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Research Article

Statistical Dependence for Detecting Whale-Watching Effects on Humpback Whales

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ABSTRACT Whale-watching is one of the fastest growing ecotourism industries and involves the observation of endangered wild cetacean species. However, this growth has raised concerns because of the negative effects this activity may have on the behavior and survival of focal species. Hence, detecting the effects of this activity requires sensitive analytical methods allowing the implementation of regulations to protect cetacean welfare. We compared the performance of different hypothesis tests from classical and Bayesian approaches to detect whale-watching effects on humpback whale (*Megaptera novaeangliae*) behavior. From a cliff located 31 m above sea level in northern Peru, we measured breathing frequency, surface time, long dive duration, directness index (i.e., path linearity), and swimming speed of humpback whales before, during, and after encounters with whale-watching boats. During 167 hours of observation, we tracked 180 humpback whale groups; 43% of groups had calves and 57% did not. Inference by null-hypothesis testing indicated significant changes only in directness index after boat encounters in groups with a calf. Other methods of inference detected moderate behavior responses as increments in the number of adult breaths, swimming speed, and dive intervals for adults and calves. Whale-watching regulations must be implemented in Peru to regulate number of boats, distance to whales, approximate speed, and time observing humpback whales. Whale-watching of humpback whales with calves should be avoided. © 2018 The Wildlife Society.

KEY WORDS anthropogenic disturbance, Bayesian inference, ecotourism, management, *Megaptera novaeangliae*, null-hypothesis test, short-term response.

Whale-watching is one of the fastest growing ecotourism industries in the world. This activity has shown a steady growth worldwide, with 13 million people undertaking whale-watching excursions in 2008 alone (O'Connor et al. 2009). This expansion has also been translated into economical benefits; in 2010, whale-watching generated 2.5 billion dollars (U.S.; Cisneros-Montemayor et al. 2010). The growth of whale-watching has raised concern amongst the scientific community because of the potential for lethal effects, such as collision events, and non-lethal effects, such as behavioral responses that may negatively affect energy expenditure, feeding, and reproductive success of cetacean species (Lusseau 2005, Bejder et al. 2006, Christiansen et al. 2014). Human disturbance is defined as "any human activity that induces changes to the contemporaneous behavior and/or physiology of one or more individuals" (Nisbet 2000:313). Human disturbance to the behavior of wild animals has been demonstrated to lead to short-term and long-term negative consequences on population wellness (Bejder et al. 2006, Weinrich and Corbelli 2009). Whale-watching initiates short-term behavioral responses in cetaceans including longer dive time intervals, decreased number of aerial behaviors such as tail slaps and side flukes, decreased group cohesion, increased swimming speed, and changes from a straight to sinuous path on movement directness (Christiansen et al. 2010, Stamation et al. 2010, Schaffar et al. 2013, Argüelles et al. 2016). The evidence of these negative whale-watching effects has motivated the implementation of whale-watching regulations and conduct codes worldwide (Orams 2000, Brownell and Oosthuizen 2004, Constantine et al. 2004, International Whaling Commission 2009).

In any given region, whale-watching activities focus on species in which behavioral patterns are context-dependent because distinct regions and habitats may serve different biological purposes (e.g., feeding, traveling, mating, calving). For instance, humpback whales (*Megaptera novaeangliae*) at feeding grounds seem to be indifferent to the presence of whale-watching vessels (Weinrich and Corbelli 2009), whereas in migratory corridors, approaching whale-watching vessels instigated deeper dives and a decrease in breathing frequencies (Corkeron 1995, Stamation et al. 2010). Moreover,

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habituation (the adaptation of cetaceans to repeated presentations of a signal) could reduce our ability to detect behavioral responses. Animals could tolerate some degree of disturbance if their benefits in terms of feeding, mating, or migrating are being threatened (Würsig and Richardson 2015). Because cetaceans are sensitive to acoustic pollution, the noise emitted by vessels may also initiate behavioral reactions before boats approach whales. Whales are subject to various and overlapping anthropogenic stressors throughout their migration, making the identification of a direct cause and effect relationship between the presence of whale-watching vessels and whale behaviors challenging. Habitat, life history, and natural behavior of cetaceans are intrinsically variable, so the magnitude of responses associated with the presence of whale-watching boats must be interpreted with caution. All these factors will likely affect our ability to accurately detect whale-watching effects (Childress and Lung 2003, Wade et al. 2012), which would have important consequences on the management of whale-watching activities. Thus, statistical methods are brought into question. Whale-watching effects are broadly studied by measuring a given behavioral response variable, often using a design that involves sampling before, during, and after the presence of whale-watching boats (Morete et al. 2007, Senigaglia et al. 2016). Behavioral variables are compared using null hypothesis significance testing (NHST) of no whale-watching boat effects on the behavior. Although, the NHST approach is commonly used, it has been criticized and shown to be not suitable in many biological and ecological situations (Carver 1978, Cohen 1988, Guttman 1985, Hilborn and Mangel 1997, Gerrodette 2011). The main criticisms about NHST rely on its high dependence on the sample size. After data are obtained a probability value (*P*-value) is estimated for the statistical test. The *P*-value is the probability of an observed effect given that the null hypothesis is true. However, with a larger sample size there would be a higher probability that the null hypothesis would be rejected correctly (i.e., the type II error is decreased; Johnson 1999). Bayesian inference has an advantage, in that it combines all factors and variables together, hence less information is lost during analysis and large sample sizes do not influence falsification of the null hypothesis. In Bayesian inference, 95% confidence intervals are interpreted as 95% credible intervals, meaning the probability that the true value of the parameter exists within the 95% interval (Johnson 1999). Thus, the magnitude of variation of the parameter can be used as criteria to assess the degree of support of the hypothesis rather than accepting or rejecting it as in NHST. Considering these caveats in NHST, it is important to consider alternative or complementary methods that could fit well in the context of ecological studies, particularly those assessing effects on charismatic and endangered species. Very few studies explore combinations of statistical methods, despite harsh criticisms of NHST over the decades (Stephens et al. 2007). An illustrative example is provided by Gerrodette (2011), who reported that model-based and Bayesian inference analyses were far more informative than NHST for detecting a population decline in the abundance of the vaquita (*Phocoena sinus*), the most endangered marine cetacean species in the world.

