



Evidence for the functions of surface-active behaviors in humpback whales (*Megaptera novaeangliae*)

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ABSTRACT

As part of their social sound repertoire, migrating humpback whales (*Megaptera novaeangliae*) perform a large variety of surface-active behaviors, such as breaching and repetitive slapping of the pectoral fins and tail flukes; however, little is known about what factors influence these behaviors and what their functions might be. We investigated the potential functions of surface-active behaviors in humpback whale groups by examining the social and environmental contexts in which they occurred. Focal observations on 94 different groups of whales were collected in conjunction with continuous acoustic monitoring, and data on the social and environmental context of each group. We propose that breaching may play a role in communication between distant groups as the probability of observing this behavior decreased significantly when the nearest whale group was within 4,000 m compared to beyond 4,000 m. Involvement in group interactions, such as the splitting of a group or a group joining with other whales, was an important factor in predicting the occurrence of pectoral, fluke, and peduncle slapping, and we suggest that they play a role in close-range or within-group communication. This study highlights the potentially important and diverse roles of surface-active behaviors in the communication of migrating humpback whales.

Key words: humpback whale, *Megaptera novaeangliae*, surface-active behavior, function, surface behavior, breach, fluke slap, peduncle slap, head lunge, pectoral slap.

Many animals living in the marine environment have adapted their communication to optimize successful transmission of signals underwater. Visual communication, particularly in deeper waters with restricted light penetration, is limited except

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in some clear shallow water environments (Richardson *et al.* 1995). In contrast, sound travels much more efficiently in water than in air as it loses comparatively less energy with distance (Richardson *et al.* 1995). As a result, sound is used by many marine animals to communicate and its use is well documented in the literature. For example, the acoustic signal repertoire of killer whales (*Orcinus orca*) includes pulsed calls and whistles (Ford 1989) and it has been suggested that some of these signals function to maintain contact and coordination within groups during close-range interactions (Ford 1989, Thomsen *et al.* 2001, Miller 2002). Similarly, it has been proposed that the signature whistles of bottlenose dolphins (*Tursiops truncatus*) are used to facilitate reunions between separated mothers and calves over small spatial scales (Smolker *et al.* 1993). On the other hand, other marine mammals may communicate over long ranges with the sounds they produce audible many kilometers from the source (Herman and Tavolga 1980). Male fin whales (*Balaenoptera physalus*), for example, produce long, patterned vocalizations thought to function over great distances as a male breeding display (Richardson *et al.* 1995, Croll *et al.* 2002). Leopard seals (*Hydrurga leptonyx*) use two distinctively different types of sounds, one for close-range interactions and one as a longer-range broadcast sound (Rogers *et al.* 1996). Consequently, it appears that marine mammals' acoustic communication may vary in function from long-distance broadcast signals to short distance within-group displays.

Humpback whales (*Megaptera novaeangliae*) are found in all oceans of the world (Clapham and Mead 1999). They use both vocally and nonvocally produced sounds as part of their acoustic communication (Payne and McVay 1971, Thompson *et al.* 1986). Humpback whale song is a complex, highly structured, and stereotyped vocal signal produced only by males and is thought to function as a sexual display (Payne and McVay 1971, Tyack 1981, Clapham 1996). This song is audible over large distances (Payne and McVay 1971) and singing whales have been acoustically tracked at ranges greater than 10 km (Frankel *et al.* 1995, Noad *et al.* 2004, Noad and Cato 2007). Social sounds, on the other hand, lack the continuous pattern of song, are produced by males, females, and calves, and are heard in many different social and environmental contexts (Silber 1986; Dunlop *et al.* 2007, 2008; Zoidis *et al.* 2008; Stimpert *et al.* 2011). The social sound repertoire of humpback whales also includes nonvocal sounds generated by surface-active behavior (Dunlop *et al.* 2007, 2010). Although the function of song has been studied extensively, the functions of social sounds are less well understood, particularly those produced as a result of surface-active behavior.

Humpback whales are one of the most surface-active of the baleen whales. Their behavioral repertoire is extensive and includes energetic leaps as well as the repetitive slapping of a pectoral fin or flukes on the water surface (Whitehead 1985, Corkeron 1995, Deakos 2002). These surface-active behaviors are thought to be part of the communication repertoire of these animals due to the audible sound made by the splashing on the surface of the water (Whitehead 1985, Deakos 2002, Dunlop *et al.* 2008). More specifically, a number of potential functions for these behaviors have been hypothesized. It has been proposed that they play a role in maintaining contact between groups (Payne and McVay 1971) and in communication within groups (Dunlop *et al.* 2008). Surface-active behaviors may also be involved in initiating or mediating social interactions (Deakos 2002, Dunlop *et al.* 2008) as they have been observed during group affiliations and disaffiliations (Baker and Herman 1984). In a more general sense, it has been suggested that breaching accentuates other forms of communication in whales and is used as a "physical exclamation point" (Whitehead

1985). However, these behaviors occur in a variety of social and environmental contexts, making it challenging to determine their specific functions. In addition, surface-active behaviors are performed by humpback whales of all sexes and in many different social contexts and as a result they probably have several functions, at least on breeding grounds (Whitehead 1985).

Surface-active behaviors are regularly observed during humpback whales' migration. Whales migrate annually between feeding grounds in high latitude waters and breeding grounds in tropical waters, a one-way trip of up to 8,000 km (Chittleborough 1965, Dawbin 1966, Clapham and Mead 1999, Stone *et al.* 1990, Rasmussen *et al.* 2007). They are believed to fast for the majority of these extended journeys and on breeding grounds, although there is evidence that individuals from some populations make feeding stop-overs (Stone *et al.* 1987, Best *et al.* 1995, Stamation *et al.* 2007, Owen *et al.* 2016). Although migrating individuals are usually fasting, the surface-active behaviors they perform appear highly energetic and successive bouts of these behaviors potentially require considerable amounts of energy (Whitehead 1985). The fact that they are performed extensively during the migratory period and on the breeding grounds, when animals would be expected to be conserving their energy, suggests that they may play an important role in the communication repertoire of humpback whales.

