

SC/66a/WW/12

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INTERNATIONAL
WHALING COMMISSION

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A. SITAR*, L.J. MAY-COLLADO[#], A.J. WRIGHT*, E. PETERS-BURTON⁺, L. ROCKWOOD^Δ AND E.C.M. PARSONS*

*Department of Environmental Science and Policy, ^ΔDepartment of Biology, ⁺Educational Psychology Program George Mason University, Fairfax, Virginia, USA.

[#]University of Vermont, Department of Biology, 109 Carrigan Drive, Burlington, VT 05405, USA.

Abstract

This study was conducted during the low tourism season of July and August 2013 to evaluate the behavioral effects of whalewatching vessels on the local resident dolphins of Bocas del Toro, Panama. Due to Bocas' high level of unmanaged whalewatching tourism with a small population of dolphins being observed, a hybrid/composite boat based survey technique called "Focal Group Scanning" (FGS) was developed. This methodology made it possible to gather more data than other methodologies and is recommended for cetaceans groups in small populations. Using AIC analysis results indicated whalewatching did affect behavior change. Dolphins were less visible when vessels were around. Dolphins travelled more in the presence of vessels. There were less deep dives, foraging activity, play, sexual behavior, and resting in the presence of whalewatching boats. Social behavior was found to be more probable when number of boats decreased. The unmanaged dolphin tourism in Bocas del Toro is causing behavioral change and decreasing important behaviors such as foraging, socializing and resting. Management is urgently required- it is highly recommended that whalewatching activity in this region be carefully monitored and the existing Panamanian regulations be strictly enforced.

Introduction

Previous studies have documented cetaceans altering their behavior as a result of vessel interactions (i.e. boats and whalewatching) (e.g. Au and Perryman 1982; Kruse 1991; Janik and Thompson 1996; DeNardo 1998, Nowacek et al. 2001; Hastie et al 2003; Parsons 2012). Thus, unmanaged and unregulated boat-based whalewatching is an anthropogenic impact to cetacean populations and as such, it has been argued that it is a type of exploitation (Orams 1999; Martinez & Orams 2011). The harm that unmanaged and unregulated whalewatching tourism causes can be both direct and indirect (Mattson et. al. 2005). The most obvious direct impacts are injuries and death caused by propeller

strikes or other boat collisions, but whalewatching boats can also cause behavioral changes (Donaldson et al. 2012). Several studies have documented cetaceans performing short-term, but immediate, behavioral changes when boats are present (Lusseau & Bejder 1997; Constantine et al. 2004; Carrera 2004; Christiansen et al. 2010; Parsons 2012; May-Collado et al. 2014; Sitar et al. 2014). One of the most serious behavioral changes recorded is a decline in foraging when boats are present (Carrera 2004; Williams et al. 2006; Stockin et al. 2008; May-Collado et al. 2014; Sitar et al. 2014). Another immediate behavioral change is that some individuals move closer to each other when boats approach (spatial distribution) (Bejder et al. 1999; 2006a; Barr & Slooten 1999).

Engine noise can mask cetacean calls, obstructing them (Erbe 2002; Nowacek et al. 2007; Tyack 2008; Jensen et al. 2009) and high levels of noise can cause temporary or permanent hearing damage (more correctly referred to as temporary or permanent threshold shifts, or TTS or PTS, respectively), especially if the distance from the boat and the cetacean in question is minor and the source level is high (Ketten 1998; Ng & Leung 2003; Mattson et al. 2005). Noise can thus disrupt echolocation, feeding, socializing, communication between group individuals and other behaviors (Bain & Dahlheim 1994; Richardson et al. 1995; Mattson et al. 2005). Van Parijs and Corkeron's (2001) documented Pacific humpback dolphin (*Sousa chinensis*) mother and calf pairs increasing whistle rates after boats have passed. They assume this is the result of mothers and calves trying to re-establish communication (Van Parijs & Corkeron 2001). Several studies have similarly reported bottlenose dolphin mothers and calves whistling repeatedly when separated or during unexpected events (e.g. Tyack, 1986; Caldwell et al. 1990; Smolker et al. 1993; Janik & Slater, 1998; Van Parijs & Corkeron 2001). It isn't surprising that mothers and calves are most disturbed by boat traffic and call out for each other repeatedly because predation and other risks for calves increase when separated from their mothers (Mann & Barnett, 1999; Van Parijs & Corkeron 2001). A few tens of meters of separation can increase the risk of a shark attack (Mann & Barnett 1999).

