rich in harmonic structure [Figs. 1(a)–1(c)]. Female calls were long, averaging 1.0 s in duration (N = 156 from 13 females, s.d. = 278.49). The majority of call energy is located in the first and second harmonic bands with a fundamental frequency of 262 Hz (Table II).

B. Inter-individual variation

1. Discriminant function analysis

Ten variables from the PAC were used to discriminate amongst thirteen female Australian fur seals using DFA. There were significant differences in individual PAC amongst females [Wilks’ lambda = 0.01, F (120, 1054) = 6.35, p < 0.01]. Discriminant analysis assigned 76% of the data correctly to individual females, which is greater than would be expected by chance alone (p < 0.0001). Assigning three or more calls correctly per individual was considered significant at the p = 0.05 level. All individuals had six or more calls correctly assigned and therefore all produced individually distinct PACs (Table III).

Roots 1–3 account for 91% of the variance of the data, suggesting that these were more important in distinguishing individuals. DUR and MIN F were strongly and positively correlated to Root 1 while Fp, END F, MAX F, and MEAN F were strongly and negatively correlated. DUR and END F were strongly and positively correlated to Root 2 while MEAN F was strongly and negatively correlated. MEAN F was strongly and positively correlated to Root 3 and Fp, IN F, MIN F, COFM, and PEAK F3 were strongly and negatively correlated (Table IV).

The training cross-validation procedure resulted in 81% of calls being correctly assigned (p < 0.0001), compared to the test case where 47% of the calls were correctly assigned. The probability of achieving the test percentage by chance is p = 0.01.

2. Classification and regression tree analysis

Initially a 15-node classification tree was pruned with cross validation. As suggested by Van Opzeeland and Van Parijs (2004) and De’ath and Fabricius (2000) the 1-SE rule was adopted, this is the smallest tree for which the cross-
TABLE IV. Results of the canonical discriminant analysis comparing the pup attraction calls of female Australian fur seals.

<table>
<thead>
<tr>
<th>Acoustic variable</th>
<th>Root 1</th>
<th>Root 2</th>
<th>Root 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>F0</td>
<td>-0.44</td>
<td>0.20</td>
<td>-0.48</td>
</tr>
<tr>
<td>DUR</td>
<td>0.49</td>
<td>0.82</td>
<td>0.33</td>
</tr>
<tr>
<td>INF</td>
<td>0.15</td>
<td>-0.13</td>
<td>-0.80</td>
</tr>
<tr>
<td>END F</td>
<td>-0.44</td>
<td>0.49</td>
<td>0.03</td>
</tr>
<tr>
<td>MIN F</td>
<td>0.41</td>
<td>-0.17</td>
<td>-0.88</td>
</tr>
<tr>
<td>MAX F</td>
<td>-0.42</td>
<td>0.22</td>
<td>0.16</td>
</tr>
<tr>
<td>PEAK F3</td>
<td>0.07</td>
<td>0.32</td>
<td>-0.61</td>
</tr>
<tr>
<td>PEAK F4</td>
<td>0.01</td>
<td>0.40</td>
<td>-0.37</td>
</tr>
<tr>
<td>MEAN F</td>
<td>-0.49</td>
<td>-0.42</td>
<td>0.99</td>
</tr>
<tr>
<td>CoFM</td>
<td>-0.07</td>
<td>0.14</td>
<td>-0.68</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>8.27</td>
<td>0.92</td>
<td>0.59</td>
</tr>
<tr>
<td>Cumulative proportion</td>
<td>0.77</td>
<td>0.85</td>
<td>0.91</td>
</tr>
</tbody>
</table>

validated error is within one standard error of the minimum and this produced a 13-node classification tree (Fig. 3). The analysis classified 74% of the calls to individuals in the training set and 51% in the test set. This result is similar to that from the cross-validation procedure in the DFA. From all calls analyzed from this analysis there was a 26% misclassification rate in the train data set and a 49% misclassification rate in the test data set. In this CART the F0 caused the first major split of the data.

