

Examining the Impacts of Ecotourism on Humpback Whales (*Megaptera novaeangliae*)

in Panama

by

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ABSTRACT

Cetacean-based ecotourism is a popular activity and an important source of revenue for many countries. Whale watching, a subset of cetacean-based ecotourism, is vital to supporting conservation efforts and provides numerous benefits to local communities including educational opportunities and job creation. However, the sustainability of whale-based ecotourism depends on the behavior and health of whale populations and is therefore vital that ecotourism industries consider the impact their activities have on whale reproductive behavior. To address this statement, behavioral data (e.g. direction change, breaching, slap behaviors, diving, and spy hops) were collected from humpback whales (*Megaptera novaeangliae*) in Las Perlas Archipelago off the Pacific coast of Panama to determine if vessel presence had an influence on whale behaviors. Studies were recorded during their breeding season from August through September in 2019. Based on 47 behavioral observations, higher boat density corresponded with humpback whales changing direction which is believed to be a sign of disturbance. This result is important given Panamanian regulations implemented on February 13 of 2007 prohibit whale-based tourism from disturbing whales, which is measured as changes in behavior. Because there is no systematic monitoring of whale watching activity to enforce the regulations, there is currently little compliance among tour operators. The integration of animal behavior research into management planning will result in more effective regulation and compliance of conservation policies.

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INTRODUCTION

Wildlife ecotourism provides growing economic benefits to many countries around the world (Hoyt, 2001; O'Connor et al., 2009; Shogren et al., 1999). In many areas, local communities rely heavily on tourism, which contributes to employment, connection with cultures, distribution of wealth, and overall increased production of the economy. For example, in 2009 cetacean-related ecotourism generated nearly two billion dollars across 119 countries (O'Connor et al., 2009). Additionally, tourists' increased exposure to species through ecotourism contributes to improved conservation awareness and increased environmental protection through education opportunities. Indeed, values of direct contact with animals elicit support for conservation and care ethics for wildlife (Highman & Lück, 2008). Whale watching has even replaced whaling in some places, generating greater revenue than consumption-based practices (Hoyt and Hvenegaard, 2010). This is especially relevant given that a rapidly urbanizing society is prompting tourists to "reconnect" themselves to nature (Curtin and Kragh, 2014). Yet, whale tourism may have negative effects on the health, communication, mortality rate, and behavior of cetaceans. Respiration difficulties, an increase in whale-vessel collisions, increased stress behavior, changes in swimming patterns, communication acoustics, and falling reproductive rates have all been documented among whale populations (Dorsey et al., 1989; Parsons, 2012; & Guzman et al., 2013) in places with active whale watching programs.

Many environmental organizations maintain the premise that tourism that is nature-based, sustainably managed, conservation supporting, and environmentally

educating should be considered “ecotourism” (Buckley, 1994). The International Ecotourism Society (TIES) defines ecotourism as “responsible travel to natural areas that conserves the environment, sustains the well-being of the local people, and involves interpretation and education” (The International Ecotourism Society, 2015). Whale watching is an ecotourism activity because it falls into all categories and has been proven to produce economical and ecologically benefitting outcomes. These ecological advantages are credited to the International Whaling Commission (IWC), who made measures to protect whales by publishing guidelines for responsible whale watching (IWC, 1997).

Ecological benefits of whale watching include the transition from whaling practices to whale watching as an alternative “use” for whales. This replacement sustains the revenue required to support local communities, cultures, and lifestyles while supporting whale welfare and conservation efforts (Wearing, et al., 2014). Additionally, whale watching has an educational value by informing the public about conservation efforts for whales and the ecosystem that is crucial for propelling environmental protection, especially for the enactment of new policies (Stamation, et al., 2007). In a related study, humpback whale watching was effective in encouraging natural resource protection and patronization of business if tour guides disseminate conservation messages to tourists (Peake et al., 2009). This practice falls under responsible whale watching guidelines, which is defined as an environmental and economical use of whales that is sustainable, promotes whale conservation, and education while simultaneously supporting local communities (O’Connor et al., 2009). The popularity of this industry has

drawbacks, as tour operators may utilize locations with little enforcement and violate the rules of responsible whale watching and whale watching regulations from their country, leading to detrimental implications to whale welfare.

Previous research suggests potential behavior changes in humpback whales in the presence of small vessels, including changes in acoustics, nursing, surfacing, and swimming behaviors, as well as changes in group size, dynamics and movement direction (Parsons, 2019). Behavioral transitions are often indicators of whale avoidance tactics used during levels of high vessel presence. Vessels high speeds and angle of approach can increase collision risk and whales' energy expenditure while decreasing the occurrence of necessary survival activities (feeding, nursing, and reproduction) (Nowacek et al., 2007). One study suggests long-term disruption could have lasting reproductive impacts on humpback whale populations (Braithwaite, et al., 2003), while other potential impacts include the inability to communicate due to “sound masking” from loud boat sounds. This could result in the reduced success of finding a mate in breeding areas, locating food in feeding areas, and further expended energy to increase call volume (Nowacek, et. al., 2007).

Panama is a great site for whale and boat interactions, especially since it is a popular spot for tourism with the Panama Canal, which only increases vessel traffic. Therefore, studies were done in the Las Perlas Archipelago (8.41 ° N, 79.02 °W) in the Gulf of Panama, which lies about 60 km southeast of Panama City (Figure 1). The archipelago comprises 250 basaltic rock islands and islets spread over 1,688 km. (Guzman et al., 2008). Humpback whales of the Southern hemisphere (*Megaptera*

novaeangliae) are charismatic megafauna that migrate to tropical areas from their feeding grounds in Chile and Antarctica. They aggregate to Panama and Costa Rica during the breeding season which extends from June to October, peaks in August and September, and which can extend into December, facilitating observational field research in Central America. There are approximately 100-300 whales that come in a single season and 900 whales across all seasons (Guzman, 2013). This population of humpback whales is considered Breeding Stock G (International Whaling Commission, 1998), which is one of the seven “stocks” that populate in the Southern Pacific (Félix and Guzman, 2014). They also undertake the longest migration distance of more than 16,000 km roundtrip from the feeding grounds to the breeding grounds (Félix and Guzman, 2014) with the entire stock using about 9,000 km of coastline (Félix, et al., 2011). Although whales are migratory for the majority of the year, they congregate in waters less than 200 meters deep for their annual breeding season. The shallow waters of the Pacific of Panama are ideal for mother humpback whales giving birth because of the assumed avoidance of competitive males pursuing females, lack of ocean turbulence, and predators (Darling & Nicklin, 2002). However, the coastal waters of Las Perlas Archipelago are a popular spot for vessel interactions, which poses higher threats of vessel collisions during these migratory seasons.

