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Usage of monophonic and biphonic calls by free-ranging resident killer whales (*Orcinus orca*) in Kamchatka, Russian Far East

O. A. Filatova · I. D. Fedutin · M. M. Nagaylik ·
A. M. Burdin · E. Hoyt

Abstract Killer whale discrete calls include types containing an overlapping high-frequency component (biphonic calls) and types without an overlapping high-frequency component (monophonic calls). In the resident killer whales of the Northeast Pacific, biphonic discrete calls exhibit higher source levels than monophonic calls, which suggests different active space and consequently different functions for monophonic and biphonic call types. In this study we investigate the potential communicative functions of monophonic and biphonic discrete calls produced by killer whales from Kamchatka (Northwest Pacific). We analyze how the usage of these calls depends on the number of pods present in the area and type of activity. Our results show that the usage of monophonic and biphonic calls in Kamchatkan killer whales depends on the number of pods in the area and is less dependent on the type of activity. Biphonic calls are more common when more than one pod is present in the area and could therefore function as markers of pod and matriline affiliation, serving mainly as cohesion signals. Monophonic calls dominated the vocalizations when a single pod was present, while in the presence of more than one pod both categories were used in equal proportions.

Keywords Killer whale · Acoustic behavior · Discrete calls · Biphonation

O. A. Filatova (✉) · M. M. Nagaylik
Department of Vertebrate Zoology, Faculty of Biology,
Moscow State University,
Vorobiovy Gory, 1/12,
Moscow 119992, Russia
e-mail: alazor@rambler.ru

I. D. Fedutin
Central Forest State Nature Reserve, Zapovednik,
Nelidovo District,
Tver, Tver region 172513, Russia

A. M. Burdin
Kamchatka Branch of Pacific Institute of Geography
of Russian Academy of Sciences,
Prospect Rybakov, 19a,
Petropavlovsk-Kamchatsky 683024, Russia

A. M. Burdin
Alaska Sealife Center,
P.O. Box 1329, 301 Railway Avenue,
Seward, AK 99664, USA

E. Hoyt
WDCS, the Whale and Dolphin Conservation Society,
29A Dirleton Avenue,
North Berwick, Scotland EH39 4BE, UK

Introduction

Biphonation is a nonlinear phenomenon in mammalian vocalizations that has received a large amount of scientific attention in recent years. Biphonation appears as two independent fundamental frequencies in a call spectrum (Wilden et al. 1998; Fitch et al. 2002). Biphonic sounds have been described in many mammals as diverse as canids (Wilden et al. 1998; Riede et al. 2000; Volodin and Volodina 2002), primates (Fischer et al. 2001; Brown et al. 2003; Riede et al. 2004), and whales (Tyson et al. 2007). The presence of biphonation in the vocalizations of different species suggests that it may play an important communicative role. However, functional interpretations of biphonation are scarce. For terrestrial mammals, it was suggested that biphonation and other nonlinear phenomena may arise from the physics of a mammalian sound production apparatus and thus may not have an adaptive

meaning for a caller (Wilden et al. 1998; Fitch et al. 2002). For example, biphonation was found in unhealthy animals including Japanese macaque *Macaca fuscata* (Riede et al. 1997), domestic dog (Riede et al. 2001), domestic cat (Riede and Stolle-Malorny 1999), as well as in humans (Herzel and Reuter 1997). However, in many species, biphonation occurs in normal calls of healthy animals (Wilden et al. 1998; Riede et al. 2000; Fischer et al. 2001; Fitch et al. 2002; Volodin and Volodina 2002; Brown et al. 2003; Riede et al. 2004). The proposed functions of this phenomenon include the enhancement of individual recognition (Aubin et al. 2000; Fitch et al. 2002; Volodina et al. 2006), increase of unpredictability, and indication of physical condition (Fitch et al. 2002). For killer whales, it was suggested that differences in directionality of the lower- and higher-frequency components in biphonic calls can provide information on the orientation of a caller to a listener (Miller 2002). Understanding the role of biphonic sounds in killer whale communication requires information on the behavioral and social contexts in which the sounds are used.

