

Short Note

Evaluating Humpback Whale (*Megaptera novaeangliae*) Social Behaviour Through Sexing Active Individuals

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Socio-ecological studies on large whales require individual identification of the animals. Ideally, the sex of the animal is also identified in order to better define the social roles of individuals within groups (Mann et al., 2000; Whitehead, 2008). Given the short time that whales remain visible at the surface, simple observation is usually ineffective as a sex determination strategy. As a result, sexing whales through molecular analysis has become an extended and convenient methodology in cetacean studies either by biopsying or collecting sloughed skin (e.g., Whitehead et al., 1990; Clapham et al., 1993; Bérubé & Palsbøll, 1996; Gendron & Mesnick, 2001; Rosel, 2003). The humpback whale is one of the species in which sloughed skin is commonly available and has been successfully used for this purpose (Clapham et al., 1992).

Humpback whales (*Megaptera novaeangliae*) have been studied off Ecuador for 20 y (see Félix & Haase, 2001, 2005; Félix, 2004; Félix & Botero, 2011; Félix et al., 2012). These whales belong to the so-called Breeding Stock G (International Whaling Commission [IWC], 2008) that migrates along the west coast of South America between the eastern tropical Pacific where breeding grounds are located and their feeding grounds along the northwestern Antarctic Peninsula (Stevick et al., 2004). In the last 5 y, collecting sloughed skin has been used as the standard sampling procedure for genetic studies focused on stock structure and sex determination, taking advantage of the energetic surface behaviours displayed by the species (Félix et al., 2012). Aerial displays from which samples have been obtained include breaching, belly flop, and slapping the surface with appendages.

Surface displays by humpback whales have been associated with a variety of social contexts and emotional states, including aggression, courtship, and dominance ranking (e.g., Herman & Antinova, 1977; Herman & Tavolga, 1980;

Darling et al., 1983; Tyack & Whitehead, 1983; Baker & Herman, 1984; Whitehead, 1985; Silber, 1986; Clapham et al., 1992; Frankel et al., 1995; Darling, 2001; Clapham, 2002; Félix, 2004). The nonvocal sounds produced when an individual hits the water surface after executing an active surface behaviour are used for communication and can be heard several kilometers away from the source (Herman & Tavolga, 1980; Dunlop et al., 2008).

Although humpback whales surface displays are well-documented in the scientific literature, few studies have focused on the meaning of particular surface displays (e.g., Whitehead, 1985; Deakos, 2002). This gap in knowledge is partially due to problems in identifying individuals during their generally unexpected performance, which makes it difficult to set an activity in its correct social context. Even more difficult is determining the sex of individuals during periods of surface activity. Therefore, it is unknown whether or not the various surface actions are sex specific.

In this paper, we present a first attempt to establish a possible association between humpback whale sex and specific surface displays during their breeding season off Ecuador. Between 2006 and 2010, we conducted 586 trips (average duration ~2 to 3 h, total effort = 1,347 h) aboard whalewatching boats 8 to 12 m in length around the Santa Elena Peninsula tip, Southeast of Ecuador (02° 10' S, 81° W) (Figure 1), as part of a long-term study on the southeast Pacific humpback whale population (see Félix & Haase, 2001, 2005). During the trips, we recorded 1,237 humpback whale groups (average sighting period was 35.53 min, SD = 25.37, range 1 to 181 min). Whales were usually approached to a distance of 50 to 100 m. Information on group size, composition, behaviour, dive time, heading, and oceanographic conditions was recorded during the sighting period. For the purpose of this work, we focus on the behavioural information related to energetic displays at

the water surface of groups for which genetic samples were collected ($n = 319$, 25.8%).

A group was defined as all individuals present within a radius of 100 m that moved in the same direction and generally maintained a coordinated breathing pattern. We defined four types of groups based on the relative size of the individuals: (1) all adult whales (A), (2) adult and subadults (AS), (3) all subadults (S), and (4) groups containing a mother/calf pair (MC). This last category was split into three subcategories in some analyses to differentiate mother/calf pair alone, mother/pair accompanied by an escort whale (MCE), and mother/calf pair accompanied by more than one whale (MC+N). In addition, we distinguished five categories for group size: (1) singletons, (2) pairs, (3) trios, (4) quartets, and (5) groups larger than four individuals.