Our study site at Peregrine Beach, Queensland, Australia, offers a rare opportunity to study the behavior of humpback whales in a variety of social and environmental contexts in order to tease apart the different functions of their surface-active behaviors. The aims of this study were therefore (1) to determine how changes in social and environmental factors correlate with the use of particular surface-active behaviors by migrating humpback whales, and (2) to infer the functions of these behaviors based on the results. Whales at this site were migrating south from the breeding grounds and have previously been recorded exhibiting many of the behaviors also observed on the breeding grounds (Brown and Corkeron 1995, Frankel *et al.* 1995, Noad 2002, Smith *et al.* 2008, Kavanagh 2014). Therefore, we hypothesized that these surface-active behaviors are primarily influenced by social factors and have a social function.

METHODS

Study Site

This study was carried out as part of the baseline research for the "Behavioral Response of Australian Humpback whales to Seismic Surveys" project (BRAHSS) (Cato *et al.* 2013). Data were collected at Peregrine Beach (26°30'S, 153°05'E) on the east coast of Australia (Fig. 1) during September and October in 2010 and 2011. The group E (i) breeding stock of humpback whales migrates annually along the east coast of Australia (Chittleborough 1965, Bannister 2005). Their southward migratory route involves a large proportion of the population traveling within 10 km of the shore along parts of the coast including at Peregrine Beach, 130 km north of Brisbane (Noad *et al.* 2004). At this site there are elevated land-based locations close to the shore, from which whales could be observed without the added disturbance of a research vessel. These factors made this an ideal location from which to study the natural behavior migrating humpback whales. For this study, data were collected from two land-based locations: (1) North Station, the balcony of an apartment building 8.6 km north of the base station at Peregrine Beach (30 m above sea level, 30 m from

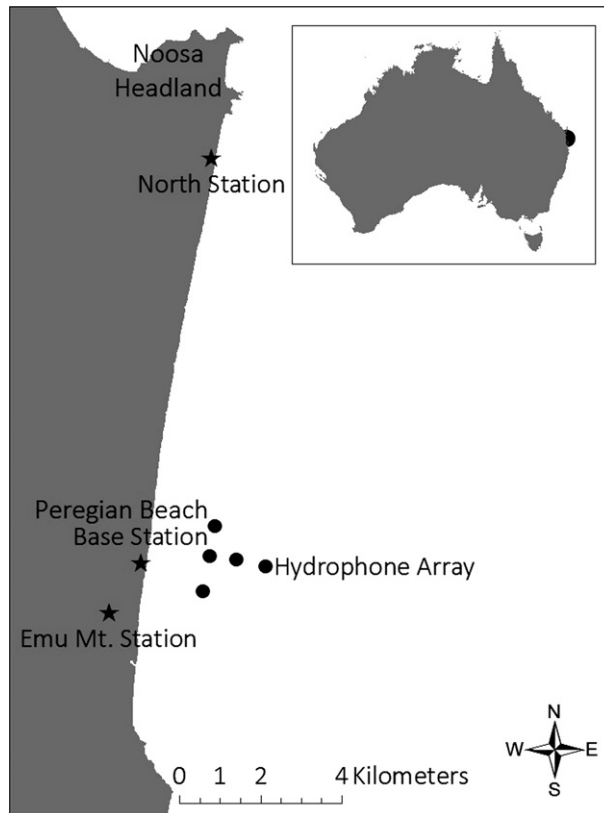


Figure 1. The study site at Peregian Beach on the Sunshine Coast of Eastern Australia. Land-based observations stations (Emu Mt. and North Station) and the location of the hydrophone array and the base station where signals from the array were transmitted are indicated.

the coast), and (2) Emu Mt. Station, the peak of Emu Mountain, 3 km south of Peregian Beach (73 m above sea level, 700 m from the coast). Both stations had unobstructed views over the sea, although the North Station's view to the north was partially restricted by Noosa headland (Fig. 1).

Data Collection

Prior to the commencement of the data collection period all observers underwent two weeks of intensive training to ensure each was proficient in the behavioral data collection methodologies used in this study. Observer proficiency was tested in a simultaneous study and, with the training provided, observer experience did not have a significant effect on the reliability and validity of the behavioral data they collected (Kavanagh *et al.* 2016).

Behavioral data on a focal group of whales were collected using a detailed ethogram (Appendix S1) and a focal sampling method (Altmann 1974, Mann 1999, Martin and Bateson 2010). We defined whales as a group if they surfaced synchronously

within 100 m of one another (Whitehead 1983, Corkeron 1995). We recorded the location of a focal group at every surfacing and the timing of every behavior observed from the group (behavior categories examined in this study are listed in Table 1). The group composition, *i.e.*, the number and type of animals in the focal group, and the occurrence of any group interactions, *i.e.*, when the focal group split or joined with another group, were also recorded (definitions in Table 2). Although a focal group of whales could be tracked successfully, data were collected for all animals in the group, as individual whales within a group were not readily identifiable from the land-based survey stations through successive dives. The average distance of the focal groups offshore was 5 km. Therefore, the majority of groups were readily identifiable through successive dives by comparing speed and course, group composition, and behavior of a group between each dive using data stored in the tracking software VADAR (Visual and Acoustic Detection and Ranging, developed by and available from EK).

