HORIZONTAL TRANSMISSION OF CALL FEATURES IN KILLER WHALE DIALECTS

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1. Introduction

In humans language passes from mother to offspring by the process of vocal learning. Vocal learning is common among birds (Kroodsma & Miller, 1996), but less studied and probably rare for non-human mammals. Among mammals vocal learning was shown only for cetaceans (Caldwell & Caldwell, 1972; Richards et al., 1984; Payne & Payne, 1985; Janik & Slater, 1997), true seals (Phocidae) (Ralls et al., 1985), some bats (Jones & Ransome, 1993; Boughman, 1998). Geographic variations in acoustic repertoires typical for many terrestrial mammals are usually a result of geographic isolation and pass from generation to generation genetically, rather than by vocal learning (Conner, 1982).

The specific vocal traditions of sympatric or neighbouring groups or sub-populations of mammals are called dialects (Conner, 1982). Ford (1991) showed that killer whale groups in the Northeast Pacific have unique vocal repertoires of discrete call types and documented various levels of sharing of discrete call types between groups: certain groups shared a number of discrete call types and others had entirely different call repertoires. The basic unit of the North Pacific resident killer whale's social organization is the "matriline", which consists of a living female and several generations of her offspring (Bigg et al., 1990). One or several matrilines comprise "pod" – a group of whales that share a unique repertoire of discrete calls. Set of pods which share a number of discrete call types is called "clan".

Killer whales acquire discrete call repertoires from their mothers through the process of vocal learning, like human children which learn the language from

their parents. Some observations suggest that not only vertical (from mother to offspring) vocal learning can occur in killer whales, but also horizontal (between adult animals). For example, Ford (1991) showed that killer whales in the wild sometimes mimic the discrete calls from the dialects of other pods, and Bain (1986) described that an Icelandic killer whale in captivity started to use calls from the dialect of its pool mate from British Columbia. However, it is not known if horizontal call type transmission is a rare incidence or a common mechanism of dialect formation and change. In human languages horizontal transmission is a common phenomena, constantly affecting the process of language development and change. The aim of this study was to examine if similarities and differences of calls in killer whale dialects can reveal the existence of horizontal transmission of vocal traditions in killer whales.

2. Methods

We examined the patterns of call sharing in 11 pods of resident killer whales from Avacha Gulf, Kamchatka, Russian Far East. Discrete calls of resident killer whales fall into two main categories: monophonic close-range calls, which are used mostly for intra-group communication, and biphonic long-range calls, which are used mostly for inter-group communication (Filatova et al., 2009). We have compared the similarity of one monophonic and one biphonic call type between killer whale pods. Monophonic K1 type represents the low-frequency squeak-like sound which is shared by all 11 pods with substantial variations between pods (fig. 1). Biphonic K5 type is higher-frequency call which is shared by all but one pod with substantial variations between pods (fig. 2). The only pod which lacks K5 type produces K6 type which is highly similar to K5 type.

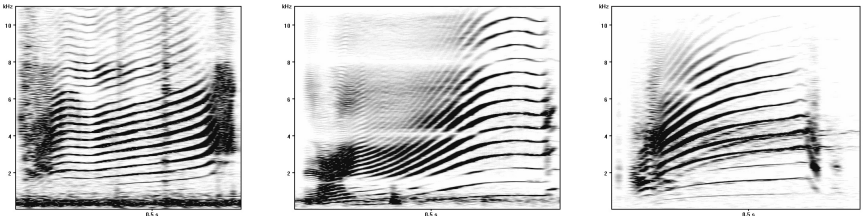

Figure 1. Examples of K1 calls from three different pods.

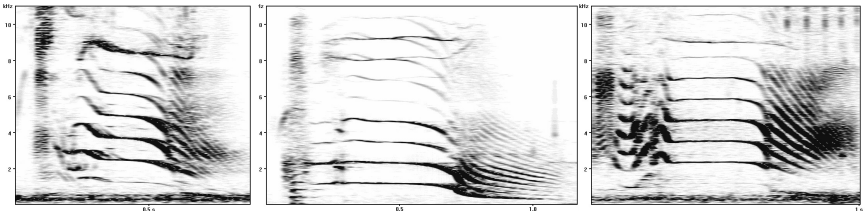

Figure 2. Examples of K5 calls from three different pods.

3. Results and discussion

We have created dendrograms of similarity by K1 and K5 calls for all 11 pods (fig. 3).

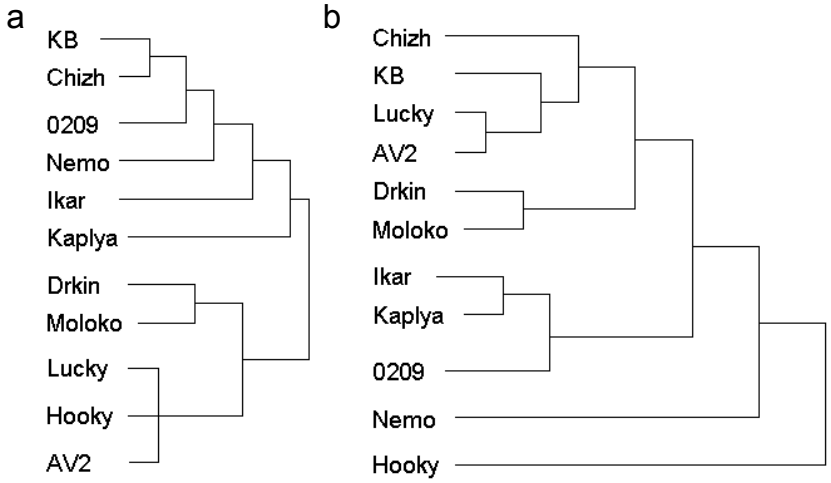

Figure 3. Dendrograms of K1 (a) and K5 (b) call type similarity for 11 pods.

