

MODELING THE EFFECT OF BOAT TRAFFIC ON THE FLUCTUATION OF HUMPBACK WHALE SINGING ACTIVITY IN THE ABROLHOS NATIONAL MARINE PARK, BRAZIL

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ABSTRACT

Since the moratorium on whaling, the Brazilian government and local Non-Governmental Organizations (NGOs) have adopted and encouraged a more sustainable use of whales as tourist attractions. Nevertheless, concerns about boat traffic impacts on whale population health have arisen, especially in protected areas such as marine parks. The Abrolhos Marine National Park is the seasonal habitat for the breeding population of humpback whales in the Western South Atlantic. We acoustically monitored 7% of the park area during 26 days using marine autonomous recording units and evaluated the responses of whales to boat traffic by measuring changes in male singing activity. The recorded humpback whale songs were analyzed to locate and count individual singers. We modeled the fluctuation in the number of singers over time in response to: number of acoustic boat events, tide height, lunar phase, hour of the day, the quadratic function of hour of day, day of the season, and presence of light. Generalized linear models were used to fit the singer count data into a Poisson distribution and log link. We found an important negative effect of boat traffic on singing activity. There is evidence that the interaction between phases of the moon and the quadratic function of hour of day also affect singing behavior. Adaptive management should aim at reducing the number of noise events per boat, which can improve the whale watching experience and reduce the impact on male singing behavior.

SOMMAIRE

Depuis le moratoire sur la pêche à la baleine, et dans une optique de tourisme durable, une utilisation plus raisonnée des baleines en tant qu'attraction pour touristes a été adoptée et encouragée par le gouvernement brésilien et les O.N.G. locales. Mais des problèmes concernant les impacts du trafic de bateaux sur la santé des populations de baleines ont toutefois surgi, particulièrement dans des secteurs protégés comme les parcs marins. Le parc national marin d'Abrolhos abrite la population reproductrice des baleines humpback du sud-ouest de l'océan atlantique. Afin d'évaluer les réponses des baleines au trafic de bateaux, nous avons réalisé des enregistrements sonores sur 7% du parc pendant 26 jours en utilisant des unités autonomes marines d'enregistrement. Ces enregistrements nous ont permis de mesurer les changements dans l'activité de chant des mâles. Les sons émis par les baleines humpback ont été détectés et les différents chanteurs ont été localisés et comptés. Nous avons modélisé les fluctuations du nombre de chanteurs au cours du temps en fonction du nombre d'événements acoustiques émis par les bateaux, de l'amplitude des marées, de la phase lunaire, de l'heure, de la fonction quadratique de l'heure, de la date, et de la présence de lumière. Des modèles linéaires généralisés ont été utilisés pour adapter le nombre de chanteurs à une distribution de Poisson et un lien log. Nous avons trouvé un effet négatif important du trafic de bateaux sur l'activité de chant. L'interaction entre la phase lunaire et la fonction quadratique de l'heure semblent également affecter le comportement de chant. Une gestion adaptative devrait viser à réduire le nombre d'événements de bruit émis par les bateaux, qui améliorerait l'expérience d'observation des baleines et réduire l'impact sur le comportement de chant des mâles.

1. INTRODUCTION

There has been a dramatic increase in the appreciation of whales as living beings, with the shift away from exploitation (whaling) to ecotourism (whale-watching). However, whale-watching has been somewhat controversial. There can be costs associated with whale-watching to individuals and populations and this activity has coexisted with whaling in many cultures [1-2]. In Brazil, since the

moratorium on whaling was initiated, whale watching has been considered a more acceptable way to coexist with these large marine mammals. The potential negative effect of whale watching on marine mammals is of special concern in breeding areas, where animals congregate and where boat noise has been shown to be disruptive to vocal behavior related to reproduction [3-4]. In their wintering grounds, male humpback whales produce a conspicuous, long, and patterned sequence of sounds denominated as "song" [5]. Various hypotheses for the function of these complex male

vocal displays have been offered, and the prevailing one is that songs are socially important, and related to reproduction [6-12]. Boat disturbances of singing behavior on breeding grounds may thus affect individual mating success, and have even more far-reaching effects on the long-term viability of populations.