A small-scale whale-watching industry, focused on the observation of humpback whales during their breeding season, started in the northern coast of Peru in 2009 (Pacheco et al. 2009, 2011; Guidino et al. 2014). The activity has expanded every year, from 1 boat operating in 2009 up to 16 boats in 2016. There are no governmental whale-watching regulations in Peru, which led to the need to operate under a voluntary conduct code (Pacheco et al. 2011). This whale-watching voluntary conduct code is based on 3 factors: the number of observing vessels, the observation time, and the distance between whales and vessels. However, no studies regarding the acceptance of the conduct code have been performed. Although, there have been efforts to transmit this conduct code to all whale-watching operators in the region, it is not clear whether all boats normally follow the conduct code. Therefore, it is important to assess whether whale-watching is affecting humpback whale behavior, particularly when this activity has been promoted as an alternative to whaling and a potential tool to foster species and environmental conservation (Garcia-Cegarra and Pacheco 2017).

We evaluated the responses of humpback whales via a suite of behavioral traits (e.g., swimming speed, directness index, breathing frequency, long dive duration, surface time) considering scenarios before, during, and after whale-watching vessel encounters in northern Peru. We also compared use of NHST (1-way analysis of variance [ANOVA] and Kruskal–Wallis) and non-NHST (Bayesian inference, likelihood ratio test, and Akaike's Information Criterion) for estimating magnitude of behavioral responses of humpback whales subjected to whale-watching.

STUDY AREA

We performed daily land-based surveys from a natural land elevation (i.e., la mesa), which provided an elevation of 31 m above sea level allowing panoramic coverage of a 7-km radius of the coastal area between Los Organos (4°10′38.23″S, 81°8.27′4.83″W) and Cabo Blanco (4°15′1.36″S, 81°13′50.17″W) where whale-watching activities take place (Fig. 1). In this area, 2 important oceanic currents converge, the cold and nutrient-rich Humboldt Current flows northward and the warm, less productive Equatorial Countercurrent flows from East to South (Spalding et al. 2007). The coastline is straight without main inlets or embayments. Observation conditions were favorable during the entire study period with 95% of days with approximately 6–10 km of visibility. We conducted observations from 15 August until 15 October 2016, encompassing the core timing of the humpback whale breeding season in northern Peru.

METHODS

Humpback Whale and Whale-Watching Boat Tracking

We used a total station (Nikon NPL-322, Nikon-Trimble, Tokyo, Japan) to record humpback whale behaviors before, during, and after an encounter with a whale-watching vessel. Whale-watching activities in the area started at 0700 and finished at 1000 because of late strong wind conditions; thus,

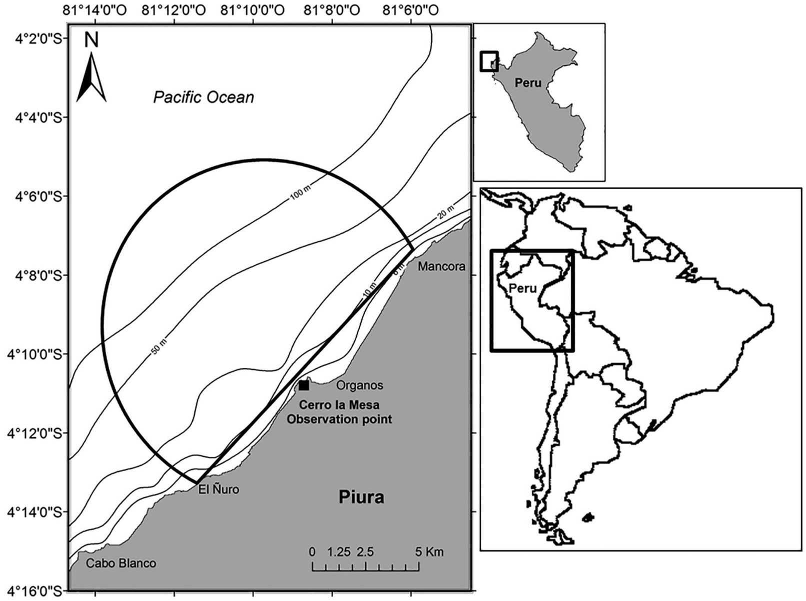

Figure 1. Our survey station in Los Organos (Northern Peru) where we surveyed humpback whale response to whale-watching boats, 2016. The semi-circle represents the 7-km radius of the panoramic view covered by the total station.

we surveyed before the departure of whale-watching boats and finished when the activity ceased in the area. The total station measured angles in the horizontal and vertical planes together with the timing of each position. Prior to tracking, 2 observers spotted humpback whales in the area using 15 × 50 Nikon binoculars under weather conditions with Beaufort sea state <3 (Beer 1996) and visibility up to 1 km. We determined group composition during the initial surface sighting. When observers were able to locate and unequivocally follow a group of humpback whales for >10 minutes, they chose that group for tracking. We defined a group as a pod of humpback whales in which individuals were within 100 m of each other, moving in the same direction and displaying a similar diving and movement pattern (Mobley and Herman 1985, Whitehead 1983). We determined mother and calf groups according to the size of the calf, estimated to be a third to a half of the length of the accompanying adult (assumed to be the mother). We classified groups according to the number of whales, the presence of calves, surface behavior (i.e., traveling, resting, mating, breach, fluke slap, pectoral fin slap; Corkeron 1995), and the presence or absence of whale-watching boats. For the analysis, we considered mother-calf and mother-calf plus escort groups as calf groups, and the rest of groups as non-calf groups (Table 1).

