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Dependence of Killer Whale (*Orcinus orca*) Acoustic Signals on the Type of Activity and Social Context[1]

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Abstract—We investigated the influence of the type of activity and the social context on the proportion of four different structural categories of stereotyped calls in the acoustic communication of Kamchatkan killer whales. Using generalized linear models, we described the dependence of each sound category on the type of activity, the number of killer whale pods and the presence of mixed-pod groups. We found that the proportion of different sound categories depended on the number of pods and the presence of mixed-pod groups, while the type of activity did not affect the proportion of sounds of different categories. Based on the observed differences we suggest that biphonic and high-frequency monophonic calls are mainly used as family and pod markers, and help to track the position of family members at long ranges, and low-frequency monophonic calls are used as close-range intra-group signals to maintain contact between pod members in the conditions of limited underwater visibility.

Keywords: killer whale, *Orcinus orca*, behaviour, acoustic communication

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INTRODUCTION

The functions of animal sounds can be explored in detail by studying the context of their use. The vocal communication of cetaceans is poorly studied, despite the fact that the acoustic channel is much more important for marine than for terrestrial animals. Relationships between vocal signals and behavioural contexts were examined in several cetacean species, including blue whales (*Balaenoptera musculus*) (Oleson et al., 2007), southern right whales (*Eubalaena australis*) (Clark, 1982), long-finned pilot whales (*Globicephala melas*) (Weilgart and Whitehead, 1990), common bottlenose dolphins (*Tursiops truncatus*) (Janik 2000), spinner dolphins (*Stenella longirostris*) (Lammers et al., 2006), common dolphins (*Delphinus delphis*) (Henderson et al., 2011) and killer whales (*Orcinus orca*) (Ford, 1989; Thomsen et al., 2002; Deecke et al., 2005; Saulitis et al., 2005; Weiß et al., 2007; Foote et al., 2008; Filatova et al., 2009; Graham and Noonan, 2010).

Most of the studies of killer whale acoustic behaviour have been conducted in the eastern North Pacific, where three main ecotypes of killer whales exist: two coastal—fish-eating and mammal-eating (Ford et al., 1998) and one offshore (Ford et al., 2011). In Russian waters, in the western North Pacific, at least two ecotypes are found—fish-eating and mammal-eating types (Burdin et al., 2005). Fish-eating killer whales have a complex social structure based on the matrilineal relatedness. The basic unit of the social structure is family, or matrilineal unit, containing a matriarch and all her descendents (children, grandchildren and grand-grandchildren). Pods contain a set of matrilines that share the same vocal dialect, while the pods with similar dialects comprise clans (Ford, 1991; Ivkovich et al., 2010).

Ford (1989) examined the acoustic behaviour of fish-eating killer whales in British Columbia and concluded that the same signals could be used in different behavioural contexts. Stereotyped discrete calls comprising a pod dialect dominated vocalization in most contexts. The relative use of different discrete calls varied with activity, but no call type was correlated exclusively with any particular behaviour. Variation in relative production of some call types between intra- and intergroup contexts was reported (Weiß et al., 2007, Foote et al., 2008; Filatova et al., 2009).

In this study we examined the roles of type of activity and social context (number of pods and presence of mixed multi-pod groupings) in the production of the

[1] The article was translated by the authors.

Number and duration (min, in parentheses) of recordings used for the analysis

Type of activity	Mixed-pod groupings	Number of pods						
		1	2	3	4	5	6	7
Foraging	No	12 (210)	10 (152)	2 (13)	1 (15)	2 (13)	2 (21)	1 (9)
	Yes	n/a	3 (31)	0	0	2 (21)	3 (19)	0
Travelling	No	12 (305)	10 (233)	3 (210)	2 (10)	1 (15)	3 (33)	1 (23)
	Yes	n/a	4 (93)	3 (43)	3 (31)	4 (98)	3 (43)	1 (7)
Socializing	No	4 (45)	3 (17)	3 (24)	0	2 (21)	0	1 (37)
	Yes	n/a	5 (61)	0	3 (22)	4 (54)	2 (28)	1 (13)

n/a—not applicable, because formation of mixed-pod groupings was possible only when more than one pod was present in the area.

major categories of killer whale stereotyped calls. Basing on our results we attempt to interpret the communicative function of the studied call categories.