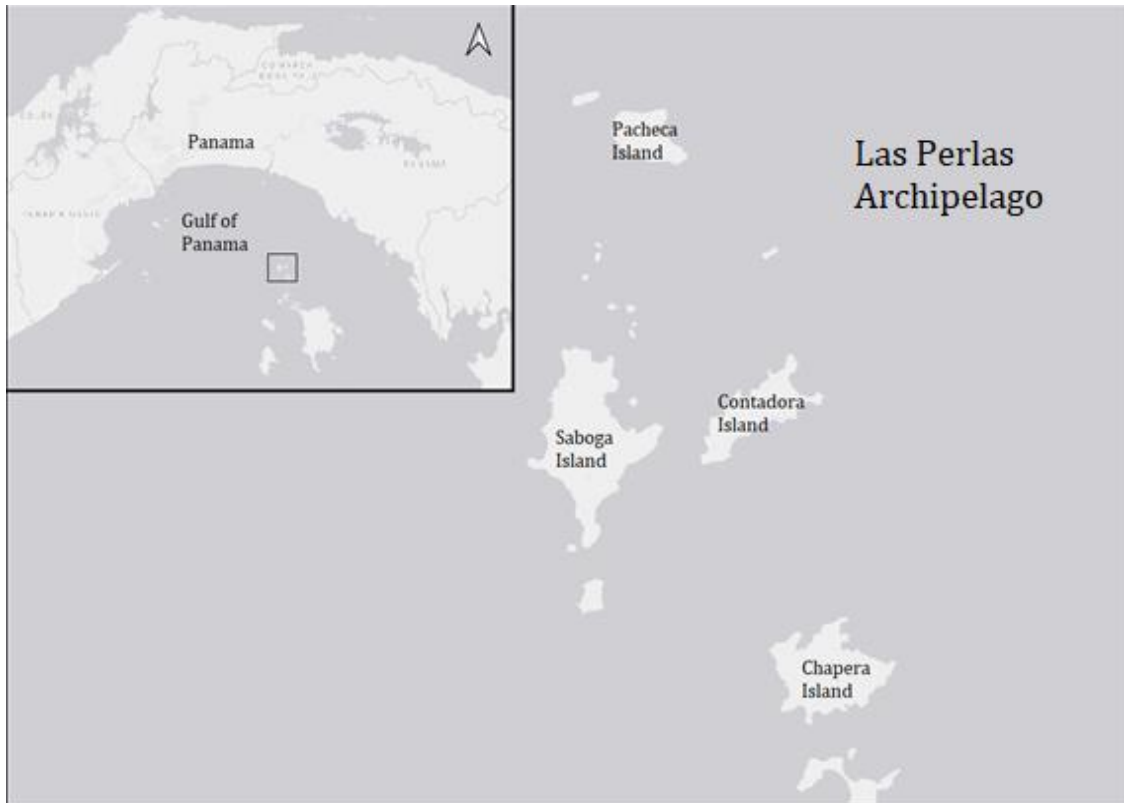


Figure 1: Map showing the study site location in the Las Perlas archipelago in Panama.

Previous research suggests human activities influence animal behavior and related physiological systems (Wikelski & Cooke, 2006), which can include drastic shifts in behavior or habituation. While researchers have documented behavioral responses to human disturbances (Bejder et al. 2006; Kight et al. 2007), habituation is more challenging to measure. Habituation may occur when sensory systems stop relaying signals to the brain in response to repeated or constant stimuli (Frost et al., 1997), or when stimuli are received in the brain, but the animal ceases to respond (Rose & Rankin, et al., 2001). Even simple forms of habituation may entail complex interactions of different mechanisms and time scales and it is linked to the reduction of hormonal stress mediators' over time (Cyr and Romero, 2009).

However, habituation has negative repercussions for species and previous studies have shown other mammals have habituated to human activity. Habituation of dolphins was initially overlooked as a threat to the species, but after two calves were found dead from their repeated interaction with vessels, many scientists wondered how many unnoticed cetaceans are killed by vessel collisions (Stone and Yoshinaga, 2000). Although Right whales can hear approaching vessels, they do not appear to respond to vessels, leading to higher death rates from vessel collisions (Nowacek et al., 2004; Richardson et. al., 1995). However, it is difficult to predict whale responses to vessels, as this may depend on their past experiences with boats and activity overtime (Minerals Management Service, 2009), but it is a primary concern, as whale habituation to vessels could lead to higher vessel collisions, thereby diminishing the population through fatal encounters with boats (Sousa-Lima and Clark, 2009).

Due to concerns about whale interactions to vessels, Panama passed resolution decree No. 0530-2017 on October 17, 2017, to control vessel disturbance on cetaceans with the goal of conserving their populations. Regulations from the earlier decree ADM/ARAP No. 1 (February 13, 2007) include that operators needing a permit for commercial operations, have a maximum of two whale-watching vessels per group, take extra care when calves are present, maintain a 250 meters distance from the whales, and limited observation times to 30 minutes per group or no more than 15 minutes when calves are involved, and obey the restriction of individuals from entering the water with whales, to prevent altering the behaviors of cetaceans (*sensu* Carlson, 2010).

Lack of enforcement from the Panamanian government has elicited the reiteration

and repeated implementation of these policies every year. While boat operators may be aware of the policies currently in place there is little structural enforcement to ensure regulatory compliance. Lack of compliance may also be the result of poor communication of regulations by the government, leaving local whale-watching companies with a lack of knowledge of these laws (Sitar, et al., 2016). Boat operation practices differ among companies; small and large boats from Panama City, and individual family-operated local businesses; enabling us to collect varying data sets and develop general ideas of current practices.