Behavioral data were collected continuously between 0700 and 1700 throughout the field season. Multiple teams of observers worked in shifts of no longer than 3 h at a time to achieve continuous data collection and to reduce the potential for observer fatigue. At any one time, two focal observation teams were located at each of the two land stations. Initially each of the four teams followed a separate group of whales. When a southbound group being followed by a North Station team was deemed to be mid-way between the two stations the group was passed onto an Emu Mt. team who dropped their group in order to continue to follow the North Station's group. The "handover" of groups between the North and Emu Mt. teams was facilitated by using UHF radios to communicate between observation stations. In addition, the VADAR tracking software used by each team was networked, allowing the teams at the North Station to see the observations recorded by the teams at the Emu Mt. Station and *vice versa* (tracking software is described below). This feature increased the ease and accuracy with which a group of whales could be handed over between stations, allowing them to be tracked for longer periods of time and over greater distances. During handover both teams (North and Emu Mt.) followed the focal group for a period of up to 30 min to ensure no behaviors were missed and to maintain the

Table 1. Behavior categories.

Behavior category	Behaviors	Definition
Breaching	Breach Half breach	A leap in which a proportion of the whale's body exits the water. The whale usually, but not always, twists in the air and lands on its dorsal or lateral aspect.
Head lunging	Head lunge	A leap in which a proportion of the whale's body exits the water with an energetic forward motion.
Fluke slapping	Fluke slap Inverted fluke slap	The entire fluke is raised out of the water and forcibly slapped against the water surface.
Peduncle slapping	Peduncle slap Peduncle throw	The entire fluke and peduncle are raised out of the water and forcibly slapped or thrown against the water surface
Pectoral slapping	Pectoral slap Inverted pectoral slap Bilateral pectoral slap	One or both pectoral fins are raised out of the water and forcibly slapped against the water surface.

Table 2. Predictor variables included in behavior models. The baseline categorical predictor variables are indicated with an asterisk (*).

Category	Variable	Description
Social context	Comp	The group composition.
	Group interaction	Involvement in an interaction with another group.
	Near group	Distance to the nearest group of whales within 10 km.
	No. of groups	The number of whale groups within 10 km.
	Near singer	Distance to the nearest singing whale within 10 km.
Environmental context	No. of singers	The number of singing whales within 10 km.
	Wind speed	Wind speed in km/h.
	Water depth	Water depth in meters.
	Distance shore	The distance in meters from shore to the group of whales
Compositions:		
Adults only (groups containing two adults only).		
Lone animals (groups containing a single adult).		
Female/calf* (a calf and a single adult, presumed to be a female).		
Female/calf/escort (a calf and two adults; a female and an escort).		
Female/calf/multiple escorts (a calf and multiple adults; a female and two, three, or four escorts).		
Multiple female/calf pairs (multiple female/calf pairs, with or without a single escort).		
Group interaction:		
Stable* (group not in the process of splitting or involved in joining with another group).		
Pre-/post-join (the 10 min period before or after a join was noted).		
Pre-/post-split (the 10 min period before or after a split was noted).		
Distance to nearest group or singer:		
Within 1,000 m, 1,000–2,000 m, 2,000–4,000 m and beyond 4,000 m.*		
Number of groups: 0, 1, 2, 3, 4, or 5+ whales within 10 km of the focal group.		
Number of singers: 0, 1, or 2+ singing whales within 10 km of the focal group.		

continuity of the track. This allowed the maximum number of individual groups to be followed accurately and handed over between stations. Focal follows varied in length depending on whether they were tracked by a single station or passed from a North to an Emu Mt. team. In the latter case, continuous focal follows of up to seven hours were sometimes possible. Whales were followed at distances of up to approximately 15 km from the observation stations, dependent on the weather conditions (factors such as the level of glare, haze, and sea state reduced visibility).

Each focal team consisted of three people: a theodolite operator, a computer operator, and a spotter. The theodolite operator used a surveyor's theodolite to (1) track the movements of whales by taking a fix on a focal group at each surfacing, and (2) observe the behavior of each animal in the focal group. Information from the fix was transmitted directly to a laptop computer running the software VADAR that automatically calculated the positions of whales using information from the theodolite's height above sea level, and the angle of elevation and azimuth of the whale. Data were processed by the program in real time and positions were displayed on the laptop screen allowing the computer operator to maintain a visual track of the whales. Along with accepting theodolite positions, the computer operator also recorded the behavioral data and information on group composition called out by the theodolite operator. The spotter, equipped with a pair of compass reticule binoculars (Kinglux waterproof 7 × 50), aided the theodolite operator in locating groups of whales upon

surfacing, taking rough positions (using compass and reticules to give the angle to the horizon) and calling out behaviors observed when necessary.

Social Context Data

Social context was described in four ways: The focal teams recorded (1) the composition of the focal group and (2) whether the focal group was involved in a group interaction, while the additional data platforms recorded (3) the presence of other groups in the area and (4) the presence of singers in the area. If a focal group was joined by another group during the course of a follow behaviors from all whales in the newly formed group were recorded and the new composition was noted. If a focal group split during the course of a follow only one of the two new groups continued to be tracked; generally, the group containing the larger number of animals was selected for continued focal follow.

Data on the presence of other groups were collected simultaneously with focal data by a fifth team of observers (referred to as the scan platform), located at the Emu Mt. Station. They recorded the locations and behaviors of all groups of whales within approximately 20 km of the Emu Mt. Station each time they surfaced, using *ad libitum* sampling (Altmann 1974, Mann 1999, Martin and Bateson 2010). This enabled the distance to the nearest whale group and the number of groups within 10 km to be calculated for each focal data observation. Distance to the nearest group was categorized for analysis as within 1,000 m, 1,000–2,000 m, 2,000–4,000 m, and beyond 4,000 m (Table 2).