We considered whale-watching boats to be with a group of whales when they were within 100–400 m of the whales, and we considered the minimum interaction time between whale-watching vessels and humpback whales to be 10 minutes to standardize the response variable recorded. We recorded the number of whale-watching boats observing a group of whales. We obtained angle data from the total station and downloaded data to a personal computer using Transit version 2.35 software (Nikon). We further processed these data using the trigonometric relationship between the vertical and horizontal angles and the known height of the total station to obtain the geographic positions of cetaceans and vessels tracked (Davis et al. 1981, Würsig et al. 1991). We did not correct geographic positions for earth curvature. Instead, we performed a preliminary analysis of tracking accuracy by a boat navigation simulating a whale, recording boat positions every 5 minutes with the total station. We recorded an error of up to 35 m of deviation for distances

Table 1. Humpback whale group composition and categories used as predictor variables during peak breeding season in Northern Peru, 15 August–15 October 2016.

Group composition	Description
Non-calf groups	
Single	One single adult or sub-adult whale
Pair	Two adults
Trio	Three adults
Competitive group	A group of ≥3 whales showing intense aerial displays (frequent breaching and leapings) presumed to be a group of males pursuing a female
Navigation group	A group of ≥3 whales swimming in same direction but not engaged in competition
Calf groups	
Mother-calf	A calf and a single adult, presumed to be the mother
Mother-calf-escort	A mother and calf pair joined by a single or more escorts
Boat encounter scenarios	
Without boat	Groups tracked in absence of boat
Before-during	Groups tracked before and during boat presence
Before-during-after	Groups tracked before, during, and after boat presence
During-after	Groups tracked during and after boat presence
With boat	Groups tracked with boat presence all the time

>4.5 km (Romero 2015). We loaded geographic coordinate positions in Google Earth (Google, Mountain View, CA, USA) using Kml Creator (http://www.apps.ingeapps.com/gtools/en/kml-creator.php, accessed 10 Oct 2016).

We used humpback whale group tracks in Google Earth to estimate swimming speeds and the variation in movement of path course. We analyzed 5 behavioral response variables: directness index and swimming speed for groups of whales and breathing frequency, long dive duration, and surface time for individuals. The directness index was equivalent to the milling index (Tyack 1982); it consisted of the distance of the complete track of a group of whales divided by the cumulative distance between surface intervals. The index ranged from 1 (animals moving in a straight line) to 0 (animals moving in a circle). We estimated mean swimming speed as the speed between 2 surfacing events. We averaged all speeds of surfacing intervals to take into account the total distance of the track. We calculated mean breathing frequency as the number of blows per minute of each humpback whale group during the tracking session. Long dive duration was the time interval when whales undertook a prolonged dive and displacement >60 seconds. Surface time was the time at the surface for breathing between long dives <60 seconds. We conducted land-based surveys under the approval of the Scientific Research Ethics Committee of the University of Antofagasta (CEIC REV numbers 039/2017 and 7298/2015).

Statistical Analysis

We estimated mean swimming speed, directness index, long dive duration, surface time, and breathing frequency of humpback whale groups with and without calves in different scenarios of whale-watching (Table 1). To test the null hypothesis of no effects on behavioral responses during boat encounter scenarios, we used NHST in 2 ways: when variables met the assumptions for parametric tests, such as swimming speed, breathing frequency for calf groups, and surface time for non-calf groups, we used 1-way ANOVA, otherwise we used the non-parametric Kruskal–Wallis test using Minitab version 17 software (Minitab, State College, PA, USA). We performed 1-way ANOVA separately for non-calf and calf groups (single, pair, trio, competitive group, and navigation groups were non-calf groups). For example, to test whether changes in swimming speed were significant for calf groups in the different vessel encounter scenarios (before-during-after = BDA; before-during = BD, during-after = DA), we considered each scenario as a factor (Fig. 2). The null-hypotheses were:

H_0: calf group mean swimming speeds were equal in BDA scenarios,

$H_0^1 : \mu_B = \mu_D$(BD),

$H_0^2 : \mu_D = \mu_A$ (DA), and

$H_0^3 : \mu_B = \mu_D = \mu_A$(BDA).

Under the model:

$$Y_i = \mu_B + \mu_D During_i + \mu_A After_i + \varepsilon_i,$$

where $During_i$ and $After_i$ are 1 for observations measured during or after the boat, respectively, and 0 otherwise and

Y_i = swimming speed change observation

μ_B = swimming speed change before the boat

μ_D = swimming speed change during the boat

μ_A = swimming speed change after the boat, and

ε_i = experimental error for ith observation.

We used non-NHST to model the behavioral responses that better explained the magnitude of whale-watching vessel encounters (see Supporting Information for additional response variable model examples, available online). We analyzed data on mean swimming speed, long dive duration, surface time, and breathing frequency separately based on a log-normal regression model under a Bayesian approach using vague priors. For instance, for mean swimming speed

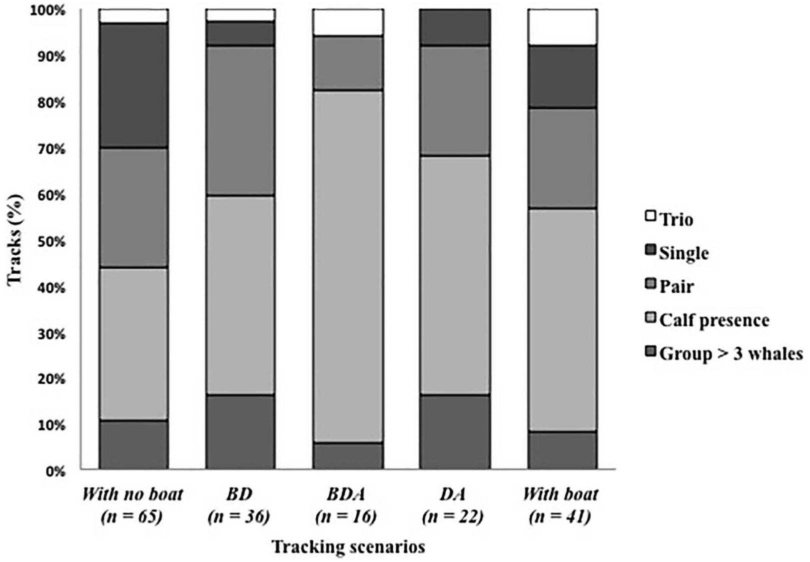

Figure 2. Percentage of humpback whale groups during the study period in the different scenarios (with no boat presence; BD = before and during boat presence; BDA = before, during, and after boat presence; DA = during and after boat presence; with boat presence; *n* = number of groups in each scenario).

