



Impacts of Whale Watching on the Behavior of Humpback Whales (*Megaptera novaeangliae*) in the Coast of Panama

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Ecotourism focused on whales and dolphins has become a popular activity and an important source of revenue for many countries. Whale watching 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 it is crucial that ecotourism industries consider the impact of their activities on whale behavior. To address this statement, we collected behavioral data (e.g., change in swimming direction, frequency of breaching, slap behaviors, diving, and spy hops) from humpback whales (*Megaptera novaeangliae*) in the marine protected area of Las Perlas Archipelago off the Pacific coast of Panama. The goal was to determine if tourist vessel presence had an influence on whale behaviors. We conducted this study during the humpback whale breeding season from August through September 2019. Based on 47 behavioral observations, we found that higher boat density corresponded with humpback whales' frequency of direction changes, which based on previous literature is believed to be a sign of disturbance. Alternatively, no changes in behavior were observed with varying boat density. This result is important given Panamanian regulations first implemented in 2007 by Resolution AMD/ARAP No. 01, 2007 prohibit whale-based tourism from disturbing whales, which is explicitly measured by changes in whale behavior. Because there is no systematic monitoring of whale watching activity to enforce the regulations, there is currently little compliance from tour operators and tourists. The integration of animal behavior research into management planning should result in more effective regulation and compliance of such conservation policies.

Keywords: ecotourism, *Megaptera novaeangliae*, disturbance, stress, behavioral ecology, animal welfare, wildlife-ecotourism

INTRODUCTION

Wildlife-based ecotourism, which includes whale watching, is identified as, "tourism based on encounters with non-domesticated animals...[which] can occur in either an animal's natural environment or in captivity" (Higginbottom, 2004). It provides economic benefits to many countries around the world (Hoyt, 2001; O'Connor et al., 2009; Guidino et al., 2020;

Wiener et al., 2020) and has increased drastically in popularity over the past 50 years. Globally, over 13 million tourists take trips to view cetaceans each year, generating over \$2 billion US dollars in revenue across 119 countries (Hoyt and Hvenegaard, 2002; O'Connor et al., 2009; Stoeckl et al., 2010; Guidino et al., 2020; Wiener et al., 2020). Whale watching industries are rapidly growing in developing countries such as Cambodia, Laos, Nicaragua, and Panama (Hoyt, 2001; O'Connor et al., 2009). While ecotourism activities have many economical, educational, and ecological benefits relating to conservation, there have been many published studies that conversely question the benefits of this form of ecotourism, proposing that these activities may be harming the wildlife involved (Parsons, 2012; Leslie et al., 2015; Larson et al., 2016). Therefore, these activities deserve a higher level of scrutiny and monitoring to ensure their ongoing sustainability and economic, community, educational, etc., contributions (Stamaton et al., 2007; The International Ecotourism Society, 2015).

The main contribution of whale watching is that it provides a stable financial alternative to the traditionally consumptive use of whales through hunting or “whaling.” The growing influx of tourists coming to watch whales provides the revenue required to support local communities and cultures while simultaneously supporting whale conservation efforts (Wearing et al., 2014). Whale watching focused on humpback whales (*Megaptera novaeangliae*) was also found to be effective in encouraging natural resource protection and patronization of local businesses, especially when tour guides take care to disseminate conservation messages to tourists (Peake et al., 2009). In addition, through specific platforms such as whale watching, the public has the opportunity to come in contact with often endangered or threatened wildlife and learn about conservation efforts (García-Cegarra and Pacheco, 2017). 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). This is especially relevant given that the rapid urbanization of society is prompting people to desire opportunities to “reconnect” themselves with nature (Curtin and Kragh, 2014).

The growing popularity of this industry also has drawbacks especially in developing countries, where regulatory frameworks are often lacking leading to a higher likelihood that animal welfare and safety regulations will be ignored (Sitar et al., 2016; Kassamali-Fox et al., 2020). Tour boat operators may intentionally or inadvertently utilize locations that experience little enforcement or actively violate the rules of responsible whale watching in the desire to attract more clients, ultimately leading to detrimental impacts on whale welfare (Corbelli, 2006; Parsons, 2012; Kessler and Harcourt, 2013; Sitar et al., 2016). Accordingly, the International Whaling Commission (IWC) established measures to protect whales and published guidelines for responsible whale watching in 1997 (International Whaling Commission, 1997). Unfortunately, with little enforcement in some countries, there are still high levels of detrimental whale interactions with non-consumptive whale-watching vessels (Parsons, 2012).