The time spent submerged by singing whales can be much longer than for non-singers (Whitehead 1981) and therefore they can be difficult to track from land-based locations. For this reason, five acoustic buoy systems were deployed in a T shape configuration in the center of the study site in 18–25 m of water (Fig. 1, Noad *et al.* 2004). Singing whales were tracked using the acoustic data recorded by these buoys and the acoustic analysis software *Ishmael* (Mellinger 2001). All acoustic recordings were made simultaneously with the land-based observations in the field and plotted by VADAR. This allowed groups containing singers to be identified and the distance to the nearest singer and the number of singers within 10 km to be calculated for each focal observation. Distance to the nearest singer was categorized for analysis as within 1,000 m, 1,000–2,000 m, 2,000–4,000 m, and beyond 4,000 m (Table 2).

Environmental Context Data

Weather conditions were obtained from the Australian Bureau of Meteorology automatic weather station at the Sunshine Coast Airport approximately 10 km south of the study site and within 1 km of the sea. Data on wind speed (km/h), wind direction (degrees), and wind gusts (km/h) were recorded half-hourly throughout the field seasons. Wind speed was selected as one of the environmental context variables because of the good correlation between noise from the sea surface and wind speed (Wenz 1962), and because wind-dependent noise is the main source of ambient noise at the site in the frequency range of the whale sounds (Dunlop *et al.* 2010). Bathymetry data on water depths in the study site (Beaman 2010) and coastline data, with distances to shore (data derived from the State of Queensland, Department of Environmental and Resource Management 2013), were also added to the data set using ArcGIS 10.0 (ESRI 2011). Spatial data were imported using the WGS1984 datum and reprojected into a projected coordinate system (transverse Mercator using

UTM Zone 56S, WGS1984 datum) for the purpose of measuring distances between objects and events.

Data Processing

Surface-active behaviors (definitions available in Appendix S1) were grouped into five behavior categories: (1) breaching, (2) head lunging, (3) pectoral slapping, (4) fluke slapping, and (5) peduncle slapping (Table 1). Focal follows were divided into 10 min time bins and for each time bin the presence/absence of each behavior category was noted using a 1 (presence) or 0 (absence). Ten minutes was chosen to ensure that most time bins contained at least one complete dive cycle (the mean length of a dive cycle, a long dive followed by its subsequent surfacing event, was $6.2 \text{ min} \pm 4.3 \text{ SD}$) (Kavanagh 2014).

Context data were either averaged across a time bin for discrete predictors (number of singers within 10 km of the focal group, number of groups within 10 km of the focal group) and continuous predictors (water depth), or the initial observation for a time bin was used for categorical predictors (group composition, group interaction, and the distances to the nearest group or singer).

Data on wind speed were available half-hourly from the weather station. All data were examined for sightability bias associated with wind speed, as well as distances both from the location of the team who recorded the focal follow and from the scan observation team who collected the social context data. Due to reduced sightability of groups with increased distance, "sightability cutoffs" were applied to the data used in this analysis. Cutoffs were based upon preliminary analysis of the raw data used in this study (where the number of behaviors recorded by land-based observers *vs.* distance from the survey platform and wind speed were examined). This indicated that behaviors were being missed beyond 15 km or in wind speeds above 30 km/hr. These results agreed with analysis carried out by Dunlop (2016) at the same study site. Therefore, conservative sightability cutoffs were applied to the sightings data (12 km from the focal platform, 10 km from the scan platform, 30 km/h wind speeds) to minimize potential bias. For the social context data collected by the scan team of observers located at the Emu Mt. Station only focal groups found within 10 km of this station were included in the analysis. Finally, any focal groups deemed to contain a singing whale were also omitted from analysis as the effect of the presence of a singer nearby, but not in the group, was one of the factors we wished to examine.

Statistical Analysis

All statistical analyses were carried out in R v3.0.1 (R Core Team 2013). Mixed effects models were used as repeated measures were taken on the same group of whales. The ID of each group of whales was included as a random effect in the model. Nine predictor variables (Table 2) were selected with which to model humpback whale behavior (following recommended modeling methodology in Burnham and Anderson 2002).

Overall collinearity was assessed and correlated predictor variables were identified using the generalized variance inflation factor ($\text{gvif}^{(1/2 \text{ df})}$), in the *car* package of R (Fox and Weisberg 2011). Variables with a $\text{gvif}^{(1/2 \text{ df})}$ value greater than, or close to 2 were removed in order of decreasing magnitude until a subset of variables remained that showed no indication of collinearity. A separate global mixed effects model was then carried out for each response variable (each behavior category) with the remaining

uncorrelated predictor variables using the *glmer* function in the *lme4* package in R (Bates *et al.* 2015). The residuals of each global model were evaluated for heterogeneity, auto-correlation, and overdispersion.

To assess the evidence for the different predictor variables included in a model, an all-subsets model selection method was carried out following Burnham and Anderson (2002) and using the *MuMIn* package in R (Barton 2013). Models were ranked according to their Akaike information criterion (AIC) values and a confidence set of models was chosen; the selected models were those with ΔAIC values < 2 (Burnham and Anderson 2002). Akaike weights for each model in the confidence set were calculated, *i.e.*, the weight of evidence in favor of a model (Burnham and Anderson 2002, Zuur *et al.* 2009). The relative importance of each predictor variable (relative to other variables in the confidence set of models) was calculated by summing these Akaike weights for all confidence set models containing them (Burnham and Anderson 2002). If a predictor variable did not occur in any of the confidence set of models its relative importance value was zero. Evidence ratios, which provide information on the support of evidence in favor of one model relative to another, were calculated for the top two models for each behavior (Akaike weight of top model/Akaike weight of next best model) (Burnham and Anderson 2002, Zuur *et al.* 2009).

