



The vocal behaviour of mammal-eating killer whales: communicating with costly calls

VOLKER B. DEECKE*†‡, JOHN K. B. FORD‡§ & PETER J. B. SLATER*

*School of Biology, University of St Andrews

†Marine Mammal Research Unit, University of British Columbia, Vancouver

‡Vancouver Aquarium Marine Science Centre

§Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo

(Received 26 January 2004; initial acceptance 23 February 2004;
final acceptance 6 April 2004; published online 9 December 2004; MS. number: A9805)

The cost of vocal behaviour is usually expressed in energetic terms; however, many animals may pay additional costs when predators or potential prey eavesdrop on their vocal communication. The northeastern Pacific is home to two distinct ecotypes of killer whales, *Orcinus orca*, called residents and transients. Resident killer whales feed on fish, a prey with poor hearing abilities, whereas transient killer whales hunt marine mammals, which have sensitive underwater hearing within the frequency range of killer whale vocal communication. In this study, we investigated how the superior hearing ability of mammalian prey has shaped the vocal behaviour of the transient killer whale ecotype. We recorded pulsed calls and the associated behavioural context of groups of transient and resident killer whales in British Columbia and southeastern Alaska. Transient killer whales produced pulsed calls significantly less frequently than residents. Transient killer whales only showed significant amounts of vocal behaviour after a marine mammal kill or when the whales were displaying surface-active behaviour. Vocal activity of transients increased after a successful attack on a marine mammal. Since marine mammals are able to detect killer whale pulsed calls and respond with antipredator behaviour, the reduced vocal activity of transients is probably due to a greater cost for calling in this ecotype resulting from eavesdropping by potential prey. The increase in vocal behaviour after a successful attack may represent food calling (informing other animals in the area about the presence of food), but is more likely to reflect an increase in social interactions during feeding and/or the fact that the cost for vocal behaviour is comparatively low after a successful attack.

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During acoustic communication, an animal transmits information to other individuals using sound signals and thus attempts to influence the behaviour of these individuals to its own advantage (Dawkins & Krebs 1978; Slater 1983). The benefits of such acoustic communication can be substantial but are offset to some degree by associated costs. Direct costs of acoustic communication include the energy required to produce sound, as well as the energy lost by not feeding during the time spent in communication. Indirect costs of acoustic communication result from passing information on to unintended

receivers (eavesdroppers). Unintended receivers may include competitors (e.g. Hammond & Bailey 2003), predators (e.g. Hosken et al. 1994; Mougeot & Bretagnolle 2000), parasitoids (e.g. Lehmann & Heller 1998; Müller & Robert 2002), or, in the case of predatory animals, potential prey.

Costs arising from eavesdropping by the prey have been documented extensively in the case of echolocating predators, animals for which vocal behaviour is an essential part of the foraging process. Studies of bats feeding on insects with good hearing abilities suggest that the vocal behaviour of the predator and the hearing abilities of the prey have coevolved (for reviews, see Fenton & Fullard 1981; Rydell et al. 1995; Fenton 2003). Costs generated by prey eavesdropping on echolocation signals have also been postulated for toothed whales (Barrett-Lennard et al. 1996; Wilson & Dill 2002). Unlike echolocation, communicative vocalizations are usually not an essential part of the foraging process. For this

Correspondence: V. B. Deecke, Marine Mammal Research Unit, University of British Columbia, 6248 BioSciences Road, Vancouver, BC V6T 1Z4 Canada (email: deecke@zoology.ubc.ca). J. K. B. Ford is at the Marine Mammal Research Program, Fisheries and Oceans Canada Pacific Biological Station, Hammond Bay Road, Nanaimo, BC V9T 6N7. P. J. B. Slater is at the School of Biology, University of St Andrews, St Andrews, Fife KY16 9TS, Scotland, U.K.

reason one might expect predators hunting acoustically sensitive prey to drastically reduce vocal communication while foraging.

Studies in the northeastern Pacific have documented the existence of distinct ecotypes of killer whale, *Orcinus orca*, that specialize on different prey (Ford et al. 1998; Saulitis et al. 2000). 'Resident' killer whales live in large, stable groups and feed only on fish, especially Pacific salmon (*Oncorhynchus* spp.). 'Transient' killer whales, on the other hand, exclusively hunt warm-blooded prey. Their primary prey in the coastal waters of British Columbia are harbour seals, *Phoca vitulina*, but transients also attack Steller, *Eumetopias jubatus*, and California, *Zalophus californianus*, sea lions, harbour porpoise, *Phocoena phocoena*, Dall's porpoise, *Phocoenoides dalli*, and Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, and they occasionally also take seabirds (Ford et al. 1998).

Both killer whale ecotypes produce three functionally and structurally distinct types of vocalizations: echolocation clicks, whistles and pulsed calls (Awbrey et al. 1982; Ford 1989). Spectrograms of the three vocalization types are given in Fig. 1. Clicks are short pulses of sound, usually produced in series, and are used in echolocation for orientation and prey detection (Barrett-Lennard et al. 1996). Whistles are tonal signals with little or no harmonic content that tend to be most common in social contexts and are thought to play a role in short-range communication (Ford 1989; Thomsen et al. 2002). Pulsed calls are the most common vocalization of killer whales and are thought to function in group recognition and coordination of behaviour (Ford 1989, 1991; Miller 2000b; Miller et al. 2004). Ford (1989) grouped pulsed calls into three categories: discrete, variable and aberrant. Discrete calls are highly stereotyped and can easily be assigned to different call types according to their structural properties. Variable calls are not stereotyped and cannot be divided into clearly defined call types. Finally, aberrant calls are structurally based on a discrete call type, but show some degree of modification. As with whistles, killer whales tend to produce aberrant calls most frequently during social interactions (Ford 1989, 1991).