C. Classification of variables

1. Potential for individual coding

From the methods of Charrier et al. (2003a), the PIC analysis results were used to rank the variables into 3 groups based on the variables’ contribution to the coding of individual distinctiveness. The first group represented a high potential for individual coding (2.5–3.0), the second showed medium potential for individual coding (1.4–1.7), and the third group demonstrated a low potential for individual coding (1.1–1.2). F0, Max F, and Mean F (PIC=2.94, 2.37 and 2.73, respectively) were classified as having a high potential for individual coding. IN F, PEAK F1, DUR, END F, and MIN F (PIC=1.50, 1.70, 1.43, 1.37, and 1.40, respectively) and PEAK F2, PEAK F3, PEAK F4, and CoFM (PIC = 1.21, 1.07, 1.06, and 1.13, respectively) exhibited a medium and low potential for individual coding, respectively (Table II).

Variables in the first and second groups are likely to be used in the individual recognition process as they were more individualized compared to those of the third group. Variables in the third group were considered unlikely to support any information about the emitter’s identity (Charrier et al., 2003a).

2. Discriminant function analysis

In the DFA, Roots 1 and 2 were dominated by the following variables: DUR, MIN F, F0, END F, MAX F, and MEAN F. These variables accounted for 85% of the data’s variance indicating that they were the most important in identifying individuals. The other three variables, INF, CoFM, and PEAK F3, were included in Root 3 and explained a further 6% of the variance. These variables may be important in separating individual females although to a lesser degree. Once again, PEAK F1 and PEAK F2 were not included in the DFA as they could not be normalized.

3. Classification and regression tree analysis

Important variables considered by primary splitters in this CART were F0, PEAK ENERGY BAND, DUR, PEAK F1, PEAK F3, and MIN F.

There are differences in the variables found to be important by all three analysis techniques, however all agree that the F0, DUR, and MIN F variables are all important in separating individual seals.

D. Peak frequency distribution in the PAC

Table III displays the most common peak energy band used by each individual and their frequency of occurrence. The results indicate that most individuals analyzed (Females 1, 2, 3, 4, 7, and 10) displayed peak frequency in Harmonic One (H1) in most replicate calls. However, some individuals displayed peak energy in Harmonic Two (H2) (Females 11, 12, 13) and Four (Females 5 and 6). There were also individuals (Females 8 and 9) that equally distributed peak energy in two harmonic bands. As a result this feature alone could only discriminate 2 out of 13 females analyzed in the

![FIG. 3. A 13-node classification tree showing how vocalizations from 13 individual female Australian fur seals split based on 10 vocal parameters.](image)


Tripovich et al.: Vocalizations in female Australian fur seals

507
current study. With the majority of callers using harmonic one (H1), the results suggest that this feature is not a good characteristic to separate individuals.

IV. DISCUSSION

For an individual seal’s call to be unique it must vary from that of other seals and be stable within the caller. This study demonstrates that the PAC produced by female Australian fur seals was correctly classified by the DFA in 76% of cases and is consistent with other previous otariid studies (74% in Antarctic fur seals, Arctocephalus gazella, Page et al., 2002; 70% in South American fur seals, Arctocephalus australis, Phillips and Stirling, 2000; 82% in Northern fur seals, Callorhinus ursinus, Insole, 1992). Call features found to be important by this study indicate that pups may rely on a combination of frequency, temporal, and amplitude-related characteristics to differentiate between the calls of their mother and those of other females. Similar results were found with respect to South American (A. australis, Phillips and Stirling, 2000) and subantarctic fur seals (A. tropicalis, Charrier et al., 2003a).

The overall structure of the PAC in Australian fur seals is generally similar to that of other otariid species. However, differences, can be noted between the species, in particular Australian fur seals have a lower fundamental frequency when compared to the other fur seals (Stirling and Warneke, 1971). This feature and other call structure variations may allow seals to discriminate among species, and result in reduced inter-breeding. Although the sample size in this study was relatively small, call stereotypy in fur seals appears to be fairly consistent with other studies with similar sample sizes (DFA analysis: South American fur seals=70%, Phillips and Stirling, 2000; Antarctic fur seals=74%, Page et al., 2002; Australian fur seals=76%, current study; subantarctic fur seals=84%, Page et al., 2002; New Zealand fur seals=88%, Page et al., 2002). Direct comparisons between studies is difficult for a number of reasons including differences in number of replicate calls per individual, acoustical features measured, and the behavioral context of recordings, all of which can affect the degree of individual distinctiveness (Bee et al., 2001). Nevertheless similarities are noted in the degree of call stereotypy of the Arctocephaline species examined to date, with DFA classification rates ranging between 70% and 88%.