To account for model selection uncertainty and to obtain robust parameter estimates, a model averaging approach was taken (Grueber *et al.* 2011) and estimates were averaged over the confidence set of models (Burnham and Anderson 2002). Model averaged estimates, with standard errors, 95% confidence intervals, *z*-values and *P*-values are presented, and significance was set a $P < 0.05$. For each categorical predictor variable, a baseline category was chosen to which all other categories would be compared in the model (indicated in Table 2). The baseline for each categorical variable was chosen based on the question being posed in the study. Model averaged estimate values indicate the probability of observing a behavior (breach, head lunge, pectoral, fluke, or peduncle slap) as the value for a continuous predictor variable increases, or compared to the baseline (in the case of categorical predictor variables). Positive estimates indicate an increased probability; negative estimates indicate a decreased probability. Model averaged estimates were not calculated for predictor variables that did not occur in the confidence set of models. It is important to note that using this method it is possible that a categorical predictor may display a high relative importance value but show no significant result in the model averaged estimates, as these are dependent on the baseline chosen. Therefore, both the relative importance and model averaged estimate results should be considered in combination.

RESULTS

Overall, 202 h of focal follow data were collected comprising 94 focal follows ranging in length from 27 to 463 min. A total of 25 focal follows were collected during September/October in 2010 and 69 in the same period in 2011. After combining data into 10 min time bins then subsettings for sightability cutoffs and the presence of singers, 795 data points remained from 76 focal follows. Of these focal followed groups, 88% displayed surface-active behaviors. The sample size for groups containing singers was low. By removing groups containing singers, one entire focal follow and part of four others, a total of 30 observations, were omitted from the analysis. To ensure that the data were representative of natural behavior (and groups were not

influenced by vessel activity), focal follows where a recreational vessel came within 2 km in more than one consecutive time bin were excluded. As a result, no vessels were recorded within 5 km of the focal group for 75% of the time bins included in this analysis.

We found a high correlation between water depth and distance from shore (gvif of 1.9). Therefore, to reduce the effect of collinearity we removed distance to shore from further analysis as it had the highest gvif. The significant results for all models are summarized in Table 3. The confidence sets of models for breaching, head lunging, pectoral slapping, fluke slapping, and peduncle slapping contained between three and eight models each (Tables 4, 5). In all cases there was considerable model uncertainty with no evidence ratios above 2.3.

Breaching Behavior

Predictor variables wind speed, group composition, and the distance to the nearest group displayed the highest model averaged relative importance values (1.0) for breaching behavior (Table 4). Breaching was more commonly observed in windier weather conditions and from groups containing multiple calves (*i.e.*, multiple female/calf pairs) when compared to those containing only a single calf (*i.e.*, single female/calf pairs) (Table 6). The presence of conspecific groups was also an important predictor, with the probability of observing this behavior decreasing significantly when the nearest neighbor was within the 1,000–2,000 m and 2,000–4,000 m categories, compared to beyond 4,000 m (Table 6). The distance to the nearest singing whale was also found to be an important predictor of breaching behavior (model averaged relative importance value of 0.68, Table 4), however no significant result was found for the model averaged estimates (Table 6).

Table 3. Model results summary table; list of significant predictor variables with explanation of model averaged estimate results for each behavior category.

Behavior category	Significant predictor		Probability of observing behavior
Breaching	Composition	Increased	For groups containing multiple female/calf pairs when compared to single female/calf pairs
	Near group	Decreased	When the nearest neighbor groups was within 1,000–2,000 m and 2,000–4,000 m categories compared to beyond 4,000 m
Head lunging	Wind speed	Increased	As wind speed increased
	Water depth	Decreased	As water depth increased
Fluke slapping	Group interaction	Increased	During pre-join and post-split periods compared to stable periods
Peduncle slapping	Water depth	Decreased	As water depth increased
	Water depth	Decreased	As water depth increased
Pectoral slapping	Group interaction	Increased	During pre-split and post-split periods compared to stable periods
	Number of singers	Decreased	As the number of singers within 10 km of the focal group increased
	Wind speed	Decreased	As wind speed increased

Table 4. Confidence sets of models for breaching, and head lunging. Akaike weights for models in confidence sets indicated by ω . The model averaged relative importance for each predictor variable was calculated by summing the Akaike weights for all confidence set models containing them. A value of 1 indicates a variable is very important and occurred in all confidence set models, a value of 0 indicates a variable is unimportant and did not occur in the confidence set models. Plus signs (+) indicate the variables included in each model.

Model	Comp	Group interaction	Near group	No. of groups	Near singer	No. of singers	Wind speed	Depth	df	logLik	AICc	Δ AIC	ω
Breaching	+		+			+	+		12	-328.32	681.0	0.00	0.37
	+		+				+		11	-329.50	681.3	0.3	0.32
	+		+			+	+	+	13	-328.08	682.6	1.59	0.17
	+		+			+	+		13	-328.26	682.9	1.95	0.14
Model averaged relative importance	1	0	1	0.14	0	0.68	1	0.17					
Head lunging	+							+	8	-160.88	337.9	0.00	0.43
								+	3	-166.30	338.6	0.69	0.3
	+						+	+	9	-160.32	338.9	0.93	0.27
Model averaged relative importance	0.7	0	0	0	0	0	0.27	1					

Head Lunging Behavior

Both water depth and group composition had high model averaged relative importance values for head lunging behavior, 1.0 and 0.7 respectively (Table 4). However, only water depth displayed a significant result for model averaged estimates (Table 6). The probability of observing this behavior decreased as water depth increased, *i.e.*, it was more commonly observed in shallower waters.

