ANIMAL BEHAVIOUR, 2007, **73**, 747–762
doi:10.1016/j.anbehav.2006.06.012

Available online at www.sciencedirect.com
ScienceDirect

Vocalizations of male bearded seals, *Erignathus barbatus*: classification and geographical variation

DENISE RISCH*†, CHRISTOPHER W. CLARK‡, PETER J. CORKERON‡, ANDREAS ELEPFANDT†, KIT M. KOVACS§, CHRISTIAN LYDERSEN§, IAN STIRLING & SOFIE M. VAN PARIJS††**

*Norwegian College of Fisheries Science, University of Tromsø,
†Humboldt University, Berlin
‡Bioacoustics Research Program, Cornell University
§Norwegian Polar Institute
**Canadian Wildlife Service
††Northeast Fisheries Science Center

*(Received 31 March 2005; initial acceptance 13 July 2005;
final acceptance 17 June 2006; published online 26 March 2007; MS. number: 8510R)*

Comparative studies of vocal repertoires over the geographical range of a species can improve our understanding of the function and evolution of animal vocalizations. They may also help to elucidate relationships between populations, where genetic studies are missing or difficult to perform. We recorded male bearded seal vocalizations from four sites throughout their Arctic distribution. We measured 16 parameters for each vocalization and examined variability using classification tree analyses. There were four major call categories: trill, ascent, sweep and moan. Trills divided further into three subcategories: trills with ascent/plume, long trills and short trills. Not all call categories were present at all sites: the ascent occurred only in Alaska and western Canada, the sweep occurred only in Svalbard and in the High Canadian Arctic, and the trill with ascent/plume occurred at all sites except Svalbard. Geographical differences between sites were apparent in repertoire size as well as in vocal structure. Furthermore, an east–west gradient in structural similarities between call types was apparent. The vocal repertoire of bearded seals seemed to be relatively stable; for example, over a period of 16 years no calls were lost or added to the Alaskan repertoire. The most likely explanation for the observed vocal differences between sites is the geographical isolation of populations by physical distance. Other factors, such as varying ecological influences (e.g. adaptation to varying ice habitats) or sexual selection, may also contribute to vocal variability and result in the observed geographical variation.

Keywords: acoustic behaviour; bearded seal; *Erignathus barbatus*; geographical variation; mating signal; trill; vocal repertoire

Geographical variation in animal vocalizations is common and widespread (e.g. Wilczynski & Ryan 1999). This variation might occur on different spatial scales. Potentially interbreeding populations of the same species may show microgeographical variations, which are the basis for true vocal dialects (Conner 1982), while geographically distant populations may show macrogeographical variations in their vocalizations. Ecological factors, such as acoustic properties of the habitat (e.g. Wiley & Richards 1982) or interspecific interactions between species in a given area (Wilczynski & Ryan 1999), are often important in forming these larger-scale variations. The evolution of anatomical features (Nevo & Capranica 1985) is

Correspondence and present address: D. Risch, F.-Engels-Str. 183, 13158 Berlin, Germany (email: denise_risch@web.de). C. W. Clark and P. J. Corkeron are at the Bioacoustics Research Program, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850-1999, U.S.A. A. Elepfandt is at the Institut für Biologie, Humboldt-Universität Berlin, Invalidenstr. 43, 10115 Berlin, Germany. K. M. Kovacs and C. Lydersen are at the Norwegian Polar Institute, N-9296 Tromsø, Norway. I. Stirling is at the Canadian Wildlife Service, 5320 122 Street, Edmonton, AB T6H 3S5, Canada. S. M. Van Parijs is at the Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1026, U.S.A.

0003–3472/07/$30.00/0

another likely contributing factor, as are intraspecific social factors that differ across geographical scales. Cultural drift can also influence acoustic variation in species that are capable of vocal learning (Slater 1986; Deecke et al. 2000). Furthermore, a number of studies have documented a genetic basis for geographical variation in various species (e.g. Lieblich et al. 1980; Kroodsma & Canady 1985; Nevo et al. 1987).

