



Individual and geographical variation in display behaviour of male harbour seals in Scotland

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Studying variations in behaviour at the individual or population level enables insight into the reproductive strategies within a species. We examined individual and geographical variation in the vocal and dive behaviour of male harbour seals, *Phoca vitulina*, which is associated with aquatic mating. This display behaviour was recorded in the Moray Firth, Scotland, from July 1994 to 1997, and in Orkney, Scotland, during July 1998. One vocalization type was apparent in the Moray Firth and two in Orkney. Time parameters (total and pulse duration) varied between males in the population in the Moray Firth. We used both frequency and time parameters in a discriminant analysis, which showed that 73.2% of individual male vocalizations could be correctly classified; 94.6% of male vocalizations from the Moray Firth and Orkney could be correctly classified according to their geographical areas. Therefore, vocal variation was greater between geographical areas than between individuals. No individual variation was apparent between dive and surface interval durations. However, individuals varied significantly in the percentage of short surface intervals. Male harbour seals showed substantial variability in the parameters affecting their vocal and dive behaviour during the mating season. We suggest that these variations may be indicative of adaptations to varying environmental challenges influencing the reproductive strategies of discrete populations.

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Studies of individual variation of behaviour in animals are important for investigating both female choice and male–male competition (Harvey & Bradbury 1991). Variations in display behaviour, such as vocalizations, are known to influence male competition (Catchpole & Leisler 1996; Levin 1996) and female choice (Bishop et al. 1995; Gray & Hagelin 1996). Variations in vocalizations on a microgeographical and geographical scale are important in determining and maintaining the social structure of a group and can be found in a range of species (Mundinger 1982; Ford 1991; Mitani et al. 1996; Weilgart & Whitehead 1997).

Several phocid species use vocalizations during the breeding season, including both land-breeding species (e.g. northern elephant seal, *Mirounga angustirostris*: Shipley et al. 1980) and aquatic-mating species (e.g. Weddell seal, *Leptonychotes weddellii*: Bartsch et al. 1992; leopard seal, *Hydrurga leptonyx*: Rogers et al. 1996). In land-breeding phocids, vocalizations by males are

thought to serve principally in male–male competition (Shipley et al. 1980; Le Boeuf & Reiter 1988). In contrast, very little is known about the function of underwater vocalizations in aquatic-mating phocids. Individual variations in vocalizations have been observed in some phocids, such as the northern elephant seal (Shipley et al. 1980). Several studies have reported geographical variations in vocalizations in aquatic-mating pinnipeds at both a local and regional scale (Thomas & Stirling 1983; Cleator et al. 1989; Asselin et al. 1993; Morrice et al. 1994; Terhune 1994; Pahl et al. 1997). For example in the Weddell seal, distinct geographical variations in vocalizations have been reported on a local scale, between six fjords (Morrice et al. 1994), and regionally, between the Palmer Peninsula and McMurdo Sound, Antarctica (Thomas & Stirling 1983).

The harbour seal, *Phoca vitulina*, is an aquatic-mating phocid (Sullivan 1981; Allen 1985; Thompson 1988; Hanggi & Schusterman 1994; Björge et al. 1995; Coltman et al. 1997; Van Parijs et al. 1997). Energetic constraints force females to forage to sustain late lactation (Bowen et al. 1992; Boness et al. 1994; Thompson et al. 1994). Therefore, they are widely distributed at sea throughout the mating season and it is unlikely that males are able to monopolize females (Thompson et al. 1994). Previous

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studies have shown that male harbour seals produce underwater vocalizations and alter their dive behaviour markedly during the mating season (Hanggi & Schusterman 1994; Bjørge et al. 1995; Coltman et al. 1997; Van Parijs et al. 1997). They display over a wide area covering the whole of the females' distribution (Van Parijs et al. 1997, 1999), but especially near the haul out sites and feeding grounds of females and on transit routes between the two (Van Parijs et al. 1997, 1999). Oestrous females show marked differences in spatial and temporal distribution between geographical areas and males clearly adapt their display behaviour to variations in female distribution between sites (Van Parijs et al. 1999).

In Scotland, male harbour seals alter their dive behaviour at the start of July, the mating season, from long foraging dives to characteristic short stereotypic dives (Van Parijs et al. 1997). Changes in dive behaviour during the mating season have also been reported in Norway (Bjørge et al. 1995) and in Canada, where shallow diving has been associated with mating season behaviour (Coltman et al. 1997). Individual variation in vocalizations of male harbour seals have been recorded in a small subset of a breeding population in California (Hanggi & Schusterman 1994). However, to date nothing is known about individual variation in male vocalizations throughout a breeding population or in different geographical areas.

We examined whether vocalizations vary between individuals throughout a population's range and between individuals from distinct geographical areas. We also determined the level of individual variation in male display diving behaviour in Scotland, U.K.