The Abrolhos National Marine Park is the most important breeding site for the southwestern Atlantic population of humpback whales [13]. Local whale-watching activity increased until 1998, and since then, the annual number of park visitors has been 4,000-5,000 people. The boat-based trips to Abrolhos provide substantial income to the small coastal towns from which the tour boats depart [14]. Increasing boat traffic from these coastal towns may put the Abrolhos humpback whale population at risk. Fortunately, as a designated Marine Park, there is the opportunity for better regulation of the potential human disturbances on the whales, while still allowing economically important ecotourism to continue.

Monitoring programs designed to improve management decisions should focus on the fundamentals of the humpback's biology: its population size, distribution, behavior, and mating system. In a marine environment, to disregard acoustic communication between individuals is to ignore their primary sensory modality which enables social interactions, and thus, the mechanisms that strongly influence reproductive success and the mating system. There is limited information about how whale vocal behavior varies through time. Studies on humpback whale singing activity have focused on geographic and temporal changes in song patterns [6, 15-24]. Only a few authors [25-28] have addressed temporal variability in the singing activity of individuals to evaluate effects of disturbances. Studies have shown an effect of noise from human activities on humpback whale singing activity [28-30] and in one case the factor that most influenced ambient noise was the total number of vessels passing within the area per unit time [31].

Here we employed advanced technologies in passive acoustics to: 1) explain the natural fluctuation in humpback singing over a 26-day period and 2) determine how the noise generated by boat traffic affects the variation in singing activity in the Abrolhos National Marine Park, Brazil. Our approach was to create multiple models incorporating variables that we hypothesized might affect singing behavior. A list of the hypotheses is presented. These hypotheses are not mutually exclusive; some of the variables may affect the others, so interaction terms between effects are included in the models. The prediction of each hypothesis is given in parenthesis and the specific variable is in bold.

H1) singing is negatively affected by boat noise (**Boats** has a negative coefficient);

H2) singing is a function of the density of whales and increases as the season progresses, peaks in September and decreases until the end of the season [32] (**Day** is not an important variable and the quadratic function, **Day**², has a negative coefficient but is not included in the models because data collection was concluded in August);

H3) singing increases linearly as the season progresses (**Day** has a positive coefficient);

H4) singing decreases as a function of density (**Day** has a negative coefficient, **Day**² has a positive coefficient);

H5) singing is intensified at night (**Light** has a negative coefficient);

H6) singing is affected by moon cycle, and will decrease during phases with moonlight (**Moon** has a negative coefficient when "Full" and positive when "New");

H7) singing increases with tide height (**Tide** has a positive effect), and;

H8) singing is a function of time of the day (**Hour**² has a positive effect; **Hour** has a negative effect).

2. METHODS

2.1. Data Collection

The Abrolhos Bank is located off the coast of Brazil between 16°40'-19°30'S covering an area of approximately 30,000km² [33]. The Abrolhos Marine National Park includes the Abrolhos archipelago in the northeast portion of the bank [34]. The local humpback whale population has been estimated at around 3,000 individuals [35], representing almost 15% of the total population of humpbacks thought to occur in the Southern Hemisphere [36]. Approximately 7% of the park area was acoustically monitored using an array of pop-ups (marine autonomous recorders developed by the Bioacoustics Research Program of the Cornell Lab of Ornithology - details at www.birds.cornell.edu/brp). Each pop-up carries an onboard clock that makes it possible to perform sound source localization and tracking of signals recorded by an array of synchronized pop-ups. Our array consisted of 4 pop-ups deployed northwest of the Abrolhos archipelago. The 4 pop-ups were programmed to record continuously from 22 July to 16 August, 2003 at a sampling rate of 2kHz.

2.2. Data Processing

The 4-channel sound files were submitted to detection and location algorithms. The detections were identified using 30 to 70 different templates of humpback whale sounds (song units) extracted from the same 24-hour recording using a custom software analysis program, XBAT (xbat.org). This detection procedure was repeated for each day of recording in order to avoid reduced detection probability due to changes in song units that are known to occur through time [18]. All XBAT detections were located using a custom location tool (Cortopassi & Fristrup, unpublished), and the resulting locations of each detected sound were checked by an experienced analyst using a browsing time window of 10 to 30s. This protocol insured that false detections and locations were eliminated and that missed humpback whale sounds were detected and located individually. Detections of boat acoustic events were done manually by an operator listening to the files and drawing a box over any continuous bout of engine sound produced by a single or multiple boats in one channel while browsing each 24-hour sound file with a window of 100-300s. The "Energy Distribution

Measurement” tool [37] was used to obtain the “center-time” of each boat event (*i.e.*, the time at which the median amplitude of the boat’s noise occurred on a given channel).

