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## Bottlenose dolphins change their whistling characteristics in relation to vessel presence, surface behavior and group composition

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Cetacean watching from tour boats has increased in recent years. However, short- and long-term impacts of this industry on the behavior and energetic expenditure of cetaceans have been documented. Although multiple studies have investigated the acoustic response of dolphins to marine tourism, there are several covariates that could also explain some of these results and should be considered simultaneously. Here, we investigated whether common bottlenose dolphins, *Tursiops truncatus*, inhabiting Walvis Bay, Namibia vary their whistle behavior in relation to boat presence, surface behavior and/or group composition. We detected an upward shift of up to 1.99 kHz in several whistle frequency parameters when dolphins were in the presence of one or more tour boats and the research vessel. No changes were demonstrated in the frequency range, number of inflection points or duration of whistles. Whistle occurrence and production rates increased when tour boats were present. High natural variation was detected in the whistle behavior of bottlenose dolphins over varying behavioral states and group composition. Anthropogenic impact in the form of marine tour boats can influence the vocal behavior of dolphins and such changes could have a long-term impact if they reduce the communication range of whistles or increase energy expenditure.



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# 1. INTRODUCTION

Wildlife tourism involving cetacean (whale, dolphin and porpoise) watching has experienced rapid growth since the 1990s (Hoyt, 2001; O'Connor *et al.*, 2009). Globally, boat-based cetacean watching generates an estimated 2.2 billion US dollars annually (IWC, 2014). Compared with captive facilities, responsible boat-based cetacean watching has been promoted as an ethically acceptable option for observing dolphins, providing a valuable forum for environmental education and promotion of conservation efforts (IFAW, 1997). However, a considerable body of work has shown that boats and boat-based cetacean watching can have multiple negative impacts on the individual, population or species (Parsons, 2012).

Relative to the observable changes in surface behavior, the impacts of boats on the acoustic behavior of cetaceans has received less attention. Changes in the characteristics of vocalizations or their production may be related to elevated levels of anthropogenic noise associated with vessel engines (Jensen *et al.*, 2009; Parks *et al.*, 2011; Pirodda *et al.*, 2012), the physical presence of boats (Pirodda *et al.*, 2015), boat type (La Manna *et al.*, 2013) or vessel behavior during encounters, and the interplay between these factors can be difficult to disentangle (see Ellison *et al.*, 2011). As cetaceans are highly acoustically oriented and rely on acoustic signals throughout their daily lives, they are particularly sensitive to elevated noise levels (Southall *et al.*, 2007).

Sound generated through outboard engines, which are typically used by small-scale cetacean watching boats, can be loud (149–152 dB re 1 $\mu$ Pa<sub>RMS</sub> at 1 m) and broadband (extending between 0.2 and 40 kHz), resulting in a significant reduction of communication range (Jensen *et al.*, 2009). Although excessive noise can cause hearing damage, and even strandings in cetaceans (Weilgart, 2007), the more relevant impacts of boat noise generated through marine tourism activities are likely to be the masking of calls (Jensen *et al.*, 2009) or biological cues (Clark *et al.*, 2009), behavioral changes (Williams *et al.*, 2006), displacement (Rako *et al.*, 2013) and stress (Rolland *et al.*, 2012).

In bottlenose dolphins (*Tursiops* spp.) long-range communication relies on whistles: narrow-band, frequency-modulated signals, ranging between 0.8 and 41.8 kHz in frequency (Schultz and Corkeron, 1994; Hiley *et al.*, 2016). In favourable conditions, these signals can propagate over tens of kilometres (Janik, 2000). Acoustic parameters and production rates may vary according to behavioral state (Jones and Sayigh, 2002; Quick and Janik, 2008; Azevedo *et al.*, 2010; May-Collado, 2013) and can be useful in predicting surface behavior (Hernandez *et al.*, 2010; Henderson *et al.*, 2011; Henderson *et al.*, 2012). For example, whistle production is usually higher during socializing contexts (Jones and Sayigh, 2002; Quick and Janik, 2008) and when animals experience stress (Esch *et al.*, 2009).

Each bottlenose dolphin uses an individually distinctive signature whistle which is acquired through vocal production learning in the first year of life (Caldwell and Caldwell, 1979; Janik and Sayigh, 2013). Around 50% of all whistles recorded from free-ranging bottlenose dolphins are signature whistles (Cook *et al.*, 2004; Gridley *et al.*, 2012) which are used to convey identity information (Janik *et al.*, 2006), facilitate group contact (Janik and Slater, 1998; Quick and Janik, 2012) and address conspecifics (King and Janik, 2013). The function of other, non-signature whistles in the dolphin's repertoire is less well understood. Non-signature whistles may include shared whistle types (King and Janik, 2015), copies of conspecifics' signature whistles (Tyack, 1986; Watwood *et al.*, 2005; King *et al.*, 2013) and non-stereotyped whistles produced by calves (Caldwell and Caldwell, 1979).

Although several studies have investigated the likely impact of boat presence on dolphin communication signals including whistles (Scarpaci *et al.*, 2000; Buckstaff, 2004; May-Collado and Quiñones-Lebrón, 2014), few have controlled for other key covariates that may influence whistle characteristics or production, such as behavioral context (Scarpaci *et al.*, 2000; Lemon *et al.*, 2006; May-Collado and Quiñones-Lebrón, 2014) or group composition. Here we investigated variation in the acoustic parameters and production of whistle vocalizations of common bottlenose dolphins (*Tursiops truncatus*) in relation to three key covariates: tour boat presence, surface behavior and group composition. We also investigated the influence of engine noise generated by the research vessel as a possible source of disturbance.

## 2. METHODS

### A. DATA COLLECTION

Data were collected between 2009 and 2014 in Walvis Bay (22°57'S, 14°30'E), central Namibia (see Table 1). The north-facing bay is shallow (mostly <15 m deep) with a muddy/sandy bottom and approximately 10 x 10 km in area. The Walvis Bay bottlenose dolphin population is small (around 100 individuals) and apparently isolated from

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other bottlenose dolphin populations along the west coast of Africa (Findlay *et al.*, 1992; Best, 2007). Walvis Bay has become a popular place for wildlife watching. A review of the industry documented eight marine wildlife watching companies operating 27 motorized tour boats in 2010 (Leeney, 2014). Encounters with bottlenose dolphins are a key attraction for the industry. Most tour boats in Walvis Bay operate with four-stroke outboard or inboard diesel motors with varying travel speeds.