During encounters when high numbers of vessels are present, whales will often exhibit a high frequency of behavioral shifts, such as direction changes, which are reflective of avoidance tactics employed when whales encounter predators (Frid and Dill, 2002; Williams et al., 2002). These behaviors, combined with the high-speeds and unpredictable approach angles often displayed by vessels, greatly increase the risk of collision (Guzman et al., 2013). In addition, whales must expend extra energy to avoid boats, while decreasing the occurrence of necessary survival activities (e.g., nursing, foraging, and reproduction; Morete et al., 2007; Stamaton et al., 2010; Schaffar et al., 2013; Fournet et al., 2018; Fiori et al., 2019). This is especially true in breeding areas that are primarily frequented by mother and calf groups because they are more susceptible to whale watching disturbances (Morete et al., 2007; García-Cegarra et al., 2019). One study suggested that long-term disruption of routine behaviors caused by high levels of negative boat and whale interactions could have lasting reproductive impacts on humpback whale populations (Braithwaite et al., 2015), while others highlight potential impacts due to the inability for whales to effectively communicate due to “acoustic masking” from loud boat sounds (Rossi-Santos, 2016; Erbe et al., 2018, p. 290). This could result in reduced success when finding a mate in breeding areas, locating food in feeding areas, and further expended energy to increase call volume or duration (Foote et al., 2004; Fournet et al., 2018; Putland et al., 2018).

Given these issues and mediating factors, the marine and coastal areas of Panama are ideal locations for observing the whale–vessel interactions and potential repercussions. Panama is a popular tourist destination due to the presence of the Panama Canal, which only serves to increase daily levels of vessel traffic through its service as an important commercial trade route. Humpback whales from the southeast Pacific population migrate from their feeding grounds in Chile and Antarctica to the tropical areas along the Pacific coasts of Central America for the breeding season (Rasmussen et al., 2007; Acevedo et al., 2017). The season extends from June to October, and sometimes December, with peaks in August and September (Guzman et al., 2015). The humpback whale population of this archipelago is estimated to be around 1,000 individuals, with about 25–50 calves born annually (Guzman et al., 2015). This population of humpback whales is identified as Breeding Stock G (International Whaling Commission, 1998), which is one of the seven “stocks” inhabiting oceans in the southern hemisphere. This specific population undertakes one of the longest migration distances (Stone et al., 1990; Acevedo et al., 2017) of more than 16,000 km roundtrip from the feeding grounds to the breeding grounds (Rasmussen et al., 2007; Félix and Guzmán, 2014; De Weerd et al., 2020), with the entire stock swimming along 9,000 km of coastline (Félix et al., 2011). Female and calf pairs tend to remain closer to shore (Glockner and Venus, 1983; Bruce et al., 2014; Oña et al., 2017) while adults prefer more direct routes in deeper waters (Félix and Haase, 2005; Rasmussen et al., 2012; Félix and Guzmán, 2014; Guzman and Félix, 2017). Mother–calf pair preference for coastal waters poses higher risks of vessel collision and entanglement in gillnets, as fishermen and commercial ships share these waters (Félix and Guzmán, 2014). Although whales are migratory for

the majority of the year, they congregate in waters less than 200 m deep for their annual breeding season. Hence, the shallow waters of the Pacific of Panama are ideal for mother humpback whales giving birth, due to the lack of competitive males pursuing the females, ocean turbulence, and predators (Flórez-González et al., 1994; Corkeron and Connor, 1999; Darling and Nicklin, 2002; Cartwright and Sullivan, 2009; Craig et al., 2014; Pitman et al., 2015). The objective of this study is to determine if tour boat number and mode of approach to whales elicit changes in their behavior frequencies in the Las Perlas Archipelago in Panama. We hypothesize that whales will decrease the frequency of certain behaviors as indicators of disturbance when boat presence increases and when boat captains are not complying with regulations.

MATERIALS AND METHODS

Study Site

This study was conducted 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, making it the fourth-largest coastal marine protected area of Panama (ADM/ARAP No. 1 from 13 February 2007; Guzman et al., 2008). We recorded behavioral responses of humpback whales in the Las Perlas Archipelago between 18 August and 6 September 2019, with observational sessions consisting of both land-based and boat-based visual behavioral studies, from a lookout point on Contadora Island (the largest inhabited island) and a ~9.75 m whale-watching vessel, respectively. 720 total minutes were recorded, with 135 min from land-based surveys and 585 min from boat-based surveys, throughout the 16 days of research. Our boat, unlike other boats, took extreme precautions to minimize our potential disturbance to the whales by following the mandated regulations such as keeping a 250 m distance, having a certified boat operator with a permit for commercial operations, and limiting observation times to 30 min per group.

Data were collected using a whale group-follow protocol, as the presence of competitive groups (i.e., a female surrounded by one or several males displaying active behaviors, such as breaching, striking, charging, and trumpeting), made it difficult to follow specific individuals (Mann, 1999). Therefore, a focal follow method was used. Variables in the data included four group types (e.g., competitive, mother–calf pair and escort, pair, and lone whale), group size, behaviors (see **Table 1**), Global Positioning System (GPS) coordinates, whale direction changes, and the number of boats within approximately 300 m of the whales. The distance was visually measured for both boat and land surveys by the researcher using Chapera island as a referential point. We then estimated how far the whale was between the boat or Contadora (the lookout point) and Chapera. Diving behavior was measured by the number of fluke dives that occurred within 15 min by a focal whale (including adults and calves). Other recorded variables were measured to characterize the environmental conditions during the survey which included the Beaufort wind scale and cloud cover (Spencer et al., 2006).