METHODS

We studied seals in the inner Moray Firth, U.K. (57°41'N, 4°0'W) during July 1993, 1994, 1995 and 1996 and in northwest Orkney, U.K. in July 1998 (59°8'N, 3°8'W; Fig. 1). The study was based throughout the Beaully and Inverness Firths (Fig. 1a). In the Moray Firth, female pupping haul out sites are limited to a few intertidal sandbars and females are highly clumped in time and space (Thompson et al. 1996). During June and July, females travel along these narrow estuaries to forage further out in the inner Moray Firth (Thompson et al. 1994; Van Parijs et al. 1997). In contrast, the study area in Orkney consisted of several dispersed islands with rocky coastlines (Fig. 1b). Here, female pupping haul out sites are much less influenced by tidal availability and females are much more dispersed (Thompson 1988; Thompson et al. 1989). Only limited information is available on foraging areas of seals from Orkney, but females appeared to travel west out to more open water to forage during late lactation (P. M. Thompson, unpublished data).

Acoustic Methodology

In the Moray Firth, we used data from 30 males for vocal analyses and from six males for dive analyses. Of these 30 males, six were identified from radiotags which

each operated at different VHF frequencies (for details of capture and tagging techniques see Dive methodology). We recorded three of the radiotagged males (M30, M34 and M39) from a 5.5-m boat during July and early August in 1994 and 1995 (Fig. 1a). M30 was recorded on 1 day for 60 min, while both M34 and M39 were recorded on 3 separate days, M34 for a total of 270 min, and M39 for a total of 180 min. Recordings were made using an AN/SSQ-41A hydrophone, a custom-made preamplifier and a Tascam four-track audiocassette recorder.

We identified the other 27 individuals by using both acoustic localization techniques and visual observations of male surface behaviour. Acoustic recordings were made at sampling stations, spaced at 2-km intervals, throughout the inner Moray Firth (Fig. 1a). At each sampling station, we used a compass bearing to identify the direction of males that were making short dives associated with mating behaviour within visual range of the boat. We recorded untagged males at sampling stations, by using a four-hydrophone array fixed to an 8.5-m boat (Van Parijs et al., *in press*). We studied a further two untagged males by using a land-based three-hydrophone array in the Kessock channel, Beaully Firth (Fig. 1a). For recordings from the boat array we used four SSQ906A(D) navy hydrophones and from the land-based array three HTI-94-SSQ hydrophones. For all recordings we used a Tascam four-track audiocassette recorder and custom-made preamplifiers (see Van Parijs et al., *in press* and Janik et al., *in press* for the design and calibration of the arrays). The frequency response of the whole system was 40 Hz to 12.5 kHz \pm 3 dB with the Tascam recorder. In July 1996, we made 30-min recordings at each sampling station from the boat array, and a total of 320 min of recordings of each of the two males over 8 days from the land-based array.

All recordings were played back on the four-track audiocassette recorder and to identify individual males we used a localization program in the Signal software package (Engineering Design, Belmont, MA, U.S.A.). In this case, we used Signal to calculate the time delay between the spectrograms generated for all recorded male harbour seal vocalizations. Each time delay corresponds to a specific hyperbola of possible source locations. The source locations for all male vocalizations were calculated and plotted on to a chart. The four-hydrophone array showed a localization error of 2.6–7.4 m and the three-hydrophone array an error of 2.4–14.9 m for sounds inside and close to the arrays (Janik et al., *in press*; Van Parijs et al., *in press*). On either side of the array the error increased with distance from the centre of the array.

Individual males were identified based on the assumption that when five acoustic locations were consistently calculated in one direction they were produced by one individual. This assumption was based on evidence that males display consistently within the same small discrete areas throughout July (Van Parijs et al. 1997; Van Parijs 1998). All acoustic locations were contrasted with the relevant compass bearing taken from visual observations of display-diving males in order to ensure that only one individual was clearly associated with the recorded vocalizations. Therefore, only vocalization data from