**Table 1. Vessels and equipment utilized for acoustic data collection between 2009 and 2014.**

Data collection	Research vessel	Recording device
February–March 2009	8 m ski boat fitted with twin 80hp 4-stroke Honda engines	Edirol UA-25 sound card to PC
June–August 2011	5.7 m rigid hulled inflatable boat (RHIB) fitted with twin 50 hp 2-stroke Mercury engines	Zoom H4n digital recorder
June–August 2012, January and June 2013 and January 2014	5.7 m rigid hulled inflatable boat (RHIB) fitted with twin 60 hp 4-stroke Yamaha engines	Zoom H4n digital recorder

Local weather conditions create calm and flat seas in the bay during the morning with stronger winds in the afternoons (usually Beaufort sea state 4 or higher). Therefore, boat surveys to conduct focal follows (Altmann, 1974) of groups were mostly carried out in the mornings when the probability of finding dolphins was highest. Surveys did not follow a set route, although searching was concentrated in areas known to be preferred by dolphins. When dolphins were sighted, an encounter began and acoustic data were collected. Standard information on the estimated group size and composition (calf present, C-P or absent, C-A) was documented at the start and end of each encounter. No focal follow lasted more than 4 h and most lasted between 1 and 2.5 h.

Data on group surface behavior and tour boat presence were point sampled every 3 min during encounters, allowing 1 min to observe and assign the behaviors. A group was defined as an aggregation of dolphins within 100 meters of one another. Due to low numbers of dolphins within Walvis Bay, it was rare to encounter more than one group within a day. Tour boats were deemed present (TB-P) during a point sample if one or more were visually estimated to be within 200 m of the focal group. If not in attendance or further than 200 m away, tour boats were considered absent from the point sample (TB-A). The behavior of dolphins encountered was assessed using a focal group sampling method whereby we assigned the predominant group behavior for the majority (> 50%) of the group to a predetermined set of behavioral states (Mann, 1999). Where appropriate, we assigned the behavior of the remaining group to a secondary behavioral category. This approach was also used if dolphins were split into subgroups, or if a small proportion of the group were engaged in an obviously different behavior (e.g. a subgroup milling while the majority of the group socialized). Behavioral states were classified as resting (R), milling (M), travelling (TR), socializing (SOC) and surface feeding (SF) adapted from Lusseau (2003, Table 2); and were designed to be mutually exclusive but together describe the entire observable behavioral budget of the population.

Underwater acoustic recordings of dolphin vocalizations were made using the equipment reported in Table 1. Throughout the study we used a single-element High-Tec HTI-96-MIN hydrophone with a frequency response of 2 Hz to 30 kHz ( $\pm 1$  dB). The recorders used sampled the data at 96 kHz. The hydrophone was weighted using a 1 cm diameter steel chain and lowered 2–3 m below the surface of the water. When dolphins were found in waters < 3.5 m deep, the hydrophone depth was reduced accordingly. Acoustic recordings were made when the research vessel was stationary, idling or travelling slowly (less than eight knots).

Our analysis focuses on the acoustic parameters and occurrence (presence and rate) of whistles. Whistles were identified in the spectrogram display of Adobe Audition CS5.5 (version 4.0, Adobe Systems Inc., San Jose, CA, U.S.A.), and Raven Pro 1.4 (<http://www.birds.cornell.edu/brp/raven/ravenversions.html>) by visually and aurally scanning the recordings. The spectrogram display was created using a Hanning window with an FFT of 512 for whistle identification. Whistles were defined as narrow-band tonal signals longer than 0.1 s in duration (Lilly and Miller, 1961; Janik *et al.*, 2013) where at least part of the fundamental frequency was above 3 kHz (Gridley *et al.*, 2015).

**Table 2. Behavioral state categories based on Lusseau (2003) to describe the repertoire of behaviors observed.**

Behavior		Definition
Resting	R	Slow, directed movement (slower than idle speed of vessel); no splashing; closely grouped or in subgroups; short, relatively constant, synchronous dive intervals
Travelling	TR	Steady movement in a constant direction; short, relatively consistent dive intervals; often much splashing
Milling	M	No net movement; individuals surfacing facing different directions; pod often changes direction; dive intervals vary. May indicate a transitory phase between other more functional behaviors like foraging or socializing
Surface feeding	SF	Animals usually dispersed; frequent direction changes; fish chases at the surface; seals and birds often in attendance
Socializing	SOC	Diverse interactive behavioral events; jumps, chases, body contact; no directed movements; dive intervals vary

Identification of signature whistles was based on the whistle type catalog created by Kriesell *et al.*, (2014) for this population identified using visual categorization and bout analysis (SIGID) (Janik *et al.*, 2013). We conducted a thorough review of the Walvis Bay signature whistle catalog, updating it where necessary and adding in new signature whistles. Additional signature whistle types were identified based on the SIGID bout analysis (Janik *et al.*, 2013). In sequences of new whistle types, if at least 3 out of 4 whistles of the same type (frequency modulation pattern) occurred within 1 to 10 seconds of each other they were considered to be a new signature whistle type and added to the catalog. To be regarded in the present analysis, all signature whistle types had to contain at least four good quality whistles (SNR 2/3, unmasked, see below for details).

