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Bioacoustics
The International Journal of Animal Sound and its Recording

ISSN: 0952-4622 (Print) 2165-0586 (Online) Journal homepage: http://www.tandfonline.com/loi/tbio20

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To cite this article: Elizabeth M. J. Zwamborn & Hal Whitehead (2016): Repeated call sequences and behavioural context in long-finned pilot whales off Cape Breton, Nova Scotia, Canada, Bioacoustics, DOI: 10.1080/09524622.2016.1233457

To link to this article: http://dx.doi.org/10.1080/09524622.2016.1233457

BIOACOUSTICS, 2016
http://dx.doi.org/10.1080/09524622.2016.1233457

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Repeated call sequences and behavioural context in long-finned pilot whales off Cape Breton, Nova Scotia, Canada

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ABSTRACT
Repeated calls are part of the vocal repertoire of a diverse array of species, often presented in sequences that take time and effort on the part of the signal producer. Rhythmic repeated call sequences make up a significant portion of long-finned pilot whale (*Globicephala melas*) vocal production, yet the function of these sequences has not been investigated until now. In this study, we explored the relationship between behavioural context and the presence of these vocal sequences using recordings of a population of pilot whales found off Cape Breton, Nova Scotia, Canada. We used a binomial logit-link generalized linear model to look for possible predictors of the presence of repeated call sequences. They were more common in recordings of socializing whales than in those of whales in other behavioural states, and least common in resting whales. These vocal repetitions were also more common with larger group size. These results suggest that sequences function in maintaining contact and cohesion within this social species, possibly also serving in individual or group identification. The context of repeated call sequences indicate that they are not primarily mother–calf interactions, as they are heard just as commonly from groups without young. Future studies of pilot whale repeated call sequences should include individual-level behaviour and detailed acoustic calling context.

ARTICLE HISTORY
Received 27 April 2016
Accepted 31 August 2016

KEYWORDS
Globicephala melas; long-finned pilot whale; repeated call sequences; communication; behavioural context; vocalizations

Introduction

Repeated calls – calls that are produced by an individual repeatedly over time, sometimes in regularly spaced sequences – are an important part of the vocal repertoires of many different species, from the territorial chirping of Japanese burrowing crickets (*Velarifictorus micado*) (Alexander 1961) and interactive calling of male American green tree frogs (*Hyla cinerea*) (Klump & Gerhart 1992), to the family-specific calls of stripe-backed wrens (*Campylorhynchus nuchalis*) (Price 1999) and "resident" killer whales (*Orcinus orca*) (Ford 1991). When a species produces a significant portion of their calls in this manner, the often striking and recurrent nature of repeated calls leads us to consider the function of the call that is being repeated, as well as that of the repetition. What is a signal's purpose if a species is willing to invest much time and effort into repeating the same call again and again? While

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Supplementary material for this article is available online at [http://dx.doi.org/10.1080/09524622.2016.1233457]

the metabolic cost of sound production for many aquatic taxa is thought to be minimal in comparison to the total energy used by an individual (Bradbury & Vehrencamp 2011), the indirect costs of detection by predators, prey or social competitors can be ecologically important (Jensen et al. 2012). Some have suggested that repetition of calls is a redundancy used to reduce masking of the signal from background noise or calls from other individuals (Brumm & Slater 2006), when transferring important information such as about future actions and identity (Bradbury & Vehrencamp 2011). However, it can be a challenge to link repeated calls to a specific function.

Cetaceans are no exception, with sequences of repeated call types having been described across a broad range of species, but only well understood in a few. The Guiana dolphin (*Sotalia guianensis)* (Duarte de Figueiredo & Simão 2009), melon-headed whales (*Peponocephala electra)* (Kaplan et al. 2014), and northern right whale dolphin (*Lissodelphis borealis)* (Rankin et al. 2007) have all been recorded making repeated call sequences for which we do not yet have an explanation of function. One possible function of repeated calls is that they act as either individual or group identifiers. Signature whistles are individually distinctive stereotyped whistles found in some delphinid species (Caldwell 1965; Janik & Slater 1998; van Parijs & Corkeron 2001) often produced in sequences with 1–10s intervals between calls (Janik et al. 2013). Individual vocal identifiers are not limited to cetaceans, being found in other taxa such as bats (Knörnschild & Von Helversen 2008), birds (Gentner & Hulse 1998) and primates (Rendall et al. 1996). In contrast to the signature whistles found commonly in cetaceans that have fusion–fission societies, in which the composition and size of groups changes over time, other whale species that live in stable matrilineal units have been found to produce group-specific identification calls. Both "resident" killer whales (Ford 1989) and sperm whales (*Physeter macrocephalus)* (Gero et al. 2016) have vocalizations linked to different levels of their social structures. With both of these species, their group-specific vocalizations can be repeated in rhythmic sequences (Ford 1989; Miller et al. 2004; Schulz et al. 2008).

