

Patterns in the vocalizations of male harbor seals

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Comparative analyses of the roar vocalization of male harbor seals from ten sites throughout their distribution showed that vocal variation occurs at the oceanic, regional, population, and subpopulation level. Genetic barriers based on the physical distance between harbor seal populations present a likely explanation for some of the observed vocal variation. However, site-specific vocal variations were present between genetically mixed subpopulations in California. A tree-based classification analysis grouped Scottish populations together with eastern Pacific sites, rather than amongst Atlantic sites as would be expected if variation was based purely on genetics. Lastly, within the classification tree no individual vocal parameter was consistently responsible for consecutive splits between geographic sites. Combined, these factors suggest that site-specific variation influences the development of vocal structure in harbor seals and these factors may provide evidence for the occurrence of vocal dialects. © 2003 Acoustical Society of America.

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I. INTRODUCTION

Geographic variation in vocal patterns may occur for a variety of reasons, such as genetic variation, founder effects, and adaptations to the environment through contextual learning. Variations in vocalizations have been shown to be genetically based in several bird species (Kroodsma and Canady, 1985; Baker and Bailey, 1987; Medvin *et al.*, 1992; McCracken and Sheldon, 1997) and a few mammals (Lieblich *et al.*, 1980; Nevo *et al.*, 1987). Founder effects appear to be relatively rare, but have been suggested to be the prob-

able cause of vocal variation in the northern elephant seal, *Mirounga angustirostris* (Le Boeuf and Petrinovich, 1974). Environmental factors affecting transmission properties can influence animals to adapt their call types to increase the likelihood of transmission, even among species that are capable only of contextual learning (e.g., Janik and Slater, 1997). Although several studies have shown geographic variation in the usage of call types or site-specific calls, few studies conclusively demonstrate which mechanisms are responsible for these differences (Nevo *et al.*, 1987; McCracken and Sheldon, 1997).

Vocal communication involves two types of learning, contextual and production learning. Contextual learning is

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defined as “associating an existing signal with a new context as a result of experience with the usage of signals by other individuals,” and production learning is defined as “signals that are modified as a result of experience with other individuals” (Janik and Slater, 2000). Vocal learning can be defined as production learning in the vocal domain. Vocal learning has primarily been studied in birds (e.g., Todt, 1975; Pepperberg, 1981; Kroodsma and Baylis, 1982; Baptista and Schuchmann, 1990; Gaunt *et al.*, 1994). Evidence for vocal learning in nonhuman mammals is still scarce, but vocal learning has been demonstrated in bats, phocid seals and cetaceans (see review in Janik and Slater, 1997). Clear evidence for vocal learning in nonhuman mammals is often difficult to obtain. To date, the most convincing evidence comes from experimental studies performed with captive animals (e.g., Caldwell and Caldwell, 1972; Reiss and McCowan, 1993).

Demonstrating vocal learning from observational data is much more difficult. In the case of marine mammals, the difficulties associated with keeping captive animals often means that observational data is the only possible source of information. Unfortunately, observational data can almost never exclude the occurrence of usage learning based on a pre-existing repertoire (Janik and Slater, 2000). Nonetheless, vocal learning has been demonstrated from observational data in humpback whales, *Megaptera novaeangliae*, in the wild (e.g., Payne and McVay, 1971; Payne *et al.*, 1983; Guinee *et al.*, 1983; Payne and Payne, 1985; Noad *et al.*, 2000).

In phocid seals, vocal learning has been clearly demonstrated in two captive harbor seals, *Phoca vitulina*, that were shown to be capable of imitating speech sounds (Ralls *et al.*, 1985). Some observational data also exist suggesting that vocal dialects between adjacent colonies in Weddell seals, *Leptonychotes weddellii*, may provide evidence for vocal learning (Green and Burton, 1988; Morrice *et al.*, 1994). However, to date, studies of geographical vocal variation in phocids have concentrated on sites that are several hundreds or thousands of kilometers apart (e.g., Cleator *et al.*, 1989; Terhune, 1994; Thomas and Golladay, 1995).