The high number of private whale watching businesses in Las Perlas Archipelago makes for an ideal research site to study whale responses to increased anthropogenic presence. Understanding the dynamic changes in human wellbeing and animal population viability are critical for establishing effective wildlife conservation strategies. Changes in behaviors may change tourist satisfaction, which elicits the popularity of ecotourism activities. Variations in socioeconomic factors benefits the local communities, which motivates many to protect and care about whales. It is therefore important to consider the coupled nature of ecological and socio-economic systems to understand the impacts of wildlife tourism on both humans and nature. The hypothesis of the study predicts that the increase in the number of boats in the whales' immediate environment will provoke higher levels of stress, which will be observable through a change in their natural behaviors. Meanwhile, controlled experiments lacking vessels should not incite changes in whales' natural behaviors.

Table 1: Summary of prior studies on the impacts of whale watching on orcas and humpback whale’s behavior.

Behaviors studied	Findings	References
Avoidance behaviors	Orca whale speed increased with increased boat presence, but no difference occurred in the linearity of the path and cardinal direction.	(Kruse, 1991)
Avoidance behaviors	Humpback whales showed avoidance behaviors 84% of the time, increasing the sinuosity of path and change in direction with increased vessel approach.	(Schaffar et al., 2013)
Group type and behavior transitions	Humpback whale calf pods were much more reactive to vessels than non-calf pods and displayed more avoidance behaviors when vessels came within 100 meters of the whale.	(Stamation, et al., 2010)
Behavior transitions	Humpback whales that engaged in surface activity were likely to switch behavior when vessel presence increased. Long term effects are associated with the loss of energy when whales react to boats.	(Schuler et al., 2019)
Behavior transitions	Orcas showed fewer foraging behaviors the closer vessels approached them, leading to a reduction in energy for foraging which could have long-term effects on orcas.	(Lusseau et al., 2009)
Behavior transitions	Humpback whales exhibited more surface behaviors with increased vessel exposure, which could lead to energetic consequences	(Di Clemente et al., 2018)

METHODS

Previous studies recorded the humpback population of this archipelago to be around 1,000 individuals, with about 25-50 calves born annually (Guzman et al., 2015). Female and calf pairs tend to remain closer to shore, while adults prefer deeper waters (Glockner & Venus, 1983; Bruce et al., 2014; Ersts & Rosebaum et al., 2003; Félix & Haase, 2003; Rasmussen et al., 2012; Oña et al., 2017; Smithea, M., 2011; Félix & Guzman, 2014; Guzman & Félix, 2017). Migratory studies found that this population of humpback whales deviate between coastal and oceanic locations during their migration, up and down the coast of South America. These preferences depend on the whale group

type, with mother-calf pairs preferring coastal routes and adults preferring a more direct route in colder oceanic waters. The mother-calf pair preference for coastal waters poses higher risks of vessel collision and entanglement in gillnets, as fisherman and commercial ships occupy shared waters (Guzman et al., 2014).

Field Work

Whale behavioral studies were conducted in the Las Perlas Archipelago off Pacific Panama (8.6°N, -79.1°W) between August 18 and September 6, 2019, consisting of land-based studies from a lookout point on Contadora Island (8.6 °N, -79.03°W) and boat-based studies in a ~9.75 meters whale-watching vessel to conduct visual observations of humpback whale behaviors. Data were collected using a whale group-follow protocol, as the presence of competitive groups (i.e. groups over three whales) made it difficult to follow specific individuals (Mann, 1999). Variables in the data included group type (competitive, mother-calf pair and escort, pair, and lone whale), group size, behaviors (see Table 2), Global Positioning System (GPS) coordinates, whale direction changes, and number of boats within 300 meters of the whale. Variables also included Beaufort wind scale and cloud cover, which are common environmental factors that could have additional influences on humpback whale behavior. A whale was considered a calf if it was less than half of the length of the accompanying whale (Chittleborough, 1965). Groups were considered competitive if there were three or more adult humpback whales within 50 meters of each other and traveling in the same direction, while pairs contained two adult whales traveling in the same direction.

Whales were considered a group if two or more individuals were moving in the same direction and less than 50 meters from each other. These humpback whale pods come to Panama to breed and give birth, which results in a high level of social interaction and explains their close contact during observations. During boat-based behavioral studies, the analysis began once humpback whales were spotted within 300 meters of the research vessel, which gave a clear view for researchers to collect data. Given the increased visibility and the use of Outland X 10x42 binoculars, land-based study sessions began once a whale was spotted within approximately 3 miles of the lookout point. Once whales were spotted, one researcher tracked the GPS coordination and direction change of humpback whales. The second researcher tracked the 11 behavior categories, group type, group size, Beaufort scale, number of boats, and cloud cover. If more than one group was spotted during a study session, the group closest to the observer was tracked. Studies occurred in good weather conditions (Beaufort wind scale < 5) but were obstructed in severe weather conditions (Beaufort scale > 5; Cloud cover = 100%), if whale sightings were lost, or if the whale group split during the observation session. At the start of each session, group type, date, number of whales, Beaufort wind scale, cloud cover, location, distance, and number of boats were all recorded. During the study, data were collected in fifteen-minute increments. While counting the number of vessels, boats were only considered in the study if it was clearly following the humpback whale group and if they were within 300 meters of it. For the controlled observations, trials consisted of zero boat presence during whale behavioral samples. As the lack of boat presence acted as the control variable, these observations could only be conducted during land-

based studies to avoid inadvertent effects from the research vessel. Additionally, whales may have been resampled at any point during the study. Photo-ID may rule this out, but was not utilized for this project. Many behaviors, such as singing, trumpeting, side flukes, and colliding were left out of the study for their low or absent sample sizes. Others were combined into a single category because of low individual incidence. Thus, head slaps, tail slaps, and pectoral fin slaps were all combined into “slap behaviors”.

