Animal Behaviour 97 (2014) 229–239

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Adult male Australian sea lion barking calls reveal clear geographical variations

Heidi Ahonen [a, b, c, *], Adam J. Stow [a], Robert G. Harcourt [a], Isabelle Charrier [b, c]

[a] Department of Biological Sciences, Macquarie University, North Ryde, NSW, Australia
[b] Université Paris-Sud, Centre Neurosciences Paris Sud, UMR 8195, Orsay, France
[c] CNRS, Orsay, France

ARTICLE INFO

Article history:
Received 19 March 2014
Initial acceptance 30 April 2014
Final acceptance 12 August 2014
Published online
MS. number: 14-00221R

Keywords:
acoustic behaviour
Neophoca cinerea
otariid
pinniped
vocal communication

Vocalizing by males plays an important role in the reproductive activities of many species. Geographical variation in the characteristics of male vocalization is well studied in birds, but largely unexplored in mammals. This study quantified the extent of geographical variation in male Australian sea lion, *Neophoca cinerea*, barking calls and examined what drives vocal differences in this species. We recorded male barking calls from seven breeding colonies separated by ca. 5–2700 km enabling us to investigate acoustic differences on both micro- and macrogeographical scales. Our results revealed significant nonuniform geographical variation across colonies. Neither genetic nor geographical distances between colonies fully explained the observed acoustic variation. We suggest that environmental or morphological factors are likely to further contribute to differences in vocal characteristics.

Geographical variation in vocalizations has been documented in a wide range of organisms including birds, mammals, frogs, lizards and insects (Catchpole & Slater, 1995; Cocroft & Ryan, 1995; Wilczynski & Ryan, 1999; Yu et al., 2011; Zuk, Rebar, & Scott, 2008). Variation can occur on different spatial scales and may be demonstrated through the production of unique call types, variations in call usage and intraindividual call differences between locations. Microgeographical variability, which is the basis for true vocal dialects, may occur between interbreeding populations of conspecifics (Mundinger, 1982). Conversely, geographically isolated populations may show macrogeographical variation in vocalizations. In species capable of vocal learning, cultural drift can influence acoustic variation (Deecke, Ford, & Spong, 2000; Ficken & Popp, 1995). Vocal learning has been described in birds and mammals; however, evidence for vocal learning in mammals is often difficult to obtain and patchy (Janik & Slater, 1997). Ecological factors such as acoustic properties of the habitat (Hunter & Krebs, 1979; Wiley & Richards, 1982), the sound environment of local biota (Nicholls & Goldizen, 2006; Pitcher, Harcourt, & Charrier, 2012; Van Parijs, Lydersen, & Kovacs, 2003) or anatomical differences between individuals (Mitani, Hunley, &Murdoch, 1999) can also explain variation in vocalizations. Such factors are often suggested as potential sources of macrogeographical variation. Furthermore, a number of studies have shown correlations between genetic partitioning and vocal distinctiveness (Kroodsma & Canady, 1985; MacDougall-Shackleton & MacDougall-Shackleton, 2001; McCracken & Sheldon, 1997; Van Parijs, Corkeron, et al., 2003).

In many mammals, males use vocalizations in social contexts either to attract females or in male–male competition (Andersson, 1994; Krebs & Davies, 1993). Male calls and the ability to correctly perceive relevant acoustic variation are therefore subject to strong selection in the context of mating success. The success of a particular call trait can vary according to social or environmental contexts and recent divergent selection among localities will be reflected by differences in call characteristics (Janik & Slater, 1997). One mammalian group in which there is clear evidence of widespread geographical variation in male vocalizations is the pinnipeds (fur seals, sea lions, walruses and true seals). However, studies of geographical variation in male vocalizations have focused mainly on phocid species (true seals), with differences in vocal repertoire and vocalization characteristics reported in northern elephant seals, *Mirounga angustirostris* (Le Boeuf & Peterson, 1969; Le Boeuf & Petrinovich, 1974), Weddell seals, *Leptonychotes weddellii* (Abgrall, Terhune, & Burton, 2003; Terhune et al., 2008; Thomas & Stirling, 1983), bearded seals, *Erignathus barbatus* (Cleator, Stirling,

* Correspondence: H. Ahonen, Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia.
E-mail address: hahonen1@gmail.com (H. Ahonen).

http://dx.doi.org/10.1016/j.anbehav.2014.09.010
0003-3472/

& Smith, 1989; Risch et al., 2007), harp seals, *Pagophilus groenlandicus* (Perry & Terhune, 1999), leopard seals, *Hydruga leptonyx* (Thomas & Golladay, 1995), and harbour seals, *Phoca vitulina* (Bjørgesæter, Ugland, & Bjørge, 2004; Van Parijs, Corkeron, et al., 2003; Van Parijs, Hastie, &Thompson, 2000). The majority of these studies have measured larger-scale geographical variations in male mating signals (Risch et al., 2007). Differences in male phocid vocalizations have been attributed to isolation of populations by geographical distance (Cleator et al., 1989; Perry & Terhune, 1999; Risch et al., 2007; Thomas & Golladay, 1995; Thomas, Puddicombe, George, & Lewis, 1988), strong site fidelity to specific breeding sites (Charrier, Mathevon, & Aubin, 2013; Terhune et al., 2008), differences in acoustic transmission properties between sites (Risch et al., 2007; Van Parijs, Corkeron, et al., 2003) and possible cultural effects with vocal learning and founder effects (Le Boeuf & Petrinovich, 1974). However, over wide geographical ranges the factors influencing vocal variation are not always clear and combinations of factors may underlie these observed differences (Van Parijs, Corkeron, et al., 2003).