Mother–calf contact is also a possible function for these repeated calls in cetaceans. With sound as the main source of communication in cetaceans, and a bond between mother and calf being generally the strongest, one might expect calves to contribute significantly directly – though vocalizations produced specifically by the calves themselves – or indirectly – through vocalizations produced by their mothers or other carers to mediate interactions with the calves – to the vocal soundscape. Studies of several delphinid species support this, showing that whistling is much more prominent in groups with calves (van Parijs & Corkeron 2001), as well as demonstrating the importance of whistling during separation and reunion (Smolker et al. 1993). In both these cases, specific whistle types were repeated, sometimes in sequence.

Repeated calls can also function in establishing contact and maintaining organization in large groups of cetaceans. Highly social species of whales and dolphins need vocal ways in which to share information such as location and movement decisions that keep groups of individuals coordinated and functioning as a cohesive unit (Janik & Slater 1998; Tyack 2000). In this case, the context in which an individual repeats a call may be also important. It has been suggested that repetition of calls can provide enough detail to give the receiver a good estimation of the location on the caller (Krebs et al. 1981; Falls 1985; Naguib & Haven-Wiley 2001).

Identifying functions of repeated calls, which may not be exclusive, brings us back to the challenge of studying how social life and communication relate to one another, both in cetaceans and more broadly. One way of addressing the function of specific vocalizations is through studying the contextual cues surrounding them. Most studies on the context of cetacean vocalizations have taken place in just a handful of species. Bottlenose dolphins (*Tursiops truncatus*) produce bray-like feeding calls (Janik 2000) and individuals meeting at sea exchange signature whistles (Quick & Janik 2012). Mothers can also use specific acoustic signals – which incorporate their signature whistles, but also include additional features such as clicks or other whistles – to call their calves (Kuczaj et al. 2015). Sperm whales, though not making tonal vocalizations, have been found to make specific click patterns called "codas" while socializing at the surface (Whitehead & Weilgart 1991).

Some of the earliest published studies of both long-finned (*Globicephala melas*) (Busnel & Dziedzic 1966) and short-finned (*Globicephala macrorhynchus)* (Caldwell & Caldwell 1969) pilot whale vocalizations include descriptions of repeated call types, some of these made in sequence. A more recent study of short-finned pilot whales showed that these repeated call types made up a significant portion of their repertoire, though the function of these is not yet understood (Sayigh et al. 2013). Listening to the population of long-finned pilot whales found off Cape Breton, Nova Scotia, Canada, we noticed not only that repeated calls were present in most recordings when the whales were vocal, but that rhythmic repeated sequences of these calls were also commonplace. These sequences were composed of the same call type made three or more times, with roughly equal spacing of six seconds or less between adjacent calls, with call types including tonal or pulsed elements and sometimes a combination of both. Because of the range of different call types that are repeated in sequences, the repetition itself is a distinctive feature of the pilot whales' vocal repertoire. It is not yet known whether each of these sequences is produced by a single individual, but prior studies have concluded that these non-overlapping sequences, in which calls have consistent amplitude, generally seem to be made by a single pilot whale (Busnel & Dziedzic 1966; Sayigh et al. 2013). Our understanding of this species' calling context in the northwestern Atlantic is limited to two reports, the first which found that frequency, duration, and calling rate of whistles varied between some contexts (Taruski 1979), and a second where whales were found to make more complex whistles and pulsed calls when displaying surface active behaviour than when resting or travelling without much activity at the surface (Weilgart & Whitehead 1990).

If repeated call sequences in pilot whales function primarily as individual or group identifiers, we would expect them to be more common when individuals are socializing or when more whales are present, than when whales are resting or involved in other behaviours for which identification seems less important. If they function as calls in a mother–calf relationship, then their presence should increase when the observed number of calves in a group increases. If they function as more general contact calls, they would be expected to occur during times when cohesion and coordination are important, such as socializing or increased group size. To investigate why pilot whales repeat calls, we relate the repeated call sequences made by long-finned pilot whales to behavioural and environmental data, to provide the first detailed description of context for these repeated call sequences.