the model fitted was:

$$\textit{mean swimming speed}_i \sim LN\left(\mu_i, \sigma^2\right), i = 1, \ldots, n,$$

where n is the sample size excluding missing observations, $LN(\mu, \sigma^2)$ denotes the log-normal distribution with location and scale parameters μ and σ, respectively, and density function given by

$$f(x) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{(\ln(x) - \mu)^2}{2\sigma^2}\right), x > 0, \mu \in \mathcal{R} \text{ and } \sigma^2 > 0,$$

with $\mathcal{R}$ the set of the real numbers and $\mu_i = \beta_0 + \beta_1 \textit{calf} + \beta_2 \textit{during boat} + \beta_3 \textit{after boat}$.

Because the DI (directness index) variable response ranged from 0 to 1, we considered a beta regression model (Ferrari and Cribari-Neto, 2004) for the analysis. In this case, the density function for beta model with mean μ and precision parameter ϕ is:

$$f(x) = \frac{\Gamma(\phi)}{\Gamma(\mu\phi)\Gamma((1-\mu)\phi)} x^{\mu\phi - 1}(1-x)^{(1-\mu)\phi - 1}, 0 < x < 1, 0 < \mu < 1 \text{ and } \phi > 0.$$

The covariates are included in the same way as previously noted.

The hypotheses of interest were:

$H_0^{(1)} : \beta_1 = 0$ versus $H_1^{(1)} : \beta_1 \neq 0$ (calf effect)

$H_0^{(2)} : \beta_2 = 0$ versus $H_1^{(2)} : \beta_2 \neq 0$ (BD)

$H_0^{(3)} : \beta_2 = \beta_3 = 0$ versus $H_1^{(3)} : \beta_2 \neq 0$ or $\beta_3 \neq 0$ (BDA)

$H_0^{(4)} : \beta_3 = 0$ versus $H_1^{(4)} : \beta_3 \neq 0$ (DA)

We tested these hypotheses using 4 measures of evidence. First we calculated 95% credible intervals (CrI). Bayesian approaches summarize their uncertainty by giving a range of values on the *posteriori* probability distribution that includes 95% of the probability. The shortest interval is called the highest posterior density interval. Next, we calculated Bayesian probability $P(\beta_j > 0)$ and $P(\beta_j < 0)$, for $j = 1, 2, 3$ and $P(\beta_2 - \beta_3 > 0)$ and $P(\beta_2 - \beta_3 < 0)$, which are the probabilities of a decrease or increase of any amount of the measured response variables under a Bayesian approach. We considered values >0.75 indicative of support for positive, $P(\beta_j > 0)$, or negative, $P(\beta_j < 0)$, relationships (Kass and Raftery 1995). We used a likelihood ratio test (LR) to compare the goodness of fit of the model considering an effect on a behavior response variable measured in relation with the non-effect model. An LR of 1 means that the model does not explain the effect on the response variable. We considered the highest LR to explain the model effect on the response variable. Finally, we used the difference in Akaike's Information Criterion (ΔAIC) to compare a model with and without a specific parameter. For example, to investigate if calf presence influenced swimming speed changes under vessel presence, we compared the hypotheses H_0:$\beta_1 = 0$ versus H_0:$\beta_1 \neq 0$ by fitting the complete model (estimating all parameters) and the reduced model (estimating all parameters with the restriction $\beta_1 = 0$). High ΔAIC values (>3) suggest that $\beta_1 \neq 0$ and calf presence influences swimming speed changes under whale-watching vessels presence. We conducted all inference statistics in R version 3.5.1 (R Development Core Team 2018).

RESULTS

We obtained 167.3 hours of land-based observations during 50 days between August and October 2016. We recorded 415 whales and used 180 focal groups for the descriptive analysis; we observed calves in 43% of humpback whale groups. More than half (57%) of groups recorded were in the presence of whale-watching boats. The most important groups in terms of their contribution to the percentage of sightings were groups with calf presence in all scenarios when whale-watching vessels were present, followed by pair groups (Fig. 2). From the 180 focal groups, we tracked a subset of 71 calf groups and 79 non-calf groups >10 minutes and included them in statistical analyses (Table 2).

Table 2. Mean values and standard deviation (SD) of rates of occurrence of behavior events of humpback whale calf and non-calf groups in northern Peru, 2016, in the scenarios of whale-watching boat presence: absence of boats, before-during, before-during-after, during-after, and with boat presence the entire time.