Harbor seals are the most widely distributed pinniped species, ranging from the eastern Baltic, westward across the Atlantic and Pacific Oceans to southern Japan. The distribution of harbor seals is such that they are exposed to a wide range of varying environmental constraints and they are composed of several subspecies (Bigg, 1981; Lamont *et al.*, 1996; Stanley *et al.*, 1996; Kappe *et al.*, 1997; Goodman, 1998; Burg *et al.*, 1999). Although harbor seals are capable of long-distance movements (e.g., Thompson *et al.*, 1989; Thompson, 1993; Ries *et al.*, 1998), populations tend to be philopatric over distances of around 100 km (Härkönen and Harding, 2001). Harbor seals are vocally versatile. They are capable of vocal learning (Ralls *et al.*, 1985) and evidence from two sites show that they exhibit geographic variation in vocalizations (Van Parijs *et al.*, 2000a). Therefore, they offer an interesting opportunity to explore vocal variation between “distant” and “neighboring” mammalian populations on a wide-ranging geographic scale. Comparisons of vocal variation at this scale have not been made previously in marine

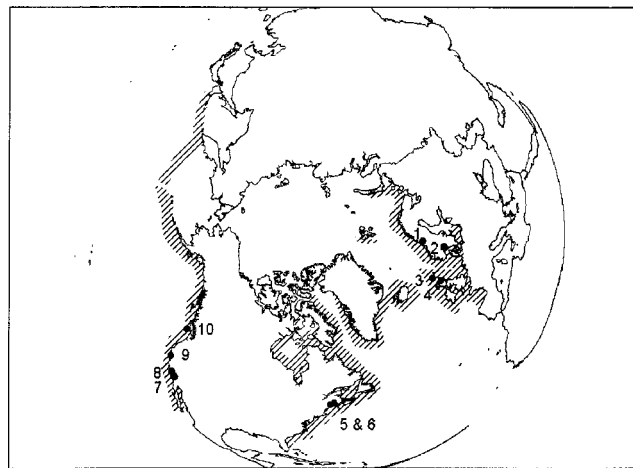


FIG. 1. Map of the Northern Hemisphere denoting the ten sites where recordings of male harbor seal vocalizations were made. The recording sites were located within (a) Eastern Atlantic Ocean—(1) Froan (FR), Norway, (2) Ursholmen (UR), Sweden, (3), the Orkneys (OR), and (4) the Moray Firth (MF), Scotland. (b) Western Atlantic Ocean—(5) Long Island (LI) and (6) St. Croix Island (SC), Eastern Canada, (c) Eastern Pacific Ocean—(7) Hopkins Marine Station, Monterey Bay (MB), (8) Elkhorn Slough (ES), and (9) Point Reyes (PR), CA and (10) Barkley Sound (BS), Western Canada. The striped lines show the distribution of the harbor seal, *Phoca vitulina*.

mammals, as few species are distributed over such a wide area.

Male harbor seals, *Phoca vitulina*, produce simple stereotyped underwater roar vocalizations for the purpose of attracting females and competing with other males (Hanggi and Schusterman, 1994; Van Parijs *et al.*, 1997; Nichol森, 2000). This study examined the vocal variation in male harbor seals from ten sites throughout the northern hemisphere, spanning most of its distribution. We hypothesized that if genetic factors control vocal variation, variation would be consistent with genetically differentiated populations and that vocal variation would increase as genetic differentiation increases with increased distances between populations. We show that genetic variation may not provide a complete explanation for geographic variation in male harbor seal vocalizations and demonstrate a possible influence of vocal dialects.