## B. VARIATION IN WHISTLE ACOUSTIC PARAMETERS

Low-frequency vessel noise can mask the low-frequency components of whistles, resulting in an apparent shift in frequency during spectrographic analysis and subsequent measurement error. To avoid this issue, we carefully filtered our data so that only high-quality whistles, with the entire contour clearly visible, were measured, even during periods with background vessel noise. This was achieved through visual assessment and grading of each whistle contour, based on the signal-to-noise ratio (SNR) as follows: 1: signal is faint but visible on the spectrogram; 2: signal is clear and unambiguous; 3: signal is prominent and dominates. High-quality whistles were those assessed as SNR 2 or 3, which had a clear start/end and were not masked by simultaneous sound. For each high-quality whistle identified, a number of acoustic parameters were measured. The duration and number of inflection points (i.e. change in slope from positive to negative or vice versa) were assessed from visual inspection of the spectrogram in Adobe Audition. Minimum and maximum frequency were automatically measured with the selection function in the spectrogram view of Raven Pro (setting Hanning window with FFT of 512, brightness 70, contrast 50) and frequency range was calculated as the difference between these values. Whistle start and end frequency were measured manually in Raven. For each whistle analyzed, we assessed whether concurrent boat engine noise was present or absent. If present, we determined whether the noise was generated from the research vessel (RV) engine/s or from one or more tour boats, or both noise sources combined. This was achieved through careful visual and aural inspection of the acoustic file. We also noted the maximum frequency of this engine noise concurrent with the measured whistle.

Each whistle contour was assigned a matching tour boat condition (TB-P or TB-A), group behavioral state (R/M/TR/SOC/SF/SUB) and calf presence (C-P or C-A) based on encounter point sample data. To account for the secondary behavioral states involving milling, which may indicate a transition between states (Quick and Janik, 2008), a mixed behavioral state (MIX) was introduced at the analysis stage. It was assigned to point samples where milling behavior was documented as the primary behavior with either socializing or surface feeding as the secondary behavior, or in cases where socializing or surface feeding was the primary behavior with milling as the secondary behavior. Other combinations of primary and secondary behaviors occurred infrequently and whistles produced during these times were therefore excluded from the analysis.

We conducted univariate statistical analyses to determine the influence of tour boat presence and engine noise on dolphin whistle parameters. Analysis was performed in R (version 3.1.1, The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) using the RStudio interface (version 0.98.1103). Visual classification via QQ-plots and histograms showed that the acoustic parameters were not normally distributed. The

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influence of tour boat presence on each of the seven parameters of dolphin whistles was therefore tested using nonparametric ANOVAs (Mann–Whitney  $U$  tests). Bonferroni correction was applied to the  $\alpha$  value, i.e.  $\alpha$  after Bonferroni correction =  $0.05/7$  comparisons =  $0.007$ . This analysis assumed that our research vessel was a constant under both the TB-A and TB-P conditions and that any effect could be caused by engine noise or the physical presence of one or more tour boats. As the research vessel was always present, whistle parameters in the absence of boats could not be tested. Also, owing to restrictions of sample size, we were not able to investigate the influence of the number of tour boats on dolphin whistle parameters.

To investigate the effect of elevated levels of engine noise on whistle parameters, we used data from when tour boats were absent and only the research vessel was present. We compared the parameters of whistles recorded when the research vessel engines were off (RV-OFF) to when one or both were on and idling but not in gear (RV-ON). Under both conditions the research vessel was stationary and no other boats were interacting with the focal group; therefore boat presence was a constant in this analysis. Parameter differences were compared using nonparametric ANOVAs (Mann–Whitney  $U$  tests) with a Bonferroni correction applied as above.

We extended our analysis to investigate the influence of surface behavior and group composition (calf presence) in addition to tour boat presence on each of the seven whistle parameters using a generalized linear model (GLM) approach. Within each of the seven models generated, explanatory co-variables were included as categorical variables. After rejection of co-linearity, the four possible predictors in each full model were (1) tour boat presence, (2) surface behavior, (3) calf presence and (4) the interaction between tour boat presence and calf presence. Sample size restriction prevented the influence of other interactions from being investigated. We applied a GLM with a gamma distributed error structure for the six response variables other than number of inflection points, as this describes right-skewed continuous positive data better than a normal distribution (Crawley, 2007). The count of inflection points was modelled as a discrete variable and, after detecting over-dispersion, the error structure was corrected by fitting a quasi-Poisson GLM. The appropriateness and assumptions for each model were checked visually by assessment of model diagnostics in R. Only the best fitting predictors, chosen via the corrected Akaike information criterion (AICc) value, were included in the final model for each parameter. Analysis of Variance type II (function 'Anova' in the 'car' library in R) was used to assess the significance of the predictors (Langsrud, 2003). Tukey contrasts as post hoc tests were calculated from the fitted model to conduct pair-wise comparisons between levels of predictors (function 'glht' in 'multcomp' library in R).

## C. VARIATION IN WHISTLE OCCURRENCE AND PRODUCTION

When assessing whistle occurrence and production rates, it is important to analyze times when all whistles produced would be recorded. To ensure this, point samples where the minimum distance of the research vessel to the group was visually estimated to be  $>100\text{m}$  were removed from analysis. To account for self noise from the research boats' engines or those of nearby tour boats which could mask dolphin whistles, we scanned all recordings for engine noise. Continuous sections were assigned an engine noise rating on a scale from one to three: level one equating to no engine noise (research vessels' engines are off and no engine noise from other boats), level two equating times when the research vessels' engines were in idle, and some low level engine noise could be detected from nearby boats and level three equating to very loud noise or unusable recording periods such as when research vessels' engines were on or there was a fault in the recording.

Recording sections and associated whistles produced concurrently with level three noise were discounted from the analysis and the amount of usable time (level one or two) per three minute point sample was calculated out of a maximum of 180 s. Whistle and signature whistle occurrence was investigated by documenting their presence or absence for sampling points with at least 60 s of usable recording time (level one or two). To investigate vocal production rates, the number of whistles and signature whistles produced during each three minute sample was counted and the amount of usable time per three minute point sample out of a maximum 180 s was included as an offset in modeling procedures. Differences in occurrence and production rate of whistles in level one and level two boat noise categories were compared using a non-parametric ANOVA (Mann-Whitney  $U$  test). As above, whistle occurrence and production rate per behavioral sampling point were linked to the associated group behavioral state, calf presence, and tour boat presence information.

We investigated the influence of several covariates on whistle and signature whistle occurrence and production rates using a generalized linear mixed model (GLMM) approach. Whistles of all quality were included in this analysis. After rejection of autocorrelation, the predictors in each full model were (1) surface behavior, (2) group composition, (3) tour boat presence. We applied a GLMM with Poisson distributed error, which is applied to count data, using the logarithm of usable seconds out of 180s as an offset and the encounter number modeled as a random effect.