Resident and transient killer whales experience differential costs for vocal communication resulting from eavesdropping by potential prey. Salmonids, the preferred prey of resident killer whales, have poor hearing abilities at the frequencies of killer whale communication (Hawkins & Johnstone 1978), suggesting that eavesdropping generates only small costs for residents. In contrast, all marine mammals have excellent underwater hearing (e.g. Renouf 1992; Au et al. 2000; Kastelein et al. 2002; Wolski et al. 2003) and can detect the communicative calls of killer whales from distances of several kilometres (Miller 2000a; Deecke et al. 2002). Harbour seals have been shown to respond to the calls of transient killer whales with anti-predator behaviour (Deecke et al. 2002) and the same is presumably true for many other marine mammals as well. Hence, vocal communication carries a high cost for transients, since potential prey animals are able to detect their vocalizations and perceive them as indicating a threat.

Barrett-Lennard et al. (1996) found that transient killer whales produce echolocation clicks far less often than

residents and attributed this to greater costs from eavesdropping. From a preliminary data set from 15 encounters with transient killer whales off British Columbia, Ford (1984) concluded that transients also use communicative vocalizations (pulsed calls) less frequently than residents. Morton (1990) compared the behaviour of resident and transient killer whales and similarly noted differences in the frequency of occurrence of vocal communication. Saulitis (1993) documented infrequent use of vocal communication in a population of mammal-eating killer whales in Prince William Sound, Alaska, suggesting that differences in the vocal behaviour of the two ecotypes are not restricted to British Columbia waters.

The objective of our study was to quantify how often resident and transient killer whales produced pulsed calls in order to determine how differential costs resulting from eavesdropping prey have shaped their vocal communication. Since mammal-eating killer whales are thought to experience a much higher cost for vocal behaviour, we predicted that transients should produce pulsed calls less frequently overall. The cost of vocal communication in mammal-eating killer whales that arises from interception by potential prey differs across behavioural contexts. This cost is highest when the animals are actively searching for prey, but can be comparatively low in other contexts when prey capture is of lower priority. We analysed how frequently vocal communication occurred in different behavioural contexts, and we predicted that vocal communication is rare when the animals are searching for prey but increases after a successful attack and during social interactions. Many species of mammals and birds vocalize in the presence of food (e.g. Elgar 1986; Chapman & Lefebvre 1990; Janik 2000). To test for such food-related calling in killer whales, we determined whether levels of vocal activity were elevated during or after a kill compared to other behavioural contexts.

METHODS

Data Collection and Classification of Behaviour

This study was carried out in the summer and autumn months (June–December) of 1999–2003 in Johnstone and Queen Charlotte Straits, British Columbia, and in Glacier Bay, Icy Strait, and Stephens Passage, southeastern Alaska. Killer whale groups were located by scanning from a boat or from elevated points on shore using binoculars. In addition, opportunistic sightings were often relayed by a network of observers including other researchers, whale-watching operators, recreational boaters and the staff of Glacier Bay National Park Preserve. Encounters where animals were first detected acoustically (i.e. by listening for their calls using hydrophones) were not used for this study. When killer whales were encountered, the identity and size of the group were confirmed by taking identification photographs of all individuals for comparison with existing catalogues (Ford & Ellis 1999; Matkin et al. 1999; Ford et al. 2000).

To monitor the vocal behaviour of a group, we moved the boat approximately 800 m ahead of the animals but