II. MATERIALS AND METHODS

Acoustic recordings were made of underwater vocalizations produced by male harbor seals from ten sites in three distinct geographic regions: the eastern and western Atlantic Ocean and the eastern Pacific Ocean (Fig. 1, Table I). Within the eastern Atlantic Ocean, two sites were located in Scotland, the Moray Firth (57° 30' N, 4° 14' W) and the Orkneys (59° 08' N, 3° 05' W), one site was in Froan Nature Reserve, Norway (64° N, 9° E) and another in Ursholmen, Sweden (58° 50' N, 10° 59' E). In the western Atlantic Ocean, two sites were located in Canada off the coast of New Brunswick, at Long Island in Passamaquoddy Bay (45° 05' N, 67° 00' W) and St. Croix Island in the St Croix River (45° 07' N, 67° 01' W). In the eastern Pacific Ocean, three of the four sites were in California, outside Hopkins Marine Station in Monterey Bay (36° 37'5 N, 121° 52'5 W), at Point Reyes (38° 02'15 N, 122° 56'41 W) and Elkhorn Slough (36°

TABLE I. The shortest distance in kilometers between the ten harbor seal recording sites.

Kilometers	Moray				Long		Barkley	Point	Monterey	Elkhorn
	Firth	Orkney	Froan	Ursholmen	Island	St. Croix	Sound	Reyes	Bay	Slough
Moray Firth (MF)	0									
Orkney (OR)	193	0								
Froan (FR)	767	624	0							
Ursholmen (UR)	422	453	584	0						
Long Island (LI)	4890	4779	4962	5223	0					
St. Croix (SC)	4888	4777	4960	5221	4	0				
Barkley Sound (BS)	7306	7118	6843	7389	4321	4318	0			
Point Reyes (PR)	8300	8119	7910	8429	4622	4620	1215	0		
Monterey Bay (MB)	8399	8220	8022	8537	4616	4614	1385	183	0	
Elkhorn Slough (ES)	8376	8197	7998	8513	4598	4596	1365	169	23	0

48° 77' N, 121° 46' 47' W) and the fourth site was in Western Canada, at Wizard Island, Barkley Sound, British Columbia (48° 51' N, 125° 09' W).

All sites from which harbor seals were recorded, except those in California and Eastern Canada, form genetically discrete populations (Lamont *et al.*, 1996; Stanley *et al.*, 1996; Kappe *et al.*, 1997; Goodman, 1998; Burg *et al.*, 1999). Sites were arranged into groups and populations according to Stanley *et al.* (1996) to allow direct comparison between vocal and genetic variation (Table II). All recordings were made between 1990 and 2000, during the mating season (eastern Atlantic sites during July and August; western Atlantic and eastern Pacific sites during May and June) except for those in Western Canada, which were recorded in November. A wide range of hydrophones was used with both digital and analog recorders, which covered the entire range of vocalizations for this species (Table III). All recordings were made with no or minimal disturbance to the seals either remotely from land or a boat from 20 m up to several hundreds of meters from the vocalizing individuals.

Throughout their geographical range, male harbor seals emit a typical roar vocalization underwater (see Hanggi and Schusterman, 1994; Van Parijs *et al.*, 1997; Bjørge *et al.*, 1995; Van Parijs *et al.*, 1999, 2000b). This roar vocalization was used for comparative analyses in this study. Recordings were analyzed as spectrograms using the BatSound analysis program (Pettersson, 1996). Only good signals, where all spectral contours were distinctly measurable, were used for these analyses (fast Fourier transforms, dt: 10 ms, df: 102 Hz, FFT size: 512, sampling frequency: 52 kHz). Four stan-

dard vocal parameters were measured (see Van Parijs *et al.*, 1999, 2000a, 2000b), the average of the lowest measurable frequency measured at both sides of the pulse, kHz (Min), the frequency with the greatest energy, kHz (Peak frequency), the total duration, seconds (Total), and the pulse duration, seconds (Pulse) (Fig. 2). These parameters were selected based on experience from previous studies, which determined the most useful variables for exploring variability in male harbor seal vocalizations [see van Parijs *et al.* (2000a, 2000b) for spectrograms with details of the measured parameters]. The number of vocalizations available for analyses varied between sites from 33 to 215 (Table II). In order to undertake balanced comparative analyses, random samples of 33 vocalizations were extracted for each site (except for Point Reyes, where only 33 samples were available). Recordings were made either at several locations (separated by more than several 100 m) within a site or at a single location where it was certain that more than one male was vocalizing. Male harbor seals have been shown to vocalize on average once every minute (see Van Parijs *et al.*, 1997), therefore a crude measure of the mean number of vocal males was calculated for all recordings using this estimate.

