biology
letters

Killer whales are capable of vocal learning

Andrew D Foote, Rachael M Griffin, David Howitt, Lisa Larsson, Patrick J.O Miller and A Rus Hoelzel

Biol. Lett. 2006 **2**, 509-512
doi: 10.1098/rsbl.2006.0525

biology
letters

Biol. Lett. (2006) **2**, 509–512
doi:10.1098/rsbl.2006.0525

Killer whales are capable of vocal learning

Andrew D. Foote[1,*], **Rachael M. Griffin**[2], **David Howitt**[3], **Lisa Larsson**[3], **Patrick J. O. Miller**[4] **and A. Rus Hoelzel**[1]

[1]*School of Biological and Biomedical Sciences, University of Durham, Durham DH1 3LE, UK*
[2]*Aquagreen Marine Research, 102 Pemberton Road, Victoria, British Columbia V8S 3R6 Canada*
[3]*Luna Research Project, PO Box 510, Alert Bay, British Columbia V0N 1A0, Canada*
[4]*NERC Sea Mammal Research Unit, University of St Andrews, Fife KY16 9QQ, UK*
**Author for correspondence* (*a.d.foote@durham.ac.uk*).

The production learning of vocalizations by manipulation of the sound production organs to alter the physical structure of sound has been demonstrated in only a few mammals. In this natural experiment, we document the vocal behaviour of two juvenile killer whales, *Orcinus orca*, separated from their natal pods, which are the only cases of dispersal seen during the three decades of observation of their populations. We find mimicry of California sea lion (*Zalophus californianus*) barks, demonstrating the vocal production learning ability for one of the calves. We also find differences in call usage (compared to the natal pod) that may reflect the absence of a repertoire model from tutors or some unknown effect related to isolation or context.

Keywords: marine mammal; learning; acoustics; mimicry

1. INTRODUCTION

Vocal learning can be differentiated into production learning, i.e. learning to alter the physical structure of the sounds by manipulation of the sound production organs as a result of experience with those of others (Janik & Slater 2000), and contextual learning, in which the comprehension or usage of a signal is learnt to be associated with a novel context (Janik & Slater 2000). Many mammalian species have voluntary motor control over the usage of their vocalizations and learn the context in which to use a call (Janik & Slater 1997). However, production learning, although widespread in birds, is comparatively rare in mammals (Janik & Slater 1997).

Vocal production learning starts with a sensory learning phase in which listening and memorizing of vocalizations from an adult tutor(s) takes place (Doupe & Kuhl 1999; Wilbrecht & Nottebohm 2003). This is typically followed by a sensorimotor learning phase in which the learner develops the motor skills necessary for normal adult vocal production by audition and matching its own vocalizations to a memorized template of those of the tutor (Marler 1991; Doupe & Kuhl 1999; Wilbrecht & Nottebohm 2003). These early vocalizations are often highly irregular, such as babble in infants (Doupe & Kuhl 1999) and subsong and plastic song in birds (Marler & Peters 1982), but gradually become more structurally stereotyped and adult-like with practice. However, this sequence of ontogenetic change in vocal patterns is not in itself evidence for vocal production learning, as it may simply be owing to physical maturation of the sound production organs (Janik & Slater 1997). Additional evidence for vocal learning can come from deafening experiments, dialects and geographical variation; however, there are caveats associated with each of these. Unequivocal evidence can include the mimicry of novel sounds not found in the animal's natural repertoire (Janik & Slater 1997; Egnor & Hauser 2004).

Although killer whale (*Orcinus orca*) calves go through an ontogenetic developmental stage of vocal production during their first year (Bowles *et al.* 1988), this may simply reflect a maturation process (Janik & Slater 1997). There are reports of adult killer whales learning their tank-mate's repertoires in captivity (Bain 1988; Ford 1991) and of mimicry by wild whales of other pod's repertoires (Ford 1991). However, it is harder to distinguish between production and usage learning when the vocalizations apparently being imitated are conspecific (see Yurk *et al.* 2002).

Resident populations of northeastern Pacific killer whales live in stable, matrifocal pods from which there has been no recruitment apart from birth and no confirmed dispersal during the three decades of observation (Ford *et al.* 2000) except in two cases, which are the focus of this paper. L98 (Luna) was first sighted in 1999 and A73 (Springer) in 2000; as their natal pods were sighted during the previous years, these are assumed to be the years they were born (Ford *et al.* 2000). However, between their first and second year, they became separated from their natal pods. L98 was re-sighted alone in July 2001 in Nootka Sound, Vancouver Island, BC and A73 in January 2002 in Puget Sound, WA. Both the whales were located away from the core range of their natal populations (Ford *et al.* 2000). Killer whales of other populations have been within acoustic range of each individual for short periods of time between separation and recording. At the time of recording, A73 and L98 were in their second and fifth years, respectively. Here, we assess evidence for vocal learning from these recordings.