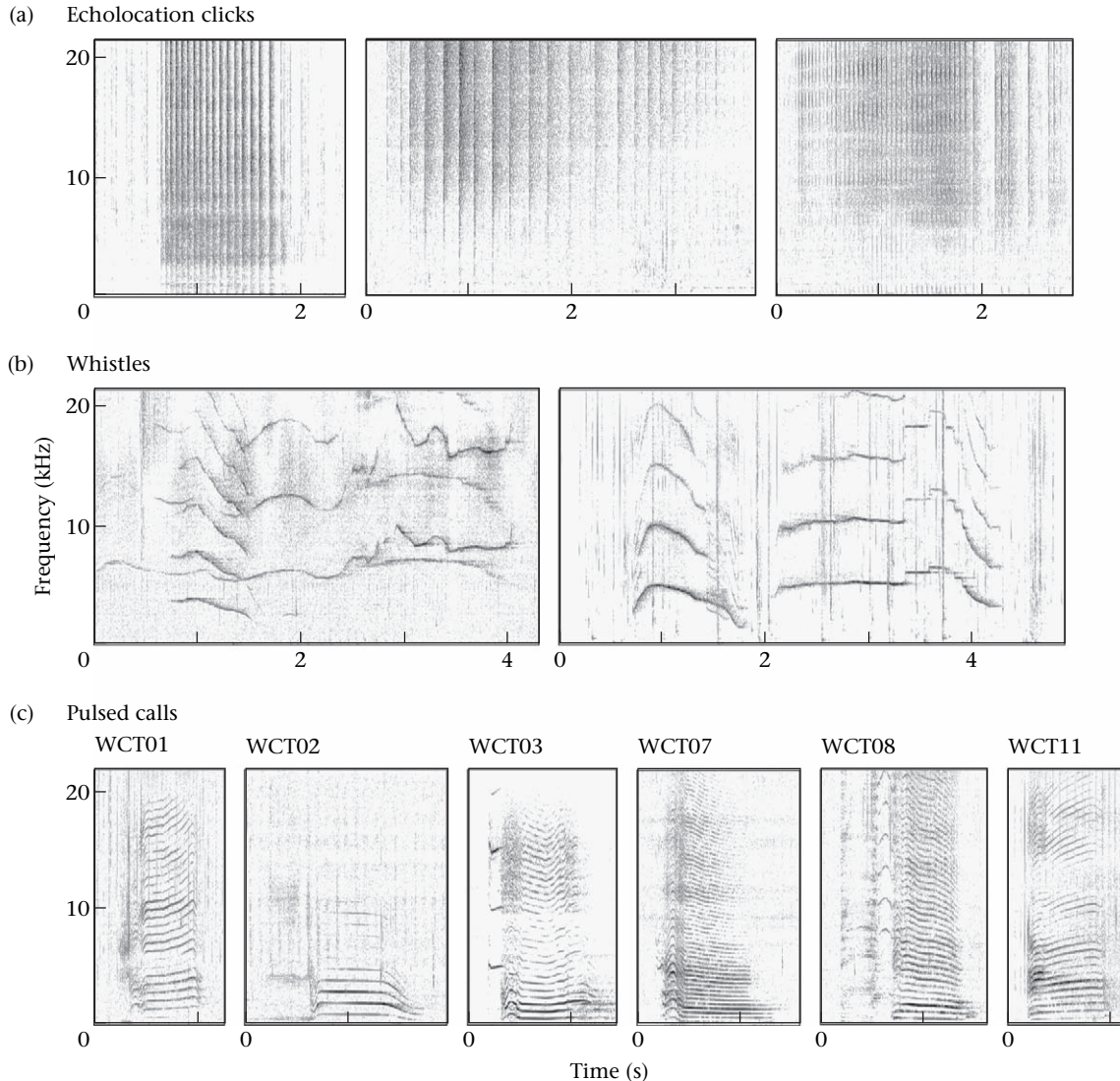


Figure 1. Spectrograms of typical echolocation click trains (a), whistles (b) and pulsed calls (c) of transient killer whales. For pulsed calls, the six discrete call types recorded in this study are shown. Sounds were digitized at 22.1 kHz, spectrograms were generated using a fast Fourier transformation size of 4096 samples, a frame length of 512 samples and 75% overlap between frames. A hamming window was used for normalization.

not in their immediate path, so that ideally they would pass the boat at a distance of about 150 m. An Offshore Acoustics hydrophone was used to monitor vocal behaviour, and each time the animals surfaced, their distance from the boat was estimated and confirmed with laser rangefinders (Bushnell YardagePro 1000 or Leica Geovid 7 × 42 BDA) whenever possible. Distances up to 500 m from the animals could be estimated with reasonable precision: in 18 instances where estimated distances could be verified with a rangefinder reading within 10 s, the average error of the estimate was 11% (standard deviation: 8%). For transient killer whales, the behaviour of the animals was noted for each such pass, and the position of the boat was determined approximately every 30 min using a global positioning system (GPS). The signal from the hydrophone and voice notes indicating the animals' distance and behaviour were recorded on separate channels of a TCD-D8 DAT recorder (Sony Corporation,

Toronto, Canada). In addition, we noted any predatory behaviour: attacks on marine mammals after which prey remains were clearly seen or could be recovered were noted as confirmed kills. If there was only indirect evidence that prey had been captured (seagulls hovering above the whales, crunching sounds on the hydrophone), this was documented as a possible kill. Behaviour was divided into categories using variables that could be easily quantified. These were swim speed (extrapolated from GPS positions), synchronicity and directionality of the animals in the group as they surfaced, and the presence of aerial and percussive behaviours such as breaching (leaping clear or partially out of the water), spyhopping (surfacing vertically and lifting the head out of the water), as well as slapping the surface with the tail flukes or flippers. We used the following five categories to classify the behaviour of transients (modified from Ford 1989; Barrett-Lennard et al. 1996).

(1) Surface-active: this behaviour category is characterized by frequent physical contact between members of the group, as well as occasional aerial and percussive behaviours including breaches, tail-slaps, pectoral slaps and spyhops. Surface-active whales typically move at speeds of less than 6 km/h, do not surface in synchrony and frequently change direction.

(2) Milling: milling whales move at speeds of less than 3 km/h and lack a clear direction. The dive sequences of individuals in the group are irregular and not synchronized and there are no aerial or percussive behaviours. Milling behaviour that we observed after a confirmed or possible kill was not included in this category (see below).

(3) Milling after kill: this behaviour is typically observed during and after a kill of a marine mammal. The dive pattern, directionality and swim speed are similar to those during milling, but often include aerial and percussive behaviours. This behaviour ends when the whales increase their swim speed and move away from the site of the kill. Only milling after a confirmed kill was included in this category.

(4) Slow travel: during slow travel, the dive sequences of the animals in a group are synchronized and the animals consistently move in the same direction for several surfacings at swim speeds of 3–6 km/h.

(5) Travel: during travel, all members of a group surface in synchrony, and consistently move in the same direction, usually within a few body lengths of each other. Swim speeds during travel exceed 6 km/h.

We found that it was impossible to consistently identify when transients were actively searching for prey. Therefore, some behaviours classified as foraging by Barrett-Lennard et al. (1996) fall into the category of slow travel in the present study.

Acoustic and Statistical Analysis

The recordings were visually and acoustically inspected for pulsed calls using the CoolEdit sound analysis package (Syntrillium 2000). Because we were primarily interested in communicative vocalizations, echolocation clicks were not investigated in this analysis (but see Barrett-Lennard et al. 1996 for a comparative analysis of the echolocation behaviour of the two ecotypes). To test for differences in call usage during different behaviour contexts, we classified pulsed calls into discrete, aberrant and variable calls (Ford 1989) and assigned discrete calls to the call types established by Deecke (2003) shown in Fig. 1. The underwater calls of resident killer whales can be heard over distances of many kilometres (Miller 2000a), whereas the calls of transient killer whales are often faint. To minimize the number of missed calls, we included in the analysis only the sections of an encounter when the whales were within 500 m of the hydrophone (i.e. recorded between consecutive surfacings within 500 m of the boat). To quantify the level of vocal activity, we calculated the rate of vocal behaviour (r) using the formula

$$r = \frac{c}{t \times i}$$

where c is the number of pulsed calls recorded while the animals were within 500 m of the boat, t is the time in minutes that the animals spent within 500 m of the boat and i is the number of individuals in the group. The unit for the rate of vocal behaviour therefore represents calls per individual per minute.

