SC/66a/WW/11

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INTERNATIONAL
WHALING COMMISSION

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ABSTRACT: A small community of bottlenose dolphins *Tursiops truncatus* residing in Dolphin Bay, Bocas del Toro, Panama is currently the target of the largest cetacean tourism operation in Panama. Boat-based tourism activities are concentrated in Dolphin Bay due to the high site fidelity of dolphins in this area and its potential importance as a calving and nursery ground for females. Many of the individuals routinely exposed to tour boats are females with dependent offspring. Previous tourism impact studies at this site show that tour boats elicit short-term changes in dolphin behavior and acoustic structure, however, the relationship of these responses to the population's biology and ecology is not clear. Animal behavior is temporally dynamic, therefore, assessing the effects of potential impacts on the time structure of behavior, such as behavioral transitions and time-activity budgets can provide useful information about the biological significance of anthropogenic disturbance. Because the time-activity budget is tied to the energy budget of individuals, information on the former can provide useful information about the energetic costs of tourism to a population. In this study, the behavioral transitions of focal dolphins in Dolphin Bay, Bocas del Toro were analyzed using transition matrix models, a time-sequencing analytical technique now widely applied to dolphin behavior to explore the potential impacts of tourism on cetaceans. First-order, time discrete Markov chain models were used to assess the effect of tour boat activities on dolphin behavioral transition probabilities in both control and impact scenarios. The effect of boat interactions was then quantified by comparing transition probabilities of both control and impact chains. Data were also used to construct dolphin activity budgets. Additionally, a Generalized Log Linear Mixed Model (GLMM) was fitted to a subset of the data containing only females with dependent calves to assess the effects of tour boats on this vulnerable age-sex class. The Markov chain analysis revealed that in the presence of tour boats, dolphins were less likely to stay in a socializing state and were more likely to begin travelling, and were less likely to begin foraging while in a traveling state. Additionally, the time-activity budgets showed that foraging decreased as an effect of tour boat presence, and travelling increased, indicating a shift in the important relationship between these two activities. The results of the GLMM showed that females with dependent calves are less likely to forage and more likely to travel when tour boats are present. These behavioral responses are likely to have energetic implications for individuals through two possible mechanisms: reduced energy acquisition and increased energy expenditure. The effect of lost foraging opportunities and increased physical demands may be more pronounced for nursing females whose physiological demands are higher and can potentially lead to poor reproductive outcomes and reduced fitness of individuals. Tour operator compliance with the ARAP No. 2007 Resolution on number and frequency of tour boats interacting with dolphins in Dolphin Bay, as well as approaching distance to females with calves is urgently needed to minimize potential long-term impacts on this small, genetically distinct population.

Introduction

It is now widely recognized that boat-based cetacean tourism can be detrimental to coastal cetacean populations and that tourism activities must be properly managed to minimize the sublethal effects of potential boat disturbance on individuals and their populations. Coastal bottlenose dolphins are the most sought after small cetacean for tourism activities due to their geographic isolation, small home ranges and high encounter rates along coastlines, rendering them vulnerable to the cumulative effects of human disturbance. Recent tourism impact studies have demonstrated that short-term behavioral changes can have long-term impacts for targeted populations by causing animals to avoid preferred habitat, disrupting energy budgets, reducing energy acquisition and/or increasing energetic expenditure (Lusseau 2004, Williams et al. 2006, Christiansen et al. 2013, Symons et al. 2014). Studies aimed at interpreting behavioral responses to tour boat disturbance have shown that changes in activity budgets, assessed using behavioral states, can reveal whether behavioral changes have energetic costs for animals (Lusseau 2003). Because the activity budget is directly related to the energy budget of individuals and populations, it can provide important information on how a population is affected by human disturbance (Neumann 2001).

