



## Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*<sup>☆</sup>

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Previous sound recordings of resident (fish-eating) killer whale groups have revealed matrilineal group-specific call repertoires and a strong tendency for calls of the same type to be produced in series. Vocal interactions between individual free-ranging animals, however, have remained unexplored because it has not been possible to identify signallers reliably with a single hydrophone. Here we link acoustic arrivals of calls on a towed hydrophone array with visual tracking of photo-identified individuals to ascribe calls to a focal animal when it was separated from other members of its matrilineal group by more than 35 m, and thereby out of visual range. We confirm that individual members of a matrilineal group share a repertoire of stereotyped calls, and we statistically examine timing of stereotyped calls produced by one individual relative to calls produced by other members of its group. Analysis of the intervals between stereotyped calls indicated that calls were produced in group bouts with a criterion interval of 19.6 s separating bouts. We were therefore careful to develop randomization tests that preserved call interval structure. Focal whales produced 36% of their calls within 5 s of a call from a nonfocal animal, four times more calls than expected by chance based upon a rotation randomization test. Consecutive calls produced by different individuals during group-calling bouts matched call type more than expected by chance. Vocal exchanges of stereotyped calls with type matching appear to be an important aspect of intragroup calling in killer whales, although the function of this calling behaviour remains to be explored.

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Many studies of acoustic communication emphasize brief interactions, called 'vocal exchanges', in which a receiver responds to a signal by signalling back within a brief interval. These vocal interactions may provide a mechanism for a respondent to direct a graded signal towards an intended receiver (Krebs et al. 1981; McGregor et al. 1992; Janik 2000), for signallers to recognize each other (Beecher et al. 1996), for the receiver to confirm reception of the signal (Sugiura 1993), or for exchange of information about the location of the callers (Falls et al. 1982).

Exchanges of matching sounds have been described in primate groups (e.g. Sugiura 1993, 1998) and between songbirds ('song-type matching', Krebs et al. 1981), and the function of vocal matching appears to depend

strongly on social context. The affiliative 'chuck' call is exchanged between captive squirrel monkeys, *Saimiri sciureus*, in a tight temporal sequence. A shift in the peak frequency of the chuck encodes the chuck as either a request or a response to a request (Biben et al. 1986; Biben 1993). Although there is little evidence that primates modify the acoustic structure of their vocalizations through learning, Sugiura (1998) showed that captive Japanese macaques, *Macaca fuscata*, respond to playback of coo calls by matching the frequency of the initial coo calls in their response. The functions of the broad class of grunts, coos, chucks and trills produced by primates have not been well studied, but these sounds appear to play a role in social reconciliation and integration or coordination of movement (Symmes & Biben 1988; Boinski 1993; Cheney et al. 1995).

In contrast, song-type matching in territorial songbirds appears to function as a threat by which the responder can target his threat to the original singer (Krebs et al. 1981; Burt et al. 2001), and vocal learning appears to play a critical role in the development of shared repertoires (Bell et al. 1998). Song sparrow, *Melospiza melodia*, males

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respond to the song of a stranger by matching the stranger's song (Stoddard et al. 1992), but respond to the song of a neighbour by singing a different song that is shared in the repertoire of the two birds (Beecher et al. 1996). Northern cardinals, *Cardinalis cardinalis*, provide biparental care to offspring, and song exchanges near the nest appear to coordinate nest approach, with males less likely to approach the nest if the female produces a matching song (Halkin 1997). Although communication serves a different function in the different contexts of territorial defence and parenting cooperation, song-type matching appears to signal 'stay away' in both cases (Halkin 1997). Song-type matching is thought to facilitate estimation of the location or range of a singer (Krebs et al. 1981), which is important in territorial defence but should also play an important role in contact signalling.

In the marine environment where light is rapidly attenuated but sound travels far, interacting individuals are forced to rely heavily on acoustic signals or cues to maintain contact with each other (Myrberg 1980). Most marine mammals range over large distances at sea, yet social species need to maintain contact and regulate interactions when individuals are out of sight of one another. Calling by the southern right whale, *Eubalaena australis*, is strongly correlated with behavioural and social context, with one call (the 'up' call) commonly exchanged between different individuals as they approach and join each other (Clark 1983). Experimental playback of various right whale sounds preferentially elicits calling and approach by receiving whales (Clark & Clark 1980). Sperm whales, *Physeter macrocephalus*, exchange patterned sequences of click sounds ('codas'; Watkins & Schevill 1977) in tight temporal sequences, particularly during intragroup social behaviours (Whitehead & Weilgart 1991). Early studies reported that codas are individually distinctive, at least over periods of a few hours (Watkins & Schevill 1977; Watkins et al. 1985). Later work reported that codas are shared by individuals from the same group (Moore et al. 1993; Weilgart & Whitehead 1993, 1997; Rendell & Whitehead 2003), but the rate of vocal matching during exchanges of these shared codas was not analysed.

