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A spatially explicit model of the movement of humpback whales relative to a source

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When measuring the response of large whales to a noise source, multiple measures of behavior are often used (e.g., horizontal movement, dive profile and surface behavior). Although this helps to determine fine-scale changes in behavior, using numerous measures means an adjustment of significance level. In addition, many of these behavioral measures do not account for the position of the source vessel relative to the animal or group. This paper develops a new measure, the ‘DDsv, which compares the distance of the group to the source vessel had they continued on their original path (expected) to their observed distance to the source vessel. An increase in DDsv implied avoidance. Baseline movements of humpback whales were then compared to a set of controls (where the vessel was moving but the air guns were not operating) and two ‘active’ treatments: vessels towing a 20 cu in air gun and a 140 cu in array of air guns, air guns firing every 11 sec. This spatially explicit model takes into account the alteration in group horizontal movement relative to the source vessel. It is a measure of displacement behavior that can be applied to other marine mammal behavioral response studies.
1. INTRODUCTION

Behavioral Response Studies (BRS) are designed to measure the response of animals (usually) to an anthropogenic noise source. Noise sources include, but are not limited to, naval sonar, seismic air gun arrays used for oil exploration, pile driving used in the construction of wind farms and vessel noise. To quantify the behavioral response to these various noise sources, the movement of a single animal, or groups of animals, is often used as the response variable. Animal, or group, movement can be measured in multiple ways: a change in travel course and/or speed (e.g. Atunes et al., 2014; DeRuiter et al., 2013; Dunlop et al., 2015; Gailey et al., 2007; Goldbogen et al., 2013; Miller et al., 2014), a change in the probability of detecting an animal in an area (e.g. Thompson et al., 2013; Tyack et al., 2011) or a change in density and/or distribution of animals in the area (e.g. Johnson et al., 2007; Muir et al., 2015; 2016; Yazvenko et al., 2007). In most cases, this change in movement behavior is attributed to animals ‘avoiding’ the source.

One of the goals of a BRS is to determine the point in time during an experiment where the subject begins to show an avoidance reaction and relate this to a received level. In other words, to estimate the lowest (i.e. threshold) received level at which a behavioral response is likely to occur. To do this, the difference between what is considered to be a response, and no response, must be determined. Previous studies have used a ‘multivariate changepoint analysis’ (e.g. Atunes et al., 2014; Miller et al., 2014), where the magnitude of change in movement between two successive time windows is used to generate a ‘changepoint’. ‘Changepoints’ are then assumed to be ‘responses’ to the source if they exceed a certain threshold value (in the Atunes et al., 2014 study this threshold was generated using baseline data). Other studies compare various movement parameters (such as course and speed travelled) of groups exposed to the noise source, to the movement of ‘baseline’ groups (e.g. Dunlop et al., 2015; Dunlop et al., 2016), and/or between various ‘treatments’ (e.g. Dunlop et al., 2015; Dunlop et al., 2016; Goldbogen et al., 2013) to determine if these parameters significantly differed. A significant difference between treatments implies a response. In the latter methodology, however, it can be difficult to determine the threshold of response, as it is difficult to decide when the response magnitude is great enough to be considered ‘significant’. In addition, using multiple response variables requires a Bonferroni correction to account for the increased chance of detecting a ‘significant’ response by chance due to the increased number of statistical comparisons. Lastly, in many previously mentioned studies, there was no measure of displacement behavior relative to the source, so any change in movement behavior was assumed to be avoidance behavior, which may not be the case.

This paper presents a novel and simple method for measuring the movement response of groups of animals (in this case humpback whales) relative to a moving source (in this case a source vessel towing air guns). It compares the predicted position of the group, had they not changed their movement, with the observed position, as a measure of movement deviance. This deviance is then related to the position of the source vessel to determine if this change in movement behavior results in groups avoiding (increasing their distance from) the noise source and therefore equates to a measure of displacement behavior.
2. METHODOLOGY

Data collection

Methods have been published elsewhere (Cato et al., 2013; Dunlop et al., 2015; Dunlop et al., 2016) and are summarised here. Experiments were carried out in September and October in 2010 and 2011 off Peregian Beach, 130 km north of Brisbane, in Southeast Queensland, Australia (26°29’S, 153°06’E) during the migration of the whales from their winter breeding grounds inside the Great Barrier Reef to their summer feeding grounds in the Antarctic. Each trial consisted of three phases – ‘before’, ‘during’ and ‘after. The ‘during’ phase involved either exposing groups of humpback whales to operating air guns (‘active’ trials), or having the vessel move along its designated transect towing non-operational air gun/s (‘controls’). In 2010, the air gun vessel was FV Ash Dar S, a 19 m West Coaster with aft trawl deck towing a single Bolt 600B air gun with 20 cu in chamber bolted into a towfish. In 2011, the vessel was RV Whale Song, a 28 m, 185 t ship with aft superstructure and towing an array of six air guns. This array included the same 20 cubic inch gun used in 2010, as well as three 40 cubic inch GI air guns, which enabled it to be used either as a 20 cubic inch source or as a 140 cubic inch source. The spacing of the air guns and timing of firing of each element were designed to maximize the horizontal transmission of sound and reduce directional differences in radiated sound level. In both years, the air guns were towed 18 m astern of the vessels, fired every 11 secs when operating and were tracked using GPS (for more details see Dunlop et al., 2015; 2016.)