Fluke Slapping Behavior

Group interaction and water depth had the highest model averaged relative importance values (1.0) for fluke slapping behavior (Table 5). Groups were more likely to be observed fluke slapping in the 10 min period prior to the focal group joining or being joined by another group (termed "pre-join") and in the 10 min period after the

Table 6. Model averaged estimates, with standard errors (SE), 95% confidence intervals (CI), *z* values and *P* values for breaching and head lunging models. Significant estimates are highlighted in bold. Estimates were only calculated for variables occurring in the confidence set of models of each behavior category (Table 4). Estimate values indicate the probability of observing a behavior as continuous predictor variables increase by one unit, or for the specified category of a categorical predictor variable when compared to the baseline category indicated (positive estimates indicate an increased probability, negative estimates indicate a decreased probability). There were no "Lone" animal samples for the head lunging analysis.

Model	Estimate	SE	Lower CI	Upper CI	<i>z</i>	<i>P</i>
Breaching predictor variables						
(Intercept)	-2.9	0.68	-4.26	-1.57	4.27	<0.001
Composition (relative to female/calf groups)						
Adults only	-1.56	1.03	-3.57	0.45	1.52	0.129
Lone animals	-0.36	0.90	-2.12	1.4	0.40	0.69
Female/calf/escort	-0.33	0.37	-1.06	0.4	0.89	0.375
Female/calf/multiple escort	-0.99	0.68	-2.33	0.35	1.45	0.148
Multiple female/calf pairs	2.47	0.77	0.96	3.98	3.2	0.001
Near group (relative to beyond 4,000 m)						
Within 1,000 m	0.35	0.44	-0.51	1.22	0.79	0.426
1,000–2,000 m	-0.71	0.35	-1.40	-0.01	1.99	0.047
2,000–4,000 m	-1.04	0.29	-1.61	-0.47	3.58	<0.001
Number of groups	0.005	0.04	-0.07	0.08	0.12	0.908
Number of singers	-0.23	0.24	-0.70	0.24	0.95	0.341
Wind speed	0.1	0.03	0.05	0.15	3.78	<0.001
Water depth	-0.004	0.01	-0.03	0.02	0.25	0.805
Head lunging predictor variables						
(Intercept)	1.38	1.07	-3.48	0.71	1.29	0.196
Composition (relative to female/calf groups)						
Adults only	-0.47	1.2	-2.82	1.88	0.39	0.696
Lone animals	—	—	—	—	—	—
Female/calf/escort	0.24	0.45	-0.65	1.13	0.53	0.56
Female/calf/multiple escort	-0.65	1.17	-2.95	1.65	0.56	0.579
Multiple female/calf pairs	1.47	1.16	0.8	3.74	1.27	0.205
Wind speed	0.009	0.02	-0.04	0.06	0.40	0.692
Water depth	-0.09	0.03	-0.17	-0.02	2.42	0.016

focal group split (termed “post-split”), when compared to stable periods when the group composition was unchanged (Table 7). Similar to head lunging, the probability of observing fluke slapping significantly decreased as water depth increased (Table 7). Although group composition displayed a high relative importance value for the fluke slapping model (0.77), model averaged estimates were not significant (Table 7).

Table 7. Model averaged estimates, with standard errors (SE), 95% confidence intervals (CI), *z* values and *P* values for fluke slapping, and peduncle slapping models. Significant estimates are highlighted in bold. Estimates were only calculated for variables occurring in the confidence set of models of each behavior category (Table 5). Estimate values indicate the probability of observing a behavior as continuous predictor variables increase by one unit, or for the specified category of a categorical predictor variable when compared to the baseline category indicated (positive estimates indicate an increased probability, negative estimates indicate a decreased probability). There were no “Near Singers Within 1,000 m” for the peduncle slapping analysis.

Model	Estimate	SE	Lower CI	Upper CI	<i>z</i>	<i>P</i>
Fluke slapping predictor variables						
(Intercept)	-0.64	0.96	-2.52	1.24	0.67	0.505
Composition (relative to female/calf groups)						
Adults only	-0.35	0.95	-2.21	1.52	0.37	0.715
Lone animals	-0.23	1.01	-2.20	1.75	0.22	0.824
Female/calf/escort	-0.02	0.42	-0.84	0.80	0.05	0.959
Female/calf/multiple escort	-0.97	1.21	-3.35	1.41	0.80	0.425
Multiple female/calf pairs	2.01	1.32	-0.58	4.60	1.52	0.127
Group interaction (relative to stable periods)						
Pre-join	2.08	0.63	0.84	3.31	3.29	0.001
Pre-split	1.01	0.82	-0.60	2.63	1.23	0.219
Post-join	1.09	0.85	-0.58	2.76	1.28	0.199
Post-split	1.69	0.74	0.23	3.14	2.27	0.023
Number of groups	-0.04	0.09	-0.22	0.13	0.49	0.628
Water depth	-0.10	0.03	-0.17	-0.03	2.88	0.004
Peduncle slapping predictor variables						
(Intercept)	-1.27	1.10	-3.42	0.90	1.15	0.249
Group interaction (relative to stable periods)						
Pre-join	0.69	0.78	-0.83	2.21	0.89	0.376
Pre-split	1.41	1.04	-0.64	3.45	1.35	0.178
Post-join	-0.22	1.02	-2.22	1.78	0.21	0.830
Post-split	-0.23	0.98	-2.16	1.70	0.23	0.818
Near group (relative to beyond 4,000 m)						
Within 1,000 m	0.03	0.29	-0.54	0.61	0.11	0.913
1,000–2,000 m	0.18	0.44	-0.68	1.05	0.42	0.676
2,000–4,000 m	0.05	0.21	-0.37	0.47	0.23	0.818
Near singer (relative to beyond 4,000 m)						
Within 1,000 m	—	—	—	—	—	—
1,000–2,000 m	0.01	0.43	-0.82	0.85	0.03	0.979
2,000–4,000 m	0.03	0.22	-0.40	0.45	0.14	0.893
Number of groups	-0.006	0.04	-0.09	0.08	0.13	0.898
Number of singers	-0.01	0.10	-0.20	0.18	0.11	0.913
Wind speed	0.002	0.01	-0.02	0.02	0.15	0.878
Water depth	-0.09	0.04	-0.16	-0.02	2.36	0.018

Peduncle Slapping Behavior

The predictor variables water depth and group interaction displayed high model averaged relative importance values for peduncle slapping behavior (1.0 and 0.73 respectively) (Table 5). However, only water depth displayed a significant model averaged estimate result (Table 7).