		Before-during dataset		**Before-during-after dataset**			**During-after dataset**		
	No boat $\bar{x}$ (SD)	**Before $\bar{x}$ (SD)**	**During $\bar{x}$ (SD)**	**Before $\bar{x}$ (SD)**	**During $\bar{x}$ (SD)**	**After $\bar{x}$ (SD)**	**During $\bar{x}$ (SD)**	**After $\bar{x}$ (SD)**	**With boat $\bar{x}$ (SD)**
With calf	$n = 21$	$n = 14$		$n = 9$			$n = 11$		$n = 16$
Directness index	0.85 (0.2)	0.92 (0.1)	0.9 (0.1)	0.6 (0.3)	0.9 (0.1)	0.67 (0.2)	0.8 (0.3)	0.9 (0.1)	0.76 (0.2)
Swimming speed (m/sec)	1.4 (0.6)	1.24 (0.5)	1.5 (0.5)	1.06 (0.6)	1.05 (0.5)	1.06 (0.6)	1.45 (0.4)	1.6 (0.4)	1.5 (0.7)
Mean breathing frequency (blows/min)	0.7 (0.5)	0.56 (0.2)	0.55 (0.2)	0.42 (0.2)	0.53 (0.1)	0.52 (±0.3)	0.51 (0.2)	0.75 (0.3)	0.5 (0.3)
Long dive duration (sec)	311 (203)	330 (146)	364 (132)	301 (184)	276 (140)	365 (178)	265 (103)	477 (366)	417 (283)
Surface time (sec)	24 (5.8)	20.9 (5)	23.2 (7)	21.2 (7)	25.8 (7.6)	23.5 (9.8)	25.9 (3.3)	25 (13)	20 (7.3)
Without calf	$n = 36$	$n = 15$		$n = 3$			$n = 5$		$n = 20$
Directness index	0.8 (0.2)	0.9 (0.1)	0.8 (0.1)	0.76 (0.2)	0.78 (0.3)	0.97 (0.01)	0.67 (0.12)	0.55 (0.1)	0.9 (0.1)
Swimming speed (m/sec)	1.7 (0.5)	1.7 (0.5)	1.8 (0.4)	1.5 (0.8)	1.7 (0.6)	2 (0.5)	1.9 (0.5)	1.6 (0.6)	1.8 (0.6)
Mean breathing frequency (blows/min)	0.8 (0.5)	0.85 (0.3)	0.87 (0.5)	0.48 (0.3)	0.6 (0.2)	0.8 (0.2)	0.8 (0.2)	0.9 (0.5)	0.7 (0.5)
Long dive duration (sec)	500 (242)	460 (311)	402 (144)	419 (239)	407 (239)	403.7 (97)	346 (142)	555 (411)	492 (298)
Surface time (sec)	20.8 (7.3)	18.3 (6.6)	24.7 (9.8)	20.7 (1.5)	12.7 (5.8)	18.7 (9)	24.8 (7)	23.8 (5.5)	24 (5.8)

Table 3. Null hypothesis significance testing (NHST) and non-NHST analysis of whale-watching boat effects on humpback whale calf and non-calf groups in northern Peru, 2016, for groups with observation data before and during boat presence. Test statistics are for Kruskal–Wallis test (*H*) or 1-way analysis of variance (*F*) and test for differences in behaviors between observations before and during boat presence. Results with an asterisk (*) were supported.

	NHST		95% credible interval			Bayesian *P* value		
Model	**Test statistic**	***P***	**Lower**	**Upper**	**Likelihood ratio**	***P*** **($\beta < 0$)**	***P*** **($\beta > 0$)**	**ΔAIC[a]**
Calf groups								
Directness index	$H_1 = 2.12$	0.146	−0.2157	0.0138	1.3570	0.9601*	0.0399	1.3895
Swimming speed	$F_1 = 1.50$	0.231	−0.1221	0.1006	1.0785	0.5728	0.4272	1.8489
Breathing frequency	$F_1 = 0.01$	0.966	−0.1007	0.1071	1.1727	0.5014	0.4986	1.6814
Long dive duration	$H_1 = 0.26$	0.613	−0.0488	0.1423	2.9079	0.1585	0.8415*	0.1348
Surface time	$H_1 = 0.85$	0.357	−0.0743	0.0673	1.3526	0.5746	0.4254	1.3960
Non-calf groups								
Directness index	$H_1 = 1.50$	0.472	−0.0913	0.0200	1.1763	0.8998*	0.1002	1.6752
Swimming speed	$F_1 = 0.67$	0.417	−0.0515	0.3581	1.0451	0.0776	0.9224*	1.9118
Breathing frequency	$H_1 = 0.21$	0.646	−0.0745	0.0285	1.4500	0.7925*	0.2075	1.2569
Long dive duration	$H_1 = 0.01$	0.963	−0.1159	0.1897	1.0481	0.3177	0.6823	1.9060
Surface time	$F_1 = 3.46$	0.076	0.0214*	0.2468*	3.1396	0.0090	0.9910*	0.2882

[a] Difference in Akaike's Information Criterion between the complete model and a reduced model (i.e., restricted to $\beta_2 = 0$).

The maximum number of whale-watching vessels with the same group of whales was 6 in 5.8% of the observations. Most of the observations (31.0%) were with 2 vessels, followed by 3 vessels (22.3%) and presence of 1 and 4 vessels shared 17.5% of observations. We observed an average of 2.79 ± 0.996 (SD) whale-watching vessels with the same group of whales with an average time of 48.2 minutes and distances ranging from 3 m to 315 m. We did not detect behavioral changes in any response variables according to the number of vessels involved in the track using NHST or non-NHST methods. At Los Organos, commercial whale-watching operates every day from July to November. In addition to commercial whale-watching vessels, other vessels such as recreational, artisanal fishing, and large cargo vessels were present in the area, but these did not follow whales. Thus, we did not consider the presence of other vessels other than whale-watching vessels in the effects on the behavior of humpback whales. However, we did not discard the fact that other vessels in the area may affect humpback whale behavior and this deserves further research. In all scenarios with whale-watching vessel present, humpback whale calf groups swam slower, performed shorter long dives, and shorter surface time than non-calf groups (Table 2). Humpback whale calf groups with whale-watching vessels showed less breathing frequency when compared with calf groups with no vessel presence. Non-calf groups in the presence of whale-watching vessels spent more time at the surface than those groups without whale-watching vessel presence.

Humpback Whale Behavior Responses

In the before-during scenario, NHST did not detect significant changes in any behavioral responses of humpback whale groups (Table 3). Bayesian inference, however, indicated that humpback whale calf and non-calf groups performed a more sinuous navigation path in the presence of whale-watching boats. Bayesian inference also indicated that humpback whale groups without calves increased mean swimming speed during vessel presence. Calf groups performed longer dives during whale-watching vessel presence. Bayesian inference statistics and 95% credible intervals demonstrated that humpback whales without calves displayed longer surface times during whale-watching vessel presence.

Table 4. Null hypothesis significance testing (NHST) and non-NHST analysis of whale-watching boat effects on humpback whale calf and non-calf groups in northern Peru, 2016, for groups with observation data before, during, and after boat presence. Test statistics are for Kruskal–Wallis test (*H*) or 1-way analysis of variance (*F*) and test for differences in behaviors between observations before, during, and after boat presence. Results with an asterisk (*) were supported.