Methods

Recordings and acoustic analysis

Recordings, photo-identification, behavioural and environmental data for this study were collected during July and August in 1998–2014 off the northwestern coast of Cape Breton Island, Nova Scotia, Canada. Two whale-watching vessels, the *Northern Gannet* and the *Double Hookup*, were used as primary research platforms. Trips were made up to three times daily, each lasting approximately 2.5 h. There were between one and three trained observers on board the vessel depending on the year.

Recordings from 1998–2000 were collected off Bay St. Lawrence (47°02′N, 60°29′W) using a VEMCO hydrophone (10–20 kHz) and a Sony TCM 5000 eV analogue cassette tape recorder. These were digitized using CoolEdit Pro (ver. 2.0) with a 16-bit sample size and a 44.1 kHz sampling rate. Those from 2013 to 2014 were collected off Pleasant Bay (46°50′N, 60°47 W) using a Cetacean Research C55 hydrophone and a Zoom H4n 4-channel Handy Recorder at the same bit size and sampling rate. The frequency response of these hydrophones was from 20 to 20 kHz for the VEMCO hydrophone, and 8–100 kHz for the C55. These sites are separated from each other by a distance of 31 km, and photo identification of pilot whales seen over the years shows that many individuals use both areas.

In both sites, the recordings were made opportunistically during encounters of groups of pilot whales, when we cut the engine and lowered the hydrophone down to a depth of 10–15 m. Encounters began when a group of whales were sighted and included all individuals within 200 m of the vessel and each other using the chain rule (see definition of party size in Clutton-Brock et al. 1982). The encounters ended when we left to return to harbour, when the whales stayed submerged for more than 10 min, or if the captain decided to observe another group that was at least 200 m away from any of the members in the previous group. A total of 329 recordings were used for analysis, with a mean estimated group size of whales present of 24.5 (SD = 19.0).

Behavioural and environmental information was recorded opportunistically in Bay St. Lawrence, while in Pleasant Bay it was taken every 10 min. Data gathered consistently in all five years included time of day, group size, group behaviour, group composition (including presence of calves under three years of age and those under one year of age), specific surface behaviours, other cetacean species present and Beaufort Sea State. Behavioural states were defined as the behaviour displayed by the majority of whales during the observation period and were recorded as outlined in Table 1.

Table 1. Definitions of group behavioural states used in this study.

Behaviour	Definition
Travelling	Steady directional movement, travelling faster than vessel's idle speed (ca. 5.5 km/hr), often displaying variable diving patterns
Socializing	Body contact between individuals, little to no directional movement, much activity at the surface, short dives
Foraging	Prolonged dives, lifting tails when diving, no directional movement, often characterized by birds feeding in association with group, little to no surface social activity with individual whales resurfacing on their own or in small groups
Resting	Either logging most of the time or travelling at a rate slower than vessel's idle speed, individuals come to the surface as a group
Other	More than one behavioural state was predominant during the observation period or it did not fall into one of the four commonly observed behavioural states listed above

Group composition included the number of adults, as well as calves with their approximate age class. Calf age class was defined and classified by physical characteristics. Calves under one year of age had visible foetal folds visible along their sides, while those from one to three years of age were grey and smaller than the general population, but lacked these folds (Auger-Méthé & Whitehead 2007).

The recordings were analysed using the acoustics software Raven Pro (Bioacoustics Research Program 2014). Final analysed recording lengths varied between 1.5 and 6.0 min with a mean of 3.58 ± 1.1 min, and only the first section of a recording was considered for those over six minutes in length. The recordings were opportunistic, and many of them were of short duration. We found that with a minimum recording length of 1.5 min and a maximum of 6 min, the probability of presence of repeated call sequences did not change substantially or significantly with the length of recording – allowing recording length to be omitted from the final model.

Spectrograms were made with a 600-point (13.6 ms) Hann window (3 dB bandwidth = 106 Hz), with a 50% overlap and 1024-point DFT. Each recording was then scored for the presence or absence of repeated call sequences, which are defined as the same call type – showing similar frequency contour and overall acoustic characteristics that can be categorized as one type of call – made three or more times at roughly regularly spaced intervals with up to six seconds between consecutive calls (Figure 1). Six seconds was chosen as a more conservative measure of the 10 seconds used in studies of bottlenose dolphins signature whistles (Janik et al. 2013) and descriptions of short-finned pilot whale repeated call sequences (Sayigh et al. 2013), as well as our preliminary scans of the recordings. This definition separates repeated calls in sequences from others repeated sporadically throughout a recording, which may be of the same call type, but without a rhythmic nature.