In the ‘before’ phase, groups of whales were ‘focally followed’ by either land or boat-based teams for at least one hour. Land-based behavioral observations were collected from two different stations: the northern station (32m elevation, 100m from the waterline) and a second station 11km to the south (73m-high hill set 700m back from the beach). Two ‘focal follow’ teams were located at each station, with a third ‘scan sampling’ team also at the southern station. Each focal follow team used a theodolite (Leica TM 1100) connected to a notebook computer running VADAR tracking software (E. Kniest, Univ. Newcastle, Australia) to track focal groups for approximately 3 - 4 h. The scan sampling team operated at the southern station only and attempted to keep track of all visible groups in the area as ‘ad lib’ observations, providing contextual data. A 5-element hydrophone array was used to acoustically tracking singing and vocalizing whales. Three boat-based platforms (a 6 m rigid hulled inflatable and two, 5.6 and 6 m, aluminum, center-console boats) were also used for data collection from focal groups. The boat was tracked continuously with on-board GPS to allow the positioning of the group relative to the boat. Boats attempted to stay within 200 m of their focal group in order to maintain visibility of behaviors whilst minimizing disturbance. ‘Baseline’ data were collected when the source vessel was not in the area.

After an hour of the ‘before’ period, the vessel moved along a pre-determined path (eastwards across the migration) for one hour at 4 knots with the air gun/s either firing or not firing while behavioral observations continued, and then stopped. Note that the air gun compressor was operating during control trials as well as active trials. At the end of ‘during’ phase, the vessel slowed again to minimum way where behavioral observations continued for another hour. Land and boat based observers
were all blind to the treatment used in each trial as well as the start of the ‘during’ phase.

Development of the response variable

Previous studies carried out during the BRAHSS study found that groups significantly changed both their diving and travel behaviour in response to the 20 cubic inch source (Dunlop et al., 2015) and the small array (Dunlop et al., 2016). We therefore collapsed group movement metrics into one response metric: the difference in distance from the source vessel between the group’s predicted position (had they not have changed their movement) and their observed position (termed DDsv) at each 10 minute intervals throughout the 60 minute ‘during’ phase. This metric relied on first calculating the group deviation distance (termed DDgp) from their predicted movement, and then making this measure relative to the position of the source vessel in terms of distance (termed DDsv).

Both DDgp and DDsv metrics relied on interpolated positions of the group at the start and end of each 10 minute time bin as the whales were usually submerged at these times. To do this, the positions of the group at the start and end of each 10 minute time bin were estimated, by assuming the whales swam in a straight line at a constant speed between the last measured position of the group in one bin and the first measured position in the next bin. These interpolated positions were ‘bin edges’. Using the ‘bin edges’, a speed and course of the group for the last 10 minutes of the ‘before’ phase (T-1; with T0 being the beginning of the exposure or ‘during’ phase) was estimated (Fig. 1) assuming straight and constant travel between those two ‘bin edge’ points. Using this speed and course, the position of the group was then predicted for the end of the next 10 minute time period (which was the first 10 minutes of the ‘during’ phase; T1), assuming a constant speed and course. The observed position of the group was the ‘bin edge’ for this time period. The distance between their observed position at the end of the 1st 10 minutes of the ‘during’ phase, and the predicted position, was then measured, to give the DDgp for the T1 time period (a measure of group deviance from their predicted pathway; DDgp1 in Fig. 1). For the T2 time period (the second 10 minutes of exposure), the predicted position was calculated using the actual T1 course and speed. This was repeated for the entire ‘during’ phase, giving 6 measures of DDgp per group (for 10 minute time periods named T1 to T6).
Figure 1. An example of the calculation of the group deviation in travel over 10 min (DDgp). The position of the whale group at T1 (10 min after the start of the ‘during’ phase) was predicted from the group’s position at the beginning and end of T-1 (last 10 minutes of the ‘before’ phase; solid red line) assuming no change in course and speed (broken blue line). This position (T1p) was compared to where the whales were observed at the end of T1 (T1o solid blue line). The distance between the group’s predicted and observed position was then measured at T1 (black arrow). This difference in the distance was the DDgp for T1.