Statistical Analysis

To measure the significance of behavior transitions due to increased boat numbers, a Chi-squared goodness of fit test was used. This method was chosen for its established ability to test the relationship between behaviors and boat presence (Bagdonavicius, and Nikulin, 2011). To normalize the data, the behavioral observations were proportionally measured and performed using a linear regression hypothesis test. Individual whales may express different behavioral responses when faced with a given dangerous scenario. Therefore, to determine if group type was a significant predictor of a whale’s behavior, a Kruskal-Wallis and a post-hoc pairwise Wilcoxon test was applied to assess which sets of behaviors had a significantly different number of direction changes from each other (Driscoll, 1996). Finally, a regression model featuring a Pearson’s product-moment test was used to test the strength or weakness between the relationship for direction changes and the number of vessels. The test is essential for drawing a best-fit line through the two variables (direction change and vessel numbers) and examining how far off the variables are from the line (Benesty, et al., 2009). All statistical analyses were performed in R version 3.6.0 and Microsoft Excel (2003).

Table 2: Description of behavior categories for humpback whale behaviors (O’Connor et al., 2009; Black, 2012; Hoyt & Hvenegaard, 2002) (*) indicates behaviors which are characteristic of avoidance or stress

Behavior Name:	Description:
Breach	Whale leaps out of the water, spinning in the air before re-entering.
*Tail-Up Dive	Whale lifts tail out of the water and attains a vertical angle for deep dives
Peduncle Arch	Whale arches its back showing the dorsal fin that usually occurs after they surface to breathe
Head Raise/Spy Hop	Raises head vertically out of the water while stationary, flippers outstretched
*Pectoral Fin Slap	Slaps flipper down onto the surface of the water
*Tail Slap	Raises flukes out of the water and slaps them on the surface
*Side fluke	Swimming on one side with one fluke extending above the surface
*Head Slap	Jumps out of the water and hits ventral side of head forcefully on surface
*Chase/Charge	Lunges at another whale, often bubble-streaming
*Strike	Intentionally hits another with flukes, underwater or on surface
Collide	Whales collide, appears to be intentional
Trumpet	Extended low-trumpet or “foghorn-like” sound from blowhole
Singing	An extended high-pitched sound made by male humpback whales
Resting	Motionless movement in which whale stays in one place
*Avoidance	Rapid change in direction to avoid a potential threat

RESULTS

Data were collected from August through September of 2019 and 47 behavioral sessions were recorded. These 47 samples consisted of 24 mother-calf pairs and escort sighting (51%), 11 competitive group sightings (23%), 7 lone whale sightings (15%), and 5 paired adult sightings (11%) (see Figure 2). The average number of individuals in a pod was 2.57 ± 1.59 with a range of 7. One explanatory variable (number of boats) and two dependent variables (direction change and behavior transitions) were compared. Mother-calf and escort pods made up 50% of the samples involving boats but were rarely observed during controlled samples, making up only 14% of the data, respectively.

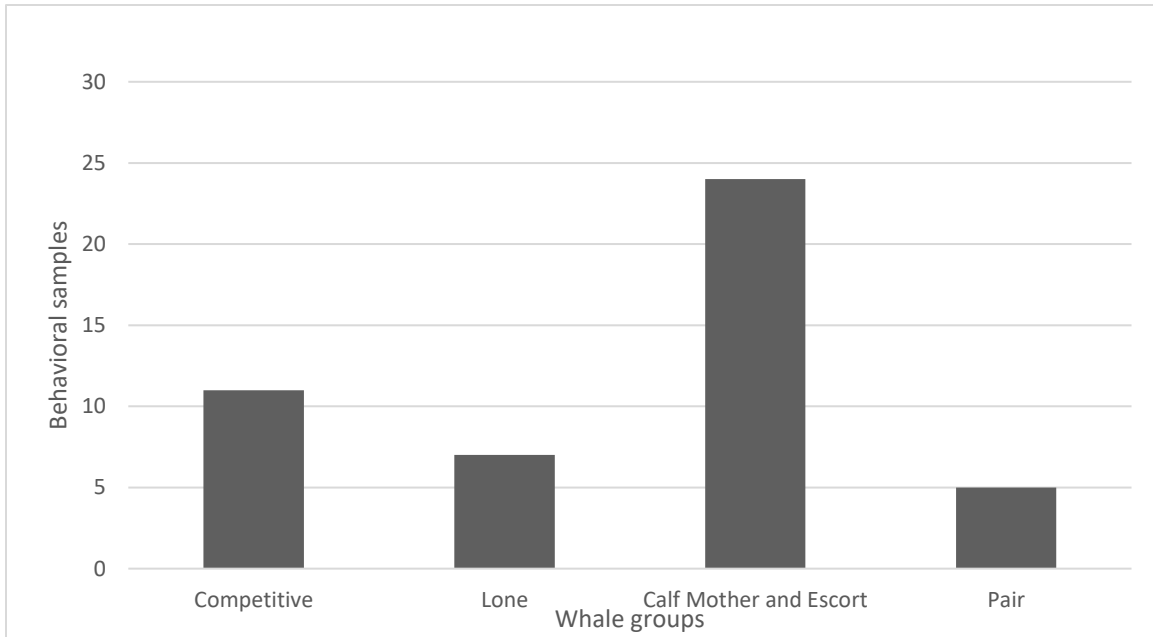


Figure 2: *Megaptera novaeangliae*. Total number of behavioral samples taken from humpback whale group types in the study.

Behavior Transitions

Behavioral observations were collected in both the absence and presence of vessels. Overall, the Chi-squared goodness of fit test indicated a significant difference among all behaviors ($X^2 = 57.1147$, $df = 9$, $p = 4.8 \times 10^{-9}$). In the presence of vessels, breaching gradually increased as boat number grew, then significantly declined ($p = 2.94 \times 10^{-7}$) with more than three boats present (2%; Figure 3). This decline in breaching often occurred when boats were chasing whales. Humpback whales were most often seen executing slap behaviors (e.g. pectoral fin slaps, tail slaps, and head slaps) during sampling with zero boats present (55% ; $p = 1.03 \times 10^{-8}$). Alternatively, the frequency of diving behavior varied widely with boat presence levels ($p = 5.53 \times 10^{-6}$) among different levels of boat presence (36% of dives occurred in sessions with two boats, 29% with four or more boats, 28% with zero boats, 5% with one boat, and 2% with three boats), but

there was no discernable pattern related to the number of vessels. While spy hops/head rises were rarely seen, they only occurred during incidences with boats present.