	NHST		95% credible interval			Bayesian *P* value		
Model	**Test statistic**	***P***	**Lower**	**Upper**	**Likelihood ratio**	***P*** **($\beta < 0$)**	***P*** **($\beta > 0$)**	**ΔAIC[a]**
Calf groups								
Directness index	$H_2 = 6.23$	0.045*	0.0263*	0.4204*	1.4933	0.0113	0.9887*	1.1980
Swimming speed	$F_2 = 0.20$	0.977	−0.1917	0.1434	1.0165	0.6477	0.3523	1.9673
Breathing frequency	$H_2 = 2.95$	0.229	−0.1676	0.0925	1.0008	0.7137	0.2863	1.9983
Long dive duration	$F_2 = 0.57$	0.576	−0.0361	0.2365	1.6965	0.0740	0.9260*	0.9429
Surface time	$H_2 = 0.65$	0.723	−0.1546	0.0643	1.0170	0.7787*	0.2213	1.9663
Non-calf groups								
Directness index	$H_2 = 1.50$	0.472	−0.0758	0.1173	1.0026	0.3760	0.6240	1.9949
Swimming speed	$F_2 = 0.65$	0.557	−0.1083	0.4130	1.0001	0.1379	0.8621*	1.9999
Breathing frequency	$H_1 = 3.24$	0.198	−0.0306	0.0965	1.6674	0.1587	0.8413*	0.9775
Long dive duration	$H_2 = 0.36$	0.837	−0.0415	0.3892	2.4668	0.0738	0.9262*	0.1941
Surface time	$F_2 = 1.31$	0.337	−0.0743	0.2494	2.3197	0.1469	0.8531*	0.3171

[a] Difference in Akaike's Information Criterion between the complete model and a reduced model (i.e., restricted to $\beta_2 = \beta_3 = 0$).

Table 5. Null hypothesis significance testing (NHST) and non-NHST analysis of whale-watching boat effects on humpback whale calf and non-calf groups in northern Peru, 2016, for groups with observation data during and after boat presence. Test statistics are for Kruskal–Wallis test (H) or 1-way analysis of variance (F) and test for differences in behaviors between observations during and after boat presence. Results with an asterisk (*) were supported.

	NHST		95% credible interval			Bayesian P value		
Model	**Test statistic**	P	**Lower**	**Upper**	**Likelihood ratio**	$P(\beta < 0)$	$P(\beta > 0)$	**ΔAIC**[a]
Calf groups								
Directness index	$H_1 = 0.1$	0.749	0.1224*	0.5297*	2.4523	0.0009	0.9991*	2.2060
Swimming speed	$F_1 = 1.7$	0.256	−0.1929	0.1387	1.0615	0.6082	0.3918	3.8806*
Breathing frequency	$H_1 = 2.52$	0.112	−0.1760	0.1004	3.9090*	0.6879	0.3121	1.2734
Long dive duration	$F_1 = 1.14$	0.316	−0.0912	0.1965	2.3250	0.2361	0.7639*	2.3125
Surface time	$H_1 = 2.27$	0.132	−0.1515	0.0751	1.3146	0.7379	0.2621	3.4529*
Non-calf groups								
Directness index	$F_1 = 0.7$	0.409	−0.0463	0.1552	1.0817	0.1524	0.8476*	1.8429
Swimming speed	$F_1 = 0.74$	0.404	−0.2314	0.2372	1.0194	0.5250	0.4750	1.9616
Breathing frequency	$H_1 = 0.02$	0.895	−0.0110	0.1304	3.3866*	0.0566	0.9434*	0.4397
Long dive duration	$H_1 = 0.01$	0.999	−0.1077	0.3285	2.4683	0.1341	0.8659*	2.1930
Surface time	$F_1 = 0.06$	0.808	−0.2260	0.1054	4.9880	0.7195	0.2805	0.7859

[a] Difference in Akaike's Information Criterion between the complete model and a reduced model (i.e., restricted to $\beta_2 = \beta_3$).

For the before-during-after scenario, NHST detected significant differences in only the calf group directness index (Table 4). Calf groups performed a more linear navigation path during whale-watching vessel presence. In contrast, Bayesian inference showed behavior differences in all response variables (Table 4). The Bayesian inference statistic and 95% credible intervals indicated an increase in linearity of the path for calf groups in the BDA scenario. Bayesian inference also indicated that non-calf groups increased mean swimming speed and all groups increased long dive durations. Humpback whales without calves also increased mean breathing frequency and displayed more surface time in the BDA scenario.

Although NHST did not detect significant behavioral responses of humpback whales in during-after scenarios, non-NHST suggested differences for all response variables (Table 5). Bayesian inference and 95% credible intervals indicated that calf and non-calf groups increased directness index after vessel presence. The AIC analysis indicated that the best model explaining decreases in swimming speed and surface time after whale-watching boat presence is the one that includes calf groups. Bayesian inference and the likelihood ratio test suggested that non-calf groups increased mean breathing frequency after whale-watching boat presence. In contrast, calf groups had a higher probability of decreasing mean breathing frequency after whale-watching vessel presence ($P[\beta < 0] = 0.6879$, $P[\beta > 0] = 0.3121$). Finally, Bayesian inference shows that non-calf humpback whale groups increased long dives durations after vessel presence (Table 5).

DISCUSSION

Overall, this study shows that whale-watching vessel presence induces short-term responses on path directness, swimming speed, breathing frequency, diving, and surface time behaviors of humpback whale groups in their breeding area of northern Peru. The detection of the effect, however, was dependent on the statistical method of choice. For example, NHST only detected significant behavioral responses of humpback whale calf group directness in the BDA whale-watching vessel presence scenario but failed to detect effects on behavioral responses in all other whale-watching scenarios. Conversely, Bayesian inference supported the hypothesis that whale-watching vessels affect the mean swimming speed, directness index, mean breathing frequency, long dive duration, and surface time of humpback whales in the breeding area in all whale-watching vessel presence scenarios. Non-NHST methods proved to be more informative tool than NHST to understand whale behavioral responses to whale-watching vessel encounters.