Statistical analysis

Data exploration

Potential behavioural and environmental predictors of repeated call sequences were explored statistically and graphically using IBM SPSS Statistics (IBM Corp 2013). The following factors were chosen for analysis: (1) Group Behavioural State (categorical; as in Table 1); (2) Group Size (continuous); (3) Number of Calves under Three Years of Age (integer); (4) Presence of Other Delphinid Species (presence/absence); (5) Beaufort Sea State (categorical) (6) Time of Day (categorical: 10:00–13:00; 13:00–16:00; 16:00–19:00; 19:00–22:00 local summer time); and (7) Year (categorical) nested within Site (categorical: Bay St Lawrence or Pleasant Bay).

Model selection

IBM SPSS Statistics was used to find social and environmental predictors for the presence of call trains using a binomial logit-link generalized linear model. Model selection was done manually using corrected AIC values (AICc). A backwards selection process was used, beginning with the inclusion of all predictors. The predictor dropped in each round was the one whose exclusion resulted in the lowest AICc, and the process stopped when excluding any predictor increased AICc.

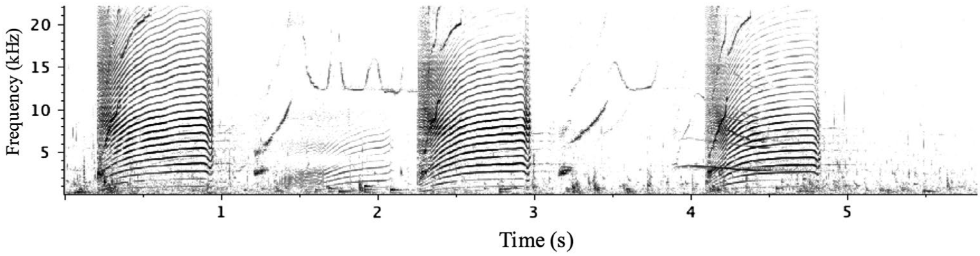

Figure 1. Example of a repeated call sequence made by a long-finned pilot whale (*Globicephala melas*), defined as the same call type is made three or more times in a row with roughly even spacing and no more than six seconds between consecutive calls.

To meet the independent assumption for modelling, only the first recording was used for each encounter in cases where there was more than one recording made. This gave 182 separate recordings. Data from all recordings were used for graphs and figures.

Results

Data exploration

From over 100hr of collected recordings, a total of 450 individual recordings that could be linked to an encounter were scored for the presence or absence of repeated call sequences. These spanned 5 different years, 221 encounters and totalled 16hrs. Of these, 329 recordings had recorded values for all chosen predictors and were used for data exploration, with 182 independent recordings being included in our modelling.

Repeated call sequences were present in 52% of recordings. The per cent of recordings with repeated call sequences varied substantially between behavioural states, with 85.4% of recordings when whales were socializing having these calls and only 22.9% of recordings during which whales were resting (Figure 2). Group size was higher for recordings with repeated call sequences than those where repeated calls were absent (Figure 3). The former had a mean group size of 28.5 individuals with a median of 22.5, while the latter had a mean of 20.1 individuals with a median of 16.5. There is some difference apparent in the presence of repeated call sequences between years, with a higher presence of repeated call sequences in 2013 and lower in 1999 (Figure 4). The prevalence of repeated call sequences was not strongly related to calf number, presence of other delphinids, sea state or time of day (Figures 3 and 5).

Repeated call sequence presence/absence model

The final model chosen included behavioural state, group size, year nested within site (Tables 2 and 3), matching the results of the exploration of the larger data-set. Time of day, number of calves, sea state and the presence of other odontocete species were excluded from the final model.

Discussion

Repeated call sequences make up a substantial portion of the known long-finned pilot whale vocal production, with this study showing that these sequences are present in over fifty