Next, the distance to the source vessel was measured at the end of each 10 min segment for both the predicted group position and the group’s actual position. The distance between source vessel and the predicted position was subtracted from the distance between the source and the observed group position to give a difference in distance to the source vessel (DDsv; Fig. 2). A positive value indicated potential avoidance and a negative value indicated potential attraction. This was repeated for every 10 minutes of the ‘during’ phase resulting in 6 measurements per group.
DDgp and DDsv were calculated all ‘control’ (n = 20 groups), ‘active’ (n = 31 groups) and ‘baseline’ (n = 20) groups as long as the groups were north of the source vessel start point at the start of the ‘during’ phase, and moving in a southward direction. For baseline data, the position of the source vessel was predicted using a simulated vessel travelling at the same speed and direction as per other experimental trials.

**Figure 2.** An example of the calculation of the Difference in Distance 10 min (DDsv). The position of the whale group at T1 (10 min after the start of the ‘during’ phase) was predicted from the group’s position at the beginning and end of T-1 (assuming no change in course and speed; broken blue line) and compared to where the whales were observed at T1 (solid blue line). DDsv for this segment (T1) was calculated as the difference in the distance between the source vessel and the group’s predicted position and the source vessel and the group’s observed position (black arrows). In both instances in this example, T1 and T2, the DDsv would have been positive as the group appeared to avoid the source vessel.
Each measure of DDgp (6 per group) was plotted against its concurrent DDsv and two different smoothing functions fitted (one for positive [red – avoidance] and one for zero and negative [blue – attraction] DDsv values; Fig. 3). Baseline data were then added separately (green; Fig. 3).

Figure 3. The relationship between the group deviation distance (per 10 minutes) and the difference in distance of the groups relative to the source vessel between the observed and predicted positions (per 10 mins). Points in red are values greater than 0 (potential avoidance) and points in blue are values less than or equal to zero (potential attraction or no response). A smoothing function was fitted to each dataset (the solid lines to illustrate the relationship between the group movement deviance and the difference in distance of the group to the source vessel due to this deviance). For comparison, the smoothing function fitted to baseline data is also shown as the green line.
To test if the group deviance significantly increased in response to the ‘control’ and ‘active’ treatments compared to the movement of the baseline groups, a Generalized Estimating Equation (GEE; Hardin and Hilbe, 2002) was carried out using ‘R’ software (R Core Development Team, 2015). This model framework was used to account for the lack of independence of model residuals (in that 6 measures were used per group). In the first analysis, the DDgp was used as the response variable (with a Gaussian distribution) and ‘treatment’ as the predictor variable (20 cubic inch, 140 cubic inch, control 1 (Ash Dar S), control 2 (Whale Song) and ‘baseline’). The analysis was then repeated (second analysis) using the DDSv (normally distributed) as the response variable. Predictions were made from the model (and plotted) and a parametric bootstrap method was used to calculate 95% confidence intervals.

3. RESULTS

Within the model (DDgp ~ Treatment, df=4, p<0.0001), groups significantly increased their distance from their predicted position in response to the 20 cubic inch air gun (p <0.0001), the 140 cubic inch air gun (p < 0.0001) and the ‘Whale Song’ controls (p = 0.004) compared to baseline groups. Baseline groups deviated from their predicted course by about 200 m, whereas groups, in response to the 20 cubic inch source, deviated by a further 200 m (95% C.I. 164 - 240 m). In response to the 140 cubic inch source and the ‘Whale Song’ control, groups deviated by a further 115 m and 165 m, respectively (Fig. 4a), compared to baseline groups. However, in response to the ‘Ash Dar S’ control, groups only deviated by a further 40 m. This deviation was not considered to be significantly different to baseline groups in the analysis model. The results suggest that a group deviation from their predicted path could be considered to be a significant if greater than 240 m (i.e. outside the confidence intervals of the baseline data).

Treatment was not a significant effect in the analysis model (DDsv ~ Treatment, df=4) as ‘responses’ ranged from negative (indicating the group approached the source) to positive (indicating the group avoided the source). This meant that, despite changes in movement behavior, at a population level groups generally neither approached nor avoided the source, resulting in a DDsv close to zero for each treatment (Fig. 4b).