Surface activity included those deliberate actions exhibited by whales other than swimming and breathing, specifically displays that implicated striking the water surface with appendages or any other part of the body. We collected sloughed skin

after whales executed one of five different behavioural displays, which we named following the terminology commonly used to describe surface activity in this species (e.g., Darling, 2001):

1. *Backward Breaching* – This includes side/twirling breaching, regardless of how much of the body cleared the water.
2. *Forward Breaching* – This is when the whale leaves the water head first and enters the water on its chin or belly (head/chin slap), regardless of how much of the body cleared the water.
3. *Tail Slapping* – Vertical movement of the tail striking the water surface with one or both sides of the flukes.
4. *Flipper Slapping* – Vertical movement of the pectoral fin striking the water surface with one or both sides of the flipper, and sometimes with both flippers in a belly up position.
5. *Tail Lashing* – Violent horizontal/vertical movement of the tail, also referred to as rear body throw/tail slashing.

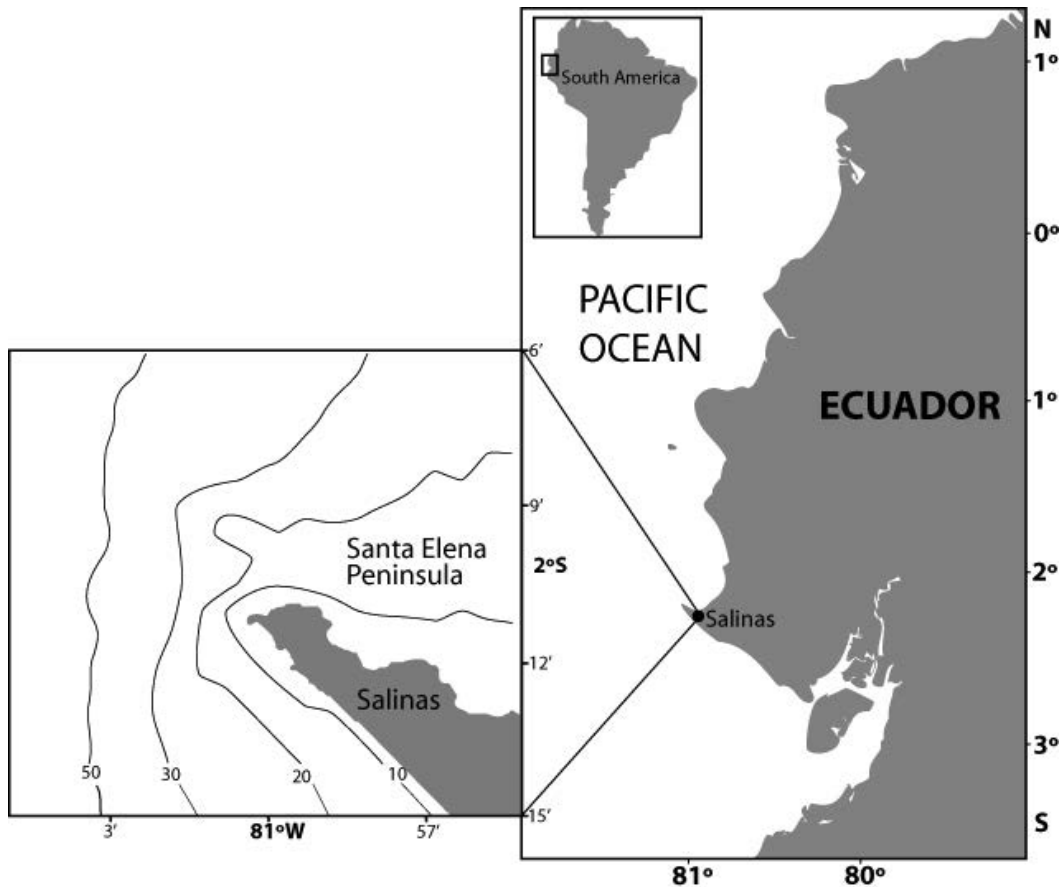


Figure 1. The study area

Usually only one animal was sampled per group, but occasionally it was possible to collect up to three samples, presumably from different individuals (details of sampling and molecular analyses can be found in Félix et al., 2012). When more than one sample was taken from the same group, any with the same sex and haplotype (as determined by mtDNA) were presumed to be the same animal and were not included in the statistical analysis. Specific molecular markers for sex determination were used following the methodology of Gilson et al. (1998). The proportion of sexes in respect to group size, composition, and surface display was compared statistically with χ^2 contingency tables.

During sightings, we recorded the number of times each display was observed, although some displays executed repeatedly—such as flipper and tail slapping—could not always be accurately counted, and the estimated rates reflect a minimum. An execution rate was determined for each display as the number of times the display was performed during the sighting by all members of the group in a period of 10 min. This was necessary due to the difficulty of identifying every active individual. Rates were compared statistically between size and age-classes by surface display using the one-way ANOVA test. The estimated activity rates are valid only for the short periods that the sighting lasted and do not necessarily represent day/season activity rates as the information may be biased towards the most active groups that are easier to spot and, thus, were of most interest to the whalewatching boats.