Sound is an important sensory system for cetaceans. They utilize it for communication, detecting the environment around them and locating prey (Au 2000; Tyack & Clark 2000; Trites & Bain 2000; Lemon et al. 2006). Ng & Leung (2003) discuss that faster

moving boats cause more noise than slow moving boats. The speed and unpredictable movement of boat traffic can also cause similar effects as engine noise (Mattson et al. 2005). When anthropogenic noise from whalewatching boats is elevated or exacerbated by enclosed areas, the ability of cetaceans to communicate or navigate is reduced (Richardson et al. 1995; Lemon et al. 2006). Scarpaci et al. (2001) documented bottlenose dolphins increased whistle rates when tourist boats were around, moreover Van Parijs & Corkeron (2001) note an increase in whistle rate when vessels were less than 1.5km from dolphins. Another potentially harmful impact of high boat traffic includes diesel fumes and oil; exposure to these over time can cause toxic harm to cetaceans (Trites & Bain 2000).

Cetaceans may be particularly vulnerable to the impact of whalewatching boats, but the impact might not be immediately apparent. Cetaceans are typically long-lived (Constantine 2014). They are also a slow-breeding species, and short-term effects like resting and foraging disturbances could have cumulative energetic costs that might have long-term, population-level effects (Constantine 2014; New et al. 2015). Realistically, it could take up to 30 years to be fully recognized as a negative impact on reproduction rate and population size (Wilson et al. 1999, Thompson et al. 2000; Constantine et al. 2004). Bottlenose dolphins (*Tursiops* spp.) are especially vulnerable to these long-term negative effects since they are one of the most exposed cetacean species to consistent and high-intensity whalewatching tourism (Constantine 2001).

It is often assumed by lay people that if cetaceans are disturbed by activities such as whalewatching they can simply swim away (Parsons pers. obs.). However, this may not always be the case. Cetaceans may be less likely to abandon their habitat even if they are being severely harassed by human disturbance. If the habitat is essential because of vital food supply and safety, and if a suitable alternative habitat is not nearby, cetaceans will remain in disturbed areas even though this exposes them to stress (Gill et al. 2001; Frid & Dill 2002; Constantine et al. 2004; Beale & Monaghan 2004a, 2004b; Beale 2007; Bejder et al. 2009).

Residential or semi-residential cetaceans (like Bocas del Toro's dolphins) are more

vulnerable to and may experience higher impacts from boat traffic (Williams et al. 1993; Schneider 1995). In reaction to whalewatching vessels, residential dolphins might avoid the vessels or possibly become habituated to them (Constantine 1999). However, serious concerns have been expressed about the use of terms such as “habituation,” “sensitisation” and “tolerance” (Bejder et al. 2009; Donaldson et al. 2012). These terms are often misused in scientific work, and there is much confusion about the term “habituation,” and as a result, these terms mislead wildlife tourism managers (Wright et al. 2007; Bejder et al. 2009). There are three terms used for changes in behavioral stress responses (Wright & Kuczaj 2007; Wright et al. 2007a; see Table 1 below). These three terms have very different definitions, and they are not interchangeable (Bejder et al. 2009; Table 2.1).

Table 1. Working definitions for categories of behavioral response and requirements for their demonstration (Bejder et al. 2009, p.181). N.B. The definition of sensitization in this table is not common in the field of physiology but is rather a definition used by Wright et al. (2007) and is more common.

Sensitization: when acclimation to one stressor increases subsequent stress responses to the original stressors (as per Romero 2004).