A study of wild bottlenose dolphins, *Tursiops truncatus*, in the Moray Firth, Scotland, used a hydrophone array to show that matched whistle exchanges between separated dolphins were more common than expected by chance (Janik 2000). The predominant whistles produced by temporarily isolated, individual dolphins from both wild and captive populations are highly distinct ('signature-whistle'; Caldwell et al. 1990; Sayigh et al. 1995). Individually distinctive whistle production also increases during voluntary separations in captivity (Janik & Slater 1998), and unrestrained captive dolphins may mimic the individually distinctive whistle of their tankmate (Tyack 1986b). Janik's (2000) study showed that matching vocal interactions do occur among wild bottlenose dolphins (see also Smolker et al. 1993), but whether the exchanged whistles are individually distinctive 'signature' whistles or whistles from a shared repertoire (Janik & Slater 1998; McCowan & Reiss 2001) remains unknown. In either case, immediate production of a matching whistle may direct the response to the initial caller (Janik 2000).

The goal of this study was to describe vocal exchanges of stereotyped calls between individual, free-ranging resident (primarily fish-eating; Ford et al. 1998; Baird 2000) killer whales within the same matrilineal group when they were out of visual range of each other. Members of these stable matrilineal groups regularly disperse to forage for up to several hours, and later reunite for social and resting activities (Ford 1989; Hoelzel 1993). Resident killer whales have a diverse repertoire consisting of whistles, echolocation clicks and burst-pulse calls. A minority (<10%) of burst-pulse calls are highly variable and are seldom repeated while the rest of the burst-pulse calls are highly stereotyped and stable. Each group of resident killer whales produces a distinctive repertoire of 7–17 stereotyped call types (Ford 1991; Deecke et al. 1999; Miller & Bain 2000). Production of stereotyped calls increases during separations, probably to aid cohesion and coordination between group members (Ford 1989). Using group recordings made with a single hydrophone, Ford (1989) found a strong tendency for a call to be followed by another call of the same type. Without being able to identify the caller, however, it was difficult to determine whether a single individual produced the entire sequence or whether the sequence represented vocal exchanges with call-type matching.

We explored exchanges of stereotyped calls by members of stable killer whale groups by using a towed hydrophone array system that allowed continuous focal observations of the vocal and surface behaviours of an identified killer whale while monitoring the vocal production of other group members (Miller & Tyack 1998). Inspection of recordings from three matrilineal groups revealed that call-type matching vocal exchanges were common. To statistically describe calling dynamics, we ascribed calls to identified individual members of one small matrilineal group, described repertoire sharing of stereotyped calls by group members, and used randomization analyses of call sequences to test whether calling by an individual is influenced by the calling of other group members. This study provides the first description of the calling behaviour of individual free-ranging killer whales.

## METHODS

We recorded sounds from matrilineal groups W3, A36 and A23 during August and September 1999 in Johnstone Strait, British Columbia. Individuals were observed from an 11-m research vessel using the focal-follow (Altmann 1974) methods described in Miller & Tyack (1998). The array was positioned to isolate one individual (the 'focal' animal) as much as possible in azimuth from other nearby killer whales ('nonfocal' animals). We determined the identity of the focal animal in the field by comparing the individually distinctive dorsal fin shape and saddle-patch markings to those in catalogued photographs of individual killer whales (Ford et al. 1994). At each surfacing, the position of the focal animal relative to the vessel was measured with laser range finders and a digital compass, and its orientation to the array was recorded (Miller & Tyack 1998).

We monitored the positions of nonfocal animals in the area during the focal follow, and analysed only the periods when the focal animal was isolated by more than 20° in azimuth. This criterion minimized the risk that signallers were misidentified, and assured that the focal animal was out of visual range of other matrilineal group members during the analysed portions of the focal follows. At a typical distance of 100 m from the vessel to the focal animal, isolation of more than 20° in azimuth corresponds to more than 35 m of separation. During these periods, we carefully ascribed calls by tracking the angle of arrival of calls and echolocation clicks from the focal and nonfocal animals. Voice notes were checked to confirm that the focal animal was widely separated in azimuth from other group members. All signaller identifications were independently checked to ensure accuracy.