2. MATERIAL AND METHODS

Recordings and visual identification of the southern resident population were made using the methodology described in Foote *et al.* (2004). From 54 recording sessions totalling 28 hours of L pod, 2831 calls were classified, as described by Foote *et al.* (2004). Recordings of L98 were made during eight recording sessions totalling 80 min in September–October 2003 and during six recording sessions totalling 289 min in March 2004 from a small vessel with the engine turned off and land-based recording sites in Nootka Sound. Four recording sessions totalling 106 min of A73 were selected from a continuous 24 h recording period in July 2002 in a holding pen in a natural bay following capture and relocation. Both were recorded at a distance of less than 500 m with a variety of hydrophones and recording equipment with a flat response between 0.1 and 20 kHz. The repertoire for A4 pod was estimated by Ford (1991). Comparisons of the relative frequency of the use of call types between L98 and L pod were done using a Mann–Whitney *U* test and between time periods for L98 using a χ^2-test.

The electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2006.0525 or via http://www.journals.royalsoc.ac.uk.

Received 2 June 2006
Accepted 15 July 2006

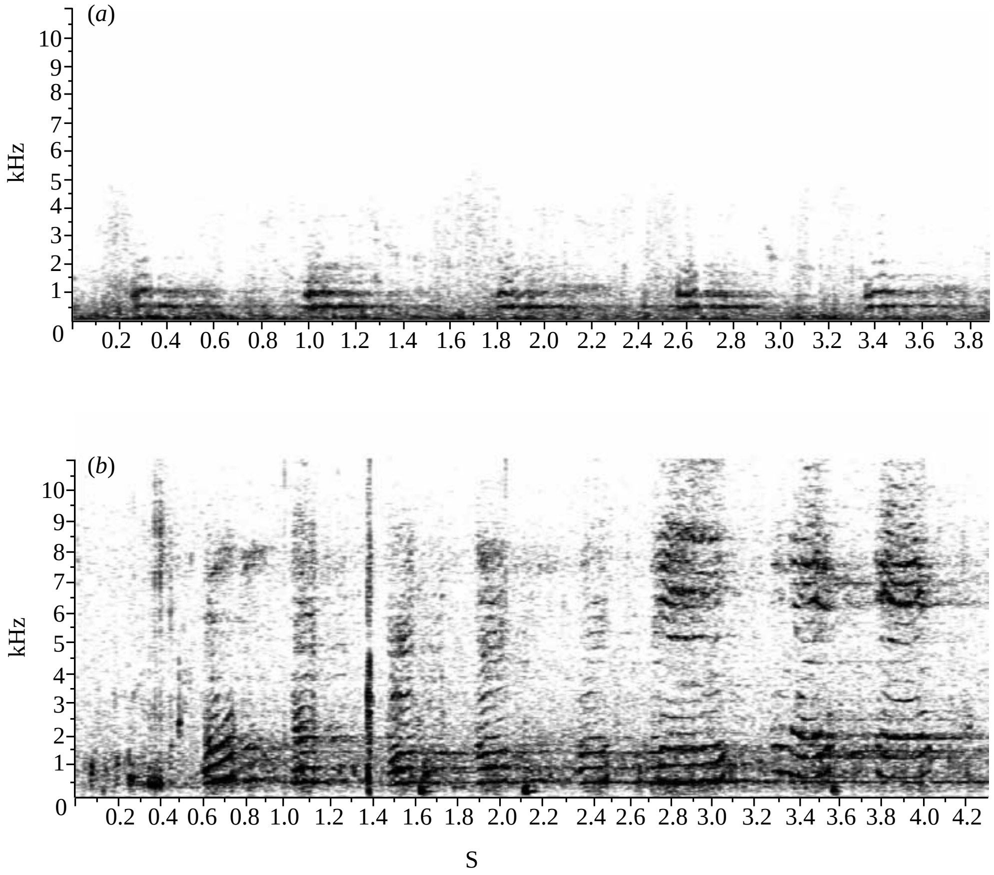

Figure 1. (*a*) Spectrogram of underwater barking of a California seal lion, *Zalophus californianus*, recorded in Tanners Bank, California in 1961. (*b*) Spectrogram of the underwater barking recorded in Nootka Sound in 2004 when only L98 and no sea lions were observed in the study area.