Term	Definition	Time course of response	Requisites to demonstrate response
Habituation	Relative persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement (Thorpe 1963, p. 61)	Longitudinal process	Sequential measures taken from the same individuals over time
Sensitisation	Increased behavioural responsiveness over time when animals learn that a repeated or ongoing stimulus has significant consequences for the animal (Richardson et al. 1995, p. 543)	Longitudinal process	Sequential measures taken from the same individuals over time
Tolerance	Intensity of disturbance that an individual. ...tolerates without responding in a defined way (Nisbet 2000, p. 315)	State	Instantaneous measurement of many individuals at one time

As an ethnological concept, habituation is a response from repeatedly being exposed to human activity and “claims of habituation are usually based on quantitative or anecdotal observations that the behaviour of animals appears to become progressively less influenced by the presence of particular anthropogenic stimuli” (Bejder et al. 2009, p. 179). However, the term habituation with regards to marine mammal response is not the same concept when referring to human behaviours. So habituation and sensitisation do not allude to specific behavioral responses that the word habituate refers to.

Behavioral habituation is the “relative persistent waning of a response as a result of

repeated stimulation which is not followed by any kind of reinforcement” (Thorpe 1963, p. 61). Habituation is, therefore, “a process involving a reduction in response over time as individuals learn that there are neither adverse nor beneficial consequences of the occurrence of the stimulus” (Bejder et al. 2009, p. 180). In conclusion, to be habituated to something is to become less influenced (less affected) to the repeated stimuli, such as whalewatching, but still continue to be physiologically stressed internally (Wright et al. 2007a, 2007b). Therefore, anthropogenic activities can still be impacting wildlife, even though the animal’s overt reaction to the activities is reduced, or has become less obvious (see Wright et al., 2007a, 2007b). Through habituation, cetaceans are even more vulnerable to boat collision because animals exhibit less avoidance behavior around vessels (Spradlin et al. 1998; Stone & Yoshinaga 2000; Woodford et al. 2002). According to Erbe’s (2002) study, the killer whale (*Orcinus orca*) study population did not exhibit the typical swim-away-response to whalewatching boats as expected from other studies (i.e. Kruse 1999; Williams et al. 2002). In Erbe’s (2002) study, killer whales did not show avoidance behaviors until whalewatching boats were 50 meters or less to cetaceans indicating that habituation could be a factor for this population (Erbe 2002).

In opposition to habituation, sensitisation is “increased behavioural responsiveness over time when animals learn that a repeated or ongoing stimulus has significant consequences for the animal” (Richardson et al. 1995, p. 543). According to Finley et al. (1990) marine mammals are less likely to be tolerant of human interaction unless there are incentives (e.g. the disturbed area is an important feeding ground) (Constantine 2001). Without such an incentive, marine mammals will likely be more sensitive to an adverse stimulus and will perform avoidance behaviors (Constantine 2001). Constantine’s (2001) study conducted on dolphins in the Bay of Islands, New Zealand, showed that their avoidance behaviors with swim-with-dolphin tourists increased over time (i.e., sensitisation occurred).

Boat traffic density is also another concern for cetaceans (Ng & Leung 2003; Constantine et al. 2004). Density of vessels has been correlated with behavioral changes in a variety of cetaceans (Adimey 1995; Williams 1999; Trites & Bain 2000; Ng & Leung 2003; Buckstaff 2004; Corbelli 2006; Parsons 2012). Bejder (2005) notes a decline in female

reproductive rate in the Indo-Pacific bottlenose dolphin (*Tursiops* sp.) population in Shark Bay, Australia that has high boat traffic. In Constantine and colleagues' (2004) New Zealand study, bottlenose dolphins showed a decrease in resting behavior when the number of boats increased. Similarly, Würsig (1996) indicates that resting behavior decreased when dolphins were exposed to repeated swimming interactions with tourists and in the presence of vessels. As resting is clearly a biologically important activity, any decrease in this behavior is significant.