Most of the studies of killer whale acoustic behavior have been conducted in the Northeast Pacific, where two main ecotypes of killer whales exist: resident (fish-eating) and transient (mammal-eating), which differ greatly in their vocal activity, as well as social organization and genetics (Bigg et al. 1987; Ford et al. 1998; Hoelzel et al. 1998; Baird and Whitehead 2000). Transient (mammal-eating) killer whales are less vocal than residents (Morton 1990; Deecke et al. 2005) because their prey can detect killer whale calls and respond with avoidance behavior (Deecke et al. 2002).

The basic unit of resident killer whale social organization is the "matriline" comprised of one to four generations of maternally related individuals (Bigg et al. 1990). "Pods" consist of one to nine matrilines observed together on 50% or more of the observation days (Bigg et al. 1990). Ford (1991) showed that pods have unique vocal repertoires of discrete call types and documented various levels of sharing of discrete call types between pods: certain pods shared a number of discrete call types, whereas others had entirely different call repertoires. Ford (1991) referred to each set of pods which shared at least one discrete call type as a "clan".

Several studies have reported that the sounds assumed to be social signals are used in different behavioral contexts (Bain 1986; Morton et al. 1986; Ford 1989; Thomsen et al. 2002). Ford (1989) showed that pod-specific, stereotyped discrete calls dominate vocalization in most contexts. An increase in the production of variable, aberrant calls and whistles was observed during socializing (Ford 1989; Thomsen et al. 2002). The relative use of different discrete calls varied with activity, but no call type was correlated exclusively with any particular behavior. Ford (1989) suggested that discrete calls function as intragroup contact

signals to maintain pod cohesion and coordinate activities, and variations in their structure carry information about the emotional state of vocalizing individuals. Miller et al. (2004) studied vocal interactions between individual free-ranging killer whales using a towed hydrophone array and showed that the whales within groups regularly exchange calls, often immediately matching the call type produced by another individual.

The evidence for the probable difference in functions of various call types comes from the work of Miller (2006), who measured source levels of different killer whale sounds and showed that discrete calls without an overlapping high-frequency component (further referred to as monophonic calls) exhibited the lower mean apparent source level than biphonic calls (calls with an overlapping high-frequency component). This variation in intensity enabled the partitioning of calls into two groups: "long-range" biphonic calls (a mean estimated active space of 10–16 km in sea state zero) and "short-range" monophonic calls (5–9 km), which suggests different functions for different discrete call types. However, these functions remain unclear. Since group members are rarely separated by more than a few kilometers, "long-range" calls could be assigned for between-group communication. In this case, it is likely that the usage of these calls could depend not only on the type of activity of the animals, but also on the number of pods present in the area.

Kamchatkan killer whales are ideal to study the role of different vocalization types in communication. The Kamchatkan coast, with wide bays and long sections of straight shoreline, is much less indented than the Northeast Pacific coast, enabling the whales to hear each other over long distances. At the same time, ecological specialization and the social structure of the study population are similar to that of the resident killer whales of the Northeast Pacific (Tarasyan et al. 2005; Ivkovich 2006).

The goal of the present study was to investigate how the usage of monophonic and biphonic discrete calls produced by Kamchatkan killer whales depends on the number of pods present in the area and the type of activity.

Materials and methods

Data collection

The materials and data used for this study were collected as part of the Far East Russia Orca Project (FEROP) around Starichkov Island (52°46′ N, 158°37′ E) in the Avacha Gulf, Kamchatka, in June–September 2005 and July–August 2006 and July–August 2007 (Fig. 1).