To compare the level of vocal activity for different behavioural contexts, we calculated the rate of vocal behaviour for each behaviour category observed in a given encounter. This means that all data points within a behaviour category are independent, but some data points in different behaviour categories come from the same encounter. Since vocal rates from the same encounter are more likely to be similar, and we tested for differences between behaviour categories, this approach is conservative. Because transient killer whales remain silent for extended periods, their vocal behaviour is not normally distributed; thus, we used nonparametric statistical tests throughout. To examine the effect of behavioural context on the level of vocal activity, we used a Kruskal–Wallis test to test for differences across behaviour categories and used Dunn's multiple contrast with tied ranks and unequal sample size (Zar 1996) to identify homogeneous subsets. To test whether vocal activity was significantly elevated after a kill, we compared the level of vocal activity while the animals were milling after confirmed kills with the level of vocal activity for the other behaviour categories during the same encounter using a Wilcoxon matched-pairs signed-ranks test. Except for Dunn's multiple contrast, which was calculated using the method described by Zar (1996), all statistical tests were carried out using the SPSS statistics package (SPSS 1999).

Comparison of Resident and Transient Killer Whales

We determined levels of vocal activity during 10 encounters with groups of resident killer whales using the methodology described above to determine whether transient killer whales vocalize less frequently than residents. Because resident groups tend to be more spread out than groups of transients, it was often unlikely that all members of a group would be within 500 m of the boat. Therefore, we calculated rates of vocal behaviour for resident killer whales using the time and the number of calls recorded while at least one group member was within 500 m. Because the calls of resident killer whales can be heard over several kilometres (Miller 2000a), it is unlikely that a significant number of calls were missed; however, if calls were missed due to animals being outside of the range of acoustic detection, this would bias the rate of vocal behaviour downward, since we used the total number of animals in the group (and not animals within 500 m) to calculate this parameter. We calculated an overall rate of vocal activity across all behaviour categories for each encounter with transient killer whales and compared these rates to the rates for residents using a Mann–Whitney U test (Zar 1996).

RESULTS

Comparison of Resident and Transient Killer Whales

We encountered 25 groups of transients in the course of the study. Group size ranged from one to 18 animals ($\bar{X} \pm \text{SD} = 5.6 \pm 4.4$) and encounters lasted between 30 and 483 min (186 ± 112 min). During an encounter, the animals spent between 2 and 58 min ($\bar{X} \pm \text{SD} = 19 \pm 14$ min) within 500 m of the boat. Group sizes for the 10 encounters with resident killer whales ranged from three to 48 animals ($\bar{X} \pm \text{SD} = 15 \pm 13.7$) and encounters lasted between 28 and 462 min ($\bar{X} \pm \text{SD} = 165 \pm 166$ min). During the encounters, at least one animal was within 500 m of the hydrophone for 4–127 min ($\bar{X} \pm \text{SD} = 32 \pm 37$ min).

Residents produced pulsed calls more frequently than transients. Median call rate across all behaviour categories for residents was 0.34 calls per individual per minute (interquartile range 0.09–1.23) compared with 0.05 calls per individual per minute (interquartile range 0.00–0.23) for transients (see Fig. 2). The difference in the call rate between the two ecotypes of killer whales was significant (Mann–Whitney U test: $U = 63$, $N_1 = 10$, $N_2 = 25$, $P = 0.023$).

The Context of Vocal Behaviour in Transient Killer Whales

For the 25 encounters with transient killer whales, the number of acoustic samples and time spent within 500 m of the boat varied between behaviour categories: travel was observed in 17 encounters (total recording time

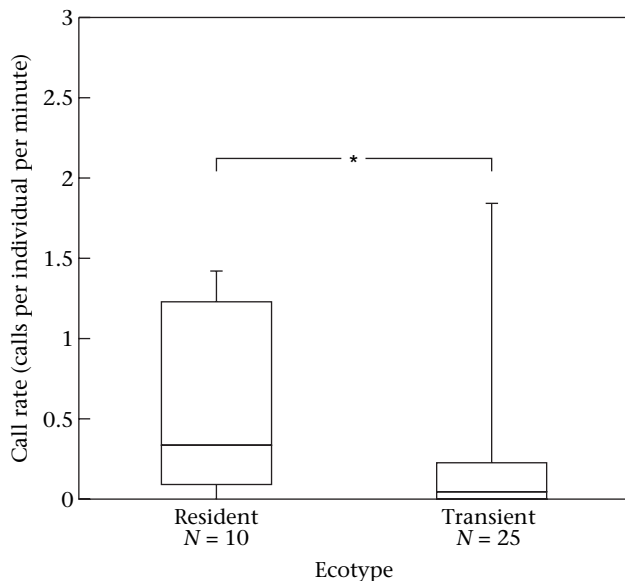


Figure 2. Differences in the rate of pulsed calls by fish-eating (resident) and mammal-eating (transient) killer whales across all behaviour categories. Horizontal bars give median call rate, boxes show the interquartile range and whiskers give the full range of call rates. $*P < 0.05$, Mann–Whitney U test.

within 500 m: 152 min), slow travel in 11 encounters (157 min), milling after kill in seven encounters (83 min), surface-active in four encounters (50 min), and milling in four encounters (12 min). The vocal rate was highest for surface-active (median call rate: 0.63 calls per individual per min; interquartile range 0.12–1.43) followed by milling after kill (median: 0.27 calls per individual per min, interquartile range 0.24–0.87). During all other behaviours, the animals were usually silent (median call rate: 0.00 calls per individual per min; interquartile range 0.00–0.00). The vocal rate differed across behaviour categories (Kruskal–Wallis test: $H_4 = 18.50$, $P = 0.001$) and vocal behaviour for milling after kill was significantly higher than during slow travel (Dunn's test: $Q_{6,10} = 3.35$, $P < 0.01$), travel ($Q_{6,16} = 3.72$, $P < 0.005$) and milling ($Q_{6,3} = 3.10$, $P < 0.02$). All other comparisons were not significant (Fig. 3).