In addition to biologically important behaviors that may be disrupted by boat traffic, animals may have locations that are important. Briggs (1991) found, for example, that killer whales are more likely to be disturbed by the presence of vessels near rubbing beaches. Cetaceans can have specific feeding grounds or important areas where socializing and feeding occurs. These locations are of great importance, and once tolerance levels have been exhausted by chronic boat traffic, cetaceans may abandon these areas (Baker & Herman 1989) and that could have an impact on the health of the population.

Dolphin Bay in Bocas del Toro, where most of the unmanaged dolphinwatching tourism occurs, is an important area for socializing (e.g. mating feeding, and rearing calves) for the resident dolphins (May-Collado 2007). If the resident Bocas del Toro bottlenose dolphins abandon Dolphin Bay because of the intolerable level of boats, what will happen to the population? Bejder et al. (2006a, 2006b) noted disturbed dolphins relocating from a site impacted by whalewatching disturbance. The resident dolphins in Bocas del Toro could decide to stay in the area and tolerate exposure to dolphinwatching activities because, although being stressful, these might be less costly in energy than fleeing to an optimal habitat (Beale 2007). This can have an even greater consequence because of chronic stress and the cumulative impact of increased energetic costs over time (Beale 2007).

The issue of whalewatching disturbance is becoming a very serious concern for the wellbeing of many targeted cetacean populations since this industry is rapidly growing

without accompanying protections and regulations (Garrod & Fennel 2004). Because authoritative regulations require extensive amounts of research and an understanding of the full implication of threats to populations, it is important to continue ongoing assessment of changes in the size of populations, in their habitat ranges, and more specifically habitat and behavioral changes due to continuous human disturbance (Constantine 1999; Constantine 2001).

This study evaluated the effects of whalewatching tourism on common bottlenose dolphins (*Tursiops truncatus*) in Bocas Del Toro Panama. The data gathered could be helpful in advocating for sustainable dolphinwatching and protective dolphin management in Bocas del Toro.

Methods

This study was conducted in Bocas del Toro, Panama from July to August 2013. Bocas is an Archipelago 9° 20' 0" N and 82° 15' 0" W, off the northeast Caribbean side of Panama, near the border of Costa Rica (Windevoxhel & Heegde 2008).



Figure 1. Map: Bocas del Toro Archipelago from Wikipedia (2015)

In this study, a hybrid/composite boat-based survey technique was developed to evaluate the effects on dolphin behavior from dolphinwatching tourism. This new method has been dubbed “Focal Group Scanning” (FGS), and it was developed to fit the specific circumstances in Bocas del Toro i.e. a high level of unmanaged whalewatching tourism and numerous vessels with a small population of dolphins being observed. FGS is semi-continuous and discontinuous sampling of dolphin behaviors. It essentially involves a focal follow but of an entire group of dolphins with a one-minute snapshot of the entire group’s activities (see Table 2.2) conducted over that period. Dolphin behaviors were recorded utilizing a one-zero discontinuous sampling method, i.e. the behavior did occur (scored as “1”) or the behavior did not occur (scored as “0”).

The survey was conducted from a four-stroke outboard motor research boats of 19 to 30 feet and with engines of 75 hp or 90 hp, respectively. Data collecting ranged from 7am to 2pm if weather and accessibility permitted. The research boat’s motor was turned off

when dolphins were spotted within a radius of 100m to minimize disturbance. Surveys were conducted throughout the Bocas del Toro Archipelago (off of Isla Popa Uno, Shark Hole, Dolphin Bay, Pastores, Almirante, Solarte, Loma Partida, Bocas del Drago, T. Oscura, Bahia Honda, Osa Perezoso, San Cristobal, Basimentos, Punta Caracol, Isla Peresozos) (see Map above), however, most surveys were conducted in Dolphin Bay because that is where the majority of dolphinwatching activity takes place (May-Collado et al. 2012).