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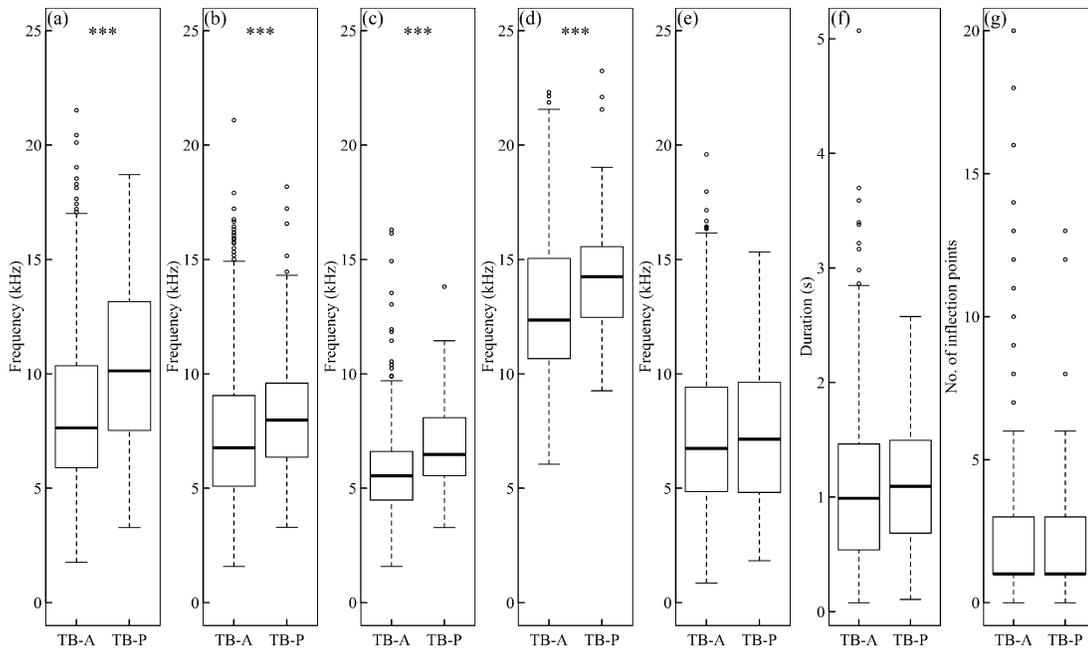
### 3. RESULTS

Between 2009 and 2014 we made acoustic recordings during 69 encounters with bottlenose dolphins in coastal Namibia. In total, more than 79 h of acoustic data were collected over varying behavioral states and group compositions.

#### A. WHISTLE PARAMETERS

A total of 3837 whistles were identified from acoustic recordings. After visual assessment of SNR, 828 whistles were considered of high enough quality to be measured and analyzed. These whistles were recorded over 36 different encounters on 35 fieldwork days. The vast majority of these whistles (98%,  $N = 813$ ) were recorded when the minimum distance to the focal group was  $\leq 100$  m. One to four ( $\bar{X} \pm SD = 1.5 \pm 0.7$ ) tour boats were present during 10 of the 36 encounters from which whistles were analyzed. Overall, 17% ( $N = 137$ ) of whistles analyzed were associated with the presence of one or more tour boats and 83% ( $N = 691$ ) were recorded when tour boats were considered absent. Group size and calf presence were correlated. Groups including calves were slightly larger ranging from seven to 50 animals than groups without calves ( $\bar{X}$  group size C-A = 9,  $\bar{X}$  group size C-P = 21). Fifty-seven per cent ( $N = 471$ ) of the measured whistles were recorded when calves were present in the focal group.

There was a net upward shift in whistle frequency when one or more tour boats were in the vicinity of focal groups. Dolphins vocalized with significantly higher minimum, maximum, start and end frequency in the presence of one or more tour boats (Fig. 1). Frequency range, however, did not differ between TB-P and TB-A conditions, nor was there a significant change in whistle duration or the number of inflection points (Fig. 1). The greatest shift in frequency was observed for start frequency (1.99 kHz) and the least for minimum frequency (1.08 kHz; refer to Heiler *et al.*, 2016, for further details).



**Figure 1. Distribution of (a) start frequency, (b) end frequency, (c) minimum frequency, (d) maximum frequency, (e) frequency range, (f) whistle duration and (g) inflection points, with one or more tour boats present (TB-P) or absent (TB-A). The horizontal line in the box represents the median; the bottom and the top of the box are the first and third quartiles. Whiskers show values within 1.5 times of the interquartile range from the boxes and outliers are plotted as single points. Asterisks (\*\*\*) mark parameters with highly significant differences between tour boat presence and absence after Bonferroni correction was applied ( $P < 0.001/7$ ).**

A visual assessment of the analyzed whistle contours recorded under the TB-P conditions when the research vessel engine was off revealed that 30% ( $N = 27$ ) of analyzed whistles were recorded when low-frequency noise attributed to one or more tour boats was under 4 kHz, 54% ( $N = 49$ ) when this noise extended up to 4 - 6 kHz and 16% ( $N = 15$ ) when it extended up to 6 - 9 kHz. Occasionally more broadband noise was apparent, either associated with gear shifts or during approach and departure of tour boats, when vessel speeds were greatest.

When tour boats were absent, the noise of the idling research vessel engine had a maximum frequency of 4 - 6 kHz and was generally quiet ( $\bar{X}$  of 10 measurements  $\pm$  SD = 20.4  $\pm$  5.3 dB, above ambient noise levels) compared to the acoustic signals of bottlenose dolphins in the vicinity. This engine noise had a moderate influence on whistle parameters, with end and minimum frequency shifting significantly upwards by 1.19 kHz and 0.7 kHz, respectively, between RV-OFF ( $N = 566$ ) and RV-ON ( $N = 125$ ) conditions. No difference was observed for any of the other five remaining parameters measured. These results suggest that (1) engine noise alone influences whistle parameters and (2) that the influence of boats (assessed by the number of parameters affected) increases when more boats are present and/or boats are moving in the vicinity of animals.