2.3. Data Sampling and Analyses

We extracted two variables from the sound recordings: 1) the response variable: “Singers” and 2) one of the predictor variables: “Boats”. The number of singers was first counted following each singing male continuously through time. Individual singing bouts (*i.e.*, time spent singing continuously by a single male, $N = 136$) varied from 30 minutes to 20.5 hours, with median duration of 90 minutes. The absolute number of singers was then counted separately in each consecutive 30 minute period as a continuous count of singers. A time series analysis was performed in version 6.2 of the S-PLUS statistical software package (S-PLUS 2003) to determine the time lag between independent samples. The autocorrelation was negligible after six 30-min periods. Thus, counts were done with a lag of 3 hours or more to avoid autocorrelation and to sample all 30-min periods of a day. The number of singers in a 1-minute count is proportional to the number of singers in continuous counts ($N = 47$; Regression through the origin: 1-Minute Count = $0.7850467 * \text{Continuous counts}$; $R^2 = 0.8963$). Given this result, the number of singers within the 5th minute of each 30 minutes sampled ($N = 141$) was used as the singer count to reduce analysis time.

The variable “Boats” was used as a measure of boat noise and is the number of boat events over each 30-min period. A boat event was counted when its center time was within the sampled 30-min period. Whales typically startle when exposed to unexpected, loud, suddenly louder or different sounds, such as a nearby engine starting up. The same sounds may not elicit a reaction if the sound is continuous and predictable, such as engine noise from a distant, approaching boat traveling at a constant speed [4, 38]. To address this observed response to noise events, cases in which the same boat’s engine was turned off and then back on with a silent interval between them were counted as two boat events. The effect of a boat’s source level and distance from the study area were also accounted for by counting every boat event that appeared on each channel of the array, even if coming from the same boat. Therefore, a higher weight was given to the boats that were louder or closer to the array and the nearby whales. The models included other measurable predictor variables that might affect humpback whale singing behavior according to the literature (Table 1). All predictor values were standardized. We excluded interactions between predictors that did not make sense and between correlated variables. Generalized linear models [39] were used to fit the singer count data into a Poisson distribution with log link. All statistical procedures were carried out in version 9.1 of the SAS statistical software package (SAS Institute 2002-2003). A

set of 70 models was explored trying to balance between under- and over-fitted models, with an effort to avoid over-fitting of the relatively small sample size. We used the Akaike information criteria [40], corrected for small sample sizes, AICc [41-42], to choose the best model in the set, *i.e.*, the model that minimizes the information loss about the system, given the data. We also used multimodel inference (model averaging) to reduce bias of the estimates [43]. The relative likelihood of model *i* versus model *j* is termed the “evidence ratio”, and a ratio of their Akaike weights (w_i) was used to compare several models and make inferences about the importance of the different predictors [44].

3. RESULTS

The singer counts ($N = 141$) varied from 0-9 (Mean = 2.62, Standard Deviation (SD) = 1.54), while boat counts ranged from 0-19 events (Mean = 2.34, SD = 4.02, Median = 0, Interquartile Range (IQR) = 3). The selected best model (Singers = Boats + Hour + Hour² + Moon + Hour²*Moon) is not convincingly the single best. If the Akaike differences (ΔAICc) are ranked from smaller to larger, the evidence ratio of the best model over each subsequent model decreases gradually, until the models become less plausible to be the best ($\Delta \text{AICc} > 10$). We then selected the models that had some support ($\Delta \text{AICc} < 10$) and included these 39 models in a 99% confidence set to recalculate the Akaike weights (Table 2) [44]. The confidence intervals for the predictors (Table 3) were estimated using the averaged model ($S = B + H + H2 + M + T + L + D + H*M + H*B + H*T + H2*B + H2*M + H2*L + H2*T + M*T$).

Table 1: Descriptions of model independent variables.

Variable	Description
Boats (B)	Integer value of the number of boat acoustic events within each sampled 30-minute period.
Day (D)	Continuous variable counted from the first day of the local humpback whale season.
Hour (H)	Continuous variable calculated based on the first hour of the first day of the humpback whale season, in half hour increments.
Hour² (H2)	Square value of Hour based on the quadratic fit of the averaged count by time of day.
Moon (M)	Phase categories (4 levels) based on NOAA Astronomical online data.
Light (L)	Binary variable based on rise and set times of the sun in Abrolhos (U.S. Naval Observatory online database).
Tide (T)	Height of tide at the end of the half hour period averaged from the hourly local values.