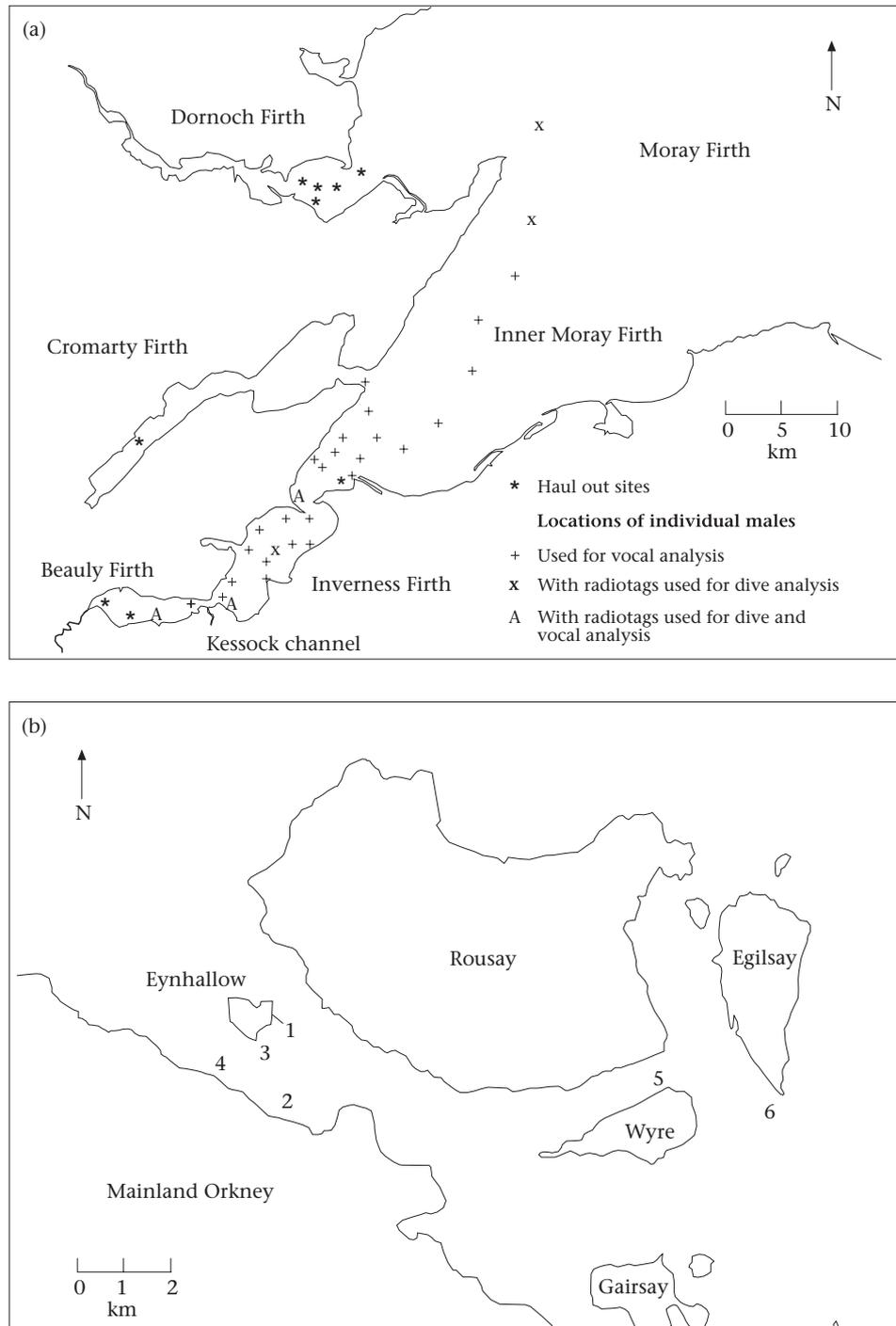


Figure 1. The locations of individual male harbour seals used in both the vocal and dive behaviour analyses. (a) The Moray Firth; (b) the Orkneys.

males located both visually and acoustically were used in the following analyses.

We also recorded male vocalizations at six sites around northwest Orkney during July (Fig. 1b). Recordings were made for 60 min at five of the sites over 2 days, while continuous recordings were made every 3 days in July at the sixth site based at Eynhallow. An SSQ906 hydrophone and a Marantz audiocassette recorder were used to record vocalizations.

We analysed all recordings as sonograms using both RTS and Signal packages (Engineering Design, Belmont, MA, U.S.A.). For standardization, and to assist comparisons, sonograms were used only where the whole of the vocalization was visible on Signal without either any background noise or distortion in the signal. A minimum of 10 vocalizations for each individual male were sampled over a frequency range of 0–5 kHz and stored in RTS and Signal computer files. We measured five vocal parameters