Through molecular analysis, we found a sex ratio of 2.15:1 skewed toward males ($n = 246$). Whales of both sexes executed the five evaluated surface displays in similar proportions since no significant difference from the expected overall sex ratio skewed towards males was found ($\chi^2_4 = 0.66$, $p > 0.05$) (Table 1). For both sexes, the most common display sampled was backward breaching (62.6% of sample); the second most frequent, also for both sexes, was tail lashing (23.1% of sample). The remaining three displays were between 2 to 5% of the sample.

Table 1. Sex proportion in the dataset in respect to the behavioural displays sampled

Display	Males		Females	
	<i>n</i>	%	<i>n</i>	%
B. breaching	106	63.10	48	61.54
F. breaching	8	4.76	5	6.41
Flipping	4	2.38	2	2.56
T. lashing	40	23.81	17	21.79
T. slapping	10	5.95	6	7.69
Total	168	100	78	100

When the dataset was organized by group size and age-class, we found no significant difference in sex proportions by display category in those cases which had sufficient frequencies for statistic comparison (Tables 2 & 3). Average surface activity was more variable in groups where males were sampled, decreasing significantly with group size ($F_{3,165} = 3.98$, $p = 0.004$), and when a female/calf pair was in the group ($F_{3,165} = 2.97$, $p = 0.033$) (Tables 4 & 5).

We analyzed groups that gained or lost individuals during the sighting period. This occurred in 95 cases (78 affiliations and 17 disaffiliations). As expected, the initial number of whales present in groups that gained members was significantly lower than the initial size of groups that lost members ($t = 3.04$, $df = 25$, $p = 0.005$; 3.76 vs 2.6 individuals/group). For both sexes (i.e., groups in which males and females were sampled), there was a significantly higher number of groups that increased in size compared with those that lost members (3.92:1 and 6.75:1, respectively) ($\chi^2 = 22.5$ and $\chi^2 = 17.09$; $p < 0.01$), suggesting that surface activity promotes the aggregation of whales.

More than one display was recorded in most groups. The modal value was two displays (29%), followed by three (27%), one (22%), four (16%), and five (6%) displays (mean displays/group = 2.55, SD = 1.17). There was no correlation between variety of displays with sighting duration ($r = 0.156$, $n = 64$ and $r = 0.02$, $n = 112$ for females and males, respectively), indicating that most surface activity occurred in short bouts any time during the sighting period.

We also tested the relationship between pairs of displays. The following significant associations were found regardless of sex composition of group: (1) flipper slapping–tail slashing and forward breaches–backward breaches occurred during sightings with a significantly higher frequency than expected if they happened independently, and (2) backward breaches–tail lashing occurred during sightings with a significantly lower frequency than expected ($\chi^2_9 = 43.61$ and $\chi^2_9 = 87.6$ for females and males, respectively; $p < 0.01$ in both cases).

In general terms, our analyses confirm that male and female humpback whales carry out the same energetic surface displays, and apparently with similar intensities, during the breeding season off Ecuador. This was an unexpected result as traditionally researchers have associated certain surface displays in this species with intraspecific competition between males (Darling et al., 1983; Tyack & Whitehead, 1983; Baker & Herman, 1984; Silber, 1986; Clapham, 1996; Félix, 2004). However, in order to optimize their contact with males during the breeding season, receptive females may use surface activity to attract males, promote competition, and/or choose

Table 2. Occurrence of five behavioural displays as a function of group size; M = male, F = female.

Display	Group size									
	Single		Pair		Trio		Quad		Larger	
	M	F	M	F	M	F	M	F	M	F
B. breaching	23	10	29	17	22	5	11	7	21	9
F. breaching	2	--	3	2	1	1	--	1	2	--
Flipping	1	1	2	--	1	2	--	--	--	--
T. lashing	8	--	17	8	8	5	2	1	5	2
T. slapping	4	2	4	3	1	1	--	--	1	1
Total	38	13	55	30	33	14	13	9	29	12

Table 3. Occurrence of five behavioural displays assessed as a function of group type (A = all adults, AS = adults and subadults, S = subadults, MC = mother/calf, MCE = mother/calf and escort, MC+N = mother/calf and more than one whale); M = male, F = female.