Table 3 details the variables included in the multivariate analysis for each model after model selection, along with a summary of the model outcomes. Results from the GLM analysis support the simpler univariate ANOVA results, showing that tour boat presence is associated with a net upwards frequency shift in whistle vocalizations for all frequency parameters measured, without any detectable change to frequency range. Model selection indicated that the presence of one or more tour boats was not a significant contributor to models describing the influence on whistle duration or number of inflection points.

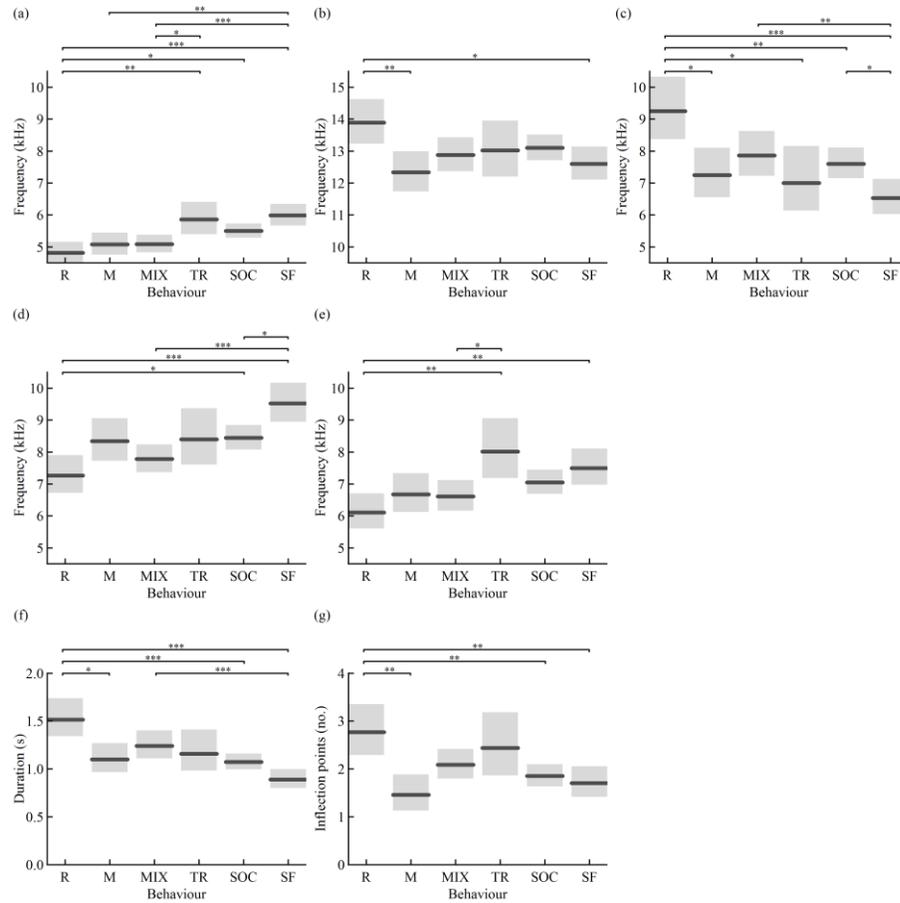
**Table 3. Summary of the best fitting model for each acoustic parameter. Predictors with 'NA' were not included in the final model (predictor selection via AICc); asterisks show level of significance for contributing predictors (\* $P \leq 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ) and '-' indicates a predictor retained in the final model but that did not have a significant effect (see text for details). Arrows indicate whether the predictor had a positive or negative effect on the acoustic parameter (applicable for binary variables only).**

Acoustic parameter	Tour boat presence	Surface behavior	Calf presence	Tour boat/Calf interaction
Start frequency	***↑	***	NA	NA
End frequency	***↑	***	*↓	NA
Minimum frequency	***↑	***	**↓	NA
Maximum frequency	***↑	*	-	***
Frequency range	-	***	-	***
Duration	NA	***	*↑	NA
Inflection points	NA	***	NA	NA

Surface behavior was identified as an important covariate significantly influencing all acoustic parameters measured. Post hoc tests (Fig. 2) identified the largest differences between resting and surface feeding, resting and socializing and, to a lesser degree, between resting and travelling. Start, end and minimum frequency were lower during resting ( $\bar{X}$  = 7.27 kHz, 6.10 kHz and 4.82 kHz, respectively) than during surface feeding ( $\bar{X}$  = 9.52 kHz, 7.50 kHz and 5.99 kHz, respectively, GLM  $P < 0.001$  for start and minimum frequency,  $P = 0.008$  for end frequency). Maximum frequency was 1.29 kHz higher during resting than surface feeding (GLM  $P = 0.029$ ). As a result, frequency range also differed between these behavioral states ( $\bar{X}$  frequency range during resting = 9.25 kHz;  $\bar{X}$  frequency range during surface feeding = 6.53 kHz). Similar patterns were detected for socializing: start and minimum frequency were lower during resting ( $\bar{X}$  = 7.27 kHz and 4.82 kHz, respectively) than socializing ( $\bar{X}$  = 8.84 kHz and 5.50 kHz, respectively, GLM  $P = 0.02$  for start frequency and  $P = 0.011$  for minimum frequency). Although not significant, maximum frequency was higher during resting ( $\bar{X}$  = 13.89 kHz) than during socializing ( $\bar{X}$  = 13.10 kHz), and in turn the frequency range of whistles recorded during resting was significantly greater than for whistles identified from socializing contexts (GLM  $P = 0.008$ ). The comparisons between resting and travelling followed a similar trend with end and minimum frequency of whistles lower during resting ( $\bar{X}$  = 6.11 kHz and 4.82 kHz, respectively) than travelling ( $\bar{X}$  = 8.01 kHz and 5.86 kHz, respectively, GLM  $P = 0.02$  for end frequency and  $P = 0.003$  for minimum frequency), and again a significant increase in the frequency range was observed between these behavioral states (GLM  $P = 0.03$ ).