Recordings were digitally transferred from multichannel Tascam digital recorders to computer for analysis using custom Matlab software. Broadband beamforming techniques were used to determine the angle of arrival of sounds recorded during the focal follow (see Miller & Tyack 1998). A visually predicted angle from the array to the focal whale was calculated at 1-s intervals by interpolating the visually observed positions of the whale at the previous and subsequent surfacings. All calls recorded during the follow were scored as having been produced by the focal or by a nonfocal whale, and the start time of each call was recorded. All calls recorded during these focal follows were classified to type using the system of Ford (1987, 1991), based on aural recognition and visual inspection of spectrograms produced in Matlab with an effective filter bandwidth of 94 Hz and a dynamic range of 50 dB. Calls were classified as variable if they did not clearly resemble any of the defined call types. All further analyses were conducted only on stereotyped calls.

### Detailed Analysis of Calling by Members of Matrilineal Group W3

To statistically describe calling by members of a matrilineal group, we examined timing of stereotyped calls produced by one individual relative to calls produced by the other members of matrilineal group W3, the only known matrilineal group from W pod (Ford et al. 1994). W pod is part of the 'R' clan of resident killer whales and produces a repertoire of stereotyped calls different from the other matrilineal subgroups observed in the summer of 1999 (Ford 1991). At the time of the study, W pod consisted of three individuals, a female (W3, estimated birth in 1940) and her two adult male offspring (W2 and W5, estimated births in 1960 and 1974, respectively; Ford et al. 1994). The recordings from group W3 were most suited for statistical analysis because we were able to ascribe stereotyped calls to all members of this small group, and their unique repertoire made it possible to be sure that nonfocal animal calls were from a member of the focal animal's matrilineal group. Members of a different pod (A5) were occasionally within acoustic range of group W3, but focal follows were conducted only when group W3 was not visibly interacting with A5 pod members.

The stereotyped calls produced by the entire group and each group member were visualized with a histogram to assess repertoire sharing. We replicated Ford's (1989, Table 5) analysis of group-calling sequences for the two most common call types (N32, N33). Using the time intervals between calls, we tested whether group production of stereotyped calls followed a simple Poisson distribution or a mixed exponential distribution by successively fitting the distribution of intervals to one- and two-process exponential models, respectively (Sibly et al. 1990). The two-process model fit the interval distribution well ( $r^2 = 0.97$ ; Fig. 1) and significantly better than the one-process model ( $F_{2,11} = 40.4$ ,  $P < 0.0001$ ; Table 1). This pattern is consistent with group members producing calls in bouts. Using the formula to minimize total time misclassified, we calculated a bout criterion interval of 19.6 s (Fagen & Young 1978; Slater & Lester 1982).

Because production of stereotyped calls by the group did not follow a simple Poisson distribution, we tested for countercalling and matched countercalling using non-parametric randomization techniques that preserved call timing of both the focal and nonfocal animals. While we could ascribe calls to the focal individual, the 'nonfocal' category included the other two animals within the group. We tested whether group members counter-called more often than expected by chance by separating all stereotyped calls recorded into the call sequence produced by the focal animal and nonfocal animals (Fig. 2a). We tallied the number of stereotyped calls produced by the focal animal within 5 s of the start time of a stereotyped call produced by a nonfocal animal. The arbitrary criterion of 5 s allowed identification of immediate exchanges in which call durations were roughly 1 s, with sound travel times between callers up to 2 s, irrespective of which animal initiated the exchange. Under the null hypothesis that the focal call sequence was produced randomly with respect to the nonfocal call sequence, we randomized call timing of different individuals by linking the start and end of each focal follow and rotating the focal animal sequence a random amount of time (Fig. 2b). For each randomization, the number of focal calls within 5 s of the

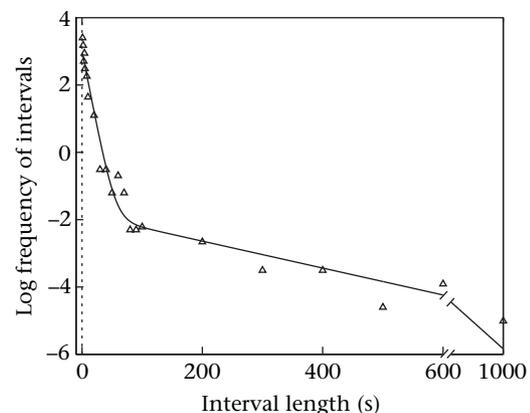


Figure 1. Log frequency of intervals between stereotyped calls produced by members of matrilineal group W3. This distribution of intervals is fit with a curve ( $r^2 = 0.97$ ) calculated as the sum of two exponential functions.

**Table 1.** ANOVA results showing variance accounted for by successively fitting a one- and a two-process model to intervals between stereotyped calls produced by group W3

	<i>df</i>	<i>SS</i>	<i>MS</i>
Mean	1	45.1	
One-process model	1	117.0	117.0
Two-process model	2	38.7	19.4
Residual	11	5.2	0.48
Total	15	206.0	

*SS*: sum of squares; *MS*: mean square.