Call parameters were log 10 transformed. Variation in vocal parameters across sites was investigated using classification trees. Tree-based methods offer a useful approach to exploring complex data. For mathematical details, see Chap. 10 in Venables and Ripley (1999); De'ath and Fabricius (2000) discuss their use with ecological data and provide a conceptually accessible approach for biologists. Classification trees are generated by repeated binary splitting of a data

TABLE II. Classification of the genetic differentiation of harbor seal populations from the ten sites used in this study according to regional and population divisions (derived from 30–34) and the number of male vocalizations recorded at each site.

Site	No. of vocalization	Estimated No. of vocal males	Subspecies		Regional	Population
Moray Firth (MF)	215	67	<i>P.v. vitulina</i>	Eastern Atlantic	Ireland-Scotland	Scotland
Orkney (OR)	197	43	<i>P.v. vitulina</i>	Eastern Atlantic	Ireland-Scotland	Scotland
Froan (FR)	62	29	<i>P.v. vitulina</i>	Eastern Atlantic	W. Scandinavia	Norway
Ursholmen (UR)	42	13	<i>P.v. vitulina</i>	Eastern Atlantic	W. Scandinavia	Skagerrak
Long Island (LI)	74	16	<i>P.v. concolor</i>	Western Atlantic	E. Canada	Miquelon/Sable
St. Croix (SC)	70	19	<i>P.v. concolor</i>	Western Atlantic	E. Canada	Miquelon/Sable
Barkley Sound (BS)	51	11	<i>P.v. richardsi</i>	Eastern Pacific	British Columbia/Washington	Washington
Point Reyes (PR)	33	4	<i>P.v. richardsi</i>	Eastern Pacific	Oregon/California	San Francisco
Monterey Bay (MB)	52	18	<i>P.v. richardsi</i>	Eastern Pacific	Oregon/California	San Francisco
Elkhorn Slough (ES)	51	11	<i>P.v. richardsi</i>	Eastern Pacific	Oregon/California	San Francisco

TABLE III. Details of the recording equipment used to record male harbor seal vocalization at each recording site.

Site	Period	Hydrophone	Recorder
Moray Firth (MF)	07–08/1995, 1996, 1997	SSQ906 (–170 dB, 5 Hz to 15 kHz)	Tascam Porta II (40 Hz to 12.5 kHz \pm 3 dB)
Orkney (OR)	07–08/1998	As above	As above
Froan (FR)	07–07/1990, 1991	Vemco VHLFS (–147 dB, 30 Hz to 20 kHz)	UHER 4400 (25 Hz to 13 kHz, –12 dB)
Ursholmen (UR)	07/08/1999	BANDK 8101 (–184 dB <i>re</i> 1 V/ μ Pa)	Sony TCD-D7 (20 Hz to 20 kHz)
Long Island (LI)	05–6/1989	Vemco VHFS (–147 dB, 30 Hz to 20 kHz)	UHER 4200 (25 Hz to 13 kHz, –12 dB)
St. Croix (SC)	05–06/1989	As above	As above
Barkley Sound (BS)	11/1999	Offshore Acoustics (149 dB V <i>re</i> 1 μ Pa \pm 3 dB, 10 Hz to 25 kHz)	Marantz PMD201 (40 Hz to 12.5 kHz \pm 3 dB)
Point Reyes (PR)	05–06/2000	HTI-ssq-41b (10 Hz to 30 kHz (–170 dB, 5 Hz to 30 kHz)	SONY TCF-8 DAT (10 Hz to 32 kHz)
Monterey Bay (MB)	05/06/1998, 1999	Int. Transducers Inc. ISOSENS™ (\pm 1 dB, 7 Hz to 10 kHz)	SignalLogic Sig32-C data acquisition board see Baggeroer <i>et al.</i> (1994)
Elkhorn Slough (ES)	05/06/1998– 2000	As above	Tascam DA-38 (20 Hz to 48 kHz)

set, so that each split minimizes the probability of misclassification of the classifying variable (in this instance, site). Splits sequentially generate the most homogeneous possible groups; equations for these are presented in Venables and