The underwater sound recordings were made from a 4-m inflatable boat while the engine was turned off. To monitor

Fig. 1 Location of the study area
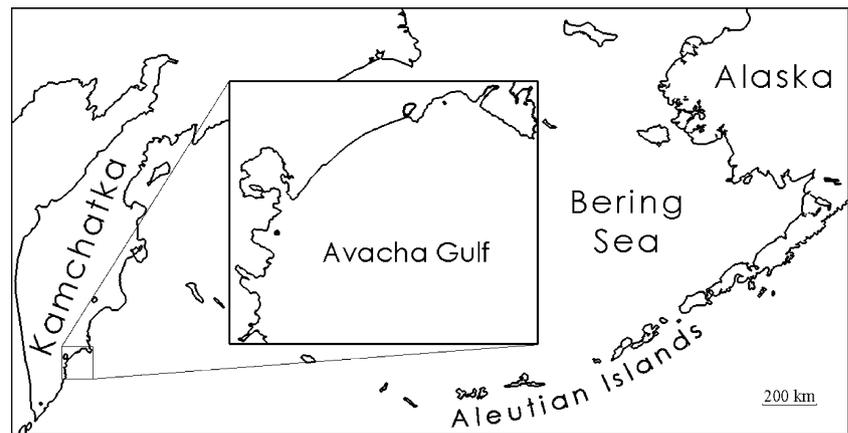
the vocal behavior of a group, we moved the boat approximately 500 m ahead of the animals and waited until they passed. If the whales were feeding or milling, we stayed at a distance of 100–500 m from them to prevent disturbance of their natural behavior. The photographic identification method of Bigg et al. (1983) was used to identify individual killer whales and groups. To make photographs, we approached the whales to a distance of 30–70 m when they were traveling, or moved the boat 200–300 m ahead of the animals and waited until they passed. Usually, the animals showed no sign of disturbance during our activities: they neither changed the type of activity nor tried to avoid the boat. In cases when the whales tried to avoid the boat, we stopped our activities and kept at a distance of at least 500 m from the group for a while, and then tried to approach again. If the group constantly avoided the boat, we quit working with that group.

During each encounter, we tried to photograph every killer whale. We estimated the number of encountered whales by looking at the photographs. In large aggregations of more than 60 animals some whales could have been missed; in large aggregations we estimate the accuracy of the number of whales at ±10 animals.

Sound recordings were made using a Sony TCD-D100 DAT recorder at a sampling frequency of 48 kHz. For omnidirectional recording, we used an Offshore Acoustics hydrophone with a bandwidth of 10 Hz to 40 kHz and a sensitivity of −154 dB±4 dB re 1 V/μPa at 100 Hz. It was lowered to a depth of 5–10 m. To localize the source of underwater sounds, we used a mobile hydrophone stereo system. This device works by separating two hydrophones using a soundproof disk consisting of a metal base 300 mm in diameter and two soundproof plastic foam plates on both sides of the base. The disk is attached to a rotating pole. The signal from each hydrophone is fed into the stereo input channels of the recording system which then feeds the left and right channels of the headphones. Rotating the device enables the operator to find the bearing of the underwater sound by listening to changes in the sounds coming from the

hydrophones. Additional details of the system can be found in Filatova et al. (2006).

The stereo system was used for separating the sounds of killer whale groups when they were close to each other. During recording, the boat was placed between the two groups and the stereo system was positioned so that the signal from each group went into a separate hydrophone. Using this method we could separately record groups that exhibited a particular type of activity. The type of activity and number of pods in the area was noted together with the orientation of the stereo system.

Study population

Photo-identification of killer whales in Avacha Gulf has been conducted since 1999, and to date we have identified most of the groups regularly visiting the area (Ivkovich 2006; Burdin et al. 2007). Both resident (fish-eating) and transient (mammal-eating) killer whales were found in the area (Burdin et al. 2007), but this study deals only with resident killer whales, because the social structure and occurrence patterns of transient killer whales are different (Morton 1990; Deecke et al. 2005).