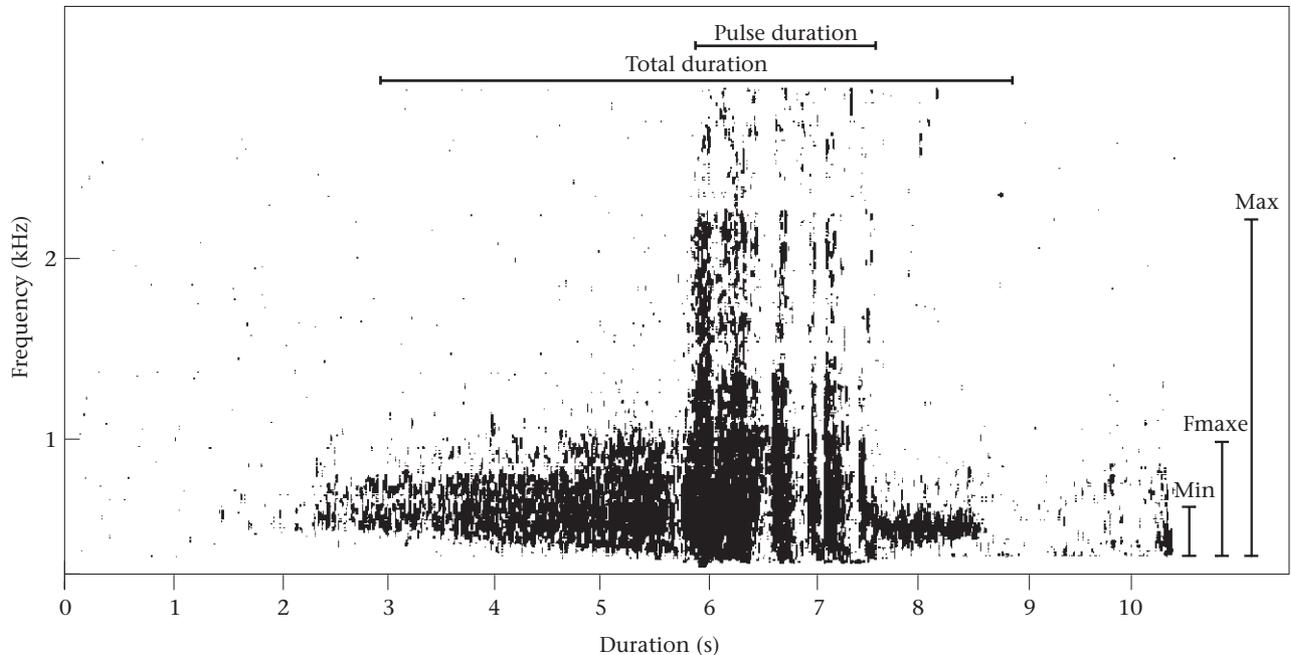


Figure 2. Spectrogram of a male vocalization indicating the five parameters measured: total duration (s), pulse duration (s), frequency with the greatest energy (Fmaxe; kHz), minimum frequency (Min; kHz) and maximum frequency (Max; kHz). Analysis settings were: frequency resolution: 31.5 Hz; sample rate: 10 000 Hz; spectrogram gain: -33.0 dB; spectrogram range: 16.0 dB.

for each vocalization: frequency of greatest energy (Fmaxe; kHz); minimum frequency (Min; kHz); maximum frequency (Max; kHz); total duration of vocalizations (Tot); and duration (s) of pulse (Pulse) (Fig. 2).

Dive Methodology

We caught and radiotagged six adult males (M30, M32, M34, M36, M38 and M39) at haul out sites in the Beaulieu and Inverness Firths, during May 1993, 1994 and 1995 (Fig. 1a). Adult males were defined as males between 80 and 120 kg (Van Parijs et al. 1997). Once the seals were secure in hand nets we sedated them with tiletamine hydrochloride and zolazepam (Zoletil, Reading, ZAC, L'Hayles-roses, France), to minimize stress and possible stress-related mortality during handling, and measured weight, length and girth (Thompson et al. 1992). An 80-g (0.06–0.09% of total body weight) VHF radiotag was then glued to the top of the head of each seal with two-part epoxy resin (Fedak et al. 1983). These transmitters were well below the maximum 5% of body weight recommended for radiotelemetry studies (Cuthill 1991). The design and positioning of tags were also chosen to minimize cross-sectional area and thus decrease drag effects whilst diving (Wilson et al. 1986). Seals generally remained quiet but alert after administration of the sedative and recovered within 30–60 min, after which they made their own way back into the water. Three display-diving males without radiotags were observed on an opportunistic basis in 1994 (total of 30 min on 1 day), 1995 (total of 56 min over 3 days) and 1996 (total of 86 min on 3 days) in the Kessock channel, Moray Firth

(Fig. 1a), to compare the display dive behaviour of radiotagged and nonradiotagged males.

We obtained radiolocations of males by triangulation using hand-held directional aerials from coastal hilltops 1–40 km away; these were accurate to $\pm 7.5^\circ$ (Thompson & Miller 1990). Dive characteristics were recorded manually for six radiotagged males on an opportunistic basis during July 1993, 1994 and 1995, whilst they were display diving (Van Parijs et al. 1997). Males were determined to be display diving when both dive and surface interval durations became short (dives of around 60 s and surface intervals of 1–30 s) and stereotypic. This behaviour contrasts with the significantly longer dive and surface interval durations (dives of around 200 s and surface intervals of 20–60 s) recorded when males were travelling, foraging or resting (as described in Van Parijs et al. 1997). Dive durations and surfacing patterns of the six radiotagged males were determined from the pattern of VHF radio signals (Wanless et al. 1988; Nielsen 1995). We measured display dive durations by noting the time between the end of one bout of radio signals and the start of the next set and surface interval durations by noting the total time that the signal was heard at the surface between each dive (Van Parijs et al. 1997).