METHODS

Data Collection

The data used for this study were collected in 2000–2011 in the central Avacha Gulf of Kamchatka peninsula. The sounds were recorded from inflatable boat with outboard engine. Sound recordings were made using Sony DAT TCD-D100 digital recorder, Zoom H4 flash recorder, Offshore Acoustics hydrophone and mobile hydrophone stereosystem (Filatova et al., 2006). Recording was made at a sampling frequency of 44.1 or 48 kHz. The photographic identification method (Bigg et al., 1983) was used to identify individual killer whales and groups.

Data Analysis

The variation in acoustic activity of killer whales was analysed across the following parameters: type of activity (travelling/foraging/socializing), number of pods in aggregation and presence/absence of mixed-pod groupings (i.e. groupings consisting of animals from different pods). We analyzed more than 32 hours of recordings made in various behavioural and social contexts (table). For the analysis we selected recordings in which the behaviour of the majority of observed animals could be classified into one of the activity types (see below).

For each recording, we defined type of activity, number of animals and pods in the aggregation, and presence/absence of mixed-pod groupings. Aggregation was defined as groupings moving together within visual range of the research boat (Ivkovich et al., 2010). A grouping was defined as animals within three body lengths of each other moving together and displaying a similar type of activity (Ivkovich et al., 2010). A grouping was considered to be mixed-pod if it consisted of animals from two or more different pods.

The activities of killer whales were divided into four categories: foraging, travelling, socializing and resting.

Foraging included all occasions in which the whales were seen carrying fish in their mouths or when their behaviour included intensive non-directional swimming, irregular diving patterns and varying swimming speeds with sudden changes in direction. A grouping was considered to be **travelling** when all of its members were moving on the same course at the same speed. **Socializing** whales demonstrated different elements of social displays: swimming on the back, rolling over each other, flipper and fluke slapping, breaching. When **resting**, whales joined together in a tight grouping and either stayed in the same place or moved slowly with highly regular and coordinated dives. We have not analysed acoustic behaviour during resting because our previous studies showed that resting killer whales were predominantly silent (Filatova et al., 2009).

Stereotyped calls of killer whales were divided into four structural categories: low-frequency monophonic calls (types K1, K4, K12, K29, K30, K31i, K34, K38, K40 and K46), high-frequency monophonic calls (types K3a, K3b, K8, K10, K11, K13, K16b, K31ii, K37, K39 and K57) and two categories of biphonic sounds, which differend in frequency of both higher and lower components (Filatova et al., 2007)—category 1 (all biphonic types except K7 and K21) and category 2 (types K7 and K21) (Fig. 1).