Display	Age-class groups											
	A		AS		S		MC		MCE		MC+N	
	M	F	M	F	M	F	M	F	M	F	M	F
B. breaching	70	31	22	11	9	4	--	2	2	--	3	--
F. breaching	3	3	3	--	2	--	--	--	--	--	--	1
Flipping	2	2	--	--	--	--	--	--	--	--	--	--
T. lashing	23	5	10	5	3	2	--	5	3	1	--	--
T. slapping	6	2	3	2	1	--	--	1	--	1	--	--
Total	104	43	38	18	15	6	--	8	5	2	3	1

Table 4. Comparison of the average group surface activity level by sex according to group size category; the bold type highlights the significant difference found in males.

Group size	Males		Females	
	display/10 min	SD	display/10 min	SD
Singleton	10.41	9.76	7.45	8.54
Pair	8.34	9.09	4.77	3.37
Trio	6.23	7.62	4.14	4.04
Quad	7.18	6.76	5.86	5.29
Larger	5.14	5.68	3.46	1.88
	$F_{3,165} = 3.98, p = \mathbf{0.004}$		$F_{3,74} = 0.84, p = 0.50$	

Table 5. Comparison of the average surface activity level in both sexes according to group type category; because of the low frequencies, the three group categories associated to mother with calf were put together in one new category (M). The bold type highlights the significant difference found in males.

Group type	Males		Females	
	display/10 min	SD	display/10 min	SD
A	7.32	8.61	4.77	5.65
AS	8.82	8.65	4.79	3.55
S	10.71	7.75	5.09	3.12
M	2.97	3.60	6.41	4.17
	$F_{3,165} = 2.97, p = \mathbf{0.033}$		$F_{3,74} = 0.84, p = 0.50$	

a mate (Darling, 2001; Deakos, 2002; Cerchio et al., 2005). The similarity between levels of surface activity for both sexes suggests that we should be cautious when attempting to infer the sex of an individual based solely on the frequency of surface displays. Our results support a similar finding in studies of migrating humpback whales off Australia that demonstrate the use of surface-active sounds in all group compositions (Dunlop et al., 2008).

The same behavioural displays were executed similarly under different social contexts by male and female humpback whales, indicating that displays may have multiple meanings for both sexes. Although behavioural studies conducted in

breeding areas reported similar displays (e.g., Herman & Tavolga, 1980; Whitehead, 1985; Darling, 2001; Clapham, 2002; Dunlop et al., 2008), our study confirms that energetic behaviours are not sex specific. The performance rate of the most frequently observed display—backward breaching—was remarkably similar for both sexes. Consequently, no definitive conclusion on the meaning of this display can be given other than it is performed in a variety of social circumstances. However, the second most frequently sampled display—tail lashing—showed some variability, suggesting an association with the social condition of sampled groups. For example, the display was

recorded in singleton immature males but not in singleton immature females. It was also sampled 4.6 times more frequently (but not significantly) in males than in females in all adult groups, supporting the belief that it is used as a form of aggression or warning toward adversary males (see Darling et al., 1983; Tyack & Whitehead, 1983; Baker & Herman, 1984; Silber, 1986). Clapham et al. (1992) suggests that females use tail slashing to reject male advances or potential escorts. The execution of this display by females in groups containing a mother/calf pair suggests that it is also used by adult females to reject male escorting; for calf protection; and, in the case of mother/calf pairs alone, as a defensive or warning response to boat presence (Félix, 2004).

The inverse relationship between group size and surface activity found in this study—particularly in groups where males were sampled—supports the belief that one role of surface activity is to act as a joining mechanism through the generating of acoustic signals for long-distance inter-group communication (Herman & Tavolga, 1980; Helweg & Herman, 1994; Félix, 2004; Dunlop et al., 2008). This would be one way in which individuals could use social recognition by conspecifics in order to establish new social interactions. Dunlop et al. (2008) suggested that slapping could contain additional information even more useful in creating aggregations than breaching. Our data support that hypothesis since we found that in most cases surface activity was not limited to breaching. Percussion sounds, such as those produced by humpback whales through surface displays, would be complementary to vocal sounds as part of their varied repertory of social sounds (Dunlop et al., 2007).

In this study, we have demonstrated that sexing humpback whales during periods of surface activity can provide valuable information on the social behaviour of breeding groups. We were aware of the limitations of interpreting humpback whale behaviour from surface activity alone. Ideally, the study of this species demands an integrated approach that combines visual, photo ID, and acoustic techniques to better understand social structure and behaviour (e.g., Frankel et al., 1995; Dunlop et al., 2008). While identification of active individuals remains challenging in groups with multiple active animals, nuclear genotyping also can be used in future studies to track active focal animals instead of groups.

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