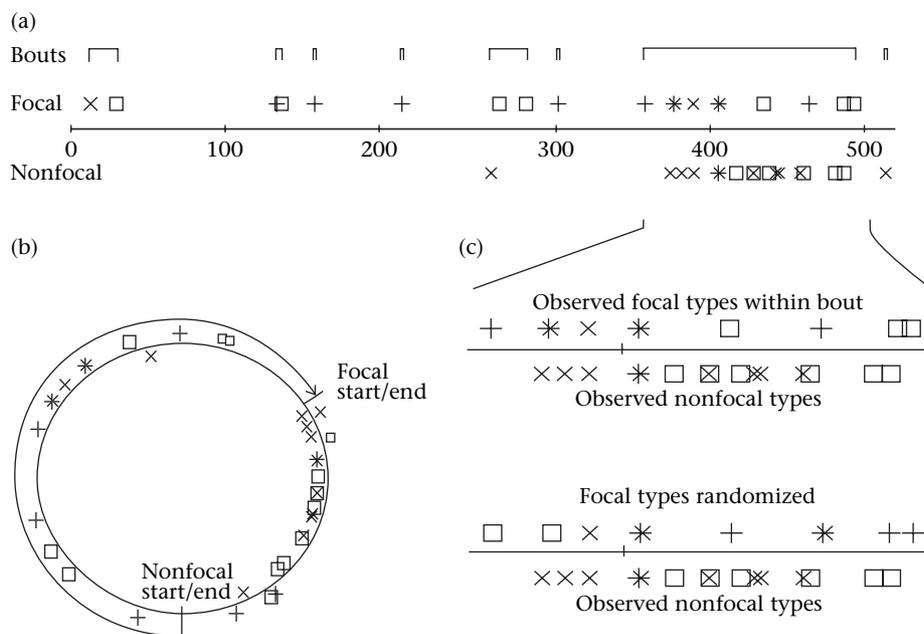
start of a nonfocal call was tallied, and a probability distribution from 10 000 such randomizations was generated and compared to the observed value. This nonparametric rotation randomization tested for dependencies in the behavioural sequences between the focal and nonfocal whales without altering the statistics of either sequence.

The rotation randomization tested for generic counter-calling irrespective of the call type produced. To test whether individuals altered their call-type production in response to calling of other group members, we examined the rate of call-type matching within vocal exchange bouts. We used the bout criterion interval calculated above (19.6 s) to divide the group call sequences into

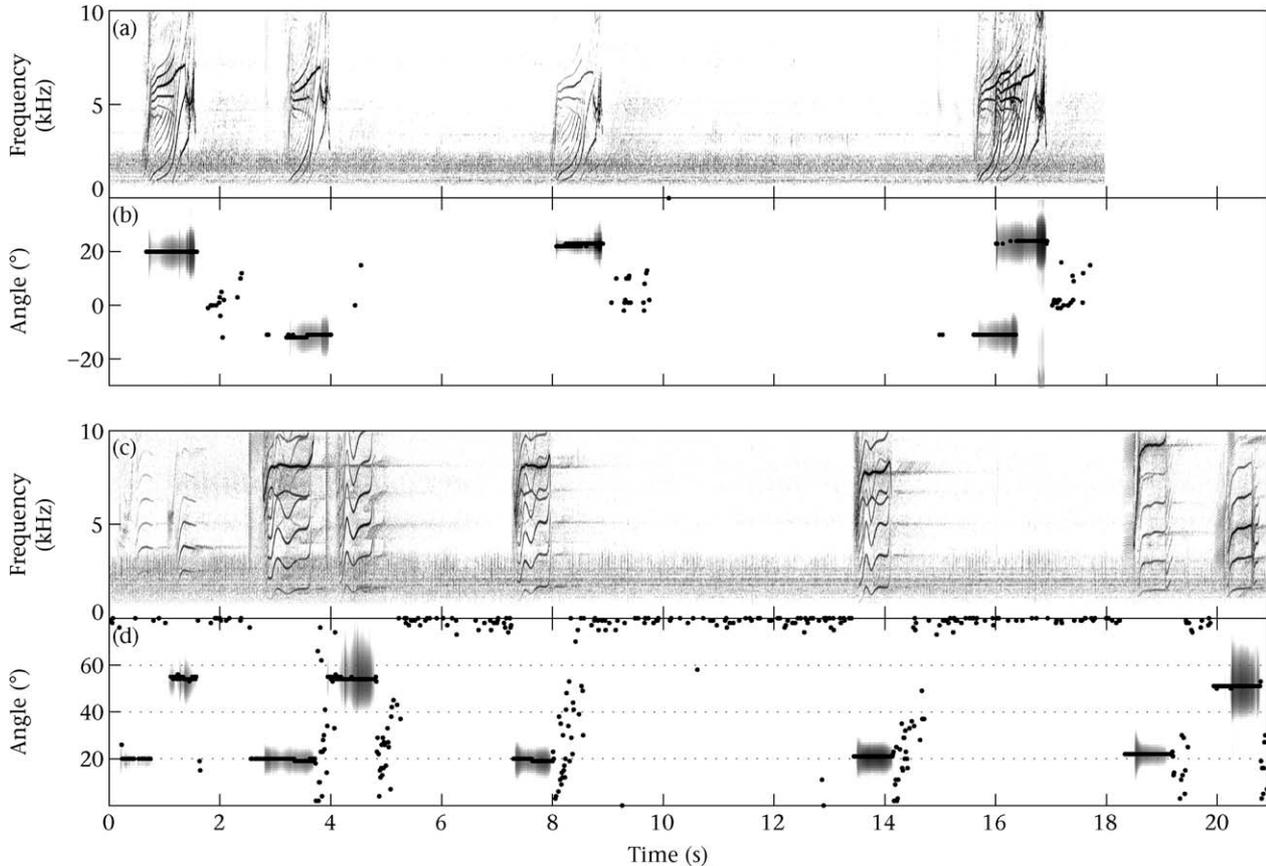
bouts (Fig. 2a). A call-type matching event was defined as a two-call sequence of the same call type within a bout where one call was produced by the focal and the other by a nonfocal whale. We tallied the number of call-type matching events across all bouts. Under the null hypothesis that the call type produced by the focal individual was selected randomly with respect to the type produced by nonfocal animals, we randomly rearranged the call types produced by the focal animal within each bout (leaving call timing and the nonfocal call types unchanged) and retallied the number of call-type matching events across all bouts 10 000 times (Fig. 2c). By randomizing the focal call types within each bout, we tested for matched counter-calling on a tight temporal scale while controlling for the potentially specific context of each bout.