Behavioral observations began when dolphins were sighted. At the beginning of each sighting, GPS coordinates, location name, weather and sea state were all recorded. The number of boats and number of dolphins present was recorded for every minute throughout the entire sighting. Sightings ended when dolphins left the area or ceased because of logistic reasons (which could include adverse weather). The boats' distance to the dolphins was also recorded. Every minute from the start of the encounter to the end, dolphin behaviors were recorded under assigned behavioral categories (e.g., forage, shallow dive, deep dive, disappear, rest, surface, socialize, play, sexual activity, mill, slow travel, fast travel, aerial and aggressive) (see Table 2). If there were any, out of the ordinary or significant activities were recorded as well.

Table 2. Behaviors recorded in this study and behavior definition

Recorded Behavior	Behavior description
Social	Socializing behaviors include dolphins interacting with each other by playful chasing, leaping, physically touching each other in play, or sexually interacting. For this study Inquisitive behaviors were included in the social category because they involved interaction with whalewatching boats, or other animals. Inquisitive behaviors include "peeping", or "spy-hopping", and voluntarily approaching a boat as if curious.
Forage:	Foraging behaviors are actions that indicate putting effort into capturing prey, fish-whacking, having prey in their mouths, consuming prey, chasing prey, circling deep dives with loud exhalations, swimming rapidly in circles (carousels), and a sequence of dives ending with a fluke dive.
Resting	Resting behaviors involve very slow movement in tight groups, traveling at about one knot. Or when dolphins are floating on top of the water still with their blowhole visible.
Slow Travel	Travel consists of slow traveling at a pace of three knots or less, and high speeds of travel with a pace faster than three knots.
Fast travel with a purpose	Purposeful travel- is considered fast travel in one direction without any action of foraging, milling or socializing.
Milling	Milling consists of different directional headings. It can be connected with socializing, play and foraging.

Deep Dive	A deep dive is when the fluke is visibly sticking out of the water
Shallow Dive	A shallow dive is when the dorsal fin and back are visible. The fluke is not visible in a shallow dive.
Disappear	This behavior describes when all dolphins in a group dive underwater and are no longer visible.
Surface	This behavior is when dolphins come up for air.
Play	Throwing objects out of the water (such as a fish) a fashion taht was not related to feeding, leaping in the wake of a boat, riding with a boat.
Sexual	This behavior is rolling (twisting, rolling around together in one place), displaying abdomen and/or penis.
Aerial	The behavior is leaping (leaping clear out of the water and re-entering head first) and porpoising (arching leaps with partial or entire body out of water)
Aggressive	This includes biting another dolphin, body slamming (a forward or side slam against the water), headbanging (head slapping the water), headbutting, head toss (abrupt head jerk), flipper/fluke strike, tail slap, and shaking body (a low scale of body thrashing, or convulsion).

To assess the potential impact of whalewatching on dolphin behaviors, the dependence of each behavior on several explanatory variables was considered using an Aikaike Information Criterion (AIC) reduction process. These variables were the number of dolphins in a group (log transformed), the presence or absence of vessels (with the exception of the research vessel), any recent changes in vessel numbers (i.e., from the previous minute to the current minute) and the location of the sighting. Boat maneuvers could not be included in this analysis against control conditions, as none could be independent of vessel presence. The original model was a binomial regression containing all the above-mentioned explanatory variables and a stepwise removal process was undertaken automatically in the program R (R Core Team 2014), until a final model was selected (Akaike 1973).

For the purposes of the analyses, explanatory variables over one minute were compared to dolphin behaviors in that minute and the following minute, with the latter required to capture any time-based activities (e.g., disappearance). The data included in the analysis was sub-sampled from the full follow data set (to every 5 minutes) to reduce autocorrelation to the greatest extent possible.

Results

Over 13½ hours (817 minutes) of whalewatching ‘occurrences’ were recorded (each occurrence was a 1-minute recording) from July to August 2013 (Table 3). Approximately 5½ hours (320 minutes) of ‘true control’ (sightings that did not have any boat activity) occurrences were recorded. Moreover, there were 732 occurrences of ‘zero boat’ activity from encounters where boat activity was recorded before and/or after, but not during the occurrence.