Table 2: Model selection results for the 39 most plausible models ($\Delta AICc < 10$). AICc values were scaled (adding the number 8) to avoid negative numbers. K = number of parameters. The best model is highlighted in bold in the table below.

Model	#	LnLikelihood	K	AICc	$\Delta AICc$	w_i	w_{21}/w_i
S = B H H2 M H2*M	21	14.4255	10	0.8412	0.0000	0.1805	1.00
S = B H H2 M T H2*M	57	14.9879	11	2.0708	1.2295	0.0976	1.85
S = B H H2 M L H2*M	68	14.6747	11	2.6971	1.8558	0.0714	2.53
S = B H H2 M H2*M H2*B	67	14.5059	11	3.0347	2.1935	0.0603	2.99
S = B H H2 M H*B H2*M	35	14.4644	11	3.1178	2.2765	0.0578	3.12
S = B H H2 M D H2*M	65	14.4276	11	3.1913	2.3501	0.0557	3.24
S = B H	42	5.4801	3	3.2149	2.3737	0.0551	3.28
S = B H H2 M L H2*M H2*L	70	15.5522	12	3.3331	2.4919	0.0519	3.48
S = B H H2 M H*M	61	13.0015	10	3.6892	2.8480	0.0434	4.15
S = B H H2 M T H2*M H2*T	69	15.0896	12	4.2583	3.4170	0.0327	5.52
S = B H H2 M T H2*M H2*B	55	15.0808	12	4.2759	3.4347	0.0324	5.57
S = B H H2 M L H2*M H2*B	51	14.7692	12	4.8991	4.0578	0.0237	7.61
S = B H H2 M T H2*M M*T	59	17.1765	14	4.9803	4.1391	0.0228	7.92
S = B H H2	31	5.6030	4	5.0881	4.2469	0.0216	8.36
S = B H H*B	43	5.4884	4	5.3172	4.4760	0.0193	9.37
S = B H H2 L	32	6.3518	5	5.7408	4.8995	0.0156	11.59
S = B M	44	6.3328	5	5.7788	4.9375	0.0153	11.81
S = B H M	41	7.3690	6	5.8888	5.0476	0.0145	12.48
S = B H H2 T	33	6.0710	5	6.3024	5.4611	0.0118	15.34
S = B H H2 M T L H2*M H2*B	53	15.2777	13	6.3108	5.4695	0.0117	15.41
S = B H H2 M H*M H2*M	66	15.2262	13	6.4138	5.5725	0.0111	16.22
S = B H H2 M	30	8.1838	7	6.4745	5.6332	0.0108	16.72
S = B M L	38	6.9107	6	6.8054	5.9641	0.0091	19.73
S = B H H2 M T H2*M H2*B M*T	54	17.4739	15	6.8923	6.0510	0.0088	20.60
S = B M T	62	6.7471	6	7.1327	6.2914	0.0078	23.24
S = B H H2 D	11	5.6376	5	7.1693	6.3281	0.0076	23.67
S = B H H2 M T	34	8.7642	8	7.5624	6.7212	0.0063	28.81
S = B H H2 M L	29	8.6338	8	7.8233	6.9820	0.0055	32.82
S = B H H2 L D	10	6.3757	6	7.8755	7.0342	0.0054	33.69
S = B H M H*B	40	7.3795	7	8.0831	7.2418	0.0048	37.37
S = B H H2 T H2*T	60	6.2251	6	8.1767	7.3354	0.0046	39.16
S = B H H2 M H2*B	39	8.2422	8	8.6065	7.7653	0.0037	48.55
S = B H H2 M H*B	36	8.2248	8	8.6414	7.8002	0.0037	49.41
S = B H H2 M T L H*B H*T H2*M H2*L	24	16.4777	15	8.8846	8.0433	0.0032	55.79
S = B H H2 M T L H2*M H2*B M*T	52	17.6475	16	9.0920	8.2508	0.0029	61.89
S = B H H2 M T L	28	9.1323	9	9.1094	8.2682	0.0029	62.43
S = B M T M*T	63	9.0888	9	9.1965	8.3552	0.0028	65.21
S = B H H2 M T H2*B	56	8.8289	9	9.7163	8.8751	0.0021	84.57
S = B H H2 M T H*B H*M M*T	64	15.9764	15	9.8872	9.0459	0.0020	92.11

Table 3: Parameter 95% confidence intervals (CIs = coefficient estimate \pm 1.96* Standard Error (SE)) for the predictors of the averaged model.