Using the threshold of response (a group deviation greater than 240 m), the responses of control and active groups, for each 10 minute period, were divided into ‘avoid’ (where this deviation resulted in an increase in DDsv), ‘attract’ (where this deviation resulted in a decrease in DDsv) and ‘no response’ (where the group deviation was less than 240 m). The corresponding DDgp and DDsv for groups ‘avoiding’, ‘approaching’ and ‘not responding’ to the source compared to baseline groups are shown in Table 1.
Figure 4. Model predictions, including 95% confidence intervals, for the group movement deviance (DDgp; a) and deviation from the source vessel (DDsv; b) for baseline groups and groups exposed to control (Ash Dar S and Whale Song) and active (20 cubic inch and 140 cubic inch) treatments.
Table 1. The group deviation and difference in distance to source (with 95% confidence intervals) for baseline groups, and those, using a threshold of response, that did not respond, avoided, or approached the source.

<table>
<thead>
<tr>
<th>Response</th>
<th>Group deviation (DDgp)</th>
<th>Difference in distance to source (DDsv)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baseline</td>
<td>199 (165, 240)</td>
<td>-28 (-7, -49)</td>
</tr>
<tr>
<td>No response</td>
<td>122 (102, 138)</td>
<td>2 (-12, 17)</td>
</tr>
<tr>
<td>Avoid</td>
<td>525 (465, 593)</td>
<td>304 (253, 350)</td>
</tr>
<tr>
<td>Approach</td>
<td>530 (467, 613)</td>
<td>-332 (-270, -390)</td>
</tr>
</tbody>
</table>

4. DISCUSSION

Groups were found to deviate significantly from their predicted pathway in response to one of the controls and both of the active treatments compared to baseline groups. In some cases, this resulted in the group increasing its distance from the source vessel (potential avoidance), but in other cases, groups decreased their distance to the source vessel. However, the general trend for baseline groups was to deviate by about 200 m from their predicted pathway resulting in them ‘approaching’ the simulated source vessel (where the source vessel would have been if a trial was underway). In other words, as these groups travelled southwards towards where the source vessel would have been, and deviated slightly from their predicted pathway, this resulted in a small negative DDsv (in the order of two body lengths). Using baseline data, however, can also give some idea of a response threshold. A deviation in group movement of more than 240 m was outside the 95% CI of the baseline data and could therefore be considered to be a significant response. Applying as the response threshold meant that groups ‘avoiding’ the source vessel did so by about 300 m and groups that ‘approached’ the source (decreased their distance to the source vessel) did so by 330 m. Other groups did not significantly deviate from their predicted pathway (did not ‘respond’) resulting in no discernable change in distance to the source vessel.

The ‘avoidance’ response of groups in the active treatments was relatively small, in that if groups deviated from their original course by about 525 m, this resulted in a 300 m deviance from the source vessel. Typical humpback whale groups at this study site travel at an average speed of 4 km/h (Noad and Cato, 2007). If continuing along the same direction, at the same speed, for another 10 minutes, a group would be expected to travel another 670 m. If, however, the group responded dramatically (i.e. swam rapidly northwards), the maximum deviation of the group from its predicted pathway would be approximately 2670 m (assuming a travel speed of 12 km/h), five times greater than observed. In this study, even the outlier groups displayed a deviance from their original course of only 1500 m, and these two groups approached the source vessel causing a ‘shut-down’ (where the experiment was halted due to groups reaching received SELs greater than 170 dB re 1µPa².s per shot, our criterion for shut down). Apart from these two groups, the maximum group deviation from their predicted pathway was just over 1000 m resulting in a 750 m deviance...
from the source vessel. Therefore, using baseline data combined with the results of previous studies, allows these ‘responses’ to be put into biological context regarding their severity.

The fact that groups all did not significantly ‘avoid’ the source vessel in response to the treatments used illustrates that changes in group movement behavior cannot simply be attributed to avoidance of the source vessel. Some groups did ‘avoid’ the source (as defined in this study), whereas others did not respond, and a few ‘approached’ the source meaning that, at a population level, their overall difference in distance to the source vessel was similar to the baseline groups. This difference in reaction could be attributed to the social context of the group. It has been hypothesised previously that single males are more likely to approach the source (McCauley et al. 2003) whereas females with newborn calves may be more likely to avoid the source (Dunlop et al. 2015; McCauley et al. 2003). The probability of a group avoiding the source is also likely to be related to its proximity to the source and/or received level (De Ruiter et al., 2013; Goldbogen et al., 2013; Miller et al., 2014; Williams et al., 2014). Therefore, further analysis should include other potential predictor variables (such as social context, proximity and received level) along with ‘treatment’ to test for these effects.

Here we have presented a simple methodology with which to relate a change in movement behavior of an animal, or group of animals, to its position relative to a moving source. This method can easily be applied to other studies and negates the need for multiple movement response variables. In addition, using baseline data, it provides a way with which to quantitatively determine a response threshold.

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