The small dolphin community inhabiting Dolphin Bay , Bocas del Toro, Panama is currently subjected to high levels of tour boat interactions year round by the local tourism industry. The dolphins in this area are long-lived, and many are year-round residents who are repeatedly exposed to tour boats over time, putting them at risk for the cumulative effects of boat disturbance. Previous impact studies at this site have shown that dolphins respond negatively to tour boats as an effect of number and frequency of tour boat interactions (May-Collado et al. 2007) and modify their whistle structure to avoid potential masking by engine noise (May-Collado & Wartzok, 2008,Quiñones-Lebrón & May-Collado, 2011). However, very little is known about the biological importance of these short-term responses to this small and genetically isolated population. This study aimed to assess the effects of tourism activities on the behavioral transition probabilities of focal dolphins living in Dolphin Bay in both control and impact scenarios, and to determine if these effects alter the time-activity budgets of dolphins. Because the time-activity budget is connected to the energy budget of individuals, we were particularly interested in determining whether tour boat interactions cause variations in the proportion of time allocated to energy acquisition (foraging) and energy expenditure (traveling) as a means of inferring the energetic consequences of tourism on individuals, and the potential for long-term detrimental effects on the population. Furthermore, we aimed to assess the effect of tour boats on the behavior of females with dependent offspring, as the sighting frequency of neonate calves in Dolphin Bay is high, suggesting its importance to females as a calving and nursery ground.

Methods

Boat surveys were conducted using a small independent research vessel in Dolphin Bay (9°13'16.7"N 82°14'14.9"W) within the Bocas del Toro archipelago. Focal follows were performed on animals with highly distinctive dorsal fins and 1 of 4 behavioral states was scored every 3-minutes using focal-animal point sampling using the following predetermined behavioral categories: foraging, resting, socializing, traveling. Only non-calves were selected as focal animals since the behavior of calves was not considered independent of that of their mothers. If the focal animal was not sighted for a maximum of 4 min and the next recorded behavior was the same as that previously recorded, I assumed that the focal animal had been engaged in the same behavior during the intervening period. If the behavior had changed between successive scorings the behavior was assumed to have changed during the intervening period. Individual follows conducted in the presence of the research vessel and without tour boats were treated as control sequences and as impact sequences when the research vessel and tour boats were present. Interactions between tour boats and focal dolphins were defined as beginning when 1 or more vessels were within 100 m of the focal dolphin and ended when the last tour boat exceeded this distance. This distance is consistent with the Panamanian government's Whale Watching Conduct Resolution (ADM/ARAP NO. 01), established in 2007 to provide guidelines on how tour boats should interact with dolphins to minimize disturbance (May-Collado et al. 2007). Follows were conducted for a minimum of 21 min (7 scans) and a maximum of 60 min (21 scans) under ideal conditions. Follows were terminated in the event of heavy precipitation and/or lightning, when sea state reached Beaufort 3, visibility deteriorated due to fog or rain, or when the focal animal was lost for more than 2 consecutive scans. This protocol was maintained during tour boat interactions to maintain behavioral consistency of the research vessel through out all control and interaction scenarios. Therefore, any differences observed in dolphin behavior were assumed to be attributable to the presence of tour boats and not the research vessel.

Data analysis

Behavioral transitions. I modeled samples of dolphin behavioral states obtained from point sampling using time discrete Markov chains (Guttorp & Minin 1995). Markov chains quantify the dependence of a succeeding event on preceding events (Caswell 2001, Lusseau 2003), while simultaneously taking into account the temporal dependence between behavioral events. This temporal dependence can be affected by any factor occurring between events. Therefore, it was possible to calculate the probability that a dolphin will change from one behavioral state to another when tour boats are either present (impact) or absent (control). This effect can then be quantified and tested for by comparing these 2 probabilities (Lusseau 2003)

Data obtained from 3-min focal animal point sampling intervals were arranged into 2-way contingency tables of preceding behavioral state versus succeeding behavioral state (Lusseau 2003). I developed 2 contingency tables: 1 for control and 1 for impact situations, depending on the presence of tour boats interacting with the focal dolphin between two behavioral samples. If no tour boat interaction occurred between two behavioral samples, the transition between these two samples was placed in a control table (no tour boats present, only research boat). If a tour boat interaction did occur between two samples, the transition was placed in an impact table (1 or more tour boats present and research boat). Following the more conservative Markov chain analysis approach, when an impact chain followed a control chain, the transition between them was discarded, as this chain could not be considered as either control or impact since it was not possible to determine the extent of the potential impact (Lusseau 2003, Meissner et al. 2015). To test the effect of tour boat presence on dolphin behavioral transitions, the impact and control contingency tables were compared using a goodness-of-fit test in R.