Kamchatkan resident killer whales have group-specific vocal dialects (Filatova 2005; Filatova et al. 2007). We have identified at least 15 pods of resident killer whales in Southeastern Kamchatka (Filatova et al. 2007). Each pod has a unique repertoire of five to ten call types; the repertoire of each pod includes both monophonic and biphonic call types (Filatova et al. 2007).

Data analysis

We analyzed more than 17 h of recordings (Table 1), including more than 6,000 discrete calls. We selected recordings in which the behavior of the majority of observed animals could be classified into one of the activity types (see below) and which were not masked by boat noise to any great extent. During sound recording our boat engine

Table 1 Number of situations and duration of recordings used to analyze the usage of different sound categories in the presence of single/few/many pods during different types of activity (duration of recordings, measured in hours, is shown in parentheses)

	Single	Few	Many	Total
Foraging	10 (3.85)	9 (1.60)	5 (0.74)	24 (6.18)
Traveling	10 (3.23)	12 (3.09)	9 (1.31)	31 (7.63)
Socializing	4 (0.47)	4 (1.18)	4 (0.71)	12 (2.36)
Resting	3 (0.92)	1 (0.1)	2 (0.14)	6 (1.16)
Total	27 (8.46)	26 (5.97)	20 (2.90)	73 (17.33)

was always turned off, but other boats were sometimes present in the area. In this paper, we did not analyze or discuss the effect of boat noise on our results because for this study we only selected recordings without boat noise.

We excluded situations when some of the animals were out of our visual range. We considered that there were some animals outside our visual range: (1) if we saw some animals moving away and then lost them while staying with another group, (2) if we heard blows but did not see animals (in good weather they can be heard farther the animals can be seen from the boat), or (3) if we heard underwater calls from a direction where we had not seen any animals.

The acoustic recordings were resampled (sampling frequency 22 kHz) and analyzed using Avisoft-SASLab Pro.

We divided the number of pods in the area into three groups: single (one pod), few (two to four pods) and many (more than four pods).

We grouped the activities of killer whales into the following categories (based on Ford 1989, Barrett-Lennard et al. 1996, Thomsen et al. 2002):

Foraging This category included all occasions in which the whales were seen carrying fish in their mouths or when their behavior included intensive non-directional swimming, irregular diving patterns, and varying swimming speeds with sudden changes in direction and short periods of high speed swimming just below the surface.

Traveling A pod was considered to be traveling when all of its members were moving on the same course at the same speed and there was no indication of feeding activity.

Resting When resting, all members of a pod joined together in a tight group and either stayed in the same place or moved slowly. Dives and surfacings became highly regular and coordinated in the group.

Socializing Socializing whales stayed grouped together and engaged in social interactions and aerial displays (e.g, breaching, flipper and fluke slapping, chases, rolling over each other, sexual interactions).

Discrete calls were divided into two categories: monophonic calls, consisting of a single frequency component and biphonic calls, which included two independently modulated frequency components (Fig. 2).

Statistical analyses

As a unit of analysis we established that a "sample" was a section of the recording when none of the parameters (number of pods and type of activity) changed. In most cases the samples were taken from the recordings on different days. In all, 73 samples were examined (Table 1). In each sample, we counted the call rate (calls per minute per animal) for biphonic and monophonic calls.

We found that the data were not normally distributed and could not be transformed to achieve normality and therefore we used nonparametric statistical tests. We analyzed the influence of each parameter on acoustic behavior. Using a nonparametric Kruskal–Wallis H-test, we compared the mean number of sounds per animal per minute across: (1) the presence of single/few/many pods and (2) the types of activity. We performed the pairwise comparisons using the Mann–Whitney U-test. Proportions of biphonic/monophonic calls were compared using an independent sample z-test for proportions. We used Bonferroni correction in all cases of multiple comparisons.