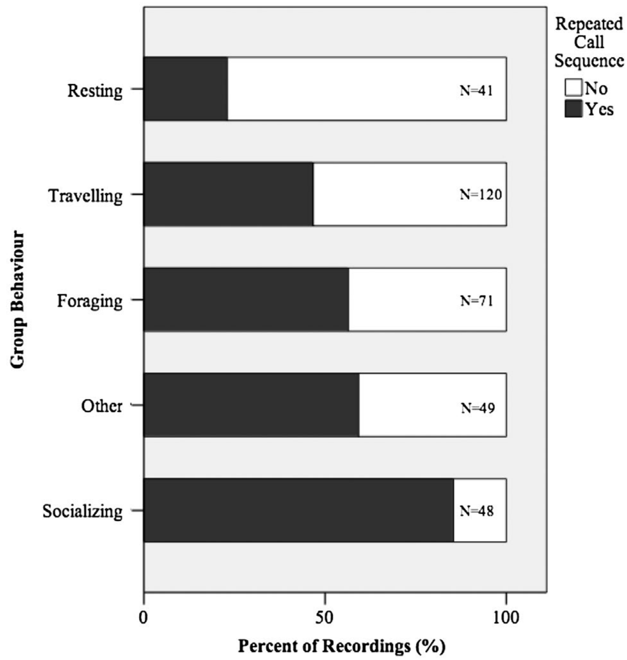

Figure 2. Per cent of recordings of long-finned pilot whales for each behavioural type that had repeated call sequences present ($N = 329$).

per cent of recordings collected off Cape Breton, Nova Scotia. There has been no prior contextual description of these vocal repetitions in this species. Analysis of the social, behavioural and environmental data collected alongside the recordings showed that group behavioural state, group size and year are predictors of the presence of repeated call sequences, while time of day, sea state, calf presence and other delphinid species present were not.

Possible functions of calls repeated in sequence

In Table 4, we suggest expected trends in the rates of production of repeated call sequences with context for potential functions. These functions are not necessarily mutually exclusive. The results are consistent with those that would be expected if the calls within these sequences were to serve as identifiers, showing a strong link between the presence of repeated call sequences and group behaviour. Resting pilot whales are often found stationary at the surface in close proximity to the other members of their group where identification would likely not be necessary, but when whales are socializing it would likely be more important to know identity for the many interactions, and sometimes joining of groups, that occur during this behavioural state. There would also be an increased need for identification with an increased groups' size, especially on the individual level (Bradbury & Vehrencamp 2011; Tyack 2000). The framework of this study does not allow for the differentiation between individual and group identifiers, and as such we will discuss them together. Sayigh et al. (2013) suggested that calls within repeated sequences in short-finned pilot whales off the Bahamas may represent individual identification akin to signature whistles found in other delphinid species, but their study itself was inconclusive about function. However, in contrast to the

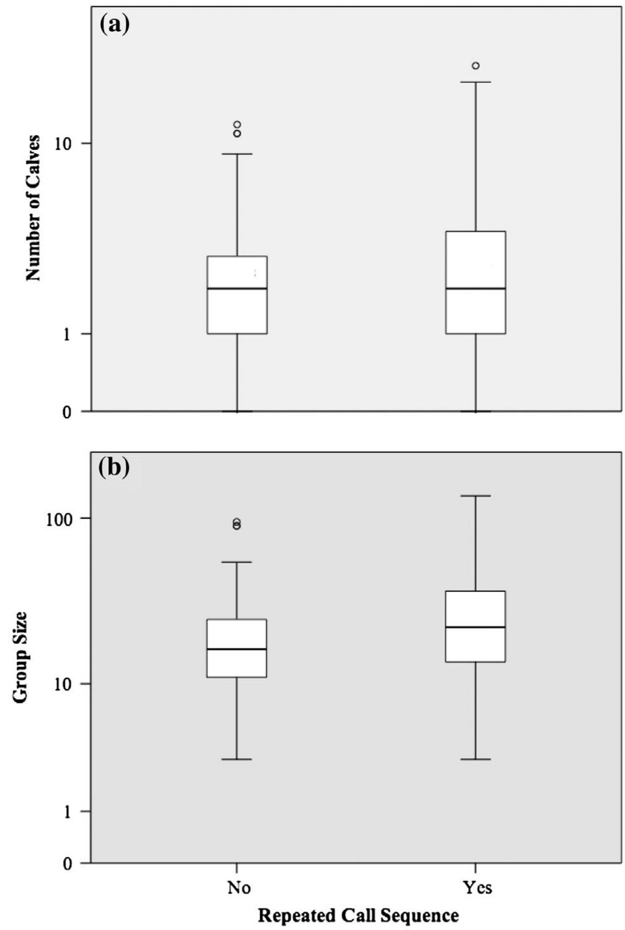

Figure 3. (a) Number of calves under the age of three in group and (b) size of group of long-finned pilot whales in relation to the presence ($N = 171$) and absence ($N = 158$) of repeated call sequences.