With the exception of one encounter, the animals produced three discrete call types (WCT01, WCT02 and WCT11; see Fig. 1) in addition to variable and aberrant calls. During a single bout of surface-active behaviour (22 August 2002) the animals frequently produced three additional call types (WCT03, WCT07 and WCT08) in addition to the more common WCT01, WCT02 and WCT11. Aside from this single encounter, visual inspection of the vocal repertoires showed no pronounced differences in the call types produced while the animals were engaged in surface-active or slow travel behaviour compared to the milling after kill category (Fig. 4).

Test for Food-related Calling in Transients

Successful attacks by transient killer whales on marine mammals could be confirmed during seven of the 25 encounters (Table 1). In an additional two encounters, indirect evidence (seagulls hovering above the whales, crunching noises on the hydrophone) indicated a possible marine mammal kill. The prey species could be identified for four of the seven confirmed kills. With the exception of one kill of an unidentified marine mammal, the animals produced pulsed calls when milling after a kill (median vocal rate: 0.27 calls per individual per min; interquartile range 0.24–0.87). No calls were recorded during any other behaviour categories in the same encounters (see Fig. 5) and the difference in vocal rate for milling after kill compared with the other behaviour categories was significant (Wilcoxon matched-pairs signed-ranks test: $T = -2.20$, $N = 7$, $P = 0.03$).

DISCUSSION

Prey Hearing and Killer Whale Vocal Behaviour

The results of this study show that transient killer whales produce communicative vocalizations only extremely rarely. Transient killer whales vocalized significantly less often than residents, and for all behaviour categories except surface-active and milling after kill, the median call rate was zero. These results are consistent with

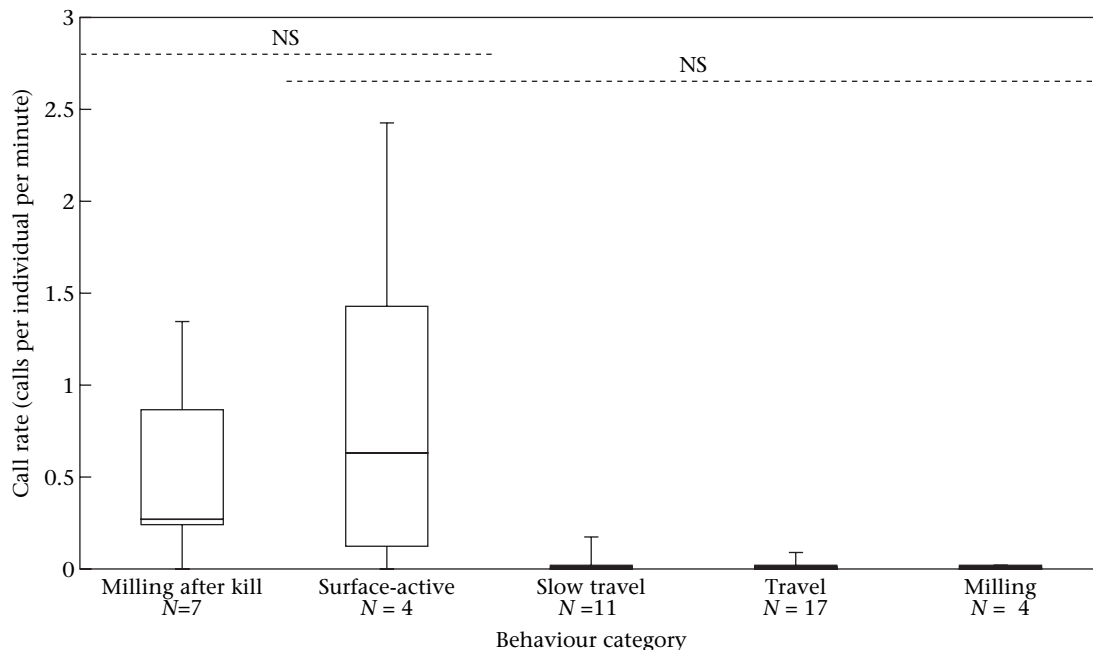


Figure 3. Differences in the rate of pulsed calls across behaviour categories in transient killer whales. Horizontal bars give median call rate, boxes show the interquartile range and whiskers give the full range of call rates. Dashed lines delineate homogeneous subsets (Dunn's multiple contrast: $P \geq 0.05$).

a significant difference in the use of echolocation by the two ecotypes (Barrett-Lennard et al. 1996). However, Barrett-Lennard et al. (1996) did not detect significant differences in echolocation use between different behaviour categories for transient killer whales.

The pronounced difference in the extent to which fish-eating and mammal-eating killer whales vocalize is consistent with a difference in the ecological cost for vocal communication arising from eavesdropping by potential prey. Eavesdropping prey do not generate large costs for residents, because their primary prey, salmonids, are unable to detect their vocalizations over a long range (Hawkins & Johnstone 1978). The cost of vocal communication for residents is therefore largely limited to the energetic cost of generating the calls. In contrast, marine mammals taken by transient killer whales can detect killer whale calls over long distances and respond to the calls of transients with antipredator behaviour (Deecke et al. 2002). Studies of capture rates and prey consumption of transient killer whales (Baird & Dill 1995, 1996) suggest that a transient killer whale needs to consume approximately the equivalent of one harbour seal each day. A typical transient group feeding on small marine mammals therefore has to make several successful attacks per day and spends a large proportion of time actively searching for prey. Eavesdropping by the prey is therefore thought to generate substantial costs for transient killer whales and our results suggest that transients have responded to this higher cost of vocal communication by restricting communication to behavioural contexts when this cost is relatively low.