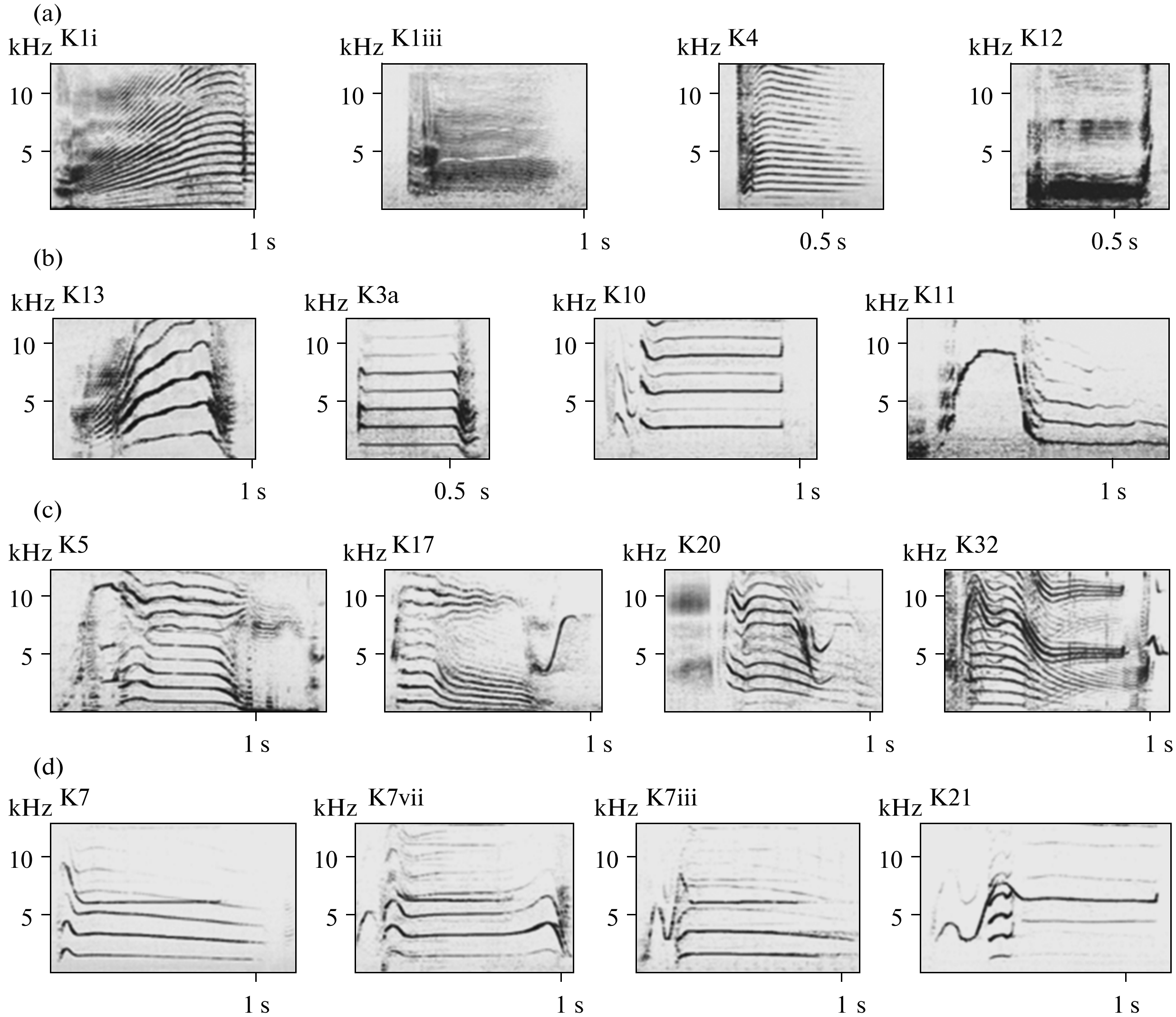

Fig. 1. Examples of sonograms of calls from four categories: (a) low-frequency monophonic calls, (b) high-frequency monophonic calls, (c) category 1 of biphonic calls, (d) category 2 of biphonic calls.

Statistical Analysis

To examine the influence of the behavioural and social context on the relative production of different sound categories, we calculated the ratio of each category in the total amount of stereotyped calls of all four categories.

We used generalized linear models to investigate whether there was a relationship between the occurrence of sounds from each category and the explanatory variables: type of activity, number of pods in the aggregation, and presence/absence of mixed-pod groupings. The type of activity and presence of mixed-pod groupings were used as nominal variables and the number of pods was fitted as a continuous variable. To test the appropriateness of the selected model, we assessed the normality and homogeneity of the model residuals and independence of the explanatory variables using the graphical model validation protocol (Zuur et al., 2009). Statistical analysis was performed in R (R Development Core Team 2011).

The relationship between the ratio of monophonic/biphonic calls and the explanatory variables was examined using proportional odds logistic regression with a binomial distribution of the response variable. Our preliminary analysis detected overdispersion, so the residuals were corrected using a quasi-binomial model by adding an overdispersion parameter φ to the variance (Zuur et al., 2009). The best model was selected by comparing the nested models by likelihood ratio test and sequentially dropping the non-significant variables.

RESULTS

The best model for the proportion of all monophonic calls included the presence of mixed-pod groupings as an only significant explanatory variable. The