Description of Group Types

A mother and calf pair consisted of a large whale (assumed to be the mother) together with a small individual one-third the length of the adult, the calf (Chittleborough, 1958; Cartwright and Sullivan, 2009). A lone whale was a single individual traveling without any other individuals observed within 50 m, while pairs contained two adult whales traveling in the same direction. Meanwhile, whales were considered a group (or “pod”) if three or more individuals were moving in the same direction and less than 50 m from each other. These groups were considered competitive if three or more adult humpback whales were within 50 m of each other, exhibiting high energy behavior. The composition of these groups usually consisted of a single female (with or without calf), with one or more males that are showing a high frequency of surface behavior and physical contact with each other (Herman et al., 2007).

Behavior Frequency

During boat-based surveys, observation began once humpback whales were spotted within 300 m of the research vessel, which gave a clear view for researchers to collect data. Land-based study sessions began once a whale was spotted within approximately 3 miles (4.8 km) of the lookout point given the increased visibility and the use of Outland X 10x42 binoculars. For both land and boat surveys, once whales were spotted, one researcher tracked the GPS coordination and direction change of humpback whales. The GPS coordinates were subjectively estimated by the researcher judging the whale’s distance between the two islands of Contadora (the lookout point) and the island of Chapera in viewpoint of the land-based studies. Researchers pinpointed the estimated location of the whale on the device’s map using a mobile device’s GPS application and recorded the coordinates. A change in direction was visually measured by considering the location and forward positioning of whales when surfacing. If the whale group surfaced in a different location and in a different facing direction than their original position, it indicated a direction change. The second researcher tracked all 15 behaviors from **Table 1** as well as group type, group size, Beaufort wind 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. If a whale or pod were spotted, then every 15 min, observations of weather conditions, and a scan of behaviors (e.g., scan sample) were conducted and then recorded. We did not record the frequency of behaviors that occurred continuously over 15 min.

While counting the number of vessels, boats were only included in a session if it was observed to be clearly following the humpback whale group and if they were within 300 m of the whale. Observation sessions that included zero boats present were considered controls. Since the lack of boat presence served as the control variable, these observations could only be conducted during land-based studies to avoid inadvertent