Guinet (1992) and Guinet et al. (2000) describe patterns of vocal behaviour of killer whales around the Crozet Archipelago in the Southern Indian Ocean that are similar

to those of our study: the animals are silent while hunting and searching for prey, but become vocal during and after an attack. Killer whales in this region are ecologically similar to North Pacific transients in that they feed on prey with good underwater hearing (marine mammals and penguins; Guinet 1992). However, genetic studies suggest that killer whales from this region are only distantly related to North Pacific transients (Hoelzel et al. 2002), which suggests that both populations have converged on similar patterns of vocal behaviour independently.

A similar system of coevolution between the vocal behaviour of predators and the hearing ability of their prey has been described for the echolocation calls of bats (e.g. Fenton & Fullard 1981; Rydell et al. 1995; Fenton 2003). Vocal behaviour in the form of echolocation is an essential part of the foraging process for these animals and the primary function of these vocalizations is orientation and detection of prey. Few studies have investigated the effect of eavesdropping prey on communicative or social vocalizations of predators. Killer whale pulsed calls are thought to be such communicative signals: it has been suggested that they function to coordinate direction of movement and behaviour state among members of a group (Ford 1989, 1991; Miller 2000b; Miller et al. 2004). Although these functions are essential to maintain group cohesion, they are not an essential part of the foraging process, especially if the animals travel within visual range of each other as transients usually do. In the case of mammal-eating killer whales therefore, eavesdropping by the prey has not only shaped the usage of vocalizations used in the foraging process (i.e. echolocation clicks; Barrett-Lennard et al. 1996) but also the usage of communicative sounds.

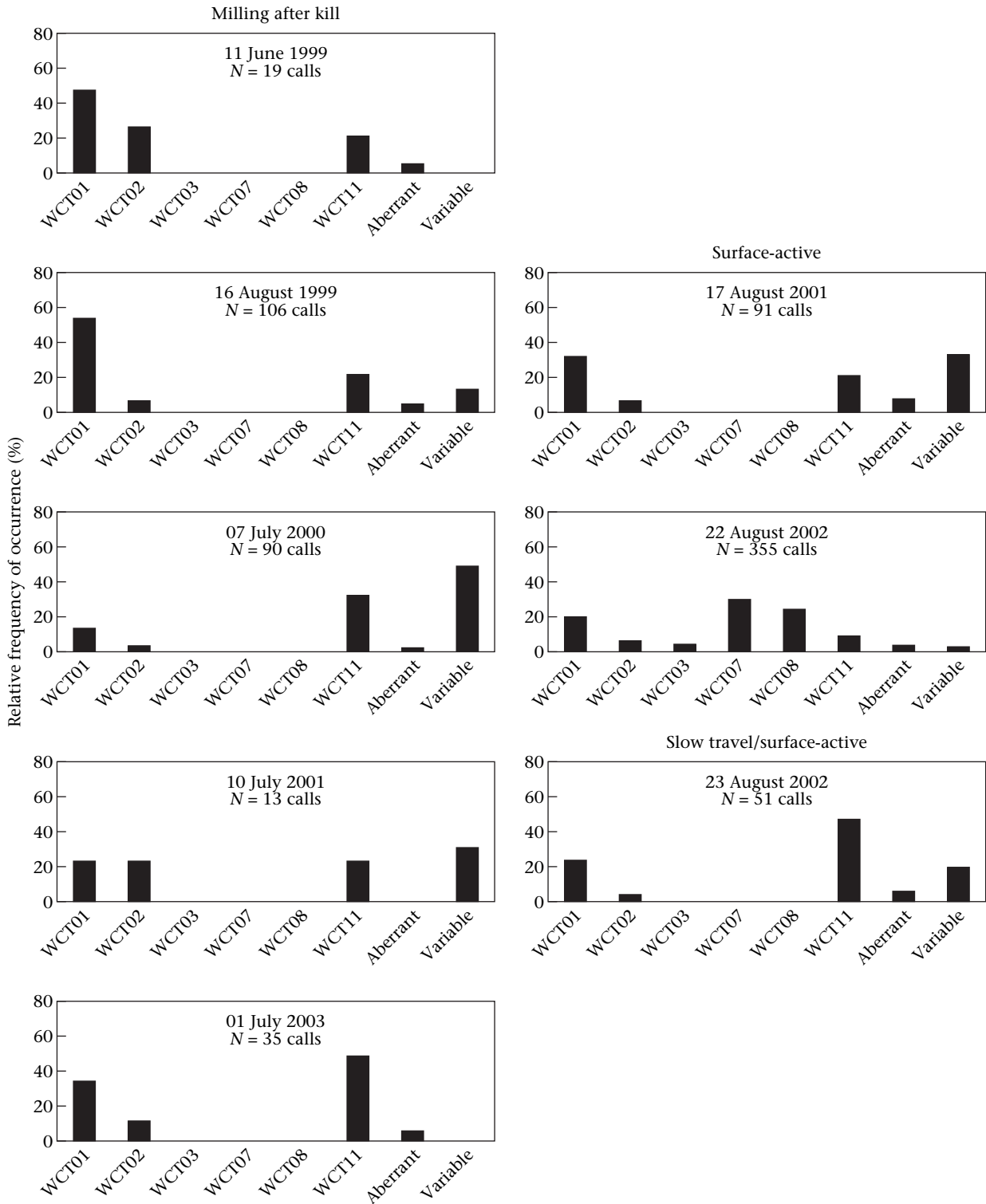


Figure 4. Call repertoires of transient killer whales while milling after a marine mammal kill (left column) compared to other behaviour states. Alphanumeric designations starting with WCT (for West Coast transient) refer to pulsed call types. Note that the recording session for surface-active behaviour on 22 August 2002 contained three call types not recorded in other sessions (see text for further details).