This study investigated the extent and causes of geographical variation in the male barking call in Australia's only endemic otariid, the Australian sea lion, *Neophoca cinerea*. Australian sea lions range across a geographical expanse of 2200 km, from the Houtman Abrolhos (28°44′34.90′S, 113°49′7.08′E), Western Australia, to The Pages Island (35°47′5.37′S, 138°17′15.29′E), east of Kangaroo Island, South Australia with approximately 80% of the species breeding in South Australian waters (Goldsworthy et al., 2009). Most (over 60%) Australian sea lion colonies are small, producing less than 30 pups per breeding episode, and a recent census estimate of ca.14 700 individuals makes this species one of the rarest otariids in the world (Goldsworthy et al., 2009; Shaughnessy, Goldsworthy, Hamer, Page, & McIntosh, 2011). Females of this species show the highest degree of genetic differentiation of any marine mammal across this geographical range (Lowther, Harcourt, Goldsworthy, & Stow, 2012). The predominant call type produced by male Australian sea lions is the barking call (Gwilliam, Charrier, & Harcourt, 2008; Stirling, 1972). Despite the occurrence of other call types in their vocal repertoire, males use the barking call in almost all social interactions. This makes their vocal repertoire the most depauperate of all otariid males (Fernandez-Juricic, Campagna, Enriquez, & Ortis, 1999; Phillips & Stirling, 2001; Stirling, 1971; Stirling & Warneke, 1971; Tripovich, Rogers, & Rogers, 2005). Gwilliam et al. (2008) showed that despite the call's simple structure, male sea lions are able to distinguish the calls of conspecifics from those of other species and can discriminate between males and females of their own species. Moreover, the barking call of male Australian sea lions has sufficient embedded information to provide the potential for individual discrimination (Gwilliam et al., 2008). Furthermore, despite this simple vocal structure, Australian sea lion males' barks were found

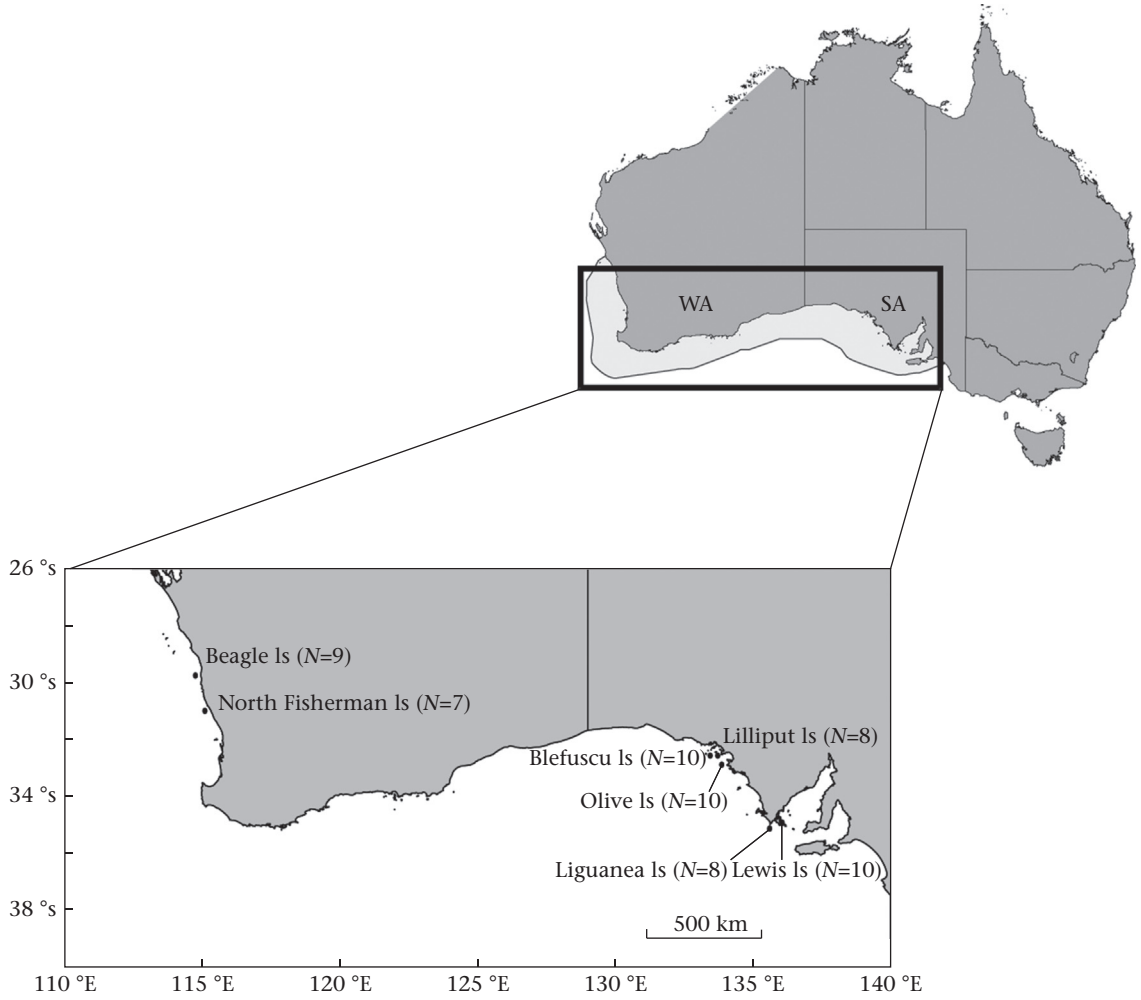

Figure 1. Location of sampling sites. Numbers in parentheses indicate the number of sampled males for each breeding colony. Highlighted area (light grey) represents the species range. WA: Western Australia; SA: South Australia.