The dendrograms show that the call similarity between pods is not consistent for monophonic K1 and biphonic K5 types: pods that have similar K1 calls have different K5 calls and vice versa. For example, KB and Chizh pods have similar K1 calls but very different K5 calls (fig. 4), while Ikar and Kaplya pods have similar K5 calls and different K1 calls (fig. 5). The classical model of killer whale dialect development suggests that pod fission and variation in discrete calls occurs gradually over several generations. According to this hypothesis, newly formed sister pods initially spend a significant amount of time together and share most of the calls of their ancestral pod. Over time, because of copying errors of calls between generations and fewer contacts between sister pods, calls change progressively and repertoires diverge. This hypothesis does not consider that killer whales can copy call features from other pods they contact with. Our

results could not be explained with the classical hypothesis, because K1 and K5 call types show different degree of divergence across pods. Applying the theory of horizontal transmission, we can explain some cases of call similarity by copying call features from other pods.

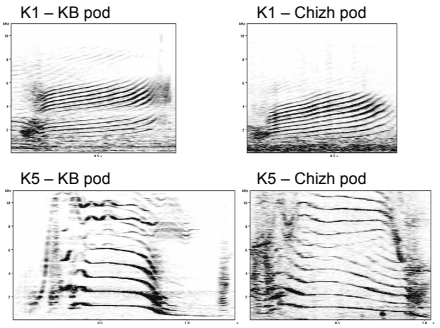

Figure 4. K1 and K5 types of KB and Chizh pods.

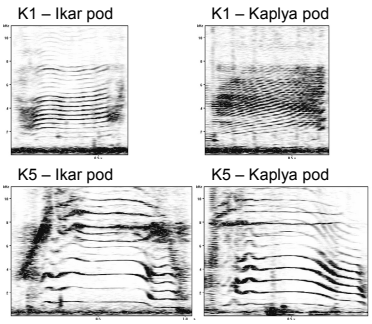

Figure 5. K1 and K5 types of Ikar and Kaplya pods.

Killer whales mate more often between clans rather than within clans (Barrett-Lennard, 2000), which suggests that they probably estimate the relationships between pods by dialect similarity to prevent inbreeding. Copying call features between pods would reduce the effectiveness of inbreeding avoidance, so we can suggest that some call types should not be affected by horizontal transmission. Therefore, some call similarities between killer whale pods are the true markers of their relatedness, and others are the results of call copying between pods, which explains the controversial patterns of call similarity between pods. This situation is analogues to similarity of native and loan words between human languages. Further investigation of killer whale dialects can probably reveal more parallels with human languages, which will enable the comparative studies that can benefit research in both fields.

Acknowledgements

If you wish to acknowledge funding bodies etc., the acknowledgements may be placed in a separate, unnumbered section at the end of the text, before the Appendices.

References

Bain, D.E. (1986). Acoustic behavior of *Orcinus*: sequences, periodicity, behavioral correlates and an automated technique for call classification. In

Behavioral Biology of Killer Whales (Ed. by B. C. Kirkevold and J. S. Lockard), pp. 335-371. New York: A. R. Liss.

Barrett-Lennard, L. G. (2000). Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis. PhD thesis. University of British Columbia, Vancouver.

Bigg, M. A., Olesiuk, P. F., Ellis, C. M., Ford, J. K. B. & Balcomb, K. C. (1990). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whaling Comm., Spec. Issue No. 12, 383-405.

Boughman, J.W. (1998). Vocal learning by greater spear-nosed bats. Proc. R. Soc. Lond. B Biol. Sci., 265, 227-233.

Connor, D. A. (1982) Dialects versus geographic variation in mammalian vocalizations. Anim. Behav., 30, 297-298.

Caldwell, M. C. & Caldwell, D. K. (1972). Vocal mimicry in the whistle mode by an Atlantic bottlenosed dolphin. Cetology, 9, 1-8.

Filatova O.A., Fedutin I.D., Nagaylik M.M., Burdin A.M. & Hoyt E. (2009) Usage of monophonic and biphonic calls by free-ranging resident killer whales (*Orcinus orca*) in Kamchatka, Russian Far East. Acta ethol DOI 10.1007/s10211-009-0056-7

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.

Janik, V.M. & Slater, P.J.B. (1997). Vocal learning in mammals. Advances in the Study of Behavior, 26, 59-99.

Jones, G. & Ransome, R. D. (1993). Echolocation calls of bats are influenced by maternal effects and change over a lifetime. Proc. R. Soc. Lond. B Biol. Sci., 252, 125-128.

Kroodsma, D.E. & Miller, E.H. (1996). Ecology and evolution of acoustic communication in birds. New-York: Cornell Univ. Press.

Payne, K. & Payne, R. (1985). Large scale changes over 19 years in songs of humpback whales in Bermuda. Z. Tierpsychol., 68, 89-114.

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

Richards, D. G., Wolz, J. P. & Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. J. Comp. Psychol., 98, 10-28.