Parameter	Lower Limit	Upper Limit
INTERCEPT	-2.4403	1.3721
DAY	-0.0283	0.1901
HOUR	-1.2365	10.5929
HOUR ²	-7.5842	1.1652
BOATS	-0.3743	-0.0954
LIGHT		
1	-0.0701	0.1121
0	0	0
MOON		
Full	-3.9447	0.8133
Last quarter	-22.5943	2.9131
New	-0.6259	0.9612
First quarter	0	0
HOUR ² *MOON		
Full	-0.7800	2.673
Last quarter	-30.8003	4.7036
New	-4.6914	1.2647
First quarter	0	0
TIDE	-0.0446	0.0620
HOUR*BOATS	-0.0177	0.0206
HOUR*TIDE	-0.0007	0.0005
HOUR ² *LIGHT		
1	-0.0405	0.0250
0	0	0
TIDE*MOON		
Full	-0.0229	0.0366
Last quarter	-0.0425	0.0707
New	-0.0155	0.0215
First quarter	0	0
HOUR ² *BOATS		
	-0.0312	0.0428
HOUR ² *TIDE		
	-0.0061	-0.0045
HOUR*MOON		
Full	-1.2013	1.7672
Last quarter	-2.9588	1.7631
New	-1.8024	1.0836
First quarter	0	0

“Boats” (B) has a negative effect and is undoubtedly the most important predictor of variation in number of singers (CI does not include zero). All the models that are plausible to be the best in the set include B as a predictor. Additionally, model 21 is 504.47 times more likely to be the best model in the set than a model which differs from model 21 only by the lack of B (not included in Table 2). Therefore, there is strong evidence to conclude that singing is negatively affected by boat noise.

“Hour” and “Hour²” are important predictors for a good model. Although their coefficient CIs may include zero, the majority of the plausible models include both predictors. Nevertheless, evidence ratios between models that exclude and include H and H2 ($w_{44}/w_{30} = 1.42$; $w_{38}/w_{29} = 1.65$) show that models that include both these predictors are less likely to be best. Therefore, there is not enough evidence to support H8: humpback whale singing behavior is affected by time.

The prediction was that singing activity would decrease

during midday but the estimated coefficient of H2 tends to negative values, contrary to the prediction. Only when we investigated the importance of the interaction between Hour² and Moon (H2*M) that the importance of H and H2 became clear. The inclusion of H2*M makes model 21 16.72 times more likely to be the best if compared to model 30. There is strong evidence that a change in the effect of “Moon” changes the effect “Hour²” on singing behavior, *i.e.*, some phases of the moon affect the temporal pattern of singing activity more than others. The main effects (H2 and M) must be kept in the model if the interaction is important. Also, H2 is a function of H, and the same rule applies. Similarly, “Moon” needs to be in the model. The change from first to last quarter has a strong negative effect on singing. Light level is unlikely to play a role given that both phases have the same percentage moon illumination. Evidence ratios ($w_{42}/w_{41} = 3.8$; $w_{31}/w_{30} = 2$) show that models that do not include “Moon” are slightly more likely to be best. Therefore the support for H6 is weak and the importance of “Moon” might also be due to the importance of the H2*M interaction. “Light” and “Day” are less important predictors. Their coefficient CIs include zero, and evidence ratios indicate that there is considerably less support for hypotheses 2-5.

The inclusion of “Tide” improves the fit of the model, and the evidence ratio indicates that model 57 is also likely to be the best in the set ($w_{21}/w_{57} = 1.85$). Nevertheless, the coefficient CI for this predictor includes zero and the estimated magnitude of its effect is very small. Inasmuch, there is little evidence to support H7, given the data. The interaction between “Hour²” and “Tide” (H2*T) seems to have an important negative effect on singing based on its CI (Table 3) but the inclusion of this predictor in the model is not as important as the inclusion of H2*M ($w_{21}/w_{60} = 39.16$), and the fit of the model that includes H2*T instead of H2*M is not very good. It is plausible that changes in tide height change the temporal pattern of singing activity, but the effect is small, and not necessarily important to explain most data variation. All the other predictors (H*M, H*B, H*T, H2*B, H2*L, and M*T) have similarly small effects and are likely unimportant variables (all coefficient CIs include zero).