To assess changes in behavioral states due to tour boat presence, transition probabilities from preceding to succeeding behavioral state were calculated following (Lusseau 2003) for the control and interaction chains separately as:

$$p_{ij} = \frac{a_{ij}}{\sum_{j=1}^{n} a_{ij}}, \sum_{j=1}^{n} p_{ij} = 1$$

where i is the preceding behavioral state, j is the succeeding behavioral state, a_{ij} is the number of transitions observed from behavioral state i to j, and p_{ij} is the transition probability from i to j in the Markov chain and n is the total number of behavioral states. Each transition is the proportion of time a succeeding behavioral state was observed following a preceding behavioral state, therefore I tested the effect of tour boat interactions by comparing the control and impact transition probability matrices for dolphin activity using a 2-sample test for equality of proportions and calculated 95% confidence intervals (CI) in R

Time-activity budgets. Following the Perron-Frobenius Theorem and from ergodic properties of Markov chains (Caswell 2001), a stationary probability distribution can be derived from control and impact chains which corresponds to the activity budget of dolphins (i.e. the proportion of time dolphins spend in each behavioral state).

The stationary distribution can be derived from the left eigenvectors of λ:

$$q_i = v_i, \sum_{i=1}^{5} q_i = 1,$$

where *i* is a behavioral state. For both control and impact situations, the activity budget was approximated by the left eigenvector of the dominant eigenvalue of the transition probability matrices (Lusseau 2003) using Eigen analysis of the contingency tables in R. Differences observed between the budgets were inherent to interactions with the tour boats. Differences between control and impact activity budgets were tested using a goodness-of-fit test, and each behavioral state in the control activity budget was compared to its corresponding behavioral state in the impact activity budget using a two-sample test for equality of proportions and 95% CI were calculated. Both tests were performed in R.

Assessing tour boat impact on females with calves

Sixty-two percent of all dolphin groups sighted from 2004-2013 were composed of calves, which suggests that Dolphin Bay is important as a calving and nursery ground for female dolphins. To analyze the potential effects of tour boats on the behavior of female dolphins with dependent calves, a Generalized Linear Mixed Model (GLMM) was used in R. I tested the model to predict effect of boats on 3 behavioral states (foraging, socializing and traveling) with previous behavior as a random effect. I also evaluated the model with the additional random effects of focal follow and individual with the GLMER function in R.

Results

Behavioral transitions

The results of the Markov chain analyses show that tour boat interactions significantly affected dolphin activity patterns by altering their transitions in behavioral states (Goodness-of-fit test, X^2 = 34.9251, df = 4, p < 0.001). However, this observed effect was not homogenous over all transitions. Overall, 2 behavioral transitions showed statistically significant differences (a = 0.05) between impact and control situations: the transition from Socializing to Traveling (X^2= 4.2156, df = 1, p-value = 0.04005) and the transition from Traveling to Foraging (X^2= 5.0145, df = 1, p-value = 0.02514). Dolphins were more likely to transition from Socializing to Traveling during tour boat interactions and were less likely to switch from Traveling to Foraging when tour boats were present (Fig. 1). Socializing dolphins were also less likely to remain Socializing during impact situations, although this difference in transition probability was not statistically significant. However, this result further indicates a shift towards traveling above all other activities during tour boat interactions. In all activities where an increase in probability was detected, traveling was the succeeding behavioral state. Conversely, the transition probability of dolphins switching to foraging was decreased across all activities, although the magnitude of difference for this activity was less pronounced.

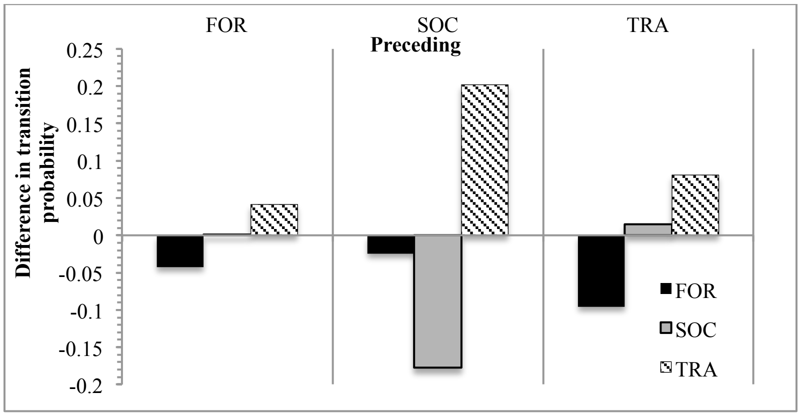

Fig 1.Effect of DW boats on transition probabilities of behavioral states of focal dolphins. Positive values indicate an increase in transition probability when DW boats are present and negative values indicate a decrease. Significant differences ($p < 0.05$) are denoted by an (*)