fission–fusion social organization of many dolphins that have signature whistles, long-finned pilot whales live in long-term social units consisting of approximately 11–12 individuals, which associate forming larger ephemeral groups (Ottensmeyer & Whitehead 2003). Is it thought that these units represent matrilines, perhaps with neither male nor female offspring leaving their natal group (Connor et al. 1998), suggesting that these calls could serve a unit-specific identification function like the those produced in other matrilineal species such as "resident" killer whales (Ford 1989) or sperm whales (Gero et al. 2016). Initial exploration of long-finned pilot whales pulsed calls showed possible group-specific characteristics, but this has yet to be investigated further and to date there is currently no concrete evidence of group-specific call types (Nemiroff 2009). With a socially complex society where individuals form stable long-term groups, identifiers either on an individual or group level are likely to be desirable. The question remains as to whether the repeated calls found in sequences are identifiers for long-finned pilot whales, or whether other parts of their vocal repertoire serve this role. Further studies categorizing these calls within repetitions for specific repeatedly

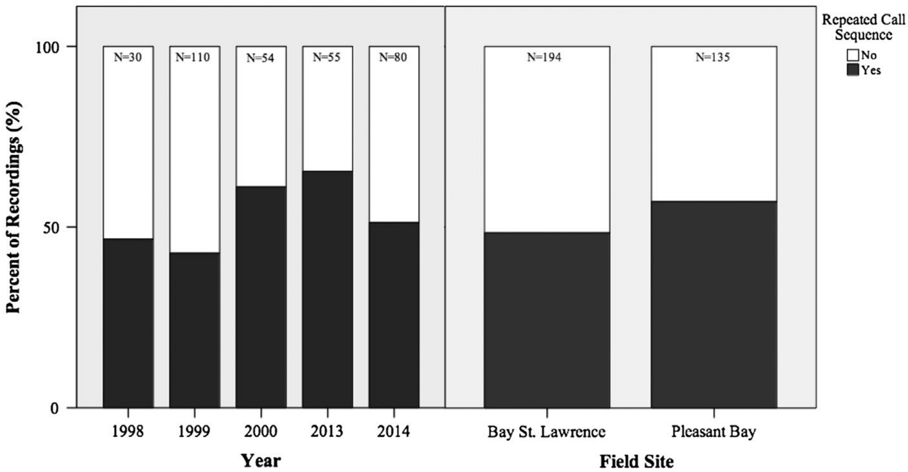

Figure 4. Year of study and field site in relation to whether repeated call sequences were present for long-finned pilot whales ($N = 329$).

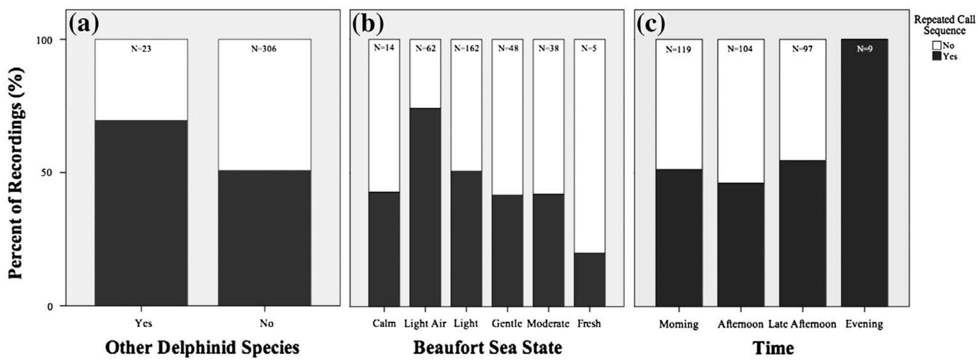

Figure 5. Per cent of recordings of long-finned pilot whales with repeated call sequences for (a) the presence and absence of other delphinid species, (b) each Beaufort Sea State with the following categories with corresponding Beaufort numbers: Calm (0), Light Air (1), Light Breeze (2), Gentle Breeze (3), Moderate Breeze (4), Fresh Breeze (5) and (c) each time of day binned into morning (10:00–13:00), afternoon (13:00–16:00) late afternoon (16:00–19:00) and evening (19:00–22:00) ($N = 329$).

Table 2. Manual backwards stepwise selection for repeated call sequence presence (REP) binomial generalized linear model with AICc values using predictors of group behaviour (GB), group size (GS), time of day (TD), number of calves under three years of age (CN), sea state (SS), presence of other delphinids (OD) and year nested within site (Y(S)).