Models investigating the effect of behavior on the number of inflection points and whistle duration also indicated a difference between resting and other behaviors. Most notably, whistles had more inflection points and were significantly longer during resting ( $\bar{X}$  = 2.77 and 1.51 s, respectively) than surface feeding ( $\bar{X}$  = 1.42 and 0.89 s, respectively) or socializing ( $\bar{X}$  = 1.64 and 1.07 s, respectively). Combined, these results indicate a systematic difference in whistle frequency, modulation and duration between resting and behavioral states associated with a higher degree of emotional arousal such as socializing and surface feeding.

The presence of calves in groups had a mixed effect on whistle parameters and was also influenced by the presence of one or more tour boats. Model results indicated that when calves were present, end frequency and minimum frequency were lower whereas whistle duration was longer (Table 3). Model selection also indicated a significant interaction between tour boat presence and calf presence for maximum frequency and frequency range (Table 3). When calves were present, whistle maximum frequency varied little with tour boat presence. However, when calves were absent, maximum frequency was significantly higher in the presence of tour boats ( $\bar{X}$  difference between C-A + TB-A versus C-A + TB-P = 2.76 kHz). As frequency range is derived from the difference between maximum and minimum frequency, this effect was reflected in a significant increase in the frequency range of whistles in non-calf groups when tour boats were absent. Model results concerning this interaction term indicate that the effect of tour boats on certain whistle parameters is influenced by the presence of calves within groups.



**Figure 2.** Changes in (a) minimum frequency, (b) maximum frequency, (c) frequency range, (d) start frequency, (e) end frequency, (f) duration and (g) inflection points for surface behavior as a predictor in the model. Black lines show the fitted value, grey boxes represent upper and lower confidence intervals (95 %); lines and asterisks above the plot indicate significant differences between behavioral states: R = resting, M = milling, MIX = mixed behavior, TR = travelling, SOC = socializing, SF = surface feeding. \* $P \leq 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

## B. WHISTLE OCCURRENCE AND PRODUCTION

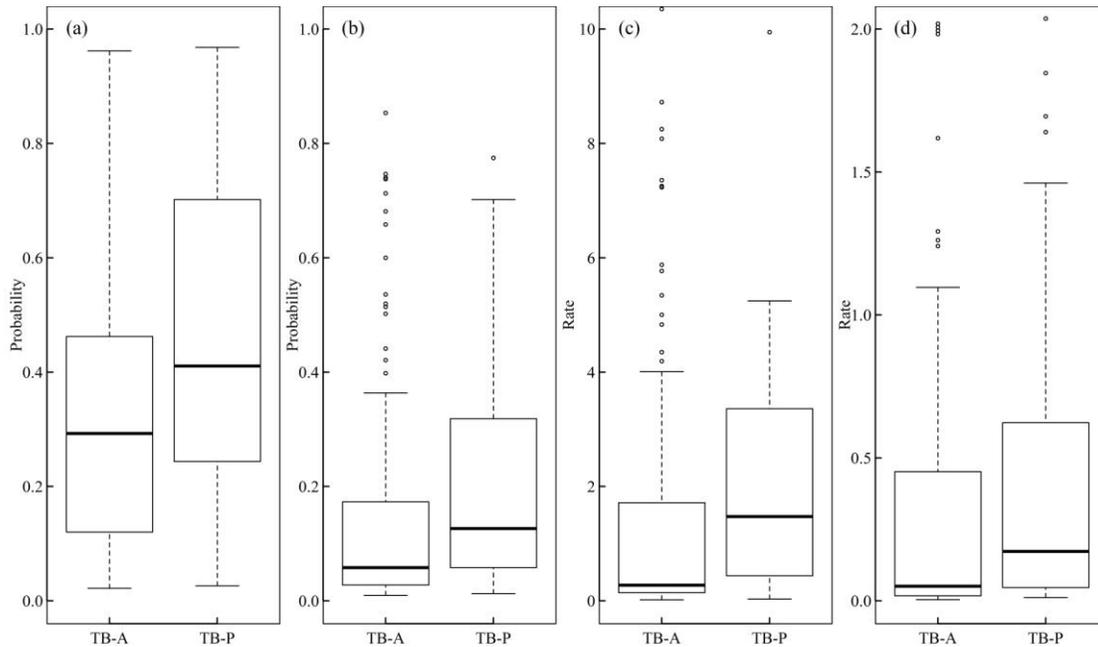
After removing point samples with missing information, saturated with only level three engine noise or collected when the focal group was > 100 m away, a total of 687 point samples remained from 58 encounters. Between one and eight tour boats were present for 22% ( $n = 153$ ) of the samples, with boats considered absent for the remaining 78% ( $n = 534$ ) samples. A total of 522 point samples from 57 encounters had 60 s or more of usable time and were analyzed for assessing whistle occurrence. Whistles were considered present in 41% ( $n = 215$ ) of the point samples. Signature whistles were present in 18% ( $n = 96$ ) of the point samples. There was no significant

difference in the occurrence or production rate of whistles recorded under boat noise one and two conditions, supporting the pooling of data under these conditions ( $\bar{X}$  rate at level one = 1.16 whistle/min,  $\bar{X}$  rate at level two = 1.45 whistle/min,  $U = 24$ ,  $P = 0.674$ ).

Table 4 details the variables included in the GLMM analysis after model selection, along with a summary of the model outcomes. The rate of all whistle and signature whistle production increased significantly when tour boats were in close proximity (200 m or less from the focal group) (GLMM  $P < 0.001$  for all whistles and GLMM  $P = 0.03$  for signature whistles, Fig. 3). Although not significant, the probability of whistles and signature whistles occurring was also greater when tour boats were present ( $\bar{X}$  prob all whistle occurrence = 0.46,  $\bar{X}$  prob signature whistle occurrence = 0.20) compared to when they were absent ( $\bar{X}$  prob all whistles occurrence = 0.33,  $\bar{X}$  prob signature whistle occurrence = 0.13, GLMM  $P = 0.50$  for both, Fig 3).