Acoustic Analyses

All statistical analyses were made using SPSS (1997).

First, the level of individual variation in all five vocal parameters was explored with both parametric two-tailed analysis of variance (ANOVA) and Tukey *t* tests in order to determine the level of variation between individual males in the Moray Firth. We applied a Bonferroni procedure to

all the data to avoid rejecting a null hypothesis from double testing of the same data (Bakeman & Gottman 1986). This lowered the threshold significance level to $P < 0.01$. These tests were justified as all vocal parameters were normally distributed (Kolmogorov–Smirnov normality test: $P < 0.0001$).

We then used a discriminant multivariate analysis comparing all five vocal parameters to determine if this test was able to extract individual seals from the Moray Firth on the basis of their vocalizations. Discriminant analysis performed a fully factorial multivariate analysis of variance using Min, Max, Fmaxe, Tot and Pulse parameters. Canonical scores were determined for each parameter and the dependent variable canonical coefficients used to produce discriminant scores. These coefficients were standardized by within-group standard deviations so that comparisons could be made of their magnitude across variables with different scale. Final classification predicted the percentage of cases correctly classified and sorted all discriminant scores into two groups: Function 1 and Function 2. Lastly, the analyses calculated the mean posterior probabilities of vocalizations being classified correctly.

Second, we explored geographical variation in vocal parameters with parametric ANOVA and Tukey t tests to determine the level of variation in vocalizations between sites. A Bonferroni procedure was applied to all the data as above.

We then used a discriminant multivariate analysis comparing all vocal parameters from Orkney and the Moray Firth to determine if this test could extract geographical variations in vocalizations between the two areas.

Dive Analyses

We examined variability in male dive parameters during July using two techniques. To measure individual variation in display dive duration between males we used parametric ANOVA and Tukey t tests, while individual variation in surface interval duration was measured with nonparametric Kruskal–Wallis and Tukey t tests. Bonferroni procedures were applied and lowered the threshold significance level to $P < 0.01$. The variation between males in the percentage of the dive that the seal spent at the surface was tested using a chi-square test. Display dive durations and surface intervals of radiotagged and nonradiotagged males were compared with ANOVA and Kruskal–Wallis tests.

RESULTS

Acoustic Analyses

Male harbour seals in the Moray Firth used only one vocalization type consisting of a broad-band roar (Fig. 3a). An ANOVA showed that there was significant variation between individuals within all five vocal parameters (Table 1). Further analysis using Tukey t tests showed that the variation between individuals was

greatest in both measured time parameters with 24 (for Tot) and 21 (for Pulse) of the individuals measured showing significant variation (Table 1). In contrast, little variation was apparent between individuals for either of the three frequency parameters measured (Table 1). Discriminant analysis results showed two major conclusions. First, vocal variability was small within an individual ($P < 0.0001$); therefore the observed variability was attributable to differences between individuals (Table 2). Second, 73.2% of the individuals could be correctly classified by discriminant analysis. Calculations of the mean posterior probability showed that classification of individuals according to their vocalizations was highly variable (Table 2).

An ANOVA of vocalizations recorded in Orkney suggested that male harbour seals in this region used two separate vocalization types (Table 3). These types varied significantly in both Min and Fmaxe values. This difference could also be noted visually by comparing spectrograms of male vocalizations (Fig. 3b, c). Therefore, we divided Orkney vocalizations into types 1 and 2 for geographical variation analyses.

An ANOVA comparing vocal parameters from the Moray Firth and type 1 and type 2 from Orkney showed that male vocalizations varied geographically (Table 4). Discriminant analysis results gave two major conclusions. First, vocal variability was small within an individual ($P < 0.0001$); therefore the observed vocal variability was attributable to differences between individuals (Table 2). Second, 94.6% of the individuals were correctly classified by discriminant analysis. The probability of each vocalization type being classified correctly was high (Table 2).

Dive Analyses

Male display dives lasted a mean \pm SE of 57.0 ± 1.14 s ($N = 1528$) and had a median surface interval of 3 s (interquartile 15, $N = 1528$; Table 5). An ANOVA showed that individuals varied in both display dive (ANOVA: $F_{5,1527} = 26.8$, $N = 1528$, $P < 0.0001$) and surface interval duration (Kruskal–Wallis: $\chi^2_5 = 620$, $N = 1528$, $P < 0.0001$). Further analysis using Tukey t tests determined that both M38 and M39 differed from other males in both dive duration and surface interval duration (M38: display dives: $t_{2,133-617} = 15.7-43.0$; surface intervals: $t_{2,96-617} = 7.7-21.6$; M39: display dives: $t_{2,133-617} = 7.1-42.5$; surface intervals: $t_{2,96-617} = 8.6-29.6$; $P_s < 0.01$). None of the other males showed significant variation from each other for either dive duration or surface interval duration ($P > 0.05$). Chi-square results revealed significant variation between males in the percentage of the dive that the seal spent at the surface (Table 5).