Table 3. Categories of survey sighting, description and number of occurrences.

Events of sightings	Description	Total occurrences
1) Whalewatching	Dolphins exposed to whalewatching activity	817
2) Control	Dolphin sighting with no boat activity	320
3) Zero boat occurrences	1 minute events with zero boats during that specific 1 minute interval	732
4) All no boat events	Total of 2) Control and 3) Zero boat occurrences	1052

AIC analysis for behavior ‘disappear’

The AIC selection process for the behavior “disappear” selected the log-transformed number of dolphins present and the presence/absence of boats (see Tables 3.1; 3.2). These variables are thus influential over the tendency of dolphins to “disappear”.

Table 3.1. AIC selection process for the first part of the analyses for TwoMinDisappear. AIC values for stepwise elimination presented.

Model	AIC
Start	566.74
Location	560.44
CngBoats	557.05
End	557.05

Table 3.2. Metrics for final model for the behavior ‘Disappear.’ TwoMinDisappear ~ a * log(No. Dolphins + 1) + b*BoatPres + c. Def Freedom = 434

Variable	Coefficient	p
log10(NoDolphins + 1)	-2.6373	<0.001
BoatPres - N	0	<0.001
BoatPres - Y	0.2066	

AIC analysis for behavior 'aerial'

For the model for 'aerial' behavior, the AIC model process selected only the log-transformed number of dolphins as being influential (Tables 4.1; 4.2).

Table 4.1. AIC selection process for the first part of the analyses for TwoMinAerial. AIC values for stepwise elimination presented.

Model	AIC
Start	274.08
Location	258.19
CngBoats	254.31
BoatPres	253.09
End	253.09

Table 4.2. Metrics for final model for the behavior 'Aerial.' TwoMinAerial ~ a * log(No. Dolphins +1) + b.
Def Freedom = 434

Variable	Coefficient	p
log10(NoDolphins + 1)	1.4069	0.045

AIC analysis for behavior 'tail slap'

The AIC reduction selected only changes in boat numbers as an influencing factor for TwoMinTailSlaps (see Tables 5.1; 5.2).

Table 5.1. AIC selection process for the first part of the analyses for TwoMinTailslaps. AIC values for stepwise elimination presented.

Model	AIC
Start	187.58
Location	178.19
log10(NoDolphins + 1)	176.34
BoatPres	174.89
End	174.89

Table 5.2. Metrics for final model for the behavior 'Tail slapping.' TwoMinTailSlaps ~ a * CngBoats + b.
Def Freedom = 434

Variable	Coefficient	p
CngBoats - D	0	0.071
CngBoats - I	-16.6689	
CngBoats - N	-1.0528	

AIC analysis for behavior ‘deep dive’

The AIC selection process found the number of dolphins (log-transformed), boat presence/absence and location to influence the behavior ‘deep dives’ (see Tables 6.1; 6.2).

Table 6.1. AIC selection process for the first part of the analyses for TwoMinDive. AIC values for stepwise elimination presented.

Model	AIC
Start	554.17
CngBoats	550.41
End	550.41

Table 6.2. Metrics for final model for the behavior ‘Diving deep.’ TwoMinDive ~ a* Location + b*log(No. Dolphins +1) + c*BoatPres + d. Def Freedom = 434

Variable	Coefficient	p
Location - Almirante	0	0.108
Location - Bahia Honda	0.7738	
Location - Basimentos	3.1779	
Location - Bocas Del Drago	0.311	
Location - Dolphin Bay	0.2809	
Location - Isla Peresosos	-14.5854	
Location - Isla Popa Uno	-0.3601	
Location - Loma Partida	1.079	
Location - Osa Perezoso	1.5359	
Location - Pastores	0.2803	
Location - Punta Caracol	-14.2005	
Location - San Cristobal	1.4138	
Location - Shark Hole	-0.1169	
Location - Solate	2.0545	
Location - T. Oscura	-0.2188	
log10(NoDolphins + 1)	1.2786	0.005
BoatPres - N	0	0.009
BoatPres - Y	-0.3712	

AIC analysis for behavior ‘shallow dive’

The AIC reduction process determined location to be an influencing variable for ‘shallow dives’ (see Table 7.1, 7.2).