Similar to other surface-active behaviors, peduncle slapping was more commonly observed in shallower waters (*i.e.*, the probability of observing it decreased as water depth increased) (Table 7).

Pectoral Slapping Behavior

Both social and environmental variables were important predictors in the pectoral slapping model. Involvement in group interactions, group composition, the number of singers in the area, wind speed, and water depth all displayed high model averaged relative importance values (>0.75) (Table 5). Similar to fluke slapping, pectoral slapping was associated with the splitting of the focal group. However, for pectoral slapping this behavior was significantly more likely to be observed in both the ten minute periods before and after the focal group was observed splitting (termed pre-split and post-split) when compared to stable periods (Table 8). Pectoral slapping was the only surface-active behavior significantly influenced by a singer predictor variable. The probability of observing pectoral slapping behavior decreased significantly with increasing numbers of singers within 10 km (Table 8). Similarly, this behavior was the only one examined to be influenced by both environmental predictors examined. Model averaged estimates indicated a significant increase in the probability of observing pectoral slapping with increasing wind speed and a decreased probability of observing pectoral slapping as water depth increased, however, this result was just above the cut off value chosen for significance in this study (Table 8). Although the composition of the focal group displayed a high model averaged relative importance value, no significant result was found for the model averaged estimates (Tables 5, 8). As discussed in the methods section, it is possible that had a different baseline been chosen a significant result may have been found.

DISCUSSION

The results of our study suggest surface-active behaviors have multiple functions within the communication repertoire of migrating humpback whales. No variable examined was important in predicting the occurrence of all behavior categories suggesting that these behaviors have differing functions. Therefore, the particular combinations of social and environmental variables that predict the occurrence of each behavior category provide insight into their potential individual functions.

We found the distance of the nearest neighbor group to be an important social variable in predicting breaching behavior. Previous research has suggested the sound made by breaching is used to signal nearby groups (Dunlop *et al.* 2008), and is more likely to be used for intergroup signaling when wind speeds, and therefore background noise levels, increase (Whitehead 1985, Dunlop *et al.* 2010). In this study, the probability of observing breaching behavior decreased significantly when the distance to the nearest group was between 1,000 m and 4,000 m compared to beyond 4,000 m, suggesting that it may be used for communication between groups, rather

Table 8. Model averaged estimates, with standard errors (SE), 95% confidence intervals (CI), z values and P values for pectoral slapping models. Significant estimates are highlighted in bold. Estimates were only calculated for variables occurring in the confidence set of models of each behavior category (Table 5). Estimate values indicate the probability of observing a behavior as continuous predictor variables increase by one unit, or for the specified category of a categorical predictor variable when compared to the baseline category indicated (positive estimates indicate an increased probability, negative estimates indicate a decreased probability). There were no "Lone" animal samples for the pectoral slapping analysis.

Model	Estimate	SE	Lower CI	Upper CI	z	P
Pectoral slapping predictor variables						
(Intercept)	-2.33	1.27	-4.82	0.15	1.84	0.066
Composition (relative to female/calf groups)						
Adults only	-0.50	1.07	-2.59	1.59	0.47	0.637
Lone animals	—	—	—	—	—	—
Female/calf/escort	-0.55	0.47	-1.48	0.37	1.18	0.238
Female/calf/multiple escort	-1.20	0.89	-2.94	0.55	1.35	0.178
Multiple female/calf pairs	1.62	0.87	-0.07	3.32	1.87	0.061
Group interaction (relative to stable periods)						
Pre-join	1.01	0.62	-0.21	2.23	1.62	0.105
Pre-split	2.34	0.73	0.91	3.76	3.22	0.001
Post-join	-0.28	0.94	-2.13	1.57	0.3	0.766
Post-split	1.49	0.72	0.08	2.89	2.08	0.038
Number of groups	-0.07	0.11	-0.29	0.16	0.58	0.56
Number of singers	-0.59	0.27	-1.12	-0.05	2.15	0.032
Wind speed	0.1	0.03	0.04	0.16	3.12	0.002
Water depth	-0.07	0.03	-0.14	0.0003	1.95	0.051

than within groups. Additionally, as we did not find group interaction to be a significant predictor of breaching behavior, this adds to the evidence that breaching is less likely to be used to mediate close-range interactions such as the splitting or joining of a group, and is more likely to be used to signal to other groups in the area. Alternatively, whales may use breaching to communicate under different acoustic conditions compared to vocal signals. However, detailed information on the detection ranges of both vocal signals and surface-active behaviors is required to accurately determine whether this is the case. Although some work has been carried out at this study site examining the source levels of the different sounds, factors such as background noise from wind or vessels, and the composition of the group, may be influential (Dunlop *et al.* 2013, 2014; Dunlop 2016). Therefore, a more in-depth knowledge of the detection ranges of both vocal signals and surface-active behaviors, under varied social and environmental conditions, is needed and currently such information is not available for this study site.