Nonradiotagged males had a mean display dive duration \pm SE of 53 ± 2.0 s ($N = 385$) and a median surface interval of 2 ± 21 s ($N = 385$). Neither display dive nor surface interval duration was significantly different from that observed for males with radiotags (display dive: $F_{2,1912} = 1.3$, $N = 1913$, $P = 0.25$; surface interval: $\chi^2_2 = 148$, $N = 1913$, $P = 0.33$).

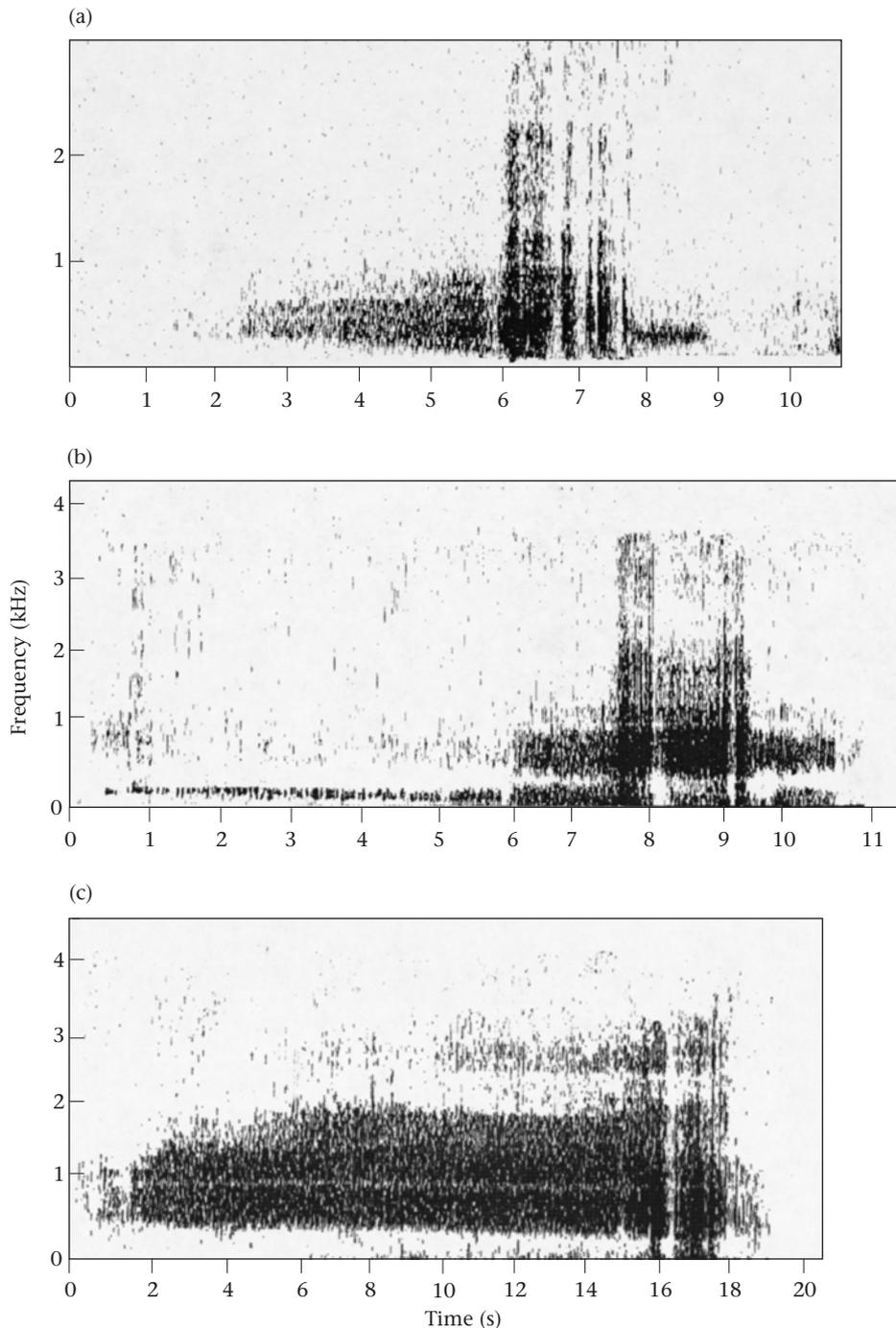


Figure 3. (a) Male vocalization from the Moray Firth, (b) type 1 vocalization in Orkney and (c) type 2 vocalization in Orkney. Analysis settings were: frequency resolution: 31.5 Hz; sample rate: 10 000 Hz, spectrogram gain: -33.0 dB; spectrogram range: 16.0 dB.