4. DISCUSSION AND CONCLUSIONS

An increase in the number of boat acoustic events negatively affects whale singing activity. Although masking makes song more difficult to detect, in our analyses the counts were made on a single minute during the 30-min period, only when boat noise was not enough to mask whale signals. The mechanism of this negative effect could, then, be: 1) male humpback whales are displaced and move outside of the location range, 2) males quit singing, or 3) a combination of 1 and 2. Clark & Altman [45] showed a decrease in the detection probability of fin whale sounds during transmissions of LFA U.S. NAVY sonar due to the same 2 possible phenomena. Variation in sound propagation can result in different radii of boat noise influence [46]. In

fact, short-term avoidance responses to ships and boats were observed at distances ranging from less than 30 m to more than 4 km for different studies [3]. Additionally, area avoidance by whales exposed to noise can last for 20 minutes to several days [3]. Long-term (almost two decades) avoidance of areas during periods of increased commercial shipping (and associated dredging activities) has been suggested for gray whales [47]. Permanent avoidance has also been hypothesized for gray whales in San Diego Bay [48], although the direct link to the whales' displacement is controversial [3]. It has been shown that whale density is inversely related to number of boats in an area [49], and our results showed a similar trend for the absolute number of vocally active male humpback whales.

It has been proposed that a higher level of singing activity at night may indicate that the male vocal display might be favored as a mating tactic in the absence of light. The assumption is that light and vision are important for competitive group formation, so that males engage in fighting as a primary mating tactic during the day, as opposite to solo singing at night [26, Cholewiak et al., unpublished]. In contrast, we found that "Light" was unimportant in explaining the fluctuations in singing behavior once we controlled for the other covariates. There was little evidence for an influence of "Tide", and if there is such effect, it is small. After we controlled for the effect of boats, the only temporal effect detected was the one linked to the changes in moon phase, *i.e.*, the temporal trend in singing activity is altered by the phase of the moon. The negative coefficient estimate of "Hour²" might then be an artifact of the small sample size for each half hour period, which ranged from 1 to 6 samples per period. This might have prevented us from detecting a real temporal trend found by others [26, Cholewiak et al., unpublished]. The most likely explanation for the decrease in singing activity during midday observed in the raw data is that it is a reflection of the effect of "Boats", which has a negative coefficient and increases during midday. Overall singing activity decreases as boat noise increases and the remaining temporal trend found is probably related to a cyclical biorhythm, influenced by the moon's phase, and maybe tidal cycle rather than related to light.

The sustainability of the whale-watching tourism industry depends on: 1) maintaining visitor numbers close to the carrying capacity of the whale watching fleet; 2) the local and regional fluctuations in the economy, and most importantly; 3) the maintenance of the resources on which the tourism relies [2]. If whales are being disturbed resulting in them moving out of the area, then current levels of whale watching activity might not be sustainable. Actions to make this human activity less distressing to whales should be implemented. Acoustic isolation of engines, scientifically-validated approach protocols, and reinforcement of regulations of numbers and speeds of boats in areas used by marine mammals are sensible measures that should be applied. Adaptive management [50] should aim at reducing the number of noise events per boat, which can both

improve the whale watching experience and reduce the impact on singing behavior for a given number of boats. It is also important to address the need for enforcement of existing management guidelines, which clearly depends on political will and better prioritization of governmental resources.

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6. REFERENCES

1. Hoyt, E. 2001. *Whale watching 2001: worldwide tourism numbers, expenditures and expanding socioeconomic benefits*. IFAW, Yarmouth Port.
2. Higham, J.E.S. & Lusseau, D. 2007. Urgent Need for Empirical Research into Whaling and Whale Watching, *Conserv. Biol.* 21:554-558.
3. Richardson, W.J., Greene Jr., C.R., Malme, C.I. & Thomson, D.H. 1995. *Marine Mammals and Noise*. Academic Press, San Diego, 576 pp.
4. Sousa-Lima, R.S., Morete, M.E., Fortes, R.C., Freitas, A.C. & Engel, M.H. 2002. Impact of boats on the vocal behavior of humpback whales off Brazil. *J. Acoust. Soc. Am.* 112:2430-2431.
5. Payne, R.S. & McVay, S. 1971. Songs of humpback whales. *Science* 173: 585-597.
6. Winn, H.E. & Winn, L.K. 1978. The song of the humpback whale, *Megaptera novaeangliae*, in the West Indies. *Mar. Biol.* 47: 97-114.
7. Tyack, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav. Ecol. Sociobiol.* 8:105-116.
8. Baker, C.S. & Herman, L.M. 1984. Seasonal contrasts in the