Food Calling in Transient Killer Whales?

Levels of vocal activity were significantly elevated after the seven confirmed kills in our study (Fig. 4). We found no clear trend in the amount of vocal behaviour recorded

in relation to the amount of food available (indicated by group size and prey type in Table 1), but this may be an effect of low sample size. Our results therefore show that vocal behaviour in transient killer whales is related to the presence of food. However, the question remains whether

Table 1. Size and composition of groups of transient killer whales, prey species, and rate of vocal behaviour for the seven encounters where successful attacks on marine mammals could be confirmed

Date	Individuals present*	Prey species	Vocal rate after kill (calls per individual per minute)
11 June 1999	T101, T101A, T101B, T102	Not determined	1.04
15 June 1999	T086, T086A, T103, T104	Dall's porpoise	0.27
16 August 1999	T018, T019, T019B, T020, T021, T022	Dall's porpoise	0.69
16 September 1999	T059, T059A, T060	Not determined	0.00
7 July 2000	T036, T036A, T036B, T063, T065, T065A, T065A1, T065B, T100, T100B, T101, T101A, T101B, T102	Harbour seal	0.26
10 July 2001	T090, T090A, T124A, T124A1, T124A2	Harbour seal	0.12
1 July 2003	T085, T085A, T085B, T101, T101A, T101B, T102	Harbour seal	1.35

*Notation follows that of Ford & Ellis (1999), who give further details about individuals.

this association indicates food calling (informing conspecifics about the presence of food). Alternatively, vocal behaviour may be food-related because vocal communication is associated with increased levels of excitement after a kill (see for example Marler & Evans 1996), because it is part of the social interactions during food sharing, or because vocal behaviour carries a comparatively small cost in this behavioural context (see Janik 2000 for a discussion of food-related calling).

Several functions have been proposed for food calling in birds and mammals, but many of these are of limited applicability to mammal-eating killer whales. Hauser & Marler (1993) argued that food calling could serve to attract related animals to a food source and thus increase an individual's inclusive fitness. Social groups of transient killer whales typically consist of individuals that are maternally related (Ford & Ellis 1999). All members of a social group either participate actively in an attack, or

are present as bystanders (Jefferson et al. 1991; Ford et al. 1998). Vocalizing if the attack is successful is therefore more likely to attract unrelated individuals than additional relatives. In many birds and primates, attracting other individuals to a food source is thought to decrease the risk of predation, and to allow the signaller to spend more time feeding and less time in vigilance (e.g. Elgar 1986; Chapman & Lefebvre 1990). Killer whales have no natural predators, and decreased risk of predation is not therefore a possible reason for food-related calling. There is evidence for aggression between the resident and transient ecotype (Ford & Ellis 1999), which suggests that vocal behaviour is as likely to attract aggressors as affiliative individuals. Marzluff & Heinrich (1991) argued that food calling in ravens may function to attract social companions to a carcass and thus to increase the chance of overcoming the defence of dominant individuals. In the Southern Indian Ocean, Guinet et al. (2000) witnessed groups of killer whales displacing others from a carcass, but such agonistic behaviours are not known from the North Pacific. Again, vocal behaviour after a kill would be as likely to attract aggressive as affiliative individuals, and the best strategy to prevent scavenging is to avoid detection altogether by remaining silent.

We found no evidence that the vocal behaviour recorded in our study served to attract other killer whales to the site of a kill. In no instance were other whales observed to join the focal group when it vocalized after a kill, even in situations where other groups were known to be nearby. Previous studies (Saulitis 1993) have noted that many, but not all, calls of transient killer whales appear much fainter than those of residents and therefore may not be audible over the long distances over which resident calls can be heard (Miller 2000a). For this reason, further studies should set out to measure the loudness of calls of transient killer whales to determine the distance over which other killer whales can detect them. Such source level measurements would also yield information about the distance over which different prey species can detect the calls of transients and hence provide a first step towards quantifying the cost of vocal behaviour.

There is therefore little evidence that the vocal behaviour recorded in our study functions to attract additional individuals to the site of a kill. An alternative explanation for why transient killer whales vocalize after a kill is that

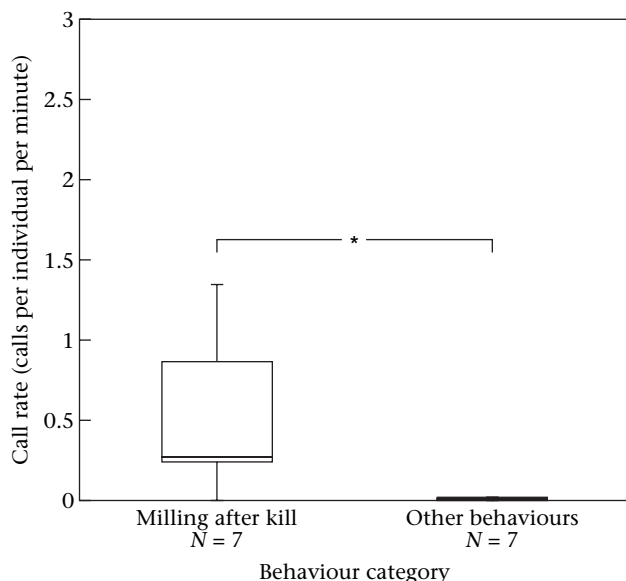


Figure 5. Differences in the number of pulsed calls recorded from transient killer whales when milling after a kill compared to all other behaviour categories during which confirmed kills of marine mammals were observed. Horizontal bars give median call rate, boxes show the interquartile range and whiskers give the full range of call rates. * $P < 0.05$, Wilcoxon test.

the cost for vocal behaviour arising from eavesdropping by potential prey is comparatively low in this context. After a successful attack, the killer whales are satiated, and may not need to hunt again for some time so that warning potential prey in the area is not very costly. In addition, attacks on marine mammals are noisy affairs: they are usually accompanied by fast swimming, aerial behaviours and hitting or ramming the prey. Potential prey animals in the vicinity may therefore already be aware that killer whales are nearby, so that there is no additional cost for vocalizing. Mammal-eating killer whales often share their prey (Jefferson et al. 1991), and sharing of prey items was common during the kills observed in this study. Vocal behaviour may be an essential part of delineating social relationships during the sharing of prey, which could also explain why it increased after a successful attack.