**RESULTS**

We recorded a total of 31 focal follows from matrilineal groups W3, A36 (part of A1 pod) and A23 (part of A5 pod; Ford et al. 1994). Sounds were analysed from 23 focal follows of matrilineal group W3, with a total duration of 274 min ( $\bar{X} \pm SD$  follow duration: 11.9  $\pm$  11.2 min). Four focal follows were conducted with members of matrilineal groups A23 and A36, for a total of 72.5 and 69 min, respectively. Vocal exchanges with call-type matching were observed from all three matrilineal groups (Fig. 3).



**Figure 2.** (a) Time series of stereotyped calls during a 510-s focal follow of matrilineal group W3 on 12 September 1999 in Johnstone Strait. Call types N32, N33, N52 and N34 are represented by the symbols  $\times$ ,  $\square$ ,  $+$  and  $*$ , respectively. Stereotyped calls produced by the focal animal (W2) are shown as symbols above the timeline, whereas calls produced by the nonfocal animals (W3 and W5) are shown below. Calls separated by less than 19.6 s are grouped into bouts delimited by brackets above the focal call sequence. In this follow, the focal animal produced 19 stereotyped calls, nine of which were within 5 s of a stereotyped call produced by a nonfocal animal. (b) A sample randomization using the rotation technique. The beginning and end of the focal and nonfocal call sequences are joined, and the focal call sequence is rotated a random amount of time (represented by the arrow) while the nonfocal call sequence remains fixed. In this representative example randomization, three calls of the focal animal fell within 5 s of a call by a nonfocal animal. A total of 10 000 randomizations resulted in a mean of 2.3 calls (maximum of 7) that fell within 5 s of a nonfocal call. (c) A sample randomization of call-type production within a bout. The top sequences are those shown in (a) between 350 and 500 s. In the bottom sequences, the focal call types are randomly assigned from the types within the bout. There were six call-type matching events in the actual data, but only four in the sample randomization. A total of 10 000 randomizations produced a mean of 4.3 (maximum of 10) call-type matching events.



**Figure 3.** Examples of vocal exchanges with call-type matching in resident killer whales. Two sound sequences are displayed as a spectrogram in each upper panel (a, c) and a 'directogram' in each lower panel (b, d). The black dots in the directogram show the angle from which most energy arrived. (a, b) An 18-s sound sequence from matrilineal group W3. The focal animal was W2 and was positioned at  $-15^\circ$  to the array, corresponding to the sound arrivals from those angles. W2 and the nonfocal animal (either W3 or W5) exchanged a series of N32 calls. (c, d) A 21-s sequence from matrilineal group A23. The focal animal was A23 (estimated birth 1947) who surfaced at  $+52^\circ$  to the array at the 10-s point in the time series. The other caller was A23's offspring A60 (born in 1992; Ford et al. 1994). A23 and A60 exchanged two N7 calls, then two N2 calls, and then two N9 calls. Note that the offspring A60 changed type with A23, rapidly matching after the type switch. The sound files associated with these sequences are available as electronic supplementary information (<http://www.elsevier.com/locate/anbehav>).