3. RESULTS AND DISCUSSION

We recorded underwater bark sounds in Nootka Sound, many in the presence of California sea lions (*Zalophus californianus*) that had spectrograms and a repetition pattern consistent with those previously reported for that species (figure 1*a*; Schusterman & Balliet 1969; electronic supplementary material). However, 39 sounds aurally identifiable as 'barks' had harmonics ranging over 10 kHz (figure 1*b*; electronic supplementary material) and occurred in short bouts of 5–10 vocalizations. Underwater sea lion barks typically have visible harmonics up to 4 kHz (figure 1*a*; Schusterman & Balliet 1969). Of these 39 unusual barks, 16 were recorded in daylight when only L98 and no sea lions were observed in the area, and a further 8 of those 16 barks were recorded within vocalization bouts consisting of recognizable killer whale calls or echolocation clicks (see electronic supplementary material). It is typical for killer whale calls to show harmonic loading to 10 kHz or more (Hoelzel & Osborne 1986; Ford 1991; Miller & Bain 2000), and some are produced by rapid pulses in the same way as California sea lion barks, and so could easily be modified to become bark-like, but a bark-type of call had not been previously reported for killer whales. In particular, it is shorter and has greater emphasis on lower frequencies than calls seen in documented killer whale repertoires. Taken together, these data strongly imply an instance of mimicry.

Under natural circumstances, most species that learn their vocalizations have a predisposition to learn only conspecific sounds (Marler 1991; Doupe & Kuhl 1999). However, cross-fostering and conditioning experiments have resulted in the adoption of heterospecific vocalizations in some species (e.g. beluga *Delphinapterus leucas*, Eaton 1979; harbour seals *Phoca vitulina*, Ralls *et al.* 1985; song sparrows *Melospiza melodia*, Marler 1991; African elephant *Loxidonta africana*, Poole *et al.* 2005). Social interaction has been found to reinforce vocal learning and mimicry in other species (Reiss & McCowan 1993; Baptista & Gaunt 1997). L98 has frequently been observed in close association with California sea lions and this may have prompted these cases of mimicry.

Even excluding the bark calls, L98 had a significantly different relative frequency of the use of call types than its natal pod (L pod). Captive killer whales have also shown repertoire distortion, such as Skana (Vancouver Aquarium), captured from K pod as a subadult. This whale produced a reduced repertoire of eight calls, and the most common (49% of recordings) was an L pod call, not recorded from K pod in the wild (Hoelzel & Osborne 1986).

The comparison of L98 recordings made six months apart indicates that there had been no change in its repertoire ($\chi^2_3=6.52$, $p=0.089$). Thus, the differences in relative call usage between L98 and