Ripley (1999, Chap. 10). With noisy data, trees can become overlarge, and pruning is used to achieve an optimal tree. Here, this was achieved using V-fold cross validation, i.e., the data were divided into ten subsets, which were tested

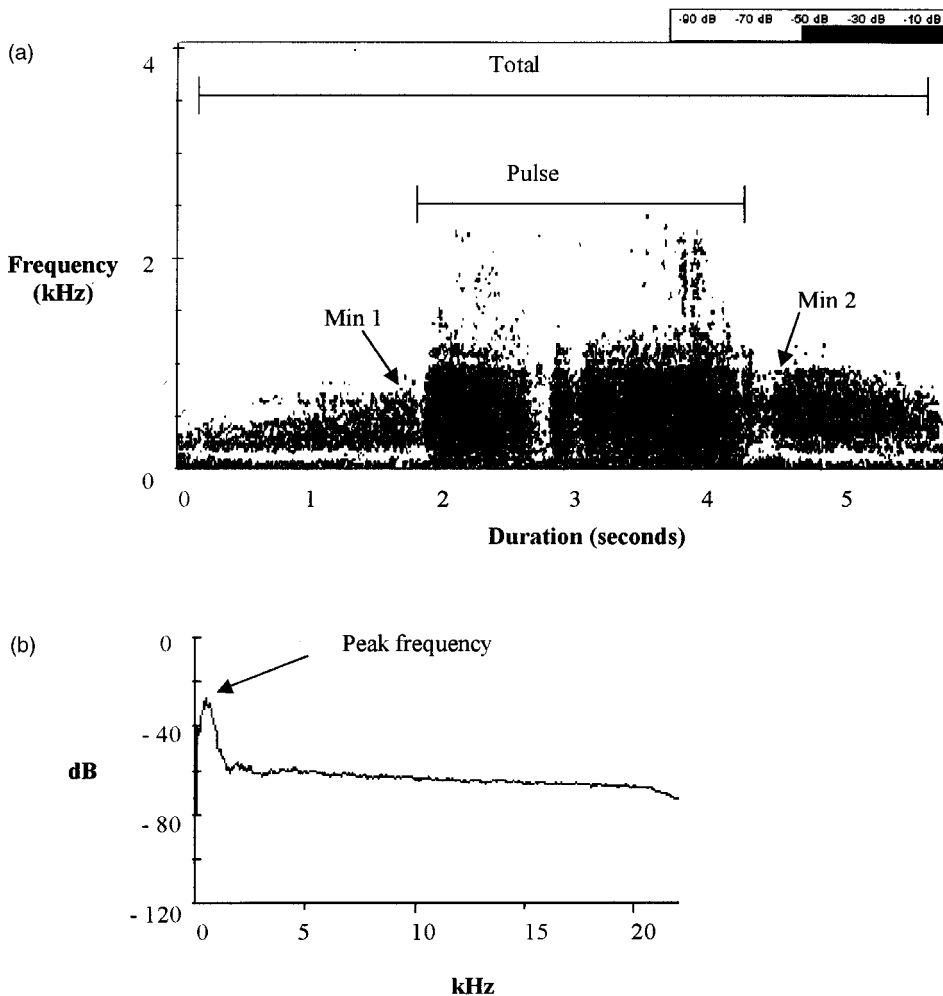


FIG. 2. A spectrogram and power spectrum of an example of a male harbor seal underwater vocalization. Four standard vocal parameters were measured, the average of the lowest measurable frequency measured at both sides of the pulse, kHz (Min); the frequency with the greatest energy, kHz (Peak frequency); the total duration, seconds (Total), and the pulse duration, seconds (Pulse).

TABLE IV. Classification of male harbor seal vocal parameters according to linear discriminant analyses.