Time-activity budgets

Markov chain analysis revealed a significant difference in dolphin activity budgets between control and impact situations (X^2= 31.0336, df = 2, p-value = <0.001). Tour boats statistically affected 2 of the 3 behavioral states in the dolphins' activity budget: Foraging and Traveling. Dolphins spent a significantly smaller proportion of their time Foraging (X^2= 22.4266, df = 1, p-value = 2.183e-06) and instead spent more time Traveling (X^2= 25.5354, df = 1, p-value = 4.343e-07) in the presence of tour boats (Fig. 2). Foraging was the dominant activity state during both control and impact situations, 61 and 48%, followed by Traveling, 32 and 45%, respectively. In impact situations, the time budget for Foraging decreased by 13% (61-48%) and the budget for Traveling increased by the same proportion, 13% (32-45%). This result indicates a shift in the strong relationship between foraging and traveling.

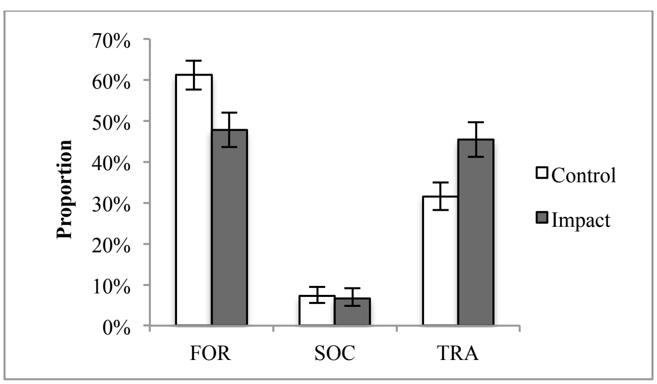

Fig 2. Effect of tour boat interactions on the activity budget of bottlenose dolphins Tursiops truncatus in Dolphin Bay. The proportion of time spent in each activity state during control (only research boat, no tour boats present) and impact (research boat and tour boats present) situations. Error bars represent 95% confi- dence intervals. (*) indicates significant differences ($p < 0.05$)

Females with calves

The results of the GLMM indicate that when auto-correlated with previous behavior as a random effect, in the presence of tour boats, females with calves are less likely to forage. When I fitted the model with the random effects of individual and focal follow, the results were insignificant. This suggests that as a whole, females with calves are less likely to forage in the presence of boats, without the added variation of focal follow or individual. Females with calves are also more likely to travel in the presence of boats, while accounting for their previous behavior, focal follow and individual. This result indicates that the effect of tour boats on dolphin traveling behavior is not homogenous, and that certain individuals travel more than others in the presence of tour boats.

Discussion

Responses to tour boat interactions are similar to those described for bottlenose dolphins at other sites. A decrease in the time spent foraging, and an attendant increase in the time spent traveling may carry energetic costs for individual animals, primarily through reduction in energy uptake and increased physical demands. Since traveling is a relatively energy consuming activity, it may lead to increased energetic demands for dolphins that are forced to increase the proportion of time they spend travelling to avoid tourist boats (Christiansen et al. 2010). This could ultimately result in reduced fitness on both individual and population levels (Lusseau 2006). Furthermore, the physiological demands of nursing females with dependent offspring are naturally higher to meet and these individuals must pend a greater proportion of time foraging to meet increased energetic demands. This study has shown that females with calves forage less and travel more in the presence of boats, although certain individuals may be more inclined to travel away from boats than others. This suggests that perhaps females who are more tolerant of boats may be using risk-avoidance strategies to balance their energy needs. The results of this study further strengthen the evidence that current tour boat practices in Dolphin Bay impact dolphin behavior and can ultimately lead to long-term deleterious effects on individuals and the population. If females utilize Dolphin Bay as a calving and nursery ground, tour boat regulations must enforce strict adherence to boat approach limits for females with calves to protect this highly vulnerable subset of the population from the effects of boat disturbance. Current levels of tour boats and frequency of interactions in Dolphin Bay may ultimately lead to a decline in population size and/or displacement from the preferred habitat of Dolphin Bay. Governmental attention to the boat tourism issue ion Bocas del Toro is urgently needed to protect the long-term sustainability of the tourism industry in this region as well as the conservation of the dolphin population.

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