- social behavior of the humpback whale. *Cetus* 5:14-16.
9. Helweg, D.A., Frankel, A.S., Mobley, J.R. & Herman, L.M. 1992. Humpback whale song: our current understanding. In: *Marine mammal sensory systems* (Thomas, J. et al., ed.). Plenum Press, New York, p. 459-483.
 10. Frankel, A.S., Clark, C.W., Herman, L.M. & Gabriele, C. 1995. Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawaii determined using acoustic and visual techniques. *Can. J. Zool.* 73:1134-1146.
 11. Darling, J.D. & Bérubé, M. 2001. Interactions of singing humpback whales with other males. *Mar. Mammal Sci.* 17:570-584.
 12. Darling, J.D., Jones, M. E. & Nicklin, C.P. 2006. Humpback whale songs: Do they organize males during the breeding season? *Behaviour* 143:1051-1101.
 13. Engel, M.H. 1996. Comportamento reprodutivo da baleia jubarte (*Megaptera novaeangliae*) em Abrolhos. *Anais de Etologia* 14: 275-284
 14. Palazzo, Jr., J.T., M. Kammers, and I. Linhares. 1994. Whalewatching sites in Brazil: a summary of available information. IWC/46/WW Working paper, 46th IWC, 8 pp.
 15. Payne, R. 1978. Behavior and vocalizations of humpback whales (*Megaptera* sp.). In: *Report on a workshop on problems related to humpback whales (Megaptera novaeangliae) in Hawaii* (Ed. by K. S. Norris & R. R. Reeves), pp.56-78. U. S. Dep. Commer. NTIS PB-280 794.
 16. Winn, H.E., Thompson, T.J., Cummings, W.C., Hain, J., Hudnall, J., Hays, H. & Steiner, W.W. 1981. Song of the humpback whale: population comparisons. *Behav. Ecol. Sociobiol.* 8:41-46.
 17. Payne, R. & Guinee, L.N. 1983. Humpback whale (*Megaptera novaeangliae*) songs as an indicator of "stocks". In: *Communication and behavior of whales: AAAS Selected Symposium 76* (Ed. by R. Payne), pp. 333-358. Boulder, CO: Westview Press.
 18. Payne, K., Tyack, P. & Payne, R. 1983. Progressive changes in the song of humpback whales songs (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii. In: *Communication and behavior of whales: AAAS Selected Symposium 76* (Ed. by R. Payne), pp. 9-57. Boulder, CO: Westview Press.
 19. Payne, K. & Payne, R. 1985. Large Scale Changes over 19 Years in Songs of Humpback Whales in Bermuda. *Z. Tierpsychol.*, 68: 89-114.
 20. Matilla, D.K. Guinee, L.N. & Mayo, C.A. 1987. Humpback whale songs on a North Atlantic feeding ground. *J. Mamm.* 68:880-883.
 21. Noad, M.J., Cato, D.H., Bryden, M.M., Jenner, M.N. & Jenner, C S. 2000. Cultural revolution in whale songs. *Nature* 408:537.
 22. Cerchio, S. Jacobsen, J.K. & Norris, T.F. 2001. Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. *Anim. Behav.* 62:313-329.
 23. Darling, J.D. & Sousa-Lima, R.S. 2005. Songs indicate interaction between humpback whale (*Megaptera novaeangliae*) populations in the Western and Eastern South Atlantic Ocean. *Mar. Mamm. Sci.* 21:557-566.
 24. Eriksen, N., Millar, L.A., Tougaard, J., & Helweg, D.A. 2005. Cultural change in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. *Behaviour* 142: 305-328.
 25. Helweg, D.A. & Herman, L.M. 1994. Diurnal patterns of behavior and group membership of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Ethology* 98:298-311.
 26. Au, W.W.I., Mobley, J., Burgess, W.C. & Lammers, M.O. 2000. Seasonal and diurnal trends of chorusing humpback whales wintering in water off Western Maui. *Mar. Mamm. Sci.* 16:530-544.
 27. Charif, R., Clapham, P.J., Gagnon, W., Loveday, P. & Clark, C.W. 2001. Acoustic detections of singing humpback whales in the waters of the British Isles. *Mar. Mammal Sci.* 17:751-768.
 28. Fristrup, K.M, Hatch, L.T. & Clark, C.W. 2003. Variation in humpback whale (*Megaptera novaeangliae*) song length in relation to low-frequency sound broadcasts. *J. Acoust. Soc. Am.* 113:3411-3424.
 29. Norris, T.F. 1995. Effects of boat noise on the singing behavior of humpback whales (*Megaptera novaeangliae*). Master Thesis. Department of Moos Landing Marine Laboratories, San Jose State University, 69 pp.
 30. Miller, P.J.O., Biassoni, N., Samuels, A., & Tyack, P.L. 2000. Whale songs lengthen in response to sonar. *Nature* 405: 903.
 31. Haviland-Howell, G., Frankel, A.S., Powell, C.M., Bocconcelli, A., Herman, R.L. & Sayigh, L.S. 2007. Recreational boating traffic: A chronic source of anthropogenic noise in the Wilmington, North Carolina Intracoastal Waterway. *J. Acoust. Soc. Am.* 122:151-160.
 32. Morete, M.E., Pace III, R.M., Martins, C.C.A., Freitas, A.C. & Engel, M.H. 2003. Indexing seasonal abundance of humpback whales around Abrolhos archipelago, Bahia, Brazil. *LAJAM* 2:21-28.
 33. Fainstein, R. & Summerhayes, C.P. 1982. Structure and origin of marginal banks off Eastern Brazil. *Mar. Geol.* 46:199-215.
 34. IBAMA/FUNATURA 1991. *Plano de Manejo: Parque Nacional Marinho dos Abrolhos. Brasília, Brazil.*
 35. Freitas, A.C., Kinas, P.G., Martins, C.C.A. & Engel, M.H. 2004. Abundance of humpback whales on the Abrolhos Bank wintering ground, Brazil. *J. Cetacean Res. Manage.* 6:225-230.
 36. Klinowska, M. 1991. *Dolphins, Porpoises and whales of the world: The IUCN Red Data Book.* Gland, Switzerland: IUCN.