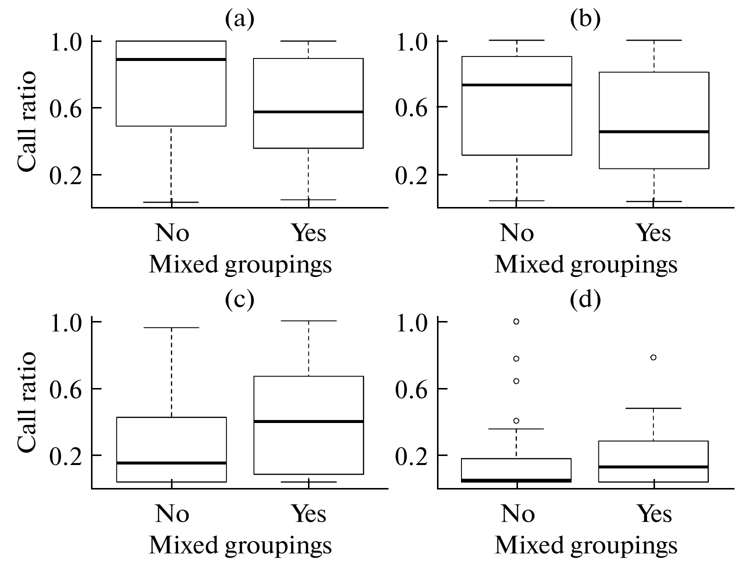

Fig. 2. Ratio of calls from different categories in presence and absence of mixed-pod groupings: (a) all monophonic calls, (b) low-frequency monophonic calls, (c) category 1 of biphonic calls, (d) category 2 of biphonic calls.

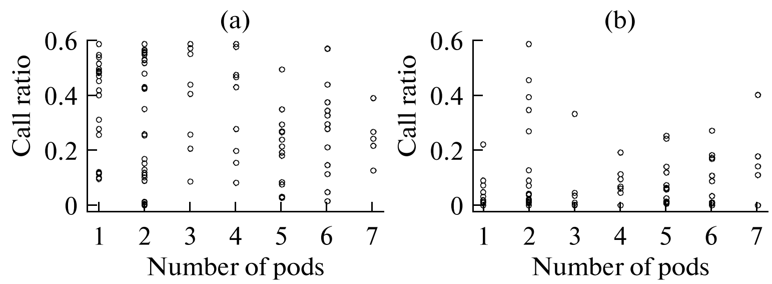

Fig. 3. Dependence of the ratio of monophonic calls on the number of pods: (a) low-frequency monophonic calls, (b) high-frequency monophonic calls.

ratio of monophonic calls was significantly lower when mixed-pod groupings were present in the area ($t_{df=106} = -2.943$, $p = 0.004$) (Fig. 2). We did not estimate the dependence of biphonic calls ratio from the context separately, because it was equal to the inverse of the ratio of monophonic calls (i.e. equal to 1 minus ratio of monophonic calls) and, therefore, had an inverse relatedness from the same parameters. So, the proportion of biphonic calls was significantly higher in presence of mixed-pod groupings, than in their absence. Although the ratio of monophonic vs. biphonic calls changed depending on the presence of mixed-pod groupings, in general the ratio of monophonic calls was higher both in presence and absence of mixed-pod groupings (Fig. 2a).

The best model for the low-frequency monophonic calls included all three variables. The proportion of low-frequency monophonic calls increased during socializing ($t_{df=103} = 2.010$, $p = 0.047$) and decreased with the increasing number of pods ($t_{df=103} = -2.219$, $p = 0.029$) (Fig. 3) and in presence of mixed-pod groupings ($t_{df=103} = -2.161$, $p = 0.033$) (Fig. 2).

The best model for the proportion of high-frequency monophonic calls included the number of pods as an only significant explanatory variable. The proportion of high-frequency monophonic calls increased with pod number with a coefficient 0.231 ($t_{df=106} = 2.827$, $p = 0.006$) (Fig. 3).

The best model for the category 1 of biphonic calls included two variables—type of activity and presence of mixed-pod groupings. The presence of mixed-pod groupings was the most significant variable: in their presence the ratio of category 1 biphonic calls was significantly higher, than in their absence ($t_{df=104} = 3.419$, $p < 0.001$) (Fig. 2). The ratio of category 1 biphonic calls slightly decreased during socializing ($t_{df=104} = -2.298$, $p < 0.024$).

The dependence of category 2 biphonic call ratio from all variables was non-significant, though the dependence from the presence of mixed-pod groupings was close to significant ($t_{df = 106} = 1.836$, $p = 0.069$). Similarly to category 1 biphonic calls, the ratio increased in presence of mixed-pod groupings (Fig. 2).

DISCUSSION

Analysis of the relationships between stereotyped calls and the behavioural and social context showed that the usage of different call categories was influenced by different parameters. The ratio of low-frequency monophonic calls decreased with increasing number of pods and in presence of mixed-pod groupings, the ratio of high-frequency monophonic calls increased with number of pods, and the ratio of biphonic calls was higher in presence of mix-pod groupings.