Results

We found that all samples recorded during group resting ($n=6$) contained no discrete calls. During resting, the whales were mostly silent or sometimes emitted a few echolocation clicks. Consequently, all samples recorded during group resting were excluded from the analysis.

Difference in percentages of monophonic and biphonic calls

We counted a total of 2,082 biphonic and 3,964 monophonic discrete calls. The percentages of monophonic and
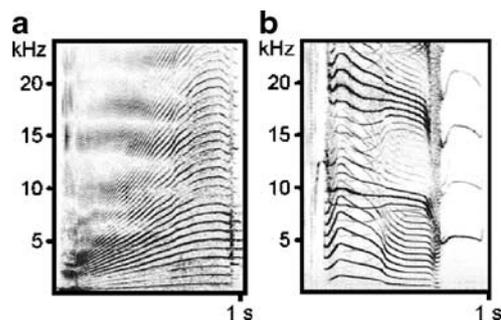
Fig. 2 Spectrograms of **a** a monophonic vocalization and **b** a biphonic vocalization

biphonic calls differed across encounters with different pod numbers (Fig. 3). In the presence of a single pod, 89.13% of discrete calls were represented by monophonic calls. In the encounters with few and many pods, the percentage of monophonic calls was lower: 47.29% and 59.80%, respectively. The proportion of calls in the encounters with single pods differed significantly from the encounters with few (z-test, $P<0.001$) and many (z-test, $P<0.01$) pods. There were no significant differences in call proportions between encounters with few and many pods. We also found no significant differences in proportions of monophonic and biphonic calls across different activity types.

Difference in call rates of monophonic and biphonic calls

The Kruskal–Wallis H-test showed significant differences in the rate of biphonic calls ($H_2=9.10$, $P=0.01$) across encounters with different pod numbers (Fig. 4). Biphonic call rate was significantly lower in the encounters with single pods than in the encounters with few (Mann–Whitney with Bonferroni correction, $U=187$, $P<0.05$) and many pods ($U=109$, $P<0.05$). The difference in the call rates of biphonic calls between encounters with few and many pods was non-significant.

The Kruskal–Wallis H-test showed significant differences in all rates of monophonic calls across encounters with different pod numbers ($H_2=6.16$, $P=0.046$) (Fig. 4). Call rate was significantly lower in the encounters with few pods than in the encounters with many pods (Mann–Whitney with Bonferroni correction, $U=133$, $P<0.05$). The differences in the monophonic call rate between encounters with single/few and single/many pods were non-significant.

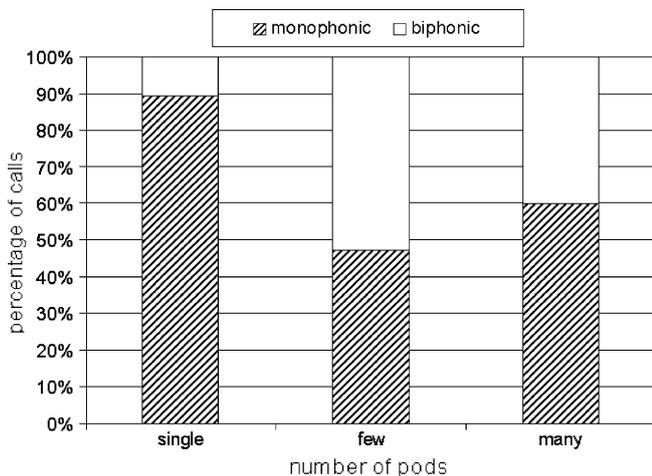The Kruskal–Wallis H-test showed no significant differences in the call rate of either monophonic or biphonic calls
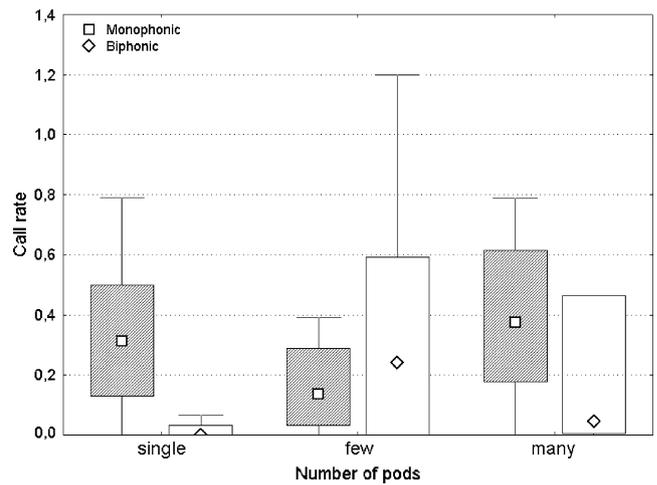