Bayesian inference results showed that humpback whale groups increased breathing frequency during and after whale-watching, but calf groups showed a higher trend of decreasing breathing frequency during and after whale-watching ($P[\beta < 0] = 0.7137$, $P[\beta > 0] = 0.2863$; Table 4). These results concur with previous studies showing that humpback whale groups with calves present are more susceptible to the presence of boats by decreasing their respiration rates during whale-watching boat presence (Baker et al. 1982, Morete et al. 2007, Stamation et al. 2010). Corkeron (1995), however, did not report significant differences in breathing rates for calf and non-calf groups in the presence of whale-watching boats in the migratory corridor of Hervey Bay, Australia. As highlighted above with the issues on NHST, Corkeron (1995) used a rather small sample size ($n = 12$, calf pods boats absent; $n = 19$ calf pods boats present) and the high standard deviation of mean breathing rates for both absence and presence of vessel scenarios might preclude the detection of significant effects in his data set. Corkeron (1995) suggested the existence of trends on whale responses, yet the lack of significance led to the conclusion of no effects. As shown in our analysis, the addition of non-NHST is useful in instances where NHST compromise the tendency of data with significance.

Humpback Whale Behavioral Responses to Whale-Watching Boats

We detected changes in directness index of humpback whale movement during whale-watching vessel presence in all scenarios and with all statistical methods. Humpback whale groups undertook a sinuous swimming path when whale-watching vessels were present but the whales' paths became linear after vessel departure (Tables 4 and 5). Whale-watching effects on path linearity have been documented in breeding and feeding grounds of humpback whales elsewhere (Scheidat et al. 2004, Lundquist et al. 2008, Timmel et al. 2008, Williams et al. 2009, Senigaglia et al. 2016). Similar responses have been observed in other cetacean species, such as southern right whales (*Eubalaena australis*) and killer whales (*Orcinus orca*), which evaded boats by adopting a more sinuous path (Williams et al. 2006, Lundquist 2007). Responses such as undertaking a linear path of movement have been attributed to the fact that cetaceans may perceive human disturbance as a potential predator, thus exhibiting an escape response (Corkeron 1995, Frid and Dill 2002, Beale and Monaghan 2004, Scheidat et al. 2004, Schaffar et al. 2010).

According to Bayesian inference statistics, humpback whale groups with calves swam slower than groups without calves and when whale-watching boats were present, calf groups tended to decrease swimming speed ($P\ [\beta < 0] = 0.6477$; Table 4), whereas non-calf groups increased swimming speed. A plausible reason for these differential responses among calf and non-calf groups could be that calves naturally swim slower than adult animals as they are developing their body and skills for migration. Increasing speed could involve an additional energetic expenditure that calves at a young age are yet not able to undertake. Mothers may adopt a vigilant attitude that may cease normal behavior, which can be translated into a reduction of swimming speed. Such responses have been observed in bottlenose dolphins (*Tursiops* spp.) with females and males reacting differently during whale-watching vessel encounters. This has been attributed to females saving valuable energy for their calves (Lusseau 2003). Morete et al. (2007) reported significant differences in humpback whale mother-calf group behaviors when whale-watching vessels were at 300 m distance, but they did not find significant differences in swimming speed, path directness, blow interval, lap, or fluke up behaviors when whale-watching vessels were <100 m distance from whales. Morete et al. (2007) argue that the low sample size in the <100-m distance scenario (6 groups of humpback whales) could have led to a type II statistical error in their analysis. We argue that the use of a Mann–Whitney test was not sensitive enough to detect behavior changes when whale-watching vessels were <100 m distance. We suggest that the use of non-NHST analyses would have helped to assess behavior responses of humpback whale mother-calf groups to different whale-watching vessel distances when the number of observations is compromised.

Our results showed that humpback whale calf groups avoided whale-watching vessels in the vertical plane by adopting a more sinuous path, longer dives, and by decreasing breathing frequency. Contrarily, non-calf groups avoided whale-watching vessels in the horizontal plane by increasing swimming speed, surface time, and breathing frequency in BD and BDA whale-watching vessel presence scenarios. At a migratory corridor for humpback whales off Australia, Stamation et al. (2010) indicated that <50% of the whales recorded showed behavioral changes in the horizontal plane (i.e., increasing swimming speed and taking a more sinuous path in the presence of whale-watching boats). Using multivariate NHST methods, analysis of similarity (Clarke and Green 1998) and analysis of similarity percent (Clarke 1993), the authors were not able to detect vertical plane avoidance responses in dive durations and diving time of humpback whales; 95% confidence intervals overlapped. For NHST, if a study is repeated an infinite number of times, the 95% confidence intervals would contain the true value of the studied parameter. When 95% confidence intervals overlap, biological or ecological parameters studied may show tendencies of change, but these are insignificant in NHST (Johnson 1999). Bayesian inference is not necessarily skewed by the overlap of the 95% confidence intervals; hence, is a more sensitive tool in detecting the magnitude of changes. When studying wild animals, which perform a wide variety of different behavior responses under human disturbance, the challenge is to detect when anthropogenic threat is affecting animal behavior. Our study provides a comparison of statistical methods for the detection of humpback whales behavioral changes in response to the presence of whale-watching vessels. Understanding the magnitude of an effect is the first step. Future studies could apply Bayesian inference on a larger sample of tracked whale-vessel encounters and provide support for the establishment of proper guidelines. The results gathered in this study demonstrate that in northern Peru whale-watching vessel presence leads to disturbance of behavioral patterns of humpback whales in the area and especially of humpback whale mother-calf groups. Mother-calf groups are particularly vulnerable as whale-watching vessels disturb nursing and calving activities. Whale-watching of mother-calf groups is forbidden in countries such as Mexico (Magdalena Bay) or restricted in observation time such as in Panama (Carlson 2012, Garrod and Fennell 2004). In addition, whale-watching companies do not respect speed limits, minimum sighting distances, maximum number of vessels, and maximum time observing whales (e.g., we observed a whale-watching vessel observing the same mother-calf group for >1 hr; Fig. 3).