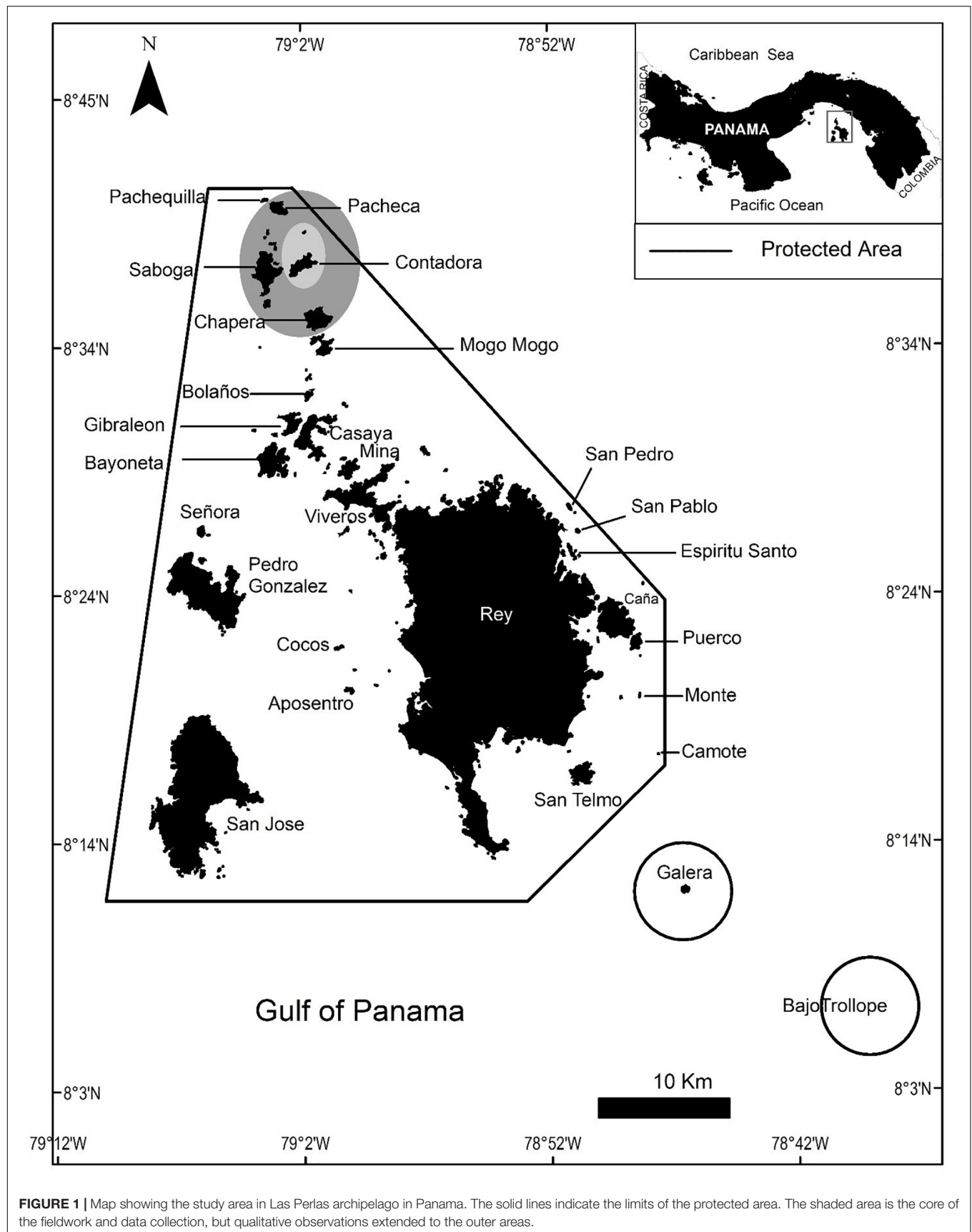


TABLE 1 | Description of behavior categories for humpback whale behaviors (based on descriptions by: Glockner-Ferrari and Ferrari (1984) and Gabriele (1992) (adapted from Bauer, 1986; Helweg, 1989; Corkeron, 1995; Darling and Nicklin, 2002).

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 the ventral side of head forcefully on surface
*Chase/Charge	Lunges at another whale, often bubble-streaming
*Strike	Intentionally hits another whale with fluke extending above the surface
Collide	Whales collide, appears to be intentional
Trumpet	Extended low-trumpet or “foghorn-like” sound from the blowhole
Singing	An extended high-pitched sound made by male humpback whales
Resting	Motionless movement in which whale stays in one place
*Avoidance	The rapid change in direction to avoid a potential threat

* indicates behaviors which are characteristic of avoidance or stress.

effects from the research vessel. Many behavioral events, such as singing, trumpeting, side flukes, and colliding, were omitted from the study given their low or absent sample sizes. Others were combined into a single category because of low individual incidence. For example, head slaps, tail slaps, and pectoral fin slaps were all combined into “slap behaviors.”

Statistical Analysis

We used a Chi-squared goodness of fit test to measure the influence of boat density on whale behavior. We used this method due to its established ability to test the relationship between behaviors and boat presence (Bagdonavicius and Nikulin, 2011). To normalize the data, we proportionally measured the behavioral observations using a linear regression hypothesis test. Individual whales may express different behavioral responses when faced with a disturbance. Thus, to determine if group type was a significant predictor of a whale’s behavior, we applied a Kruskal–Wallis and a *post hoc* pairwise Wilcoxon test to assess which sets of groups had a significantly different number of direction changes from each other (Pohlert, 2014). Results are reported as mean $\pm$ standard error followed by the *p*-value. Finally, we used a regression model featuring a Pearson’s product-moment test to test the strength or weakness between the relationship between direction changes and the number of vessels. Such a 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 regression line (Benesty et al., 2009). Both boat and land-based studies were included in every analytical test. We performed all statistical analyses in R version 3.6.0 (R Core Team, 2017) and Microsoft Excel (2003).

RESULTS

Between August and September 2019, we recorded 47 behavioral sessions. Groups with mother and calf pairs and mother–calf and escort groups were pooled for analysis due to the low sample size of mother–calf and escort groups (three groups total). These 47 samples consisted of 24 mother and calf pairs and escort sightings (51%), 11 competitive group sightings (23%), seven lone whale sightings (15%), and five paired adult sightings (11%). The average number of individuals in a pod was 2.57 with a range of one individual to a maximum of eight individual whales in the study. Thereafter, we compared the explanatory variable (number of boats) and two dependent variables (direction change and behavior). 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.

Behavior State Transitions

We collected behavioral observations in both the absence and presence of vessels. Overall, the Chi-squared goodness of fit test indicated a significant difference among all behaviors ($X^2 = 57.1147$, $p < 0.001$). In the presence of vessels, breaching gradually increased as boat numbers grew, then significantly declined with more than three boats present (2%; **Figure 2**). 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%). Alternatively, the frequency of diving behavior (e.g., tail up-dives) varied widely 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 situations when boats were present.