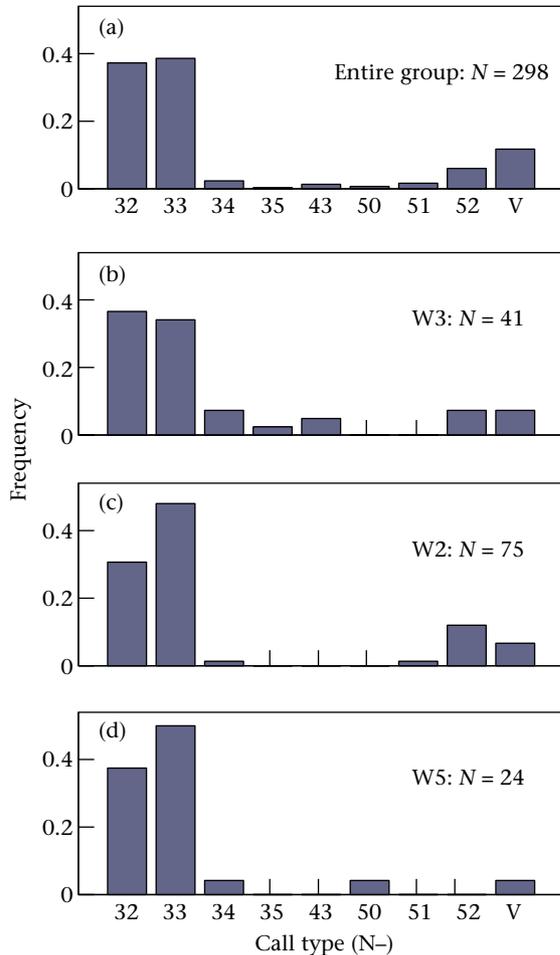
Of 298 stereotyped and variable calls recorded from matrilineal group W3, 140 (47.0%) were ascribed to an identified caller (Table 2). Of these 140 calls, 113 (80.7%) were stereotyped calls produced by the focal animals, 18 (12.9%) were stereotyped calls produced by an identified nonfocal whale, and the remaining 9 (6.4%) were variable calls. Most calls ascribed to the focal animal (88/113) arrived within  $10^\circ$  of the predicted angle. In a few cases (25/113) during boat manoeuvring, stereotyped calls whose angle of arrival was  $10\text{--}20^\circ$  from the predicted angle were ascribed to the focal animal. During two

**Table 2.** Sample size of focal follows and identified calls

	Individual		
	W3	W5	W2
Number of follows	4	9	10
Number of days	1	2	4
Minutes followed	30.8	104.6	138.6
Calls identified	41	24	75

follows, all three callers in matrilineal group W3 could be identified from detailed voice notes of the positions of widely separated nonfocal individuals.

Eight stereotyped call types were recorded from matrilineal group W3 (Fig. 4). The frequency of production of stereotyped calls by the group closely matched Ford's (1991, Figure 16) distribution from recordings made during 1981–1983. One call type occurred repeatedly but had not been previously catalogued, so it was assigned a new number (N52: see electronic supplementary information for an example of this call type: <http://www.elsevier.com/locate/anbehav>). We did not observe call type N42, which was very rare in the sample reported by Ford (1991). N32 and N33 were the most common call types, accounting for 75.8% of all calls recorded. Variable calls comprised 11.7% of all calls. Analysis of call sequences of the entire group showed a statistically significant tendency for each of the two most common call types to be repeated in series (N32:  $G_1 = 24.59$ ,  $P < 0.0001$ ; and N33:  $G_1 = 37.99$ ,  $P < 0.001$ ), matching the previous finding of Ford (1989) that calls of the same type tend to be produced in series in group recordings.



**Figure 4.** Percentage frequency of call types produced by the three members of matrilineal group W3. On the X axis, 'V' refers to variable calls not clearly matching one of the stereotyped forms. (a) All calls from the group. (b–d) Calls ascribed to an individual animal.