Competitive groups comprised most of the data in terms of amount of behaviors observed. More than 62% of behaviors were observed in eleven competitive groups ranging from three to eight individuals within each pod. Mother-calf and escort groups provided 20% of the behavioral data, followed by 16% seen in five pairs, and seven lone whale samples falling in last at only 2% of the behavioral data. Breaching was the only behavior that was not predominately expressed by competitive whale groups. This occurred primarily with paired groups (40%), followed by mother-calf and escort pods (36%). Competitive groups were only observed breaching in 23% of the samples and lone whales were always found to display the lowest frequency of activities (< 2%).

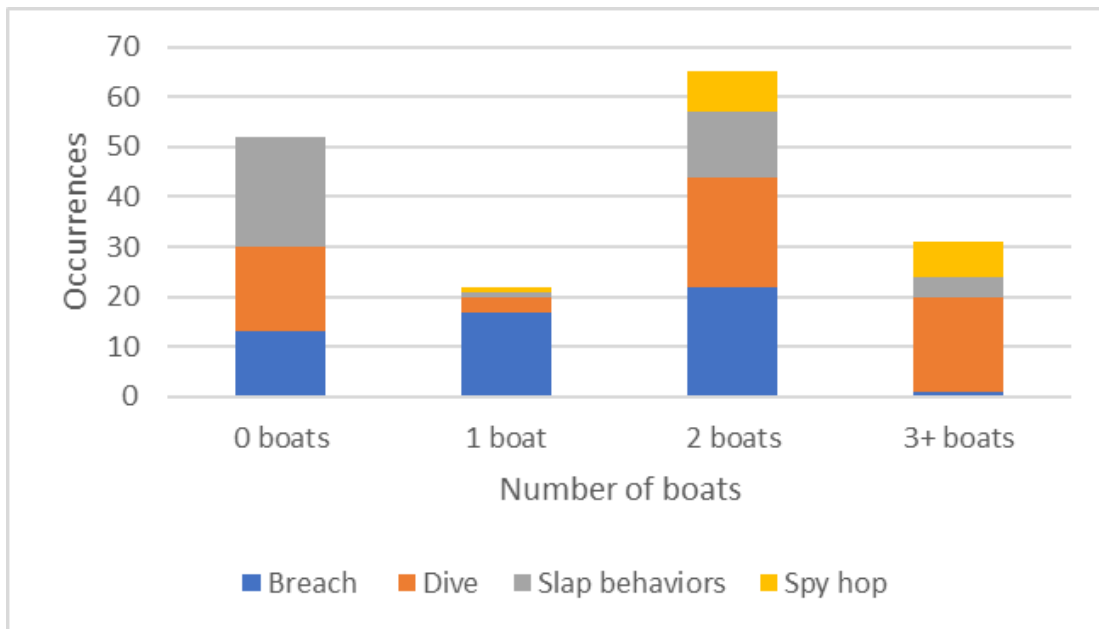


Figure 3: *Megaptera novaeangliae*. Total number of categorized whale behavior occurrences observed during varying boat presence while conducting group-follow behavioral samples.

A linear regression model of the proportion of behavioral transitions presented no clear indication of significance of change with varying boat numbers (Breach $p = 0.351$, Dive $p = 0.6918$, Slap $p = 0.641$, and Spy hop $p = 0.4206$).

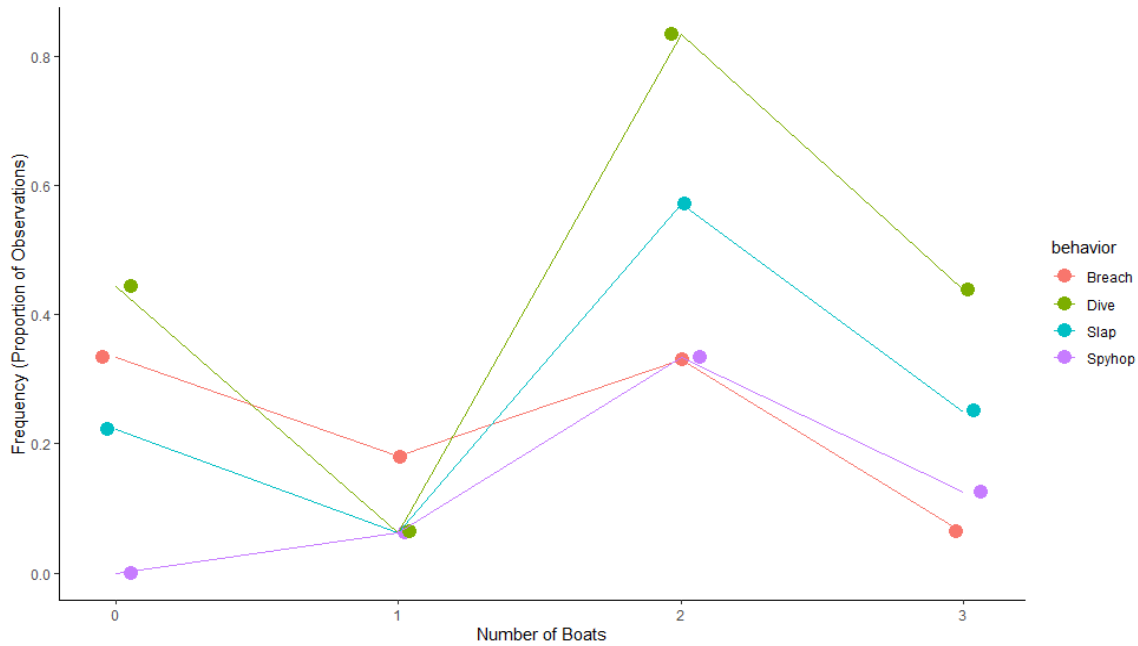


Figure 4: The frequency of behavioral observations as a proportion of the total numbers of observations for each boat type.