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 samples, five pair groups provided 16%, and seven lone whale samples accounted for only 2% of the behavioral data. Breaching was the only behavior that was not predominately expressed by competitive whale groups. Competitive groups made up 23% of the breaching while other non-competitive groups made up the other 77%. This occurred primarily with paired groups (40%), followed by mother–calf and escort pods (36%) and lone whales (<2%). In addition, a linear regression model (**Figure 3**) capturing the proportion of behavioral transitions presented no clear indication of significance of change

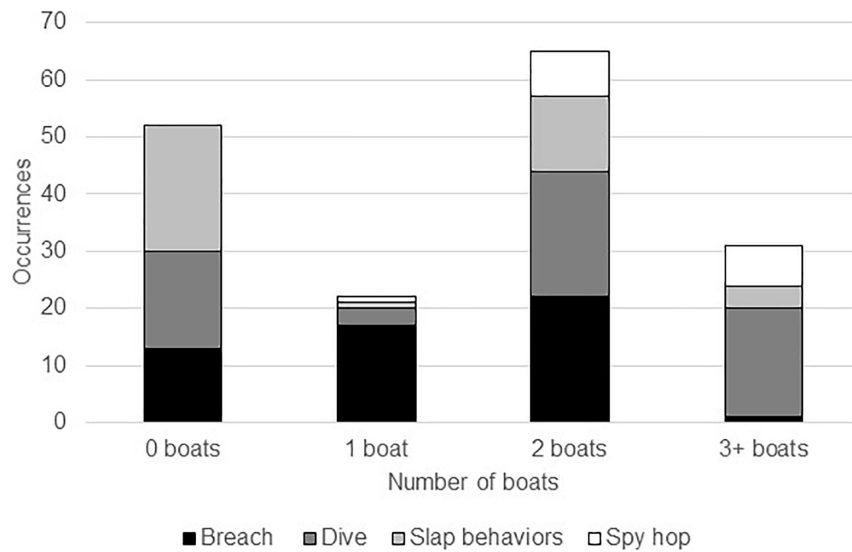


FIGURE 2 | *Megaptera novaeangliae*. Total number of categorized whale behavior occurrences observed during varying boat presence while conducting group-follow behavioral samples.