Strategies to Avoid Detection by Prey

It has been suggested that some echolocating predators have developed echolocation signals outside of the hearing range of their prey to avoid detection (e.g. Rydell & Arlettaz 1994; Fullard & Dawson 1997; Pavey & Burwell 1998). In theory, transient killer whales may be able to avoid detection by vocalizing at frequencies that are inaudible to pinnipeds or other cetaceans. The area of best hearing of killer whales lies between 18 and 42 kHz (Szymanski et al. 1999), and much of the energy of killer whale vocal communication is concentrated in this frequency band (Miller 2000a).

Because high frequencies show greater attenuation in water than lower frequencies, the cost of shifting communication to a higher-frequency band is a decrease in the distance over which calls of equal amplitude can be heard. Two common prey species, the Pacific white-sided dolphin and the harbour porpoise, have excellent high-frequency hearing (up to 128 and 140 kHz, respectively; Tremel et al. 1998; Kastelein et al. 2002), so that any upward shift in the frequency of communication would have to be substantial in order to avoid detection. Restricting communication to low frequencies would eliminate directional cues that are thought to be functionally important in killer whale vocal communication (Miller 2000a). This is because the longer wavelengths of low-frequency sounds cannot be focused by the melon (Miller 2000a), which is the fatty tissue on the rostrum of cetaceans thought to act as an acoustic lens. Harbour seals, California sea lions, and presumably Steller sea lions, all have good underwater hearing as low as 1 kHz (Schusterman et al. 1972; Wolski et al. 2003), so that again, any downward shift in frequency would have to be substantial. Given these trade-offs and constraints, it therefore appears that limiting vocal communication is the only strategy to minimize detection by all potential prey.

Costly Calls and the Evolution of Cooperation

The term cooperation can be applied to situations where two or more individuals coordinate their behaviour to achieve a common goal (e.g. Goodall 1986; Jefferson et al.

1991). One would expect cooperation to evolve in situations where the individual fitness gain of two or more animals coordinating their behaviour in the long term outweighs the gain of one animal acting alone. The results of this study combined with those of Barrett-Lennard et al. (1996) and Deecke et al. (2002) suggest that stealth and surprise are important elements of the hunting strategy of transient killer whales. This requires behaviour to be coordinated since, in order to avoid detection, all individuals in a group must refrain from vocalizing. A similar reduction in acoustic communication has been reported for chimpanzees, *Pan troglodytes*, when hunting monkeys (Boesch & Boesch 1989; Boesch & Boesch-Achermann 2000) or when groups patrol territory borders or move inside the territory of a neighbouring community (Goodall 1986; R. W. Byrne, personal communication).

In situations where group hunters attack acoustically sensitive prey by stealth, the costs and benefits of coordinating behaviours are exaggerated. In most other situations where coordination of behaviours is required primarily to overcome physical or behavioural defences of the prey, group hunters that fail to cooperate will have a capture success close to that of solitary hunters. This implies that there is a benefit for coordinating behaviour, but there is no cost for the lack of coordination between group members in addition to the costs of group living (e.g. competition and interference). However, in a situation where stealth substantially increases the probability of a successful attack, lack of coordination carries a significant added cost: if one individual in the group vocalizes while the others hunt silently, the success of every individual in the group will drop below the success of an individual hunting alone. Where group living has evolved, the coordination of vocal behaviour is therefore the only stable strategy for predators hunting acoustically sensitive prey.

Acknowledgments

C. Brignall, D. H. Chadwick, N. Dedeluk, F. Nicklin, P.-A. Presi, G. M. Weingartner, M. Wong and H. Yurk provided essential help with the field work. We are grateful to G. M. Ellis for his help with all aspects of this study, especially for supplying information on the identity of killer whale groups. We thank L. G. Barrett-Lennard, J. and M. Borrowman, J. DeBoeck, B. and R. Lamont, B. and D. Mackay, C. O. Matkin, D. R. Matkin, A. B. Morton, E. L. Saulitis, J. Watson and R. M. C. Williams, as well as the staff of Glacier Bay National Park and Preserve for valuable logistic support. The spectrogram of call type WCT03 comes from a recording generously supplied by F. Thomsen. All research was conducted under valid research permits from the U. S. National Marine Fisheries Service (permits no. 545-1488-02 and 473-1433-04), Fisheries and Oceans Canada, and Glacier Bay National Park and Preserve (permit no. GLBA-00016). Earlier drafts of this manuscript benefited greatly from comments by L. G. Barrett-Lennard, M. B. Fenton, H. C. Gerhardt, K. E. McComb, M. G. Ritchie, H. Yurk and an anonymous referee. We gratefully acknowledge the kind support from the following institutions: Glacier Bay

National Park and Preserve, BBC Natural History Unit, and National Geographic Magazine. This study was funded by the Vancouver Aquarium Marine Science Centre, BC Wild Killer Whale Adoption Program, as well as National Oceanographic and Atmospheric Administration, and North Pacific Marine Science Foundation through the North Pacific Universities Marine Mammal Consortium. During part of this study, V. B. D. was supported by a DAAD-Doktorandenstipendium aus Mitteln des 3. Hochschulsonderprogramms.

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