The three most common call types (N32, N33, N34) were recorded from all three individuals (Fig. 4), another (N52) was recorded from two individuals, and the four rarest types (N35, N43, N50, N51) were recorded from only one individual. Although we lack evidence that these call types are shared by all of the members of group W3, the high probability of not detecting these rare calls from more than one individual in our sample makes it impossible to conclude that they are not shared. For example, type N51 was only recorded from W2, and comprised 1.68% of the group sample. If we assume that the other two individuals (W3 and W5) produce this call at the same rate, then out of the 65 calls ascribed to W3 and W5 there is a probability of  $(1.0000 - 0.0168)^{65}$ , or 0.33, that call type N51 would not be observed from W3 and W5. The probabilities that call types N35, N43 and N50 would only be observed from individual W3, W3 and W5, respectively, were 0.71, 0.26 and 0.45.

Of the 113 stereotyped calls produced by the focal whales, 41 (36%) occurred within 5 s of a call produced by a nonfocal whale. We compared this observed value to the distribution expected by chance from rotating the focal sequence a random amount of time relative to the

nonfocal sequence and tallying the number of focal calls within 5 s of a nonfocal call (Fig. 2b). The observed value greatly exceeded the mean  $\pm$  SD of  $10.5 \pm 4.4$  calls generated by 10 000 randomizations and was highly statistically significant ( $P < 0.0001$ ). This finding indicates that calling by individual killer whales is closely synchronized to calling by other group members.

Calls of focal and nonfocal individuals occurred in 39 bouts with a mean duration of 6.3 s. Within these bouts, we observed 50 call-type matching events, defined above as a two-call sequence of the same type with one call produced by the focal and the other by a nonfocal animal. When the call types produced by the focal animal within each bout were randomly rearranged 10 000 times (Fig. 2c), the mean  $\pm$  SD number of call-type matching events was  $41.6 \pm 3.4$ , significantly lower than the observed value ( $P = 0.018$ ). Call-type matching events within group bouts occurred 20% more than expected by chance, suggesting that the call type produced by one group member influences the type subsequently produced by another.

## DISCUSSION

In the context of stereotyped calls given by a killer whale out of visual range of other group members, our results suggest that both the timing and types of calls produced are strongly influenced by the calling behaviour of other group members. Members of group W3 produced 36% of calls within 5 s of a call by another group member, roughly four times more calls than expected by chance. Calling bouts of killer whale groups consist of multiple individuals countercalling in tight temporal exchanges much more than would be expected if animals called independently. Detailed analysis of calling by members of matrilineal group W3 confirmed that free-ranging killer whales share at least the most common calls in their matrilineal group's repertoire. Call-type matching was common within group bouts, with callers roughly 20% more likely than expected by chance to match the immediately preceding call type of another individual. Because we randomized call-type production within each bout, we controlled for possible specific contexts of different bouts. Similar vocal exchanges with call-type matching were also observed from members of matrilineal groups A23 and A36.

While our analysis revealed dependencies between the calling sequences of different killer whales within a matrilineal group, it is difficult to conclude that a behavioural sequence from one individual directly influenced that of another based on observational data alone. It is theoretically possible that an unrecognized cue stimulated the animals to produce similar calls close in time. However, because the focal individual was always out of visual contact of other individuals, such a cue would probably need to be acoustic, and no such cue was apparent in our analyses. Although playback experiments are needed to confirm that a call shapes another individual's vocal response, this descriptive study provides strong evidence that killer whales exchange stereotyped calls of the same

type when one or more group members are out of visual range of the others.

The nonparametric rotation randomization test was a simple and effective means of testing the interdependence of the complex calling sequences of focal and nonfocal animals. When events are clumped in bouts, as were the call sequences in this study, simple randomization of event times within one sequence will bias the statistic towards finding a dependency between two sequences. For example, in the rotation randomization conducted under the null hypothesis in this study, 2.5% of randomizations had more than 21.4 focal calls within 5 s of a call by a nonfocal animal. Using a simple event-time randomization, the 2.5% threshold would be reduced to 18 calls. This effect is due to the breakup of clumped bout events in the simple event-time randomization, which alters the statistics of the sequence and inflates the probability of a type I error. The nonparametric rotation randomization used here allows testing of dependencies between behavioural sequences without altering the statistics within each sequence, and may be preferable to parametric analyses of complex sequences.

The similar distribution of call types recorded from group W3 and the tendency for calls of the same type to be repeated in series in this and Ford's (1989, 1991) studies suggest that our sample represents typical calling behaviour of resident killer whales. Ford & Fisher (1983) and Ford (1991) described occasional differences in amplitude and reverberation patterns of calls recorded from dispersed individuals as indirect evidence that several individuals were involved in exchanges, but this study is the first analysis of individual calling dynamics. We have statistically documented call-type matching vocal exchanges in one matrilineal group of resident killer whales and also observed call-type matching vocal exchanges from members of two additional matrilineal groups in 1999 (Fig. 3). Although more work is needed to study calling by individual killer whales, the results of this study, supported by previous results from group recordings, suggest that vocal exchanges with call-type matching is an important aspect of the calling behaviour of dispersed resident killer whales.