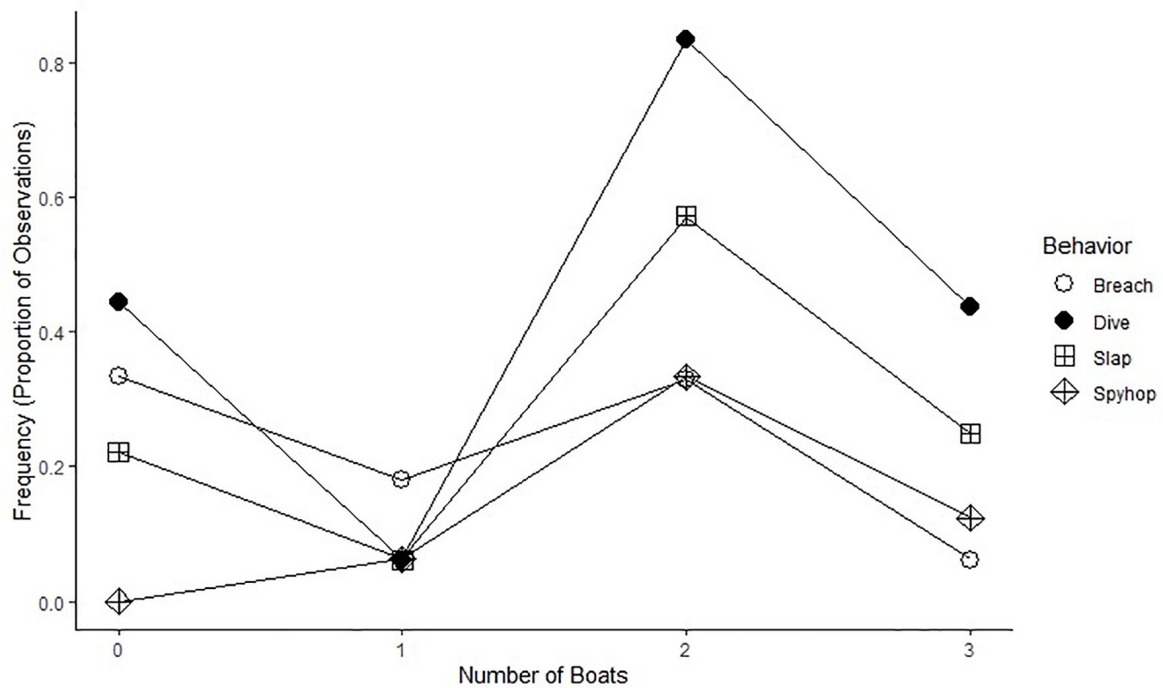


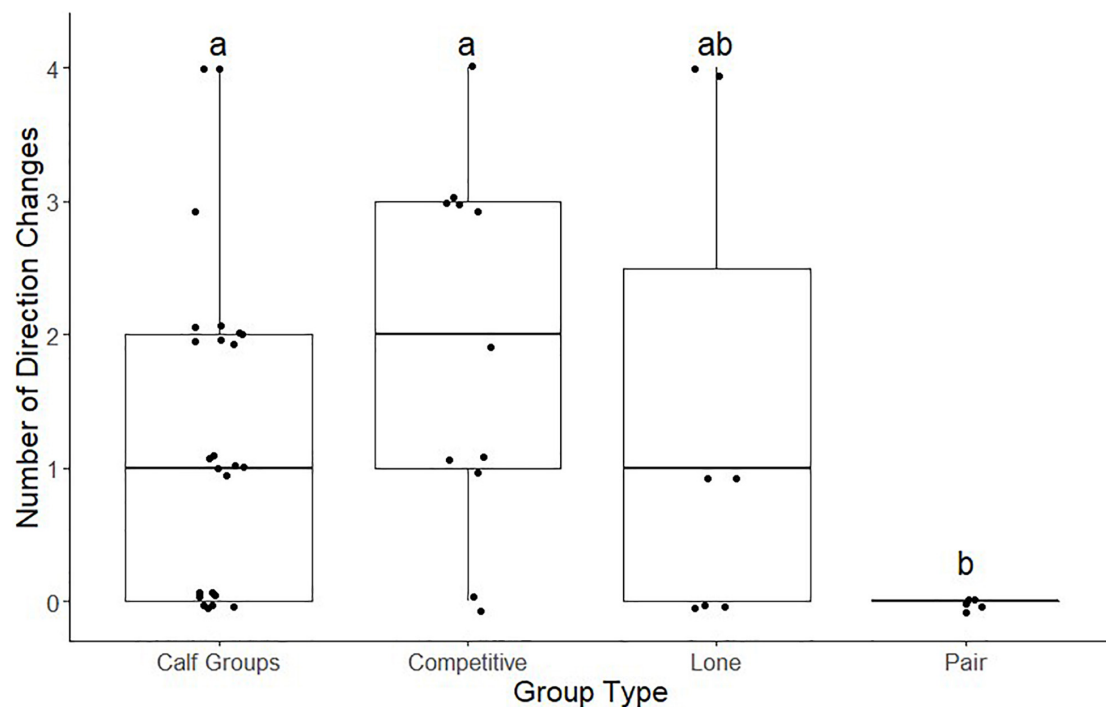
FIGURE 3 | The frequency of behavioral observations as a proportion of the total numbers of observations for each boat type.

with varying boat numbers (Breach: $R^2 = 0.42$, $p > 0.05$; Dive: $R^2 = 0.09$, $p > 0.05$; Slap: $R^2 = 0.13$, $p > 0.05$; Spy hop: $R^2 = 0.34$, $p > 0.05$).

Direction Change and Group Type

We conducted a *post hoc* pairwise Wilcoxon test (Figure 4) to assess which group types exhibited a significantly different

number of direction changes from each other. Of the comparisons across all whale group types, the pair versus competitive group type and pair versus calf group type were the only pairwise comparisons rejected ($Z = 1.68$, 16 ± 0.474 , $p < 0.05$; $Z = 1.68$, 29 ± 0.486 , $p < 0.05$, respectively). The rest of the pair-wise comparisons, therefore, supported the null hypothesis, which assumes little to no



However, the breaching frequency decreased once vessel numbers exceeded two boats. It is also possible that crowding from multiple boats limited surface area, restricting available space for whales to breach. Whale breaching has also been theorized to be a form of play, especially when exhibited by calves (Whitehead, 1985), which could explain the relatively high involvement of calf pairs in breaching. Alternatively, breaching may also be a tactic for male humpback whales to display their physical abilities when seeking a mate, which explains the high breach count that also occurred in pairs and competitive groups (Whitehead, 1985; Darling and Nicklin, 2002; Pacheco et al., 2013). Unfortunately, due to boats being more inclined to violate the existing whale-watching regulations, the high levels of whale-chasing exhibited by vessels could negatively influence the stress level of the whales, reducing their breaching. These behaviors could eventually be replaced with an increase in avoidance behaviors, such as direction change and longer dive times (Stamation et al., 2010).

The number of slap behaviors increased when the number of boats declined. This observation supports the theory that if a whale is close to another group, they will communicate through slapping behavior (Shapiro, 2008). 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 (Deakos, 2002; Herman et al., 2007). This behavior was especially evident in this study as Panama is a hotspot for breeding humpback whales, with increased competitive behaviors exhibited between males and females.

Competitive groups had the highest incidences for three of the four observed behaviors: slap behaviors, spy hopping, and diving. However, these results may differ from other studies conducted at different times of the year because whale behavior changes dramatically during breeding seasons (Corkeron, 1995; Stamation et al., 2010; Schaffar et al., 2013).

Tail slaps are the most common surface behavior observed, most likely because they are not associated with high energetic costs (Noren et al., 2009; Segre et al., 2020). Therefore, humpback whales may only resort to breaching when noise pollution (such as that caused by high vessel presence) increases, as the sound of breaching travels much farther than the noise of a tail or pectoral fin slap. Schuler et al. (2019) attribute the change in surface behavior to the disparity between the weight and surface area of a whale's tail versus that of their body. Researchers of previous studies also found an increase in vessel number 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 2).