Therefore, for the stereotyped calls we showed the tendency to decrease the proportion of low-frequency monophonic and increase the proportion of biphonic and high-frequency monophonic calls with the complexity of the social context: in presence of the mixed-pod groupings and, to a lesser extent, with increasing number of pods. It is interesting to note that the high-frequency monophonic calls had an inverse tendency comparing to the low-frequency monophonic calls: their ratio increased with the number of pods.

Our results suggest that low-frequency monophonic and biphonic calls play different roles in killer whale acoustic communication. It appears that biphonic calls function as markers of pod and matriline affiliation, serving mainly to maintain the contact between the related individuals on a distance. These calls are more common when animals occur in mixed groupings, consisting of members of different pods. In this situation whales from the same pod often travel in different groupings far away from each other, therefore they need signals allowing to recognize pod members and maintain contact on a distance.

So why are the biphonic calls used for the distant communication between the related animals? The presence of two independently modulated frequency components in biphonic calls may increase the probability of call type recognition for the sounds degraded during the transmission through water and masked by background noise. Using biphonation to improve sound recognition was showed, for example, in king and emperor penguins, where biphonation enhances the ability of parent–chick and mate–mate recognition (Aubin et al., 2000). Volodina et al. (2006) showed that biphonation may function to enhance individual recognition in the dhole, *Cuon alpinus*.

Another possible reason why biphonic calls are used for the long-distant communication may be due to the differences in directionality of the lower- and higher-frequency components. Miller (2002) showed that the relative energy in the high-frequency component was significantly greater when animals were moving toward the hydrophone array than away from it. It is likely that animals can use this feature of biphonic calls to identify signaler's orientation relative to the listener's position. The similar study was conducted with dholes and showed the possibility to identify the orientation of calling animal by its biphonic calls (Volodin et al., 2006).

Miller (2006) showed that the source level differed across call types of fish-eating killer whales of British Columbia. Low-frequency monophonic calls had the lowest source level, while the higher biphonic calls had the highest source level. No such study was conducted for the Kamchatkan killer whales, but on the distance of 8–10 km we have heard mostly biphonic calls, though in fact killer whales use monophonic calls more often. This may indicate that biponic calls of Kamchatkan killer whales are generally louder, than monophonic. Apparently the higher source level allows killer whales to use these calls on longer distances, monitoring the position and movements of animals from their pod and, probably, from other pods.

What are the functions of low-frequency monophonic calls? In our recordings they occurred much more often than biphonic calls. The lower ratio of low-frequency monophonic calls in presence of mixed-pod groupings suggests that they may be used as intragroup close-range contact signals. The visibility underwater is often just several meters, so acoustic communication is needed even at close range. Close-range contact signals exist in many species which need to maintain contact despite limited visibility, including common bottlenose dolphins (*Tursiops truncatus*) (Janik and Slater, 1998), orangutans (*Pongo pygmaeus*) (MacKinnon, 1974), baboons (*Papio cynocephalus*) (Cheney et al., 1995). Close-range cohesion calls were described in many primates: prosimians (Macedonia, 1986), Old World (Gautier and Gautier, 1977) and New World (Snowdon, 1989) monkeys, and apes (Harcourt et al., 1993). For example, gorillas (*Gorilla gorilla*) have usually used close-range contact calls when separated from group or before changing group activity type, or when being too close to one another, especially during foraging (Harcourt et al., 1993). Generally, most contact calls of primates have tonal structure and rather low frequency (Oda, 1996), similarly to the low-frequency monophonic calls of killer whales.

Contact calls are common in passerine birds, which also often have to maintain contact in limited visibility in the dense foliage. Bird calls function to signal about food, maintain contact between individuals, synchronize movements and resolve the aggressive and sexual conflicts (Marler, 2004). So, these calls can be used in a variety of behavioural contexts, which is also typical for killer whale stereotyped calls.

Type of activity did not influence significantly on the usage of most call categories. Ford (1989) also did not find any direct relationship between the activity type and particular call type usage. Apparently stereotyped calls of killer whales do not serve as markers of any specific type of activity and have more complex functions.

In summary, we suggest the following model of stereotyped call usage of Kamchatkan killer whales. Biphonic calls are used mostly as matriline and pod markers and help animals to monitor the position of conspecifics on a distance. The ratio of these calls increases in presence of whales from other pods, because in this situation there is a need to discern between calls from own and stranger pod members. Functions of high-frequency monophonic calls appear to be similar to those of biphonic calls. Low-frequency monophonic calls are used as close-range intra-group signals to maintain the contact between pod members in conditions of limited underwater visibility.

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