37. Cortopassi, K. A. 2006. <http://www.birds.cornell.edu/brp/research/algorithm/automated-and-robust-measurement-of-signal-features>.
38. Watkins, W.A. 1986. Whale reactions to human activities in Cape Cod waters. *Mar. Mamm. Sci.* 2:251-262.
39. McCullagh, P. & Nelder, J.A. 1989. *Generalized Linear Models*. 2nd Ed. Chapman & Hall, New York, NY.
40. Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In: *Second International Symposium on Information Theory*. (Eds B. N. Petrov and F. Csaki.) pp. 267–281. Akademiai Kiado: Budapest.
41. Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. *Comm. Stat., Theory and Methods* A7:13-26.
42. Hurvich, C.M. & Tsai, C-L. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297-307.
43. Buckland, S.T., Burnham, K.P. & Augustin, N.H. 1997. Model selection: an integral part of inference. *Biometrics* 53:603–618.
44. Burnham, K.P. & Anderson, D.R. 1998. *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag: New York, 488 pp.
45. Clark, C.W. & Altman, N.S. 2006. Acoustic Detections of Blue Whale (*Balaenoptera musculus*) and Fin Whale (*Balaenoptera physalus*) Sounds During a SURTASS LFA Exercise. *IEEE J. Oceanic Engineering* 31:120-128.
46. Watkins, W.A. & Goebel, C.A. 1984. Sonar observations explain behaviors noted during boat maneuvers for radio tagging of humpback whales (*Megaptera novaeangliae*) in the Glacier Bay area. *Cetology* 48:1-8.
47. Bryant, P.J., Lafferty, C.M. & Lafferty, S.K. 1984. Reoccupation of Laguna Guerrero Negro, Baja California, Mexico, by gray whales. P. 375-387 In: Jones, M.L., Swartz, S.L. & Leartherwood, S. (Eds.). *The gray whale, Eschrichtius robustus*. Academic Press, Orlando, Fl. 600 pp.
48. Rice, D.W. & Wolman, A.A. 1971. *The life history and ecology of the gray whale (Eschrichtius robustus)*. *Am. Soc. Mammal., Spec. Publ.* 3, 142 pp.
49. Baker, C.S. & Herman, L.M. 1989. Behavioral responses of summering humpback whales to vessel traffic: experimental and opportunistic observations, *Final Rep. No. NPS-NR-TRS-89-01*. United States Department of the Interior, National Park Service, Anchorage, Alaska.
50. Blumstein, D.T. 2007. Darwinian Decision Making: Putting the Adaptive into Adaptive Management. *Conserv. Bio.* 21:552-553.



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