Thirteen acoustic features were analyzed in order to evaluate their importance to call individuality in female Australian fur seals. Six frequency (F0, MAX F, MEAN F, IN F, END F, and MIN F), one temporal (DUR), and one amplitude related feature (PEAK F1) displayed high to medium PIC values. Five of the preceding features (F0, MEAN F, END F, MIN F, and DUR) and to a lesser degree accounting for 6% of the variance of the data, IN F, PEAK F3, and COFM, were also important in the DFA. In the CART analysis F0, PEAK F1, PEAK F3, MIN F, and DUR were important. Given the results, CoFM, PEAK F2, and PEAK F4, were not considered valuable in discriminating individuals. Although a slightly different range of variables were identified as important for call individuality by all three methods (PIC, DFA, and CART), they agree that the F0, DUR, and MIN F variables were important in separating individual seals. Similar results were reported by Charrier et al. (2003a), where in female subantarctic fur seals, the fundamental frequency and the duration of the PAC were identified, by PIC analysis, as important.

In the current study, the initial, end, and minimum frequencies of the first harmonic were found to be important in separating female callers. Previous studies of subantarctic fur seals and king penguins indicate that the start of calls may contain more information encoding an individual’s identity than the rest of the call (Charrier et al., 2003b; Jouventin et al., 1999). Although the current study indicates that the features at the start of PACs were important in individual discrimination, it also suggests that the end and minimum frequencies are also important. Playback studies manipulating the PAC would be advantageous to determine whether a pup’s ability to recognize its mother is based on these call features.

Previous research on call individuality has reported duration and peak frequency to be important to an animal’s identity. In South American (Phillips and Stirling, 2000) and subantarctic fur seals (Charrier et al., 2003a) duration is a key feature in distinguishing female callers, while studies on northern fur seals (Callorhinus ursinus) proposed that the duration of a call explained more of an emotive or arousal state of the individual caller rather than providing cues on an individual’s identity (Insole, 1992). However, in the current study duration, PEAK F1 and PEAK F3 were found to be important to individuality, while PEAK F2 and PEAK F4 were not considered to be important. This result indicates that PEAK F2 and PEAK F4 are not good individuality markers and may express the emotive state of a caller. Similarly, squirrel monkeys (Saimiri sciureus) have been shown to alter the peak frequency of their vocalizations with different behavioral states (Fichtel et al., 2001).

Frequency modulation has been shown to be an important characteristic of individual recognition in king penguins (Jouventin et al., 1999), subantarctic (Charrier et al., 2003a) and South American (Phillips and Stirling, 2000) fur seals. In contrast, the frequency modulation of calls in the present study was not regarded as important in separating female callers when compared to the other variables examined. Further, it is unknown whether frequency modulation is important in individual recognition in other otariid species, as this feature has only been examined in a few studies to date. There may also be cases where the variables measured may not be totally representative of frequency modulation in calls, as was suggested by Charrier et al. (2003a).

Functionally vocal recognition has important consequences to pups who are trying to locate their mothers for nourishment. Based on the parent-offspring conflict theory (Trivers, 1974) we expect the burden of reunion to be placed more on pups. Unsuccessful pair reunions may result in a mother’s reproductive loss, however, for the pup, pair reunions ultimately means survival or death. For that reason there are distinct selective pressures for reunion between a mother and her young (Insley, 2001). Recent studies have suggested an asymmetry of recognition, however, mutual
recognition has been shown in orioids (Trillmich, 1981; Inseley, 2001; Charrier et al., 2002, 2003b). In this study we found that the PAC produced by mothers could be assigned in 76% of cases using DFA, which would suggest that pups have the ability to actively find their mothers. The model presented here in this study may have some shortcomings, as suggested by the low cross validation results in both DFA and CART. This may indicate that pups discriminate female callers by different or additional call variables not included in this study. To further explore this area of vocal recognition, playback studies where a pup’s ability to recognize its mother’s voice should be tested. Additionally this process would determine those features involved in the vocal recognition process.

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