Step	Model	AICc	Δ AICc
1	REP ~ GB + GS + TD + CN + SS + OD + Y(S)	255.18	16.73
2	REP ~ GB + GS + CN + SS + OD + Y(S)	250.20	11.74
3	REP ~ GB + GS + SS + OD + Y(S)	247.99	9.54
4	REP ~ GB + GS + OD + Y(S)	240.26	1.81
5	REP ~ GB + GS + Y(S)	238.45	0.00
6	REP ~ GB + GS	238.62	0.16

Table 3. Summary of final binomial generalized linear model predictors for the presence of repeated call sequences in long-finned pilot whales with the null hypothesis being that there are no differences in repeated call presence between different behavioural and environmental contexts ($N = 182$).

Parameter	Coefficient	*p*-value
Group Behaviour**		0.034
Socializing	1.20	0.059
Other	0.18	0.766
Foraging	0.52	0.261
Travelling	0.00	
Resting	−0.79	0.124
Group Size**	0.03	0.011
Year (Site)*		0.078
1998	−0.60	0.410
1999	−0.84	0.097
2000	0.06	0.920
2013	0.57	0.277
2014	0.00	

Note: *Significant at $p < 0.10$; **significant at $p < 0.05$.

Table 4. Potential functions of repeated call sequences along with whether a positive (↑), negative (↓),or unknown (↓↑), or no effect (-) relationship of repeated call sequences would be expected for each predictor, and the results of the model of the collected data.

Predictor	Identifier	Mother-Calf	Cohesion	Model
Resting	↓	↓	↓	↓
Travelling	↓↑	↓↑	↓↑	–
Foraging	↓↑	↓↑	↓↑	–
Socializing	↑	↓↑	↑	↑
Group Size	↑	–	↑	↑
Calf Number	–	↑	–	–
Other Delphinids	↓↑	↓↑	↓↑	–
Sea State	–	↑	↑	–
Time of Day	↓↑	↓↑	↓↑	–
Year (Site)	↓↑	↓↑	↓↑	–

encountered groups are needed to determine whether these calls may function in identification and whether this would be at an individual or group level.

Our data did not support the hypothesis that repeated call sequences primarily function in mother–calf relationships – either for maintaining contact between a calf and its mother through reciprocal vocalizations or these vocal repetitions being specifically made by either calves or their mothers – as the number of calves in a group had no effect on whether these vocal repetitions were present. Research on infant pygmy marmosets (*Cebuella pygmaea*) showed a form of "infant babbling" in which certain call types were repeated many times, while mature individuals in this species may make the same call only once or twice in sequence (Elowson et al. 1998). These calls were likely both important in the process of vocal development and essential for attracting the attention of the caregiver. In cetaceans, beluga (*Delphinapterus leucas*) calves show the same babbling characteristics during vocal development (Vergara & Barrett-Lennard 2008). In long-finned pilot whales, the calves stay with their mothers for many years, perhaps even both sexes remaining for life in this matrilineally based species (Connor et al. 1998). Because the number of calves in a group does not affect the presence or absence of these vocal repetitions, it does not support the function of these repeated call sequences being primarily about mother–calf relationships. It is possible that mother–offspring contact calls are not part of these repeated call sequences, but take another form such as the low-frequency pulsed calls produced by beluga calves (Vergara & Barrett-Lennard 2008).

The calls within repeated sequences could also function as a form of contact call, a hypothesis which is also supported by the results of this study. The repeated sequences were made with higher frequency when whales were socializing, at moderate frequency when foraging and travelling, and at low frequencies when resting. This pattern supports their role in group coordination and cohesion, since socializing involves many interactions and pilot whale social gatherings, sometimes involving hundreds of whales, can often create an apparently chaotic social environment. Resting whales are often grouped closely at the surface and would have little need of maintaining contact between whales already within visual distance who are not actively changing locations. Directionality found in the upper frequency component of killer whale repeated calls that are biphonated – having both an upper and lower frequency component produced simultaneously – supports the theory that these calls may function in cohesion and coordination (Miller 2002). Similarly, pilot whales also use biphonated calls (Nemiroff 2009), which are found in many of the repeated call sequences they produce. Group size was also found to influence the presence of these repeated call sequences, which makes sense as more individuals means there would be a greater need for coordination, identification and other potential functions that these calls may have (Bradbury & Vehrencamp 2011), as well as there being more individuals to produce them. In addition to short-term cohesion, rhythmic repeated call sequences might also function in long-term social bonding amongst the stable long-term units of pilot whales, as has been suggested for overlapping and matching vocalizations in sperm whales (Schulz et al. 2008).