DISCUSSION

Male harbour seal vocalizations in Scotland varied individually and geographically. [Hanggi & Schusterman \(1994\)](#) showed that male harbour seals at Point Lobos in California, U.S.A., used five types of vocalizations and that males differed in vocalization types. In contrast, the harbour seal populations in our study had only one vocalization type in the Moray Firth ([Fig. 3a](#)) and two in Orkney ([Table 3](#), [Fig. 3b, c](#)). [Hanggi & Schusterman's](#)

(1994) recordings were made in a small, enclosed area of ca. 183×91 m. In contrast, in our study, recordings were made over several hundreds of kilometres (ca. 700 km^2) throughout the inner Moray Firth. Therefore, we suggest that the low number of vocalization types in the Moray Firth is not due to insufficient sampling, but is more likely to be due to variation between these two populations. In the Moray Firth, individual variation in vocalization types was therefore not observed as only one vocalization type was apparent. However, males did vary

Table 1. The five vocal parameters ($\bar{X}\pm SE$) measured for 30 male harbour seal in the Moray Firth, NE Scotland during July 1994, 1995 and 1996

Vocal parameters	$\bar{X}\pm SE$	ANOVA				t test			
		F	df	N	P	t	df	N	P
Min (kHz)	255.4±6.6	111.4	29,711	712	<0.001	17–118	2,9–132	30	<0.01
Max (kHz)	1312.8±78.2	836.2	29,740	741	<0.001	12–69	2,9–133	30	<0.01
Fmaxe (kHz)	650.2±7.8	60.6	29,744	745	<0.001	22–206	2,9–132	30	<0.01
Tot (s)	4.8±0.4	32.1	29,744	745	<0.001	6–26	2,9–132	30	<0.01
Pulse (s)	1.4±0.13	10.8	29,690	691	<0.001	12–124	2,9–133	30	<0.01

ANOVA and *t* tests explored the extent of individual variation between males in the vocal parameters: minimum frequency (Min), maximum frequency (Max), the frequency with greatest energy (Fmaxe), the total duration (Tot) and the pulse duration (Pulse). The range of *t* values is shown.

Table 2. Summary of the Wilks' λ functions determined through discriminant analysis, testing individual variation in male vocalizations within the Moray Firth and geographical variation in vocalizations between the Moray Firth and Orkney

Site	Test of functions	Wilks' λ	χ^2	df	P	% correct classification	Mean posterior probability
Moray Firth	1–5	0.001	4351	145	<0.0001	73.2	43±0.04%
	2–5	0.054	1955.5	112	<0.0001		
	3–5	0.204	1063.6	81	<0.0001		
	4–5	0.469	506.4	52	<0.0001		
	5	0.811	139.9	25	<0.0001		
Moray Firth versus Orkney Type 1 and 2	1–2	0.261	1133.7	10	<0.0001	94.6	MF: 94±0.65%
	2	0.802	186.27	4	<0.0001		O1: 82±0.24%
							O2: 86±0.43%

Table 3. The five vocal parameters ($\bar{X}\pm SE$) measured for male harbour seal vocalizations type 1 and type 2 in northwest Orkney during July 1998

Vocal parameters	Type 1	N	Type 2	N	ANOVA			
					F	df	N	P
Min (kHz)	306.0±16.0	171	595.6±23.0	553	84.2	1,222	223	<0.0001
Max (kHz)	2687.0±128.0	131	2526.7±235.0	30	0.3	1,159	160	0.56
Fmaxe (kHz)	1322.0±21.0	171	1533.1±50.3	53	20.7	1,222	223	<0.0001
Tot (s)	14.6±0.4	171	14.5±0.6	53	0.04	1,222	223	0.85
Pulse (s)	3.0±0.01	171	2.9±0.2	43	0.2	1,222	223	0.65

See Table 1 for definitions of parameters.

in total and pulse duration (Table 1). Once again, this contrasts with the Californian study, where individual variation was observed between five males within the measured frequency parameters: minimum, maximum and mean frequency (Hanggi & Schusterman 1994). This suggests that male harbour seals show variability in the parameters that vary between geographical areas.

Our results also showed that 73.2% of the individual males could be correctly classified by a discriminant analysis that used both time and frequency parameters (see Acoustic analysis). They clearly showed that individual variation can be found throughout the range of a population. The mean posterior probabilities, however, showed that only a few individuals had clearly distinctive vocalizations (see Acoustic analysis). Therefore, it is

unlikely that male harbour seal vocalizations in the Moray Firth vary enough to be used effectively as a means for identifying individuals on a regular basis.