Fig. 4 Rate of monophonic and biphonic calls across encounters with different pod numbers. *Rectangles* and *Diamonds* give the median number of calls, *boxes* show the percentiles (25–75%), and *whiskers* give the non-outlier range

across samples recorded during foraging, traveling, and socializing (Fig. 5). Although call rates did not differ statistically across activity types, there were some non-significant changes in their usage (Fig. 5). Monophonic call rate was highest during socializing and biphonic call rate was highest during foraging.

Discussion

Our results show that the usage of monophonic and biphonic calls in Kamchatkan killer whales depends on the number of pods in the area. Monophonic calls dominated the vocalizations when a single pod was present,
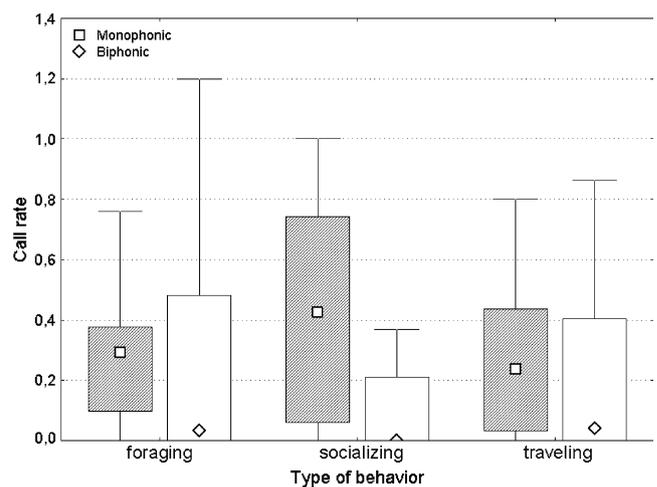

Fig. 3 The percentages of monophonic and biphonic calls across encounters with different pod numbers

Fig. 5 Rate of monophonic and biphonic calls across samples recorded in different activity types. *Rectangles* and *Diamonds* give the median number of calls, *boxes* show the percentiles (25–75%), and *whiskers* give the non-outlier range

while in the presence of more than one pod both categories were used in equal proportions. This probably indicates different roles for these groups of signals in communication. We suppose that biphonic calls are employed as markers of pod and matriline affiliation, serving mainly as cohesion signals. These calls are more common when more than one pod is present in the area, and in this situation animals may need to discern their own pod members and whales from other pods. The joining of two independently modulated frequency components into a common vocalization may function to increase the probability of call type recognition, which is especially important in long-distance communication in noisy environments, when the signal may substantially degrade during the transmission to a listener. In king and emperor penguins, biphonation enhances the ability of calls to propagate through penguin bodies in a colony and provides additional cues for 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*. This species often faces the problem of communication in conditions of dense vegetation, which also impedes the signal propagation.

Another possible function of biphonation in killer whale calls is related to the differences in directionality of the lower- and higher-frequency components. Miller (2002) showed that the relative energy in the high-frequency components was significantly greater when animals were moving toward the hydrophone array than away from it. It is likely that this difference could help the whales to determine the direction of movement of the caller.