**Table 4. Summary of the best fitting model for whistle and signature whistle occurrence and production rate. Predictors with 'NA' were not included in the final model (predictor selection via AICc); asterisks show level of significance for contributing predictors (\* $P \leq 0.05$ , \*\*  $P \leq 0.01$  and \*\*\*  $P \leq 0.001$ ) and '-' show none significant predictors.**

	Tour Boat Presence	Surface behavior	Calf presence
All whistle occurrence	-	***	***↑
Signature whistle occurrence	-	***	*↑
All whistle rate	***↑	***	***↑
Signature whistle rate	*↑	***	*↑

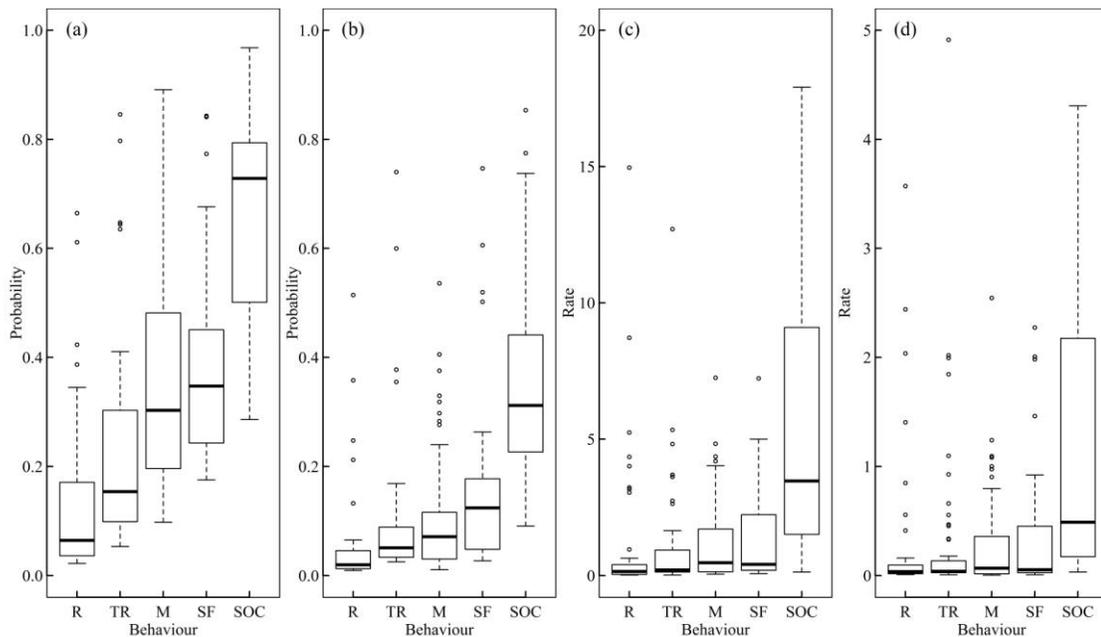


**Figure 3. Predicted probability of occurrence and predicted vocal production rates (no. per min) for all whistles (a and c respectively) and for signature whistles (b and d respectively) with tour boat absence (TB-A) and presence (TB-P). The horizontal line in the boxes represents the median; the bottom and the top of the box are the first and third quartiles. Whiskers show values within 1.5 times of the inter-quartile range from the boxes.**

There was a strong influence of surface behavior on whistle production. When ordered by likely communication need, with resting considered the behavioral state with the lowest likely need and socializing the highest, there is a

clear trend of increasing probability of occurrence and vocal production rates across behavioral states for all whistles and signature whistles analyzed (Fig. 4.). Model summaries identified the greatest differences between resting ( $\bar{X}$  prob all whistle occurrence = 0.1 ,  $\bar{X}$  prob signature whistle occurrence = 0.06) and the other behaviors for all whistles and signature whistles (e.g. socializing  $\bar{X}$  prob all whistle occurrence = 0.69 ,  $\bar{X}$  prob signature whistle occurrence = 0.37,  $P < 0.001$  for both when compared to resting). Rates of whistle production followed a similar trend, with the highest production rates observed during socializing behavior ( $\bar{X}$  = 10.57 whistles/min and  $\bar{X}$  = 2.59 signature whistles/min) compared to resting (Fig 4).

Calf presence was associated with an increased probability of whistle and signature whistle occurrence (C-P:  $\bar{X}$  prob all whistle occurrence = 0.68,  $\bar{X}$  prob signature whistle occurrence = 0.32, C-A:  $\bar{X}$  prob all whistle occurrence = 0.27, GLMM  $P < 0.001$ ,  $\bar{X}$  prob signature whistle occurrence = 0.09, GLMM  $P = 0.03$ ). Production rates were also greater in groups containing calves (C-P:  $\bar{X}$  = 9.32 whistles/min,  $\bar{X}$  = 2.41 signature whistles/min, C-A:  $\bar{X}$  = 1.76 whistles/min,  $\bar{X}$  = 0.47 signature whistles/min, GLMM  $P < 0.001$  for all whistles and GLMM  $P = 0.02$  for signature whistles).



**Figure 4 . Predicted probability of occurrence and predicted vocal production rates (no. per min) for all whistles (a and c respectively) and for signature whistles (b and d respectively) under different surface behavioral states: R = resting, TR = travelling M = milling, SF = surface feeding and SOC = socializing. The horizontal line in the boxes represents the median; the bottom and the top of the box are the first and third quartiles. Whiskers show values within 1.5 times of the inter-quartile range from the boxes.**

## 4. DISCUSSION

Acoustic communication in bottlenose dolphins relies on whistle vocalizations. Within the fission–fusion society in which dolphins exist, these signals are used to maintain group cohesion (Janik and Slater, 1998), facilitate group joins (Quick and Janik, 2012) and address conspecifics (King and Janik, 2013). Whistles may also be used to share information on food patches (King & Janik, 2015). This study suggests that the acoustic parameters and production of whistle vocalizations vary naturally according to behavioral context and group composition, but are also influenced by tour boat presence. Our results are consistent with a short-term acoustic behavioral response, with animals shifting the frequency of their whistle vocalizations upwards when boats are close by and increasing their whistle use and whistle production rates.