Our study provides evidence for the existence of geographical variation in male harbour seal vocalizations (Table 4). Our discriminant analysis correctly classified 94.6% of male vocalizations from the Moray Firth and Orkney according to their geographical area (see Acoustic analysis), suggesting that male harbour seals vary geographically in the vocal parameters measured. The results from the discriminant analysis suggest that geographical variations in vocalizations are more distinctive than variations in vocalizations between males. Furthermore, visual comparisons of published data on both mean time and frequency parameters measured for male

Table 4. ANOVA between vocal parameters recorded in two geographical areas, the Moray Firth (MF) and Orkney

Vocal parameters	ANOVA				Tukey <i>t</i> test					
	<i>F</i>	<i>df</i>	<i>N</i>	<i>P</i>	MF versus type 1			MF versus type 2		
					<i>F</i>	<i>N</i>	<i>P</i>	<i>F</i>	<i>N</i>	<i>P</i>
Min (kHz)	123.2	2,935	936	<0.0001	18.6	884	<0.0001	48.6	730	<0.0001
Max (kHz)	29.0	2,901	902	<0.0001	0.001	873	<0.0001	0.4	742	0.53
Fmaxe (kHz)	942.3	2,967	969	<0.0001	55.7	917	<0.0001	63.4	769	<0.0001
Tot (s)	425.8	2,969	969	<0.0001	170.0	917	<0.0001	19.8	769	<0.0001
Pulse (s)	24.4	2,915	915	<0.0001	4.8	763	<0.03	10.6	719	<0.0001

Orkney vocalizations were divided into type 1 and type 2 for analysis (see Results). See Table 1 for definitions of parameters.

Table 5. Descriptive statistics ($\bar{X} \pm \text{SE}$) for the display dive durations, surface interval (SI) durations and the percentage of the dive that the seal was at the surface for all six males radiotagged in the Moray Firth during 1993, 1994 and 1995

Seal no.	Dive duration (s)	<i>N</i>	SI (s)	<i>N</i>	% of SI duration	<i>N</i>	χ^2		
							χ^2_s	<i>N</i>	<i>P</i>
M30	86.4 ± 2	134	5 ± 15	134	70	6	334	135	<0.0001
M32	64.4 ± 2	322	5 ± 16	322	63	6	1088	323	<0.0001
M34	49.7 ± 1	618	3 ± 17	17	75	6	3457	619	<0.0001
M36	29.4 ± 2	65	1 ± 3	65	73	6	1970	161	<0.0001
M38	76.0 ± 11	96	4 ± 7	96	59	6	136.8	98	<0.0001
M39	43.4 ± 3	293	2 ± 1	293	56	6	1232	294	<0.0001
All	57.0 ± 1	1528	3 ± 15		68	36		1528	

vocalizations in California (Hanggi & Schusterman 1994), in Froan, Norway (Bjørge et al. 1995) and our data from Scotland (Tables 1, 3) show obvious variability between all three sites. Therefore, we suggest that geographical variation is prevalent between continents and not just between more localized geographical regions (Table 4).

Vocal variations have been described in a few pinniped species on the individual, local and geographical levels (Shiple et al. 1980; Thomas & Stirling 1983; Hanggi & Schusterman 1994; Morrice et al. 1994). However, very little, to our knowledge, is known about environmental influences on vocal repertoires in the context of reproduction. Harbour seals are the most widely distributed of pinnipeds, occur in breeding groups of one or two up to several hundred females and can be found breeding on a variety of habitats including ice, intertidal sand bars and rocky beaches (Bigg 1981). Therefore, populations in different areas will face a varying range of environmental challenges. In Scotland, male harbour seals show geographical variations in their spatial and temporal distribution, in direct parallel with variations in the distributions of oestrous females between sites (Van Parijs et al. 1999). We suggest that variations in pinniped vocalizations reflect the adaptations of reproductive strategies in populations influenced by differing environmental challenges.

Males in the Moray Firth engaged in short stereotypic dive behaviour during the mating season (Table 5; Van Parijs et al. 1997). These dives were not influenced by the

presence of radiotelemetry devices (see Dive analyses). These results contrast with data from other studies where male dive durations were considerably longer (Moray Firth: mean dive duration 0.57 min, median surface interval 0.03 min, calculated from Table 5; Norway: mean dive duration 3.34 min, mean surface interval duration 0.53, Bjørge et al. 1995; Canada: mean dive duration 3.0 min, mean surface interval duration 1.31 min, Coltman et al. 1997). Furthermore, in previous studies, male harbour seals were observed making several vocalizations per dive (Bjørge et al. 1995; Coltman et al. 1997), whilst male harbour seals in the Moray Firth were observed vocalizing only once every display dive (Van Parijs et al. 1997). Individual variation was apparent in the percentage of short surface intervals made by each male (Table 5); however, there was no variation between either display duration or total surface interval duration (see Dive analyses).

In conclusion, our study has shown that there is variability in vocal and dive behaviour of male harbour seals at both the individual and geographical level. Comparisons of these data with published data from other studies around the world provide evidence of even greater variation throughout their range. We suggest that individual or geographical variation in male vocal and dive behaviour is the result of adaptations to different environmental challenges. These challenges may influence factors such as acoustic transmission properties, female distribution and access to haul out sites. Further

studies are needed to investigate the factors influencing variability in male harbour seal reproductive strategies.

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