Kilometers	Moray Firth	Orkney	Froan	Ursholmen	Long Island	St. Croix	Barkley Sound	Point Reyes	Monterey Bay	Elkhorn Slough
Moray Firth	25	8	0	0	0	0	0	0	0	0
Orkney	0	33	0	0	0	0	0	0	0	0
Froan	0	0	33	0	0	0	0	0	0	0
Ursholmen	0	0	0	33	0	0	0	0	0	0
Long Island	0	0	0	0	19	14	0	0	0	0
St. Croix	0	0	0	0	14	19	0	0	0	0
Barkley Sound	0	0	0	0	0	0	33	0	0	0
Point Reyes	0	0	0	0	0	0	0	33	0	0
Monterey Bay	0	0	0	0	0	0	0	1	31	1
Elkhorn Slough	0	0	0	0	0	0	0	0	0	33

against each other (see Venables and Ripley, 1999, Chap. 10, for details). Analyses were carried out in R version 1.4.0 (Ihaka and Gentleman, 1996), using the RPART library version 3.1-5 for classification trees, and the MASS library version 6.3-2 for other analyses.

III. RESULTS

The mean number of vocal males estimated at each recording site ranged from 4 to 67, with only one site having less than 10 individuals present (Table II). Linear discriminant analysis was carried out using sites as the predictor variable. The first two discriminant axes explained 96.6% of the variance in call parameters. Predictions from the discriminant analysis resulted in 38 misclassifications (11.5% of all classifications). Of these, 28 were between St. Croix and Long Island (14 misclassifications for each site), eight were of calls from the Moray Firth classified to Orkney, and two Monterey Bay calls were misclassified, one each to Point Reyes and Elkhorn Slough (Table IV).

An initial 12-node classification tree was pruned using cross-validation. Using the 1-SE rule [i.e., the smallest tree for which the cross validated relative error rate is within one standard error of the minimum (De'ath and Fabricius, 2000)] suggested that the appropriate descriptive tree was one with ten nodes (Fig. 3). This tree is shown in Fig. 4. In the figure, the vertical depth of each split indicates the proportion of total variation in the data explained by that split. Splits early in the tree (i.e., nearer the top of the page) explain more of the variability in the data than those later in the tree (i.e., towards the bottom of the page). In this tree, most Atlantic sites (Froan, Ursholman, St. Croix, and Long Island) split early from the Pacific sites. However, the two Scottish sites, Moray Firth and Orkney, split from Californian sites after the other Pacific site, Barkley Sound. No individual call parameter was consistently responsible for consecutive splits (Fig. 4).

In this tree there was 37 (11.2%) misclassifications of calls most (24) due to Long Island calls being classified as St. Croix calls. However, this division explained a relatively small proportion of the remaining deviance, as indicated by the short vertical lines to the LI and SC nodes in Fig. 3. Six calls from the Moray Firth were misclassified as Orkney calls, and one Orkney call was reciprocally misclassified.

Three Point Reyes calls were misclassified as Monterey Bay calls, and three Monterey Bay calls were misclassified as Elkhorn Slough calls.

IV. DISCUSSION

This study shows male harbor seals show clear geographic variation in vocalizations at the oceanic, regional, and population level. The misclassification of calls classified to neighboring nongenetically distinct populations provides further evidence for regionally distinctive vocalizations. These results are in general agreement with the findings of genetic structure of harbor seal populations at oceanic and regional levels (Lamont *et al.*, 1996; Stanley *et al.*, 1996; Kappe *et al.*, 1997; Goodman, 1998; Burg *et al.*, 1999). Since harbor seals are regionally philopatric on the scale of several hundred kilometers, mixing between populations is likely to be limited and genetic barriers between harbor seal populations appear to present a likely explanation for most of the observed vocal variation displayed in this species.