The ultimate aim of most noise-induced vocal modification is to maintain the signal-to-noise ratio of calls during increased ambient noise (Hotchkin and Parks, 2013). Elevated anthropogenic noise levels may promote these frequency shifts in vocalizations (Lesage *et al.*, 1999; Morisaka *et al.*, 2005; Ansmann *et al.*, 2007; Parks *et al.*, 2007; Luís *et al.*, 2014). The small motorized boats often used for cetacean watching tend to generate most noise in the low- to mid-frequency ranges (Lesage *et al.*, 1999; Lemon *et al.*, 2006; Jensen *et al.*, 2009) and several studies focused on cetacean vocal parameters have identified an upward frequency shift or increase in minimum or mean

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frequency associated with boat presence (Lesage *et al.*, 1999; Parks *et al.*, 2007; Luís *et al.*, 2014). When viewing dolphins in close proximity (< 200 m) the tour boats operating in Walvis Bay were usually stationed with idling engines or manoeuvring slowly. The associated engine noise generated, the frequency of which was measured when occurring concurrently with analyzed whistles, was mostly under 6 kHz but extended up to 9 kHz. Thus the frequency shift we observed (ranging on average between 1.08 kHz and 1.99 kHz depending on the parameter measured) may not shift the entire whistle contour above the masking noise generated by tour boat engines, but may reduce masking effects at times when boat noise is present but low and limited to the lower frequency ranges. An upward shift in whistle frequency adopted by dolphins may therefore help reduce vocal masking by tour boat engine noise and could help increase transmission of communication calls such as whistles.

Recent studies, however, have argued that noise-induced frequency shifts may principally be explained as an epiphenomenon of the Lombard effect (reviewed in Brumm and Zollinger, 2011). In several bird and mammal species, the Lombard effect is associated with a range of other changes in vocal output, including a rise in fundamental frequency (Dabelsteen, 1984; Nelson, 2000; Tressler and Smotherman, 2009; Ritschard and Brumm, 2011; Nemeth *et al.*, 2013; Hotchkin *et al.*, 2015). Dolphins can readily adjust the amplitude of their calls (Au & Benoit-Bird, 2003; Tyack, 1985) and in echolocation production, an increase in click source level is associated with an increase in click central frequency (Au *et al.*, 2016). Thus a behavioral adaptation whereby dolphins attempt to increase their call amplitude above masking noise to minimize any reduction in whistle communication range might also explain the frequency shift we observed. Previous studies investigating the Lombard effect in cetaceans did not investigate concurrent changes in signal frequency (Scheifele *et al.*, 2005; Holt *et al.*, 2009) or failed to demonstrate a frequency shift associated with increased amplitude (Parks *et al.*, 2011; Holt *et al.*, 2015). However, as this research area is in its infancy, a possible coupling between the Lombard effect and other noise-induced vocal modifications in cetaceans warrants further investigation (Hotchkin *et al.*, 2015).

In relation to whistle frequency parameters, we can summarize our findings by saying that dolphins in Walvis Bay increase the frequency of some whistle parameters when boats are present, with some of the changes observed attributed to engine noise. However, we found a stronger effect with an increasing number of boats present (i.e. the RV versus RV plus one or more tour boats), which included times when tour boats were moving rather than stationary, indicating that several factors may contribute to enhance the observable effect. We cannot, however, argue whether our results are principally explained by animals shifting whistle frequency higher to reduce masking effects, as a by-product of increasing call amplitude above background noise, or a combination of these explanations which are not mutually exclusive.

Surface behavior was strongly linked to variation in all whistle parameters measured, the most striking differentiation occurring between resting behavior and behaviors associated with a higher state of emotional arousal such as socializing and surface feeding (Fig. 2). In general, the patterns identified across a range of mammalian species (Briefer, 2012) appear to hold true for the bottlenose dolphin population studied here, as we found an upward shift in most parameters of the fundamental frequency (start, end and minimum frequency) during behaviors associated with higher states of emotional arousal. Interestingly, maximum frequency did not fit this trend, as this parameter was higher during resting than the more aroused states, resulting in an increased frequency range used during resting. In addition, the duration of whistles, which was longest during resting and shortest during surface feeding and socializing, opposes the general but less consistent pattern in other species of longer call duration in states of greater arousal (Briefer, 2012).

The presence of tour boats was associated with a significant increase in the production rate of whistles and signature whistles. Whistles, and in particular signature whistles are known cohesion calls (Janik and Slater, 1998; Janik and Sayigh, 2013) and an increase in whistling rate during boat presence could help dolphins maintain contact or re-establish contact during periods of tour boat interaction (Van Parijs and Corkeron, 2001; Buckstaff, 2004; Guerra *et al.*, 2014). This may be particularly necessary in groups containing calves, as signature whistles are often involved in facilitating reunions (Smolker *et al.*, 1993; King *et al.*, 2016). Under noisy situations, animals may increase the production rate of calls to increase redundancy and maintain communication (Janik, 2009). Increases in signature whistle production have also been linked to stressful situations (Esch *et al.*, 2009) and the rise in whistle production during tour boat presence may be indicative of a heightened arousal of animals during tour boat interaction.

Surface behavior was linked to differences in production rates of whistles and signature whistles. The biggest difference was observed between resting and behaviors with heightened arousal or greater need for communication (e.g. surface feeding and socializing). Other studies including those conducted on both cetaceans (Díaz López and Bernal, 2009; Stimpert *et al.*, 2015) and terrestrial animals (e.g. Mitani and Nishida, 1993; Digby *et al.*, 2014) have shown changes in vocal production rates linked to changes in behavior, where the highest rates of production were associated with the highest arousal behaviors (Briefer, 2012). The high natural variability in vocal production rates must be accounted for when investigating the influence of anthropogenic activities on dolphin vocal behavior, by considering many covariates simultaneously, as conducted in this study.

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Our results have indicated that tour boat presence influences dolphin whistling behavior and this could have a negative influence on the bottlenose dolphin population in Walvis Bay if the communication range of whistles is reduced (Jensen *et al.*, 2009), energy expenditure is increased (Holt *et al.*, 2015) or animals become stressed (Rolland *et al.*, 2012). Such effects would be compounded if combined with other behavioral responses to tour boat presence that increase energy expenditure, for example increased socializing or travelling (Christiansen *et al.*, 2010; Indurkha, 2012).

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