In phocid seals, male mating signals vary in several species, including northern elephant seals, *Mirounga angustirostris* (LeBoeuf & Peterson 1969), grey seals, *Halichoerus grypus* (Davies 2003), harbour seals, *Phoca vitulina* (Van Parijs et al. 2003b; Bjørgesæter & Ugland 2004), harp seals, *Phoca groenlandica* (Perry & Terhune 1999), leopard seals, *Hydrurga leptonyx* (Thomas & Golladay 1995) and Weddell seals, *Leptonychotes weddellii* (Thomas & Stirling 1983; Thomas et al. 1988). Some of the phocid species are widely distributed and are therefore excellent subjects for studying geographical variation in mating signals. We focused on male mating vocalizations in the bearded seal, the largest of the Arctic phocids. Bearded seals mate aquatically (e.g. Van Parijs et al. 2001, 2003a). During the breeding season, males produce elaborate underwater vocalizations to advertise their breeding condition and/or to maintain aquatic territories (e.g. Burns 1981; Cleator et al. 1989; Terhune 1999; Van Parijs et al. 2001, 2003a). Whether females produce some of these calls is unclear, but recent captive studies (Davies et al. 2006) support the claim that only males are vocally active during the breeding season (Ray et al. 1969). Three independent studies have categorized bearded seal vocalizations from Alaska (Budelsky 1992), Canada (Cleator et al. 1989) and Svalbard (Van Parijs et al. 2001); each has used a slightly different classification system. However, to allow comparison in space and time, the consistent classification of the vocal repertoire of a species is crucial. Using previous classification systems of bearded seal vocalizations as a baseline, in this study we combined perceptual and classification tree methods to classify vocalizations.

There is a debate regarding the existence of two subspecies of bearded seals. Citing significant differences in skull morphology, Manning (1974) concluded that the division between. *E. b. barbatus* (Erxleben 1777), ranging from the eastern Canadian Arctic east to the Laptev Sea and including the North Atlantic, and *E. b. nauticus* (Pallas 1811), ranging from the central Canadian Arctic west to the Laptev Sea, is justified. Kosygin & Potelov (1971), studying skull morphology also, did not support this finding. No further studies have addressed this question. Several studies have used vocalizations to complement morphological and molecular data to infer phylogenetic relationships within species (e.g. Nikol'skii et al. 1987; Stanger 1995; Martens 1996). However, the different factors involved in signal evolution contribute to this process on different scales and with varying efficacy, so the acoustic variation between two populations does not necessarily reflect linear genetic distances between them. For example, similar habitats can influence convergence in acoustic signals between genetically distant populations (McCracken & Sheldon 1997). Even though the relation between genetic and acoustic isolation is thus difficult to assess, an acoustic approach can prove useful to give a first approximation of population distance, especially where genetic studies are lacking because of high costs or difficult logistics (McGregor et al. 2000).

Our main aim in this study was to explore the degree of geographical variation and isolation of the acoustic repertoire of bearded seals from four geographically distant sites. We compared a unique data set of bearded seal recordings from Alaska with recordings collected in the Canadian Arctic and in Svalbard. If we assume that vocal similarity correlates with genetic distance, then acoustic differences should be apparent, especially between populations, which are assumed to be reproductively isolated. Animal vocal behaviour can change substantially over time (e.g. Payne 1985; Trainer 1989; Noad et al. 2000). Since the different recordings compared in this study were acquired over a period of nearly 30 years, we cannot rule out the possibility of temporal effects on the results of the geographical comparison. However, long-term studies suggest that pinniped vocal repertoires are generally stable over long periods (Terhune 1994; Insley 2000; Serrano & Terhune 2002). We examined the long-term stability of the bearded seal repertoire by documenting the occurrence of call types over a period of 16 years of continuous recordings in Alaska.

METHODS

Sampling Procedures and Measurements

We obtained recordings of male bearded seals from four sites during the April–June mating season of this species. At each site recordings were acquired over several years between 1972 and 2001 in Alaska (1985, 1992–1993, 2000–2001), Svalbard (1999–2000), western Canadian Arctic (1972–1975) and the Canadian High Arctic (1976, 1981–1982; Fig. 1, Appendix Table A1). The Alaska and Svalbard recordings were each acquired at a single location (Point Barrow, Alaska and Kongsfjorden, Svalbard), whereas the Canadian recordings came from several locations. Based on their geographical origin, we divided these recordings into two data sets: Canadian High Arctic and western Canadian Arctic. This was done to account for some geographical variation of bearded seal vocalizations within the Canadian Arctic, while at the same time ensuring that the sample size for each region was sufficiently large to conduct statistical analyses.

Recordings were made with a variety of hydrophones and recording equipment. In Alaska an AN/SSQ-57A sonobuoy unit was connected to either a TEAC R61-D cassette recorder (50 Hz–24 kHz ± 3 dB), a TEAC RD130T DAT recorder (50 Hz–12 kHz ± 0.5 dB) or a PC Hard Drive (50 Hz–12 kHz ± 0.5 dB). In Svalbard a HTI-96-MIN (High Tech. Inc., Gulfport, MS, U.S.A.) hydrophone was connected to a Sony TCD-D8 DAT recorder (20 Hz–22 kHz ± 1 dB). In Canada a 6050C (International Transducer Corp., Santa Barbara, CA, U.S.A.) hydrophone was connected to a Uher 4200 Stereo recorder (30 Hz–25 kHz ± 4.5 dB at 19 cm/s).