It is possible that the calls within repeated sequences could have multiple functions. Many contact calls have been found to also contain information on sender identity, which is especially important in ephemeral groups as individuals need to determine the identity of others as well as advertise their own (Kondo & Watanabe 2009). This is likely the case for bottlenose dolphins, who use signature whistles more frequently during socializing (Quick & Janik 2008) and separation (Janik & Slater 1998) than other contexts suggesting that they also are important not only for identity, but also for cohesion and coordination within a group.

In addition to these inferences about function, the analysis of presence and absence revealed other attributes of repeated call sequences. Time of day was not indicated as a significant predictor, suggesting that pilot whales do not have a diel pattern associated with calls repeated in sequences, as has been found for specific types of calls for some other cetacean species (Risch et al. 2013). These patterns are often related to the behavioural context of the specific sounds, as is shown in studies of both echolocating odontocetes (Carlstrom 2005; Soldevilla et al. 2010) and calling blue whales (*Balaenoptera musculus*) that showed diel patterns in these vocalizations related to foraging behaviours (Wiggins et al. 2005). However, our research only covers daylight hours and a more comprehensive study including the nocturnal activities of this species will have to be conducted to determine if there are larger scale diel patterns present. Sea state and the presence of other delphinids were also not determined to be important predictors of repeated call sequences in pilot whales. Year nested within site was included in the final model, but the model without this term is also well supported, as it was not a strong predictor of sequence presence. The inclusion of year as a predictor may hint towards other important factors, perhaps environmental drivers such as regional productivity and climate change, which were not included in the model.

The repetitive nature of calls in sequence

Regardless of the function of pilot whale calls repeated in sequences, the recurrent nature of the vocalizations themselves is striking. Repetition may be a measure to reduce signal masking due to background noise or the calling of others (Brumm & Slater 2006). In very vocal, group-dwelling species like pilot whales, this would seem a useful strategy to make sure one's voice is heard. It could also be that some of these sequences are the result of a form call-matching between two or more pilot whales, or perhaps even a type of rhythmic duetting, as is found in other species (Deecke et al. 2000; Miller et al. 2004; Schulz et al. 2008). There is evidence for call-matching in cetaceans being used as a means of contact between individuals that are not within sight of each other (Miller et al. 2004) leading to a potential purpose for the repeated call sequences found in pilot whales in maintaining group contact and cohesion. These sequences may also allow the whales receiving the calls to estimate the approximate location of the calling whale as has been found in other species (Naguib & Haven-Wiley 2001; Miller 2002; Miller et al. 2004).

Future directions and summary

The resolution of only using basic behavioural states and working with groups instead of individual whales limit our knowledge of the specific contexts in which these repeated call sequences take place and the evaluation of alternate functions. The definition of 'travelling' in this study included both groups of whales travelling in a tight configuration with a pace barely above the vessel's idle speed and groups moving fast (20 km/hr) and spread out over hundreds of meters. If repeated call sequences function in maintaining contact and cohesion within a group, it would be expected that there would be few of them heard in the former situation and more in the latter. Similarly, contact calls would seem to be most necessary when animals regroup after a dive while foraging, but perhaps not as important when everyone is down feeding. Future studies of the behavioural context of focal individuals relative to their production of repeated call sequences would give us a better understanding of the function of these vocal repetitions. In addition to this, localization of a calling individual's respective position within a group could be used to further study the context of specific vocalization types in free-ranging pilot whales. In conclusion, repeated call sequences in long-finned pilot whales likely function as either identifiers, contact calls, or both. However, this study does not support mother–offspring communication as the main function of these vocal repetitions.

Acknowledgements

We would like to thank all the past graduate students, research assistants and volunteers for helping to collect and organize the data used in this study, as well as the captain and crews on both whale-watching vessels, the *Double-Hookup* (Captain Mark's Whale and Seal Cruise) and *Northern Gannet* (Captain Cox's Whale Watch), for facilitating our field work. We thank Andy Horn and Laura Feyrer for manuscript comments. Thanks also to the Natural Sciences and Engineering Research Council of Canada (NSERC) for providing us with the funds needed to conduct fieldwork. Finally, we would like to thank both NSERC (graduate scholarship) and the Dr. Patrick Lett Fund for financial support for E.Z.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) [grant number RPGIN\06534-2014].

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