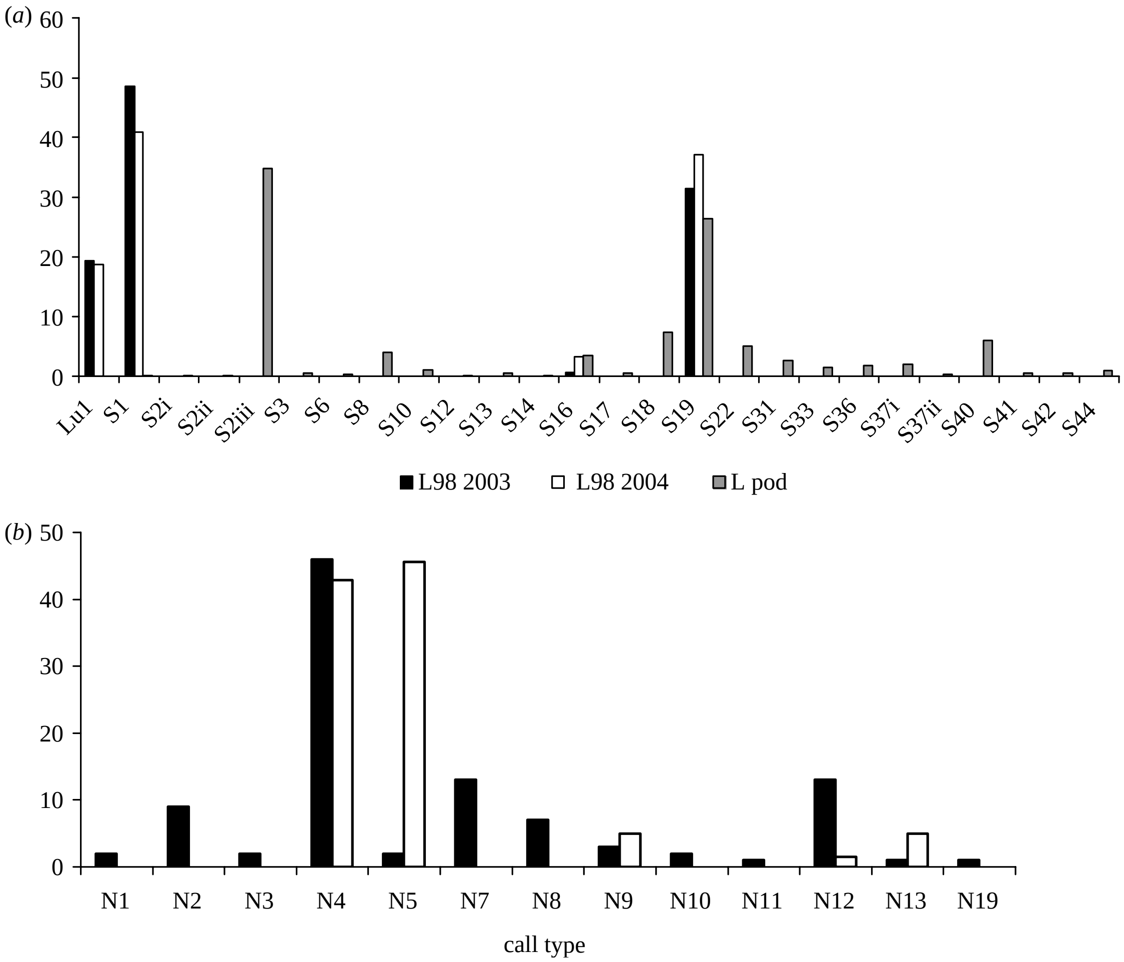

Figure 2. The relative frequency of the use (%) of call types by (*a*) L pod and L98 in 2003 and 2004 and (*b*) A73 and A4 pod.

L pod are not owing to recording L98 during a repetitive vocal bout uncharacteristic of its normal vocal output.

L98's most commonly used call type, S1 (J pod's dominant call), was used in significantly different mean proportions per recording session by L98 (50.0%) than by L pod (0.04%; $u=324.0$, $p<0.01$). Previous studies using a different set of recordings did not record a single example of the S1 call type from L pod (Hoelzel & Osborne 1986; Ford 1991). Neither the call type Lu1 nor the barking call type were recorded from the southern resident population, even though this sample represented over 100 hours recorded over nearly 30 years (Foote *et al.* 2004). L pod's most common call type, S2iii, (mean call usage of 21.4% per recording session), was not recorded from L98 ($u=237.0$, $p<0.05$).

Although there can be intra-pod variation in the relative frequency of the use of call types (Miller & Bain 2000), L98's natal matriline (L2) was present in many of our L pod recordings and so selective recording of L pod matrilines cannot fully account for the large difference seen between L pod and L98.

A73 also showed some usage differences compared to its natal pod, but these could be owing to the small sample or abnormal context. Although killer whale call types are generally not context-specific, there can be broad call usage differences between contexts (especially for 'social' compared to other behaviours; Hoelzel & Osborne 1986; Ford 1989). However, the temporarily restrained individual (A73) is much more similar in relative call usage to its natal pod than the free-ranging individual (L98) for which there is a larger dataset spanning six months (figure 2). This and the consistency of L98 in different recording sessions suggest that context cannot fully explain the magnitude of difference between L pod and L98.

Call types within a pod's repertoire that have an overlapping tonal component would be detectable over longer ranges in certain directions (Miller 2006). However, L98 used a relatively even proportion of call types with (S19) and without this component (S1, S16 and Lu1); therefore, it does not appear to have selected call types based solely on transmission properties.

The mimicry data strongly indicate that killer whales are capable of vocal production learning. The data on differential call usage by L98 are more difficult to interpret. Isolation from an L pod tutor could have been a factor, suggesting a role for usage learning in the natal pod. However, we cannot exclude alternative explanations related to the potential influence of context on L98's vocal behaviour.

We thank Kenneth Balcomb, Center for Whale Research, Richard Osborne, the Whale Museum, Paul Spong and Helena Symonds, Orcalab and Cheryl Tipp, British Library

Sound Archive for acoustic recordings. Dave Bain, Ron Schusterman and Brandon Southall gave valuable comments on the bark spectrogram and sound files. Funding was provided by the Luna Stewardship Project and the Luna Research Project.