Direction Change and Group Type

A post hoc pairwise Wilcoxon test was made to assess which sets of group types had significantly different number of direction changes from each other. Of the comparisons across all whale group types regarding the number of direction changes exhibited, the pair versus competitive group type and pair versus calf group type were the only pairwise comparisons rejected ($p = 0.046$). The rest of the pair-wise comparisons therefore supported the null hypothesis, which assumes little to no difference occurred among the number of direction changes for each group type. A box plot was made to

visualize the comparisons (Figure 5) and a more in-depth description of the pairwise comparisons can be found in Table 3.

Table 3: Summary of pairwise comparisons using Wilcoxon rank sum test to evaluate direction change differences between whale group types.

Comparison	p-value	Conclusion
Competitive vs. Calf Group	0.301	Don't Reject the Null
Lone vs. Calf Group	0.864	Don't Reject the Null
Pair vs. Calf Group	0.046	Reject the Null
Lone vs. Competitive	0.864	Don't Reject the Null
Pair vs. Competitive	0.046	Reject the Null
Pair vs. Lone	0.130	Don't Reject the Null

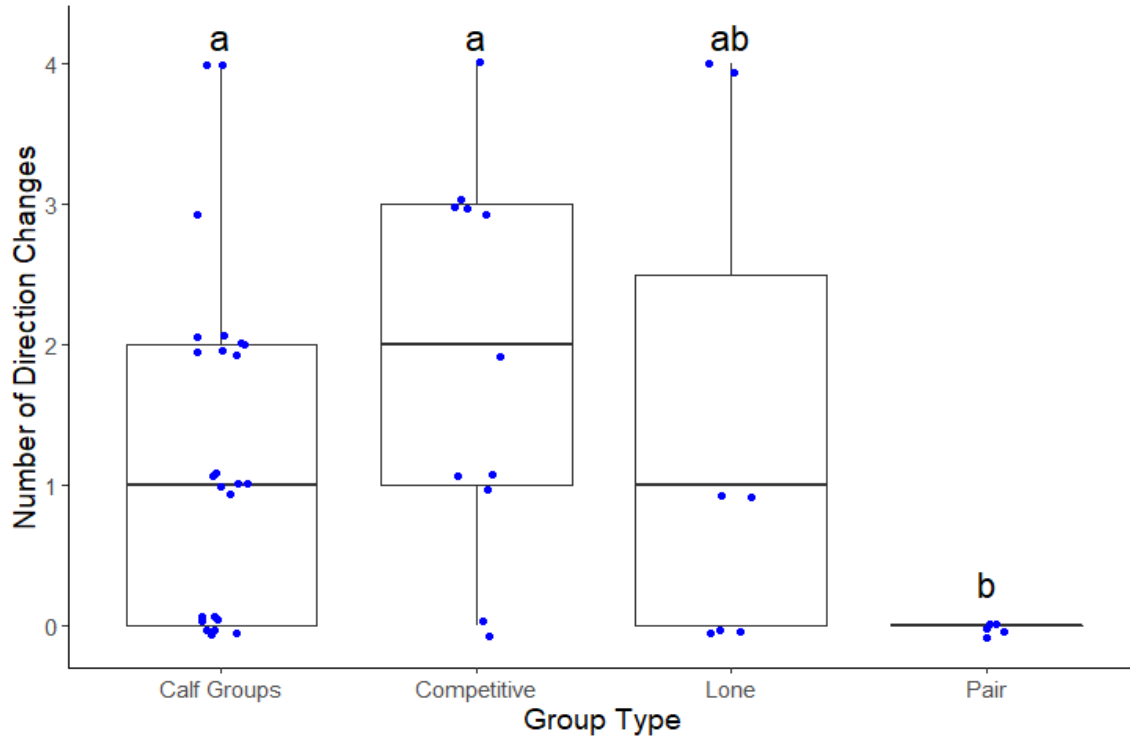


Figure 5: *Megaptera novaeangliae*. Box plot comparing the number of direction changes of four different whale group types (competitive groups, lone groups, calf groups and pairs). Groups with shared letters are not significantly different.

Relationship of Direction Change to Number of Vessels

As the number of vessels during a behavioral sample increases, whale direction changes increase. Using a linear regression model, direction change and the number of vessels produced a positive relationship ($R^2 = 0.38$, $p = 3.36 \times 10^{-6}$; Figure 6). Few direction changes occurred when zero boats were present, with only one occurrence of a competitive group changing direction once during a controlled observation; however, the number of observations within each treatment was unequal. Observations with one boat occurred most frequently (34%) followed by four or more boats (22%), zero boats (20%), two boats (15%), and three boats (9%). Mother-calf and escort groups had the most amount of direction changes, with 26 total direction alterations (see Figure 6). This result

may be attributed to calf-mother-escort groups being the most observed group type (51% of samples).