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

The linear regression model displayed no clear indication of different behavior event frequencies when correlated with varying vessel numbers. This result could be an indication of habituation

TABLE 2 | Categories of behaviors used in this study from prior studies on the impacts of whale watching on orcas and humpback whale behavior.

Behaviors studied	Findings	References
Avoidance behaviors	Cetaceans increased their path sinuosity but decreased the linearity of their path with vessels present.	Senigaglia et al., 2016
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	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	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	Blue whales showed fewer foraging behaviors the closer vessels approached them, leading to a reduction in energy for foraging which could have long-term effects on Blue whales.	Guilpin et al., 2020
Behavior	Humpback whales exhibited more surface behaviors with increased vessel exposure, which could lead to energetic consequences.	Di Clemente et al., 2018

to anthropogenic presence and noise, which poses additional risks (Richardson et al., 1995; Stone and Yoshinaga, 2000), as well as the range of different types of vessels which vary in their acoustic volume. With Panama being one of the central ports in the global cargo-shipping network, higher levels of vessel traffic will likely only increase the risk of whale-vessel collision (Kaluza et al., 2010; Guzman et al., 2013). While the risk of collision with larger ships has been reduced due to the passage of the Gulf of Panama Traffic Separation Scheme in 2014 (CITE), the lack of regulation enforcement among non-commercial ships means potentially hazardous collisions between cetaceans and vessels (Panama Maritime Authority, 2014).

This is an observational study and we did not experimentally manipulate boat numbers. Thus, the number of samples differs between boat numbers. 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 (Darling and Nicklin, 2002; Williams et al., 2002; Lusseau and Bejder, 2007; Morete et al., 2007; Stamation et al., 2010; Schaffar et al., 2013; Fiori et al., 2019; Schuler et al., 2019).

Direction Change and Group Type

We suggest that the whale group type was not a significant predictor of the number of direction changes exhibited. The significant difference between pairs versus competitive groups and pairs versus groups found in Las Perlas Archipelago may be the result of competitive groups being in a setting where they must be vigilant and always watching their competitors; however, this attentive attribute may cause them to exhibit stress-based behaviors to avoid boats. The concern of energy costs

is especially relevant with regard to calf groups since it seems whale watching vessels prefer following calf groups due to their playful behavior. As calves may feel more threatened by boats than other group types, Panamanian regulations have extra laws to protect calves, given their vulnerable state. We saw a significant difference even with a small sample size, but a greater number of samples would clarify the extent of the relationship. Nevertheless, these results support findings from previous whale behavioral reports. In one study, group type was included as an explanatory variable to predict dive time, swim speed, and directness index and found the relationship between group type and the other variables had no significance and did not lead to a better fitting model (Schaffar et al., 2013). Unfortunately, we were unable to measure changes in swim speed in this study. Another study found pods with calves exhibit higher levels of activity compared to non-calf pods (Stamations et al., 2010). This supports the results of our study, which showed groups with calves executing the largest number of direction changes. However, due to the small sample size of this study, no other conclusions can be confidently derived regarding whether whale behavior can be predicted by the whale group type.

Relationship of Direction Change to Number of Vessels

The results of this study displayed a positive correlation between the direction change and the number of vessels present, with most of these changes being exhibited by pod groups containing calves (**Figure 5**). Calves are especially vulnerable to increased vessel presence due to the higher likelihood of vessel collision, less knowledge of vessel movement, and decreased ability to partake in essential behaviors such as feeding, nursing, and learning how to care for themselves (Scheidat et al., 2004; Stamations et al., 2010). This may explain why calf groups had the highest sum of direction changes compared to all other whale pod types since vessels had a higher preference for chasing whale groups with calves. Results from this study show clear indications of behavioral change being a consequence of increased vessel presence, violating Panama's regulation that prohibits vessels from "chang[ing] the behavior of cetaceans" (*sensu* Carlson, 2010).

Previous research suggests that the proximity of boats is a robust predictor of the number of directional changes a whale might exhibit (Schaffar et al., 2013). As direction change is a tactic humpback whales use to avoid predators, this avoidance behavior may also be utilized when faced with a boat, which could be viewed as a perceived threat (Schaffar et al., 2013; **Table 2**). Several researchers suggest direction changes are also related to stress and could indicate an increased level of physiological disturbance (Kruse, 1991; Beale, 2007; Schaffar et al., 2013; Schuler et al., 2019; see **Table 2**). Thus, while avoidance behavior may ensure self and group preservation, it also 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 (Beale, 2007; Lusseau et al., 2009).

Regulatory Implications and Compliance

Due to concerns about whale interactions with vessels, Panama initially passed Resolution Decree ADM/ARAP No. 1 on 13 February 2007, to control the level of vessel disturbance on cetaceans to conserve their populations. Regulations from this decree require operators to have 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 m distance from the whales, and limited observation times to 30 min per group or no more than 15 min 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. Better enforcement protocols must, therefore, be enacted to better 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 been shown to be successful in fisheries management plans and has alleviated illegal, unreported, and unregulated (IUU) fishing (Schmidt, 2005). Alternatively, lack of compliance may also be the result of poor communication from the government concerning the regulations, leaving local whale watching companies and boat operators with a lack of knowledge about the existence of these laws (Sitar et al., 2016, 2017).