Bain, D. E. 1988 An evaluation of evolutionary processes: studies of natural selection, dispersal, and cultural evolution in killer whales (*Orcinus orca*). Ph.D. thesis. University of California, Santa Cruz.

Baptista, L. F. & Gaunt, S. L. L. 1997 Social interaction and vocal development in birds. In *Social interaction and vocal development in birds* (ed. C. T. Snowdon & M. Hausberger), pp. 23–40. Cambridge, UK: Cambridge University Press.

Bowles, A. E., Young, W. G. & Asper, E. D. 1988 Ontogeny of stereotyped calling of a killer whale calf, (*Orcinus orca*) during her first year. *Rit. Fisk.* **11**, 225–250.

Doupe, A. & Kuhl, P. K. 1999 Birdsong and speech: common themes and mechanisms. *Annu. Rev. Neurosci.* **22**, 567–631. (doi:10.1146/annurev.neuro.22.1.567)

Eaton, R. L. 1979 A beluga imitates human speech. *Carnivore* **2**, 22–23.

Egnor, S. E. & Hauser, M. D. 2004 A paradox in the evolution of primate vocal learning. *Trends Neurosci.* **27**, 649–654. (doi:10.1016/j.tins.2004.08.009)

Foote, A. D., Osborne, R. W. & Hoelzel, A. R. 2004 Environment: whale-call response to masking boat noise. *Nature* **428**, 910. (doi:10.1038/428910a)

Ford, J. K. B. 1989 Acoustic behaviour of resident killer whales (*Orcinus orca*) around Vancouver island, British Columbia. *Can. J. Zool.* **67**, 727–745.

Ford, J. K. B. 1991 Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Can. J. Zool.* **69**, 1454–1483.

Ford, J. K. B., Ellis, G. M. & Balcomb, K. C. 2000 *Killer whales: the natural history and genealogy of Orcinus orca* in British Columbia and Washington, 2nd edn. Vancouver, Canada: UBC press.

Hoelzel, A. R. & Osborne, R. W. 1986 Killer whale call characteristics: implications for cooperative foraging strategies. In *Behavioral biology of killer whales* (ed. B. Kirkevold & J. S. Lockard), pp. 373–403. New York, NY: Alan R. Liss.

Janik, V. M. & Slater, P. J. B. 1997 Vocal learning in mammals. *Adv. Stud. Behav.* **26**, 59–99.

Janik, V. M. & Slater, P. J. B. 2000 The different roles of social learning in vocal communication. *Anim. Behav.* **60**, 1–11. (doi:10.1006/anbe.2000.1410)

Marler, P. 1991 Song-learning behavior: the interface with neuroethology. *Trends Neurosci.* **14**, 199–206. (doi:10.1016/0166-2236(91)90106-5)

Marler, P. & Peters, S. 1982 Subsong and plastic song: their role in the vocal learning process. In *Acoustic communication in birds, volume: song learning and its consequences* (ed. D. E. Kroodsma & E. H. Miller), pp. 25–50. New York, NY: Academic Press.

Miller, P. J. O. 2006 Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *J. Comp. Physiol. A* **192**, 449–459. (doi:10.1007/s00359-005-0085-2)

Miller, P. J. O. & Bain, D. E. 2000 Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Anim. Behav.* **60**, 617–628. (doi:10.1006/anbe.2000.1503)

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S. & Watwood, S. 2005 Elephants are capable of vocal learning. *Nature* **434**, 455–456. (doi:10.1038/434455a)

Ralls, K., Fiorelli, P. & Gish, S. 1985 Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*. *Can. J. Zool.* **63**, 1050–1056.

Reiss, D. & McCowan, B. 1993 Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. *J. Comp. Psychol.* **107**, 301–312. (doi:10.1037/0735-7036.107.3.301)

Schusterman, R. J. & Balliet, R. F. 1969 Underwater barking by male sea lions (*Zalophus californianus*). *Nature* **222**, 1179–1181. (doi:10.1038/2221179a0)

Wilbrecht, L. & Nottebohm, F. 2003 Vocal learning in birds and humans. *Ment. Retard. Dev. Disabil. Res. Rev.* **9**, 135–148. (doi:10.1002/mrdd.10073)

Yurk, H., Barrett-Lennard, L., Ford, J. K. B. & Matkin, C. O. 2002 Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Anim. Behav.* **63**, 1103–1119. (doi:10.1006/anbe.2002.3012)