By rapidly responding to a vocal signal, the respondent in a vocal exchange directs the response signal clearly to the original caller (Krebs et al. 1981). The acoustic structure of the response (i.e. matching, repertoire matching) provides specific information to the original signaller as well as eavesdroppers, where the social context of the participants may determine the function of the display. An interesting question is how such behaviour functions in the social life of cetaceans (Janik 2000) compared to the better-studied terrestrial species. The vocal repertoire and behaviour of killer whales have similarities to many repertoire songbirds. Calls are apparently acquired by social learning (Yurk et al. 2002), and coarse observations suggest that call types are not context specific but are interchangeable across behaviours (Ford 1989). However, the social context of stable matrilineal groups of resident killer whales is clearly more similar to that of stable matrilineal primate groups than to that of territorial songbirds. Intragroup calling by killer whales is unlikely

to be a sexual advertisement display because both sexes produce calls and calling is not associated with breeding activities, as observed in humpback whales, *Megaptera novaeangliae* (Tyack 1986a).

In both primate and killer whale matrilineal groups, individual animals are closely associated within a group over a long period. Group living for mothers and offspring may provide benefits in terms of cooperative foraging (Barrett-Lennard et al. 1996) or alloparental care (e.g. Waite 1988), but also may entail costs such as resource competition (Trivers 1974; Bertram 1978). Individuals within stable groups may use communication to increase social cohesion and to mediate cooperation when such behaviour is beneficial and, conversely, to signal a desire to avoid social contact when it entails costs in terms of resource competition and/or interindividual conflict. A benefit of employing this focal-follow technique with resident killer whales is that we can ascribe vocal and visually observable behaviour to individuals whose patterns of association and life history have been well described over a 29-year photo-identification study (Bigg et al. 1987, 1990; Olesiuk et al. 1990; Ford et al. 1994). Future descriptions correlating calling behaviour with individual status and behaviour could reveal intragroup dynamics including dominance hierarchies and mechanisms regulating the spatial structure of groups (Rose 1992; Samuels & Gifford 1997).

The costs and benefits of social behaviour for members of resident killer whale matrilineal groups are likely to depend critically on the individual relationships between group members, and the strength of the cost or benefit will largely be a function of the physical distance between the parties. In the specific context of this study, where the focal group member was out of visual range of other group members, vocal exchanges probably modulate the movement of the participants in the exchange. It has been suggested that song-type matching improves the ability of participants in the exchange to localize each other, because each respondent provides itself with a model that can be compared with the degraded signal arriving from the other party (Krebs et al. 1981; Falls 1985). Familiarity with the details of call structure may improve receivers' ability to recognize propagation effects on signals (i.e. reverberation) and thereby improve receivers' ability to estimate their distance to a calling group member (Naguib & Wiley 2001). The received structure of killer whale calls is also strongly affected by the orientation of the signaller (Schevill & Watkins 1966; Miller 2002). In addition to signalling its location (Krebs et al. 1981), a caller may signal its orientation and direction of movement to intended receivers (Miller 2002; Lammers & Au 2003).

Part of the social function of type matching vocal exchanges observed in this study may be for group members to reciprocally signal both their positions and movement trajectories almost simultaneously. We also observed instances in which an individual called without a response from other group members. Of the 113 stereotyped calls produced by a focal whale in recordings from group W3, 32 (28%) were separated by 60 s or more from the nearest call of a different whale. Such calls may function differently from those produced during exchanges (Sugiura 1998).

The potential for vocal exchanges to modulate social behaviour between individuals within a group of killer whales focuses attention on the ability of killer whales to recognize each other based upon the acoustic structure of their calls (Bertram 1978). The separated individuals in our study did not produce strongly individually distinctive contours like those produced by isolated bottlenose dolphins (e.g. Janik & Slater 1998). The calls in the group repertoire do not appear to be specific to any one individual (Fig. 4). Four of eight call types were recorded from only one individual, but the sample of identified calls was too small to expect to observe these rare calls from more than one individual, and their rare use discounts their potential importance in individual recognition. Inspection of minor variations in calls (Miller & Bain 2000) produced by different individuals suggests that such variations are not individually specific, but that these minor features are also matched in vocal exchanges (P. J. O. Miller, unpublished data). Future analyses, and possibly playback experiments, should be done to explore how individual identity might be encoded in other calls or in the detailed structure of shared stereotyped calls (e.g. Rendall et al. 1996, 1998).

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