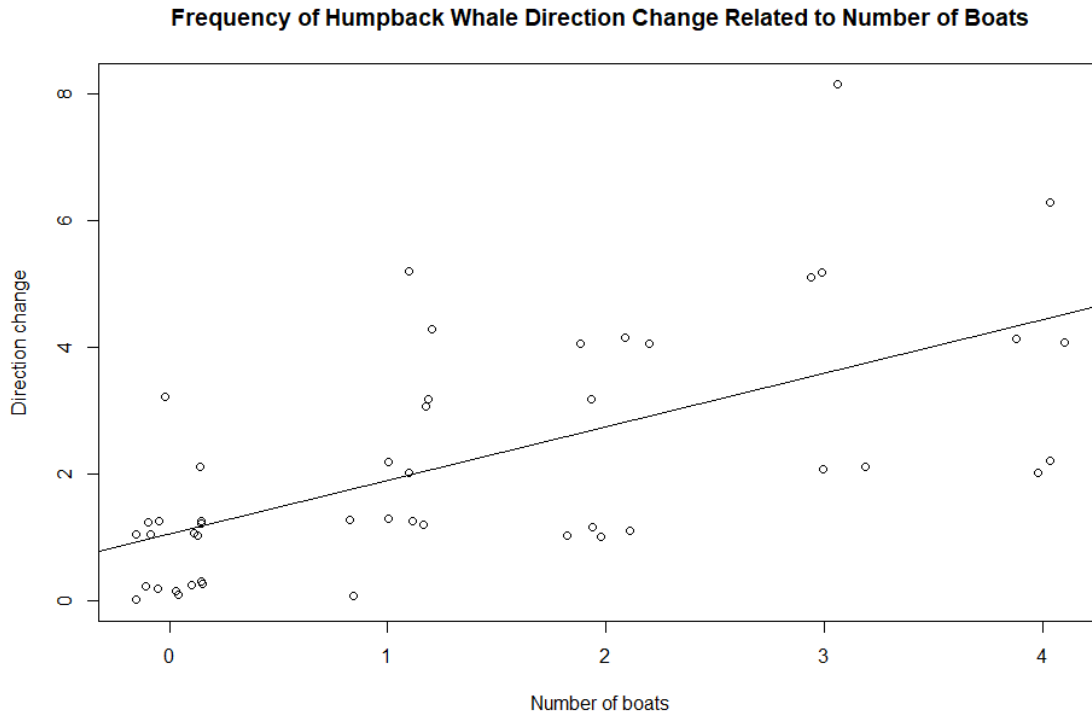


Figure 6. *Megaptera novaeangliae*. Observed correlation between the number of boats and the total number of direction changes while conducting group-follow behavioral samples.

DISCUSSION

Behavioral observations show that boat density appears to correspond with humpback whales altering their behaviors. This study suggests that these indicators are a sign of disturbance, but more studies are required to strengthen this assumption. This result is important, given that Panamanian regulations prohibit the disturbance of whales, which includes any change in whale behavior.

Behavior Transitions

The number of boats present had varying effects on the four behaviors measured: breach, diving, slap behaviors, spy hop. It is theorized that breaching represents a communicative tactic caused by whales slapping their bodies on the surface when vocalization is obstructed (Kavanagh, 2017; Whitehead, 1985). There are numerous factors that can cause vocalization hindrance such as high wind speeds, rain, and vessel noise. Whale communication in this environment could have been blocked by enhanced vessel noise, leading to an increase in the measured behaviors. This is reflected in the results, as vessel number increase appeared to be associated with higher incidences of breaching (Figure 3). However, breaching frequency decreased once vessel numbers exceeded two boats. This result may link to the many incidences of boats continuously violating speed, distance, and angle of approach. “Leapfrogging” (i.e. boats slowly approach whales at a short distance and then speed up to intercept the whale), occurred often during studies and has been found to disturb groups (Johnson, 2006) and it is possible that crowding from boats limited surface area, restricting available space for whales to jump. However, whale breaching could also be a form of play, especially for calves (Whitehead, et al., 1985), which could explain their relatively high involvement of calves in breaching activities (36%) in calf groups from the study. Alternatively, breaching may also be a tactic for male humpback whales to display their physical abilities when seeking a mate. This is indicated in the high breach count that occurred in pairs and competitive groups (40% and 23% respectively). Unfortunately, due to boats being more inclined to violate the existing whale-watching regulations, the high levels of

whale-chasing exhibited by vessels could influence stress adaptability of the whales, reducing their desire to breach. It is likely that these behaviors could be eventually replaced with an increase in avoidance behaviors, such as direction change, longer dive time, etc.

Slap behaviors increased when the number of boats in the sample declined. This observation supports the theory that if a whale is close to another group, they will communicate through slapping behavior (see Shapiro, 2008). Panama is a hotspot for breeding whale, which leads to increased competitive behaviors between males and females. Whales of both sexes slap their fins to communicate or gain attention when seeking a mate. Females specifically use this slapping tactic since they do not sing (Herman, et al., 2007; Deakos, 2002).

Competitive groups dominated in three of the four behavioral categories: slap behaviors, spy hopping, and diving. However, results may differ from other reports (Blair et al., 2016) conducted at different times of the year because whale behavior changes dramatically during breeding seasons. Tail slaps are the most prevalent surface behavior, most likely because they are not associated with high energetic costs (Noren et al., 2009; Segre et al., 2020). Thus, humpback whales may resort to breaching when noise pollution (vessel presence) increases because the sound of breaching travels much farther than the noise of a tail or pectoral fin slap. Schuler et al., 2019 attributes the change in surface behavior to the disparity between the weight and surface area of a whale's tail versus that of their body. Previous studies also found vessel increase to cause humpback whales exhibiting surface behaviors to switch from surface activity to traveling. This may have

long term effects on individuals and groups because of the high energy expenditure of reacting to the boats (Schuler et al., 2019; Table 1).

Spy hops or head raises occurred less frequently than the other documented behaviors, but more occurred during sessions of high boat presence. Scientists predict spy hops ensue when whales wish to view activities above the surface (Galvin, 2006; Pitman, 2003) and as spy-hopping only occurred in the study when vessels were present, the whales were most likely curious about the vessels following them, thereby supporting the hypothesis.

On the contrary, depending on the type of analysis and the way behavioral change is defined, some of the behavioral transition results can be compressed or expanded. Therefore, certain measures may minimize the appearance of certain changes. The linear regression model (see Figure 4) displayed no clear indication of behaviors transitioning when faced with varying vessel numbers. This result could be an indication of habituation, which only poses additional risks. Habituation to vessel noise only heightens their vulnerability to collision, resulting in severe injury or death to involved cetacean. Higher vessel traffic resulting from Panama being one of the most central ports in the global cargo-shipping network only increases their risk of vessel collision (Kaluza et al., 2010). Since this is an observational study and the study did not experimentally introduce boats, the number of samples differs between boat numbers as you can see in Figure 3. Further studies are required to confirm if humpback whales in the Las Perlas Archipelago display the same behavioral responses that whale groups exhibit in published studies.