Proposed functions of biphonation in terrestrial mammals also include the breaking of monotony in vocal sequences in order to escape habituation in listeners and an indication of the physical condition of a caller (Fitch et al. 2002). However, it is unlikely to be the case for killer whales because biphonic discrete calls are highly stereotyped in this species and occur as a normal and substantial part of the repertoire of each individual (Ford 1991).

Miller (2006) showed that source levels differ across call types in Northeast Pacific resident killer whales. The low-frequency monophonic calls exhibited the lowest mean apparent source level whereas high-frequency biphonic calls showed the highest source levels. No attempt was made to estimate the source levels and active space for the Kamchatkan killer whale acoustic signals; but while listening for calls from a distance of about 10 km, we usually heard biphonic call types. By comparison, at close distance, monophonic calls were used twice as often as biphonic ones. This indirectly indicates that biphonic calls have higher source levels than monophonic calls. The probable high source levels make biphonic calls detectable at long range, which allow the animals to monitor the position and movements of their own pod members as well as animals from other pods.

Weiss et al. (2007) showed that in the Canadian northern resident killer whale community, family-specific call types were emitted at higher rates, whereas "low-arousal" call types were used less frequently in the presence of matrilines from different pods, subclans, or clans. We recorded no calls during the group resting of Kamchatkan killer whales, which suggests the absence of "low-arousal" calls similar to that of the Canadian northern residents (Ford 1989). The biphonic calls of Kamchatkan killer whales appear to be more pod-specific and discrete than the monophonic call types (Filatova et al. 2007) and might be similar in function to the family-specific call types of Canadian northern resident killer whales.

The function of monophonic calls is less clear. In the samples that were analyzed in this study, they occurred twice as often as biphonic calls. Miller (2006) showed that monophonic calls have lower source levels than biphonic calls. This, along with the fact that monophonic calls dominated the vocalizations when a single pod was present, suggests that monophonic calls may be used as close-range intragroup contact signals. In terrestrial animals, the role of the visual channel is considered to be more significant than acoustics for short-distance communication. However, the visibility underwater is often poor, such that aquatic animals can hardly see each other even at a distance of 10–20 m. Close-range acoustic contact signals exist in many species which need to maintain contact in conditions where visibility is limited, including common bottlenose dolphins (*Tursiops truncatus*) (Janik and Slater 1998), orangutans (*Pongo pygmaeus*) (MacKinnon 1974), baboons (*Papio cynocephalus*) (Cheney et al. 1995), and dholes (*Cuon alpinus*) (Volodin and Volodina 2002).

The monophonic call rate was relatively high during all encounter types. However, the monophonic call rate was significantly higher during the encounters with many pods compared to the encounters with few pods. It is possible that the high rate of biphonic calls during the encounters with few pods reduced the need of monophonic call usage. In the encounters with many pods, by contrast, the presence of many whales from different pods created a complicated social environment and in these conditions the usage of both monophonic and biphonic calls could be vital for successful communication.

We found no differences in biphonic and monophonic call rates between activity types. Ford (1989) also found that no call types were associated exclusively with any particular activity type. This may indicate that killer whale discrete calls are not just activity markers and that their functions are more complex, or that it is the sequence of calls rather than isolated calls that is of importance in coordinating group movements within specific activities.

Although call rates did not differ statistically across activity types, there were some non-significant differences in their usage when different types of behavior were compared (Fig. 5). Monophonic call rate was highest during socializing. Socializing is a close-range affiliative context (Thomsen et al. 2002) and the increase of the monophonic call rate during socializing is in accordance with our hypothesis that monophonic calls are close-range intra-group contact signals.

In conclusion, in Kamchatkan killer whales biphonic discrete calls function mostly as pod markers and help whales to define pod affiliation and monitor the position of each other at long range when more than one pod is present in the area. In contrast, monophonic calls are less dependent on the number of pods and may be used as close-range intragroup contact signals to maintain contact in underwater conditions with limited visibility.

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