MANAGEMENT IMPLICATIONS

Although the Peruvian legislation for the whale-watching industry is currently under construction, we recommend that whale-watching regulations should be implemented in the country. As proposed by Pacheco et al. (2011), observations should be ≤25 minutes, ≤3 vessels should observe the same group of whales, vessel speed should be reduced when reaching 400 m distance between the vessel and the whales, and vessels should maintain a distance of 100 m from the whales during observation, and we propose after this study that mother-calf groups should be avoided for observation. We recommend that current effort must be placed in sharing whale-watching guidelines among all whale-watching operators. Because of the difficulties for obtaining

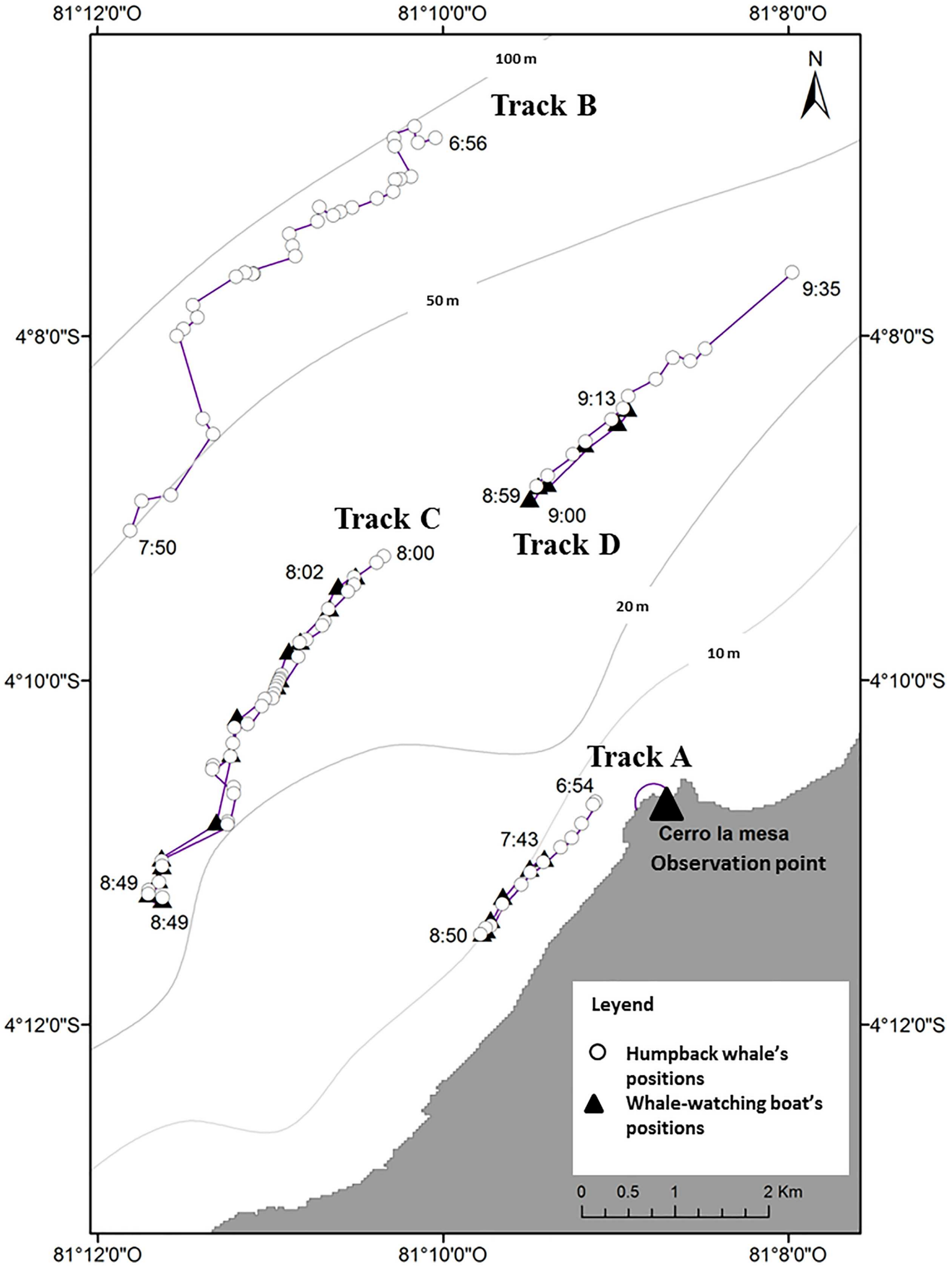

Figure 3. Example of a tracking session from Cerro la Mesa land-based observation point (31 m above sea level). The tracking took place on the 20 September 2016. A group of mother-calf humpback whales was first sighted at 0654 swimming slowly in southwest direction (Track A). They were joined by 1 whale-watching vessel at 0743 that stayed with the group until 0850. A group of 5 humpback whales was observed at 0656 swimming fast in a southwest direction (Track B). The whales showed a competitive group behavior, with strong breaths and active surface behavior. The group was not joined by any whale-watching vessel. At 0800 a mother-calf group of humpback whales was tracked swimming in a southwest direction (Track C). They were joined by 2 whale-watching vessels at 0802 and vessels stayed with the whales until 0849. Mother and calf groups showed a sinuous navigation path during whale-watching vessels encounter. A pair of humpback whales was sighted at 0900 followed by 1 whale-watching vessel (Track D). Whales were swimming in a northeastern direction and the vessel stayed with the whales until 0913. The whales were tracked after the whale-watching encounter until 0935.

short-term responses data (e.g., large sample size data in the field), we strongly recommend the application of non-NHST methods. Non-NHST methods allow the use of a small sample size to interpret trends in behavioral responses and provide more consistent results that can be proposed for management issues. This model could be applied to other cetacean species subjected to different human pressures around world.

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