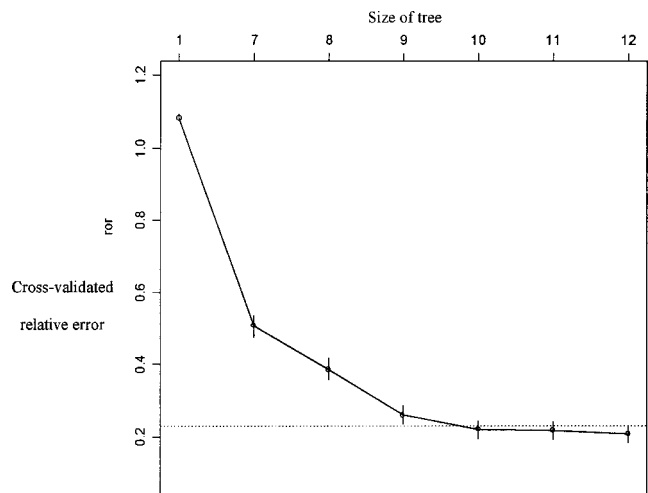


FIG. 3. Cross-validation results of an initial 12-node classification tree of male harbor seal vocalizations from ten sites. Points show the cross-validation relative errors and their standard errors from a ten-fold cross-validation for the classification tree of harbor seal vocalizations by site. Using the 1-SE rule [i.e., the smallest tree for which the cross-validated relative error rate is within one standard error of the minimum (De'ath and Fabricius, 2000)] suggests that the appropriate descriptive tree was one with ten nodes. The horizontal dashed line shows the cutoff point when using the 1-SE rule. Values along the x axis were chosen automatically to provide the most informative graph.