Direction Change and Group Type

In this study, whale group type was not always found to be a significant predictor for the number of direction changes exhibited. Significance appeared between pairs versus competitive groups ($p = 0.046$) and pairs versus calf groups ($p = 0.046$). This significance may be the result of competitive groups in a setting where they must be vigilant, always watching their competitors; however, this attentive attribute may cause them to react in a stressed-based way to avoid boats. Energy cost concern are especially prevalent in calf groups since it seems whale watching vessels prefer following calf groups for their playful behavior (Figure 2). Calves may feel more threatened by boats than other group types, which comes as an extra concern, since Panamanian regulations have extra laws to protect calves, given their vulnerable state. We saw this significance even with a small sample size, but more samples would clarify the extent of the relationship. Nevertheless, results show trends supported by previous whale behavioral reports. In one study, group type was included as an explanatory variable to predict dive time, swim speed, and directness index. This study had comparable results as it found this relationship had no significance and did not lead to a better fitting model (Scaffar et al. 2013). Another study found pods with calves to increase their activity compared to non-calf pods (Stamation, et al., 2010). This supports the results, as our study showed calves executing the most amount of direction changes. However, due to the small sample size ($n = 47$ trials) of this study, no other conclusions can be confidently drawn on whether whale behavior can be predicted by whale group type.

Relationship of Direction Change to Number of Vessels

The results displayed a positive correlation between direction change and the number of vessels. This study records a total of 62 direction changes, with most of these changes occurring in pod groups containing calves (Figure 6). Calves are especially affected by vessel presence because of the increased dangers associated with higher likelihood of vessel collision, less knowledge of vessel movement, and decrease of essential behaviors such as feeding, nursing, and learning how to care for themselves (Stamation, et al., 2010). This may explain why calf groups had the highest sum of direction changes compared to all other whale pod types, especially since vessels had a higher preference for chasing whale groups with calves. Results from this study show clear indications of behavioral change as a consequence of increased vessel presence, violating Panama's regulation declaring that "It is prohibited to change the behavior of cetaceans" (*sensu* Carlson, 2010).

Previous research (Schaffar et al., 2013) suggests that the number of boats is a robust predictor of the number of direction changes a whale will exhibit. Direction change is a tactic humpback whales use to avoid predators, suggesting this is an avoidance behavior utilized when faced with a boat, which could be viewed as a perceived threat (Schaffar et al., 2013; Table 2). Several studies suggest direction changes are also related to stress and could indicate boat presence increases physiological disturbance (Schaffar et al., 2013; Kruse, 1991; see Table 1). Such avoidance behavior may ensure self and group preservation, but it comes at a physiological cost to the organism: not only can increased levels of stress negatively impact an organism's health,

but it can also inhibit normal whale behavior and interactions, which can disrupt social interactions (mother-calf pair in particular), mating, and foraging (Lusseau, 2009).

Long-Term Impacts

This study does not address the potential long-term impacts from disturbance, but these short-term impacts may indirectly lower reproduction rates (Morete et al., 2007). This can occur through drowned out vocalizations and a reduction in the likelihood of whales finding mates from vessels changing whale group dynamics and direction (Weilgart, 2013). Additionally, whale health can be negatively affected through chronic levels of stress, increases in their energy expenditures, and discontinuation of essential behaviors such as feeding, resting, nursing, etc., when exposed to disturbance (Parsons, 2012). A constant change in behavior and less concentration on survival activities could potentially diminish their populations and could be an especially prevalent concern for pods with calves, as whale watching vessels prefer following calf groups for their charismatic physical characteristics and playful behaviors. Given their vulnerable state, Panamanian regulations contain extra provisions to ensure the protection of whale calves.

In the Las Perlas Archipelago, whale watching is economically beneficial to Panama and generates significant income to the local communities involved. Whale watching has strong links to human success, as the industry creates employment opportunities and provides ecosystem services to tourists, residents, and boat operators. However, if disturbance of the whales continues, the population may permanently

abandon areas where whale-watching industries frequently visit (Dean, et al., 1985).

Therefore, whale watching industries would suffer, damaging the Panamanian economy.

Future Studies

There is a chance that behavior and stress are not necessarily coupled in a way that we can observe, which may explain why some of the whales did not seem to change their behaviors with increased vessel interaction. Thus, animals may not show avoidance behaviors but have high levels of stress hormones. To resolve this issue, physiological studies should occur. Biopsy samples could measure the amount of cortisol in their tissue and blubber samples, which would be a direct way of determining their stress levels. Additionally, social surveys should be collected from tourists, local communities, and boat operators to help us understand their impression of the whale watching industry and generally, whether there is a conservation and education value of whale watching. These surveys could also present additional knowledge of how well regulations are being communicated to boat operators. Finally, further behavioral studies should continue with better measuring tools. The use of a theodolite tool would produce accurate distance measurements between vessels and whales, which is essential for understanding if distance impacts their behaviors. Additionally, drones could also collect more accurate behavioral samples with less invasive observations. Visual observations could be maintained more consistently by drone due to the optimal viewing angles. Vessel based observations can only be made while the whale is surfacing. Better enforcement protocols should take place to ensure vessels are abiding by Panama's regulations. To reduce vessels from violating whale watching regulations, a satellite-based monitoring system

should be implemented to track the activities of these vessels. This technology has already shown to be successful in fisheries management plans and has alleviated illegal, unreported, and unregulated (IUU) fishing (Schmidt, 2005).

CONCLUSION

Panama has strict whale watching operation regulations that are not being followed in the Las Perlas Archipelago. At multiple points throughout the duration of the study, the researchers observed all laws pertaining to vessel regulations being broken at least once by other boats. The lack of monitoring and enforcement of these regulations may result in more audacious decisions from boat operators, resulting in harmful and often lethal collisions with adult whales and calves. At the very least, these preliminary results display behavior fluctuations related to vessel presence, which is illegal according to Panamanian protocols (*sensu* Carlson, 2010). It is highly recommended that communication and education occur with boat operators to discuss regulations and the importance of abiding by the law. The purpose of this study is not to eradicate whale watching, but to persuade industries to abide by responsible whale watching protocols. Responsible whale watching develops an interdependent relationship between people and whales: people gain from the ecosystem services provided by whales and economic income from this tourism industry, while whales could directly benefit from less stress from vessels and indirectly from tour guides expanding environmental awareness and enlightening tourists of environmental or conservation issues. Continued whale research, monitoring, and modeling efforts in Panama must be implemented to better inform

management decisions for stricter regulatory and enforcement protocols that are vital to minimize disturbance on this vulnerable population of humpback whales.

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