In summary, Panama has strict whale watching operation regulations that are not being followed or enforced in the Las Perlas Archipelago. At multiple times throughout this study, we observed all laws pertaining to vessel regulations being broken at least once by boats. The on-going lack of regulation enforcement may result in more audacious decisions from boat operators in the future, leading to harmful or even lethal collisions with adult whales and calves. At the very least, these results show increased changes in whale behavior when vessels are present, which is illegal according to Panamanian protocols (*sensu* Carlson, 2010). Thus, it is highly recommended that both boat operators and tourists be educated about regulations and the importance of abiding by the law. While the purpose of this study was not to propose the eradication of whale watching, it was to highlight the potential harm being done due to the lack of compliance with 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 benefit from less stress from vessels and indirectly from tour guides expanding environmental awareness and enlightening tourists about environmental or conservation issues. Continued whale research, monitoring, and modeling efforts in Panama must be implemented to better inform management decisions regarding stricter regulatory and enforcement protocols that are vital to minimize disturbance on this vulnerable population of humpback whales.

Conclusion and Future Research Recommendations

Although our study is limited to the short-term impacts of boat vessel presence on humpback whale behavior, long-term changes in behavior may indirectly lower reproduction rates (Lusseau and Bejder, 2007). This can occur through drowned out vocalizations and a reduction in the success of whales finding mates due to vessels altering whale group dynamics and travel direction (Weilgart, 2013). Additionally, whale health can be negatively affected due to chronic levels of stress, increases in energy expenditures, and discontinuation of essential behaviors such as feeding, resting, nursing, etc. (Parsons, 2012). Constant changes in behavior and less concentration on survival activities could result in eventual population declines over time, as groups with calves are the most vulnerable, especially as whale watching vessels prefer following calf groups for their charismatic physical characteristics and playful behaviors. Due to this increased vulnerability, Panamanian regulations need to contain extra provisions to ensure the protection of whale calves (*sensu* Carlson, 2010).

However, behavior and stress may not necessarily be coupled in a way that can be easily observed. This was evident in this study when some whales did not appear to change their behaviors despite increased levels of vessel interaction. It has been proven that animals may not exhibit avoidance behaviors, but nevertheless experience high levels of stress hormones (Schuler et al., 2019). For this reason, additional physiological studies are recommended. Previous studies have shown that biopsy samples of cortisol found within blubber samples can provide measurements of stress levels over several weeks to a month, which would provide insight into how stress levels may fluctuate throughout an entire whale watching season as the number of tourist boats changes (Noren and Mocklin, 2012; Teerlink et al., 2018). Alternative cortisol collection methods including fecal (Wasser et al., 2000; Rolland et al., 2005; Hunt et al., 2006; Burgess et al., 2013) and blowhole spray have also been shown to provide more acute measurements of stress related to vessel presence.

Future behavioral research should also include the use of more accurate measuring methods and tools. For example, the use of a theodolite tool would produce accurate distance measurements between vessels and whales, which is essential for understanding if distance impacts whale behaviors. Unmanned aerial systems (UAS) (drones) would allow for the collection of more accurate behavioral samples via less invasive observational methods (Torres et al., 2018). Visual observations could also be maintained more consistently by drones due to optimal viewing angles, as traditional vessel-based observations can only be made while the whale is surfacing. Additional social surveys should be collected from tourists, local communities, and boat operators to help us understand their impression of the whale watching industry and whether whale watching is, generally, of value.

In Las Perlas Archipelago, whale watching generates income for local communities. It also creates employment opportunities and provides ecosystem services to tourists, residents, and boat operators. However, if disturbances to these whales continue unabated, it may lead to the eventual abandonment of the

Archipelago by the population, as has occurred in other popular whale-watching locations elsewhere in the world (Dean et al., 1985). The satisfaction of tourists is vital to the ongoing sustainability of the Panamanian ecotourism industry, as a report by the World Bank in 2005 found that two-thirds of all visitors to Panama were motivated to visit the country due to environmental or ecotourism reasons and income from international tourists totaled 7% of the GDP (World Bank, 2005, p. 9). Decreases in tourist motivation to partake in ecotourism activities such as whale watching potentially cause the industry to suffer, thereby affecting the Panamanian economy. This is already somewhat evidenced by the drastic decrease in tourism caused by the COVID-19 pandemic. Understanding the dynamic changes in human well-being and animal population viability are critical for establishing effective wildlife conservation strategies. Variations in socioeconomic factors that benefit the local communities can motivate more people 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.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Smithsonian Tropical Research Institute and the Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

AA is the primary author and this research is a component of her M.S. thesis paper. HG, BP, KS, and LG contributed to the overall idea, writing, research, data collection, and analysis of this paper. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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