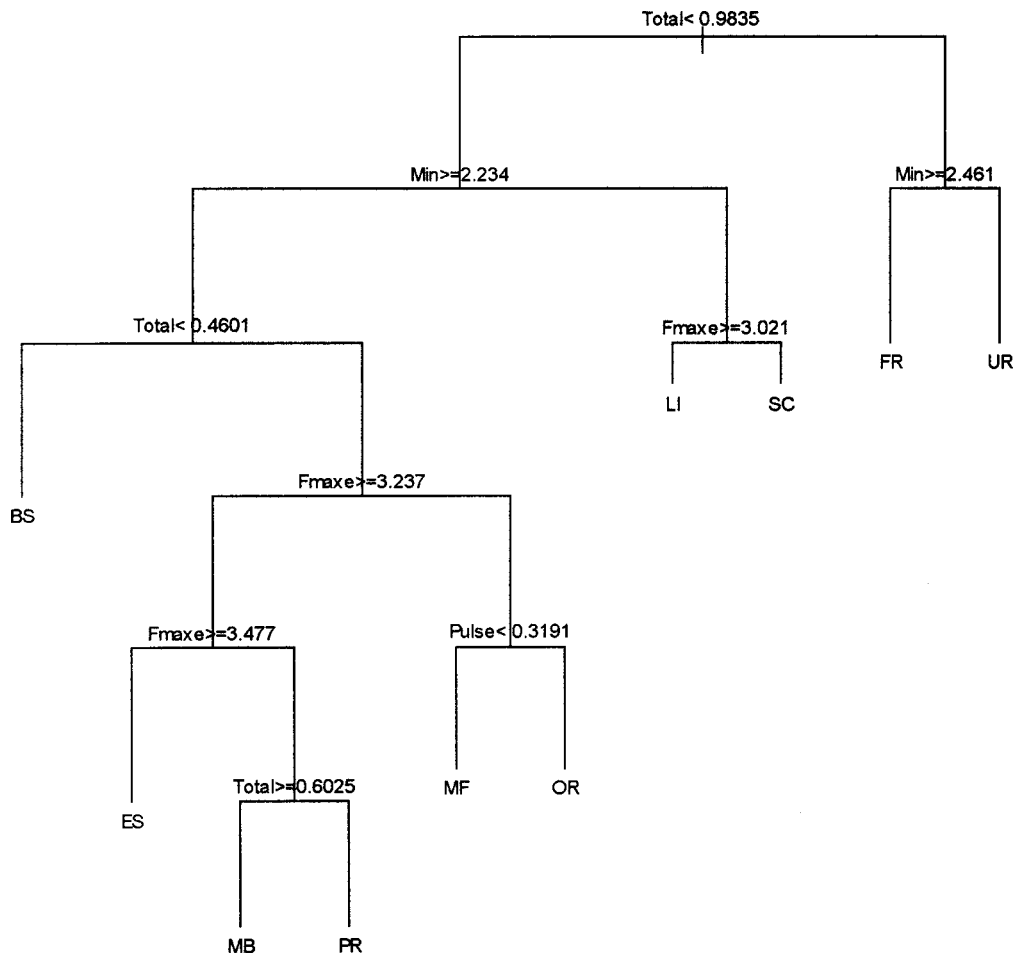


FIG. 4. A ten-node classification tree showing how male harbor seal vocalizations from ten sites throughout their distribution split, based on log 10 transformed data of the four measured vocal parameters [total duration, s (Total), pulse duration, s (Pulse), frequency with the greatest energy, kHz (Peak frequency), and lower frequency, kHz (Min)]. The vertical depth of each split indicates the proportion of total variation in the data explained by that split. Splits early in the tree (i.e., nearer the top of the page) account for more of the variability in the data than those later in the tree (i.e., towards the bottom of the page). The recording sites labels are as in Fig. 1.

However, genetics alone is unable to explain all the observed vocal variation for three main reasons. First, vocal variation between sites in California did not reflect known genetic structure. Population genetic structure (based on mtDNA) demonstrated little genetic variance between Californian populations, suggesting that regional groups mix in the geographic area (Stanley *et al.*, 1996). In addition, individuals have been shown to move between Monterey Bay and Elkhorn Slough sites for haul out purposes (Eguchi, 1998). In contrast, there was clear vocal variation between Californian sites. Furthermore, Monterey Bay and Point Reyes split from Elkhorn Slough, even though Monterey Bay is much closer in physical distance to Elkhorn Slough. We suggest that these results provide evidence for the existence of site-specific vocal dialects in Californian harbor seals.

Second, Scottish (Moray Firth/Orkney) sites split from other Atlantic sites and were classified alongside the western Pacific sites. If genetic barriers were responsible for vocal variation, we would expect these sites to be classified within the Atlantic region. A small-scale comparative analysis of the two Scottish sites showed evidence for geographic variation (Van Parijs *et al.*, 1999). However, this between site variation was considerably reduced when sites were compared

within the analyses of this study. It is important to note that small-scale comparative studies, comparing only a few sites, may overly simplify the factors influencing vocal development.

Finally, no one specific vocal parameter was responsible for classifying the sites. All parameters were responsible for the creation of nodes at different stages throughout the classification tree analysis. This suggests that variation in vocalizations may be driven by site-specific selection for changes in certain vocal parameters, providing further support towards the possible existence of vocal dialects in this species.

There may be other possible explanations for the observed variation. Geographic variation in vocalizations could have arisen as a result of ecological influences. Harbor seals occur over a wide region, spanning a range of environments (Bigg, 1981). Studies have shown that male harbor seals exhibit plasticity in the timing of their vocal behavior in response to environmentally driven variation in female distribution (Van Parijs *et al.*, 1997, 1999). Aquatic harbor seal mating habitats differ between riverine, estuarine, and open ocean areas. For example, narrow, shallow, and muddy habitats are likely to affect vocal transmission very differently from deep open ocean habitats. Similarly, habitats with high

ambient noise will affect vocal transmission substantially compared with environments that contain less ambient noise. It is reasonable to assume that differing habitats could influence sound propagation and encourage vocal variation.

Another possible explanation for some of the observed vocal variation in this study could be individual variation in male vocalizations (Van Parijs *et al.*, 2000a). However, as recordings came from multiple individuals at all sites, it is therefore unlikely that individual variation will have influenced the clear divisions that are observed in this study.

Over a wide geographic area the factors influencing vocal variation are not clear-cut. Instead a combination of factors appears to be responsible for the observed variance. While genetic barriers provided a partial explanation for the observed patterns in harbor seal vocalizations, site-specific variations also appear to be a significant factor influencing vocal patterns. Male harbor seals appear to exhibit vocal dialects, with both vocal learning and selective pressures for the evolution of vocal structure influencing the vocalizations of this species.

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