Fluke slapping behavior may play a role in close-range and between-group communication as it was more likely to occur in groups prior to joining with another group and after animals split from a group. These results indicate that it is potentially important in eliciting or mediating these social interactions. The use of fluke slapping by humpback whales has also been seen on the Hawaiian breeding grounds and in the coastal waters off Ecuador in a similar context, during group interactions (Baker and Herman 1984, Felix and Haase 2001), supporting this hypothesis. Baker and Herman (1984) and Silber (1986) suggested that fluke slapping is an agonistic

behavior in humpback whales, and likely to be used within competitive groups, where a number of males are competing for access to a female. These studies recorded incidences of fluke strikes, where a whale used its fluke to physically strike another animal. However, in our study, fluke slapping was observed in the absence of other animals and without striking other animals. In addition, fluke slapping was also observed from all group compositions, including those containing only females and calves, (*i.e.*, female/calf pairs and multiple female/calf pairs) and therefore may have multiple functions depending on the composition of the group. Specifically, as we found that groups containing multiple female/calf pairs engage in fluke slapping, and this behavior may function as a form of play in young humpback whales (either practice of adult behaviors or as social play), particularly when multiple calves occur together. However, due to the data collection constraints of this study (data could only be collected at the level of the group), we were unable to separate the behaviors of individuals with a group. This kind of individual level information should be the focus of future research and would enhance our understanding of the functions of specific behaviors for both adults and calves.

Similar to a study by Deakos (2002), who found that pectoral slapping may be used during the splitting of a group on breeding grounds, we found that the occurrence of this behavior significantly increased before and after splitting. This suggests that pectoral slapping is used for close-range or within-group communication by humpback whales, possibly to initiate or mediate splitting. In addition, that the distance to the nearest neighbor group was not an important predictor in this model (this predictor did not occur in the confidence set of models, Table 4) suggests that this behavior is used to communicate within a group rather than between groups. Finally, that humpback whales use pectoral slapping for close-range communication is supported by the evidence that, as with breaching, its occurrence increases with increasing wind speeds. This may indicate that the use of pectoral slapping is increased in high wind speeds to improve detection of this close-range communication method in noisier environments.

Variables representing the social context of whales were not the only important predictors of surface-active behavior. Environmental contexts such as wind speed, discussed above, and water depth, were also found to be important. The probability of observing head lunging, fluke slapping, and peduncle slapping behavior decreased significantly with increasing water depth (and this was the only significant predictor in the head lunging and peduncle slapping models). It is possible that groups of whales traveling in deeper waters offshore may be more focused on migrating south when compared to those in shallower waters inshore, which may be more focused on social behavior. Alternatively, if as previous research has shown at other sites, the composition of a group influences whether whales use shallower or deeper waters, this may influence the surface-active behaviors observed in different water depths: the composition of a focal group was an important predictor of most of the surface-active behaviors examined in this study (high model averaged relative importance values). On wintering grounds humpback whale female/calf pairs or groups containing calves display a preference for shallow waters, possibly to avoid predators or harassment from other whales (Smultea 1994, Ersts and Rosenbaum 2003, Craig *et al.* 2014). Previous research at this study site has shown that travel speed and course are generally not influenced by water depth (Kavanagh 2014), however, more research is needed into the compositions and social behavior of the groups using shallower and deeper waters, to better understand why water depth was associated with the use surface-active behaviors. As humpback whales

are a migratory species, potentially migrating through waters of very varied depth, it is important to understand more clearly the reason this environmental factor influences their behavior.

In this study both environmental and social variables were important in predicting the surface-active behavior of migrating humpback whales at our study site. However, only water depth was significant in the head lunging and peduncle slapping models. Group interaction and composition were important, but not significant, to head lunging and peduncle slapping respectively. As such, peduncle slapping may play a role in group interactions, however, from our results their specific function within these interactions remains unclear. Head lunging and peduncle slapping have previously been associated with aggressive behavior in humpback whales and recorded to occur within competitive group interactions (Baker and Herman 1984, Silber 1986). However, in this study neither was observed as frequently as other surface-active behaviors and thus a larger sample size may be required to tease out their potential functions.

Although singing whales were heard frequently at the study site the variables representing their presence were only significant in predicting the occurrence of one of the five surface-active behaviors examined in this study, pectoral slapping. The probability of observing pectoral slapping significantly decreased as the number of singers in the area increased. Research has shown that singers may use the sounds generated by surface-active behaviors to locate other groups of whales in the area (Noad 2002, Smith 2009). On breeding grounds, females with calves are thought to avoid contact with males in an attempt to prevent injury to their young calves in competitive groups, where multiple males compete for access to the female (Baker and Herman 1984). Calves are generally older when on migration than on breeding grounds and may not be as vulnerable to injury. In addition, competitive groups of males are not seen as frequently on migration as on breeding grounds and the risk of attracting multiple males may be reduced during this time. However, singing males are still regularly heard during the southward migration. The results of this study suggest that, during the southward migration at least, whales generally do not alter their surface-active behavior in response to the presence of singers. However, it is possible that the behavior of specific group types (*i.e.*, females/calf) or individuals (females) may be influenced. In addition, the presence of singing whales may influence other aspects of humpback whale behavior, not considered here, such as their movement or diving behavior. Therefore, future research should examine under what contexts individual whales use surface-active behaviors and how their diving and movement behavior may be influenced by the presence of singers.

The results of this study suggest that surface-active behaviors have multiple functions within the communication repertoire of migrating humpback whales. We have shown that the role of each behavior may change depending on the category of behavior in question and the social and environmental context in which they occur. In addition, their importance to the communication of these animals is supported by the fact that they perform successive bouts of these behaviors, which may require substantial amounts of energy, during a period of fasting when they would be expected to conserve energy. Our results not only highlight the potential function of these behaviors within the context of the communication of humpback whales but also provide baseline information on normal behavior of migrating humpback whales.

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SUPPORTING INFORMATION

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Appendix S1. Behavioral ethogram.