Table 7.1. AIC selection process for the first part of the analyses for TwoMinShallowsDives. AIC values for stepwise elimination presented.

Model	AIC
Start	563.92
CngBoats	561.42
log10(NoDolphins + 1)	559.42
BoatPres	557.66
End	557.66

Table 7.2. Metrics for final model for the behavior 'Shallow dives.' TwoMinShallowsDives ~ a Location + b*Def Freedom = 434

Variable	Coefficient	p
Location - Almirante	0	0.011
Location - Bahia Honda	-1.5404	
Location - Basimentos	0.6931	
Location - Bocas Del Drago	-1.4534	
Location - Dolphin Bay	-0.9931	
Location - Isla Peresosos	-15.7202	
Location - Isla Popa Uno	-2.4567	
Location - Loma Partida	-0.8473	
Location - Osa Perezoso	0.1335	
Location - Pastores	-0.2595	
Location - Punta Caracol	-15.7202	
Location - San Cristobal	0.2513	
Location - Shark Hole	-0.4418	
Location - Solate	-1.2528	
Location - T. Oscura	-0.665	

AIC analysis for behavior 'slow travel'

The behavior 'slow travel' was selected as having a relationship to change in boats and boat presence or absence (see Tables 8.1; 8.2).

Table 8.1. AIC selection process for the first part of the analyses for TwoMinTravSlow. AIC values for stepwise elimination presented.

Model	AIC
Start	481.78
Location	478.13
log10(NoDolphins + 1)	476.13
End	476.13

Table 8.2. Metrics for final model for the behavior 'Slow Travel.' TwoMinTravSlow ~ a * CngBoats + b*BoatPres + c. Def Freedom = 434

Variable	Coefficient	p
CngBoats - D	0	0.041
CngBoats - I	-0.827	
CngBoats - N	0.488	
BoatPres - N	0	0.067
BoatPres - Y	0.4234	

AIC analysis for behavior 'forage'

The AIC reduction process determined that foraging was dependent upon boat presence or absence and location (see Tables 9.1; 9.2.).

Table 9.1. AIC selection process for the first part of the analyses for TwoMinForage. AIC values for stepwise elimination presented.

Model	AIC
Start	543.92
CngBoats	541.19
log10(NoDolphins + 1)	539.41
End	539.41

Table 9.2. Metrics for final model for the behavior 'Forage.' TwoMinForage ~ a * Location + b*BoatPres + c. Def Freedom = 434

Variable	Coefficient	p
Location - Almirante	0	0.003
Location - Bahia Honda	-16.62573	
Location - Basimentos	0.53085	
Location - Bocas Del Drago	0.06133	
Location - Dolphin Bay	-0.06212	
Location - Isla Peresosos	0.78217	
Location - Isla Popa Uno	-0.13412	
Location - Loma Partida	1.00405	
Location - Osa Perezoso	-15.97644	
Location - Pastores	-0.22701	
Location - Punta Caracol	-16.88251	
Location - San Cristobal	0.68273	
Location - Shark Hole	1.76385	
Location - Solate	16.68369	
Location - T. Oscura	0.56517	
BoatPres - N	0	<0.001
BoatPres - Y	-1.38943	

AIC analysis for behavior 'social'

The AIC process selected the number of dolphins (log transformed) and changes in boat numbers as influencing the occurrence of social behavior (see Tables 10.1; 10.2).

Table 10.1. AIC selection process for the first part of the analyses for TwoMinSocial. AIC values for stepwise elimination presented.

Model	AIC
Start	457.57
Location	454.03
BoatPres	452.36
End	452.36

Table 10.2. Metrics for final model for the behavior ‘Social.’ $\text{TwoMinSocial} \sim a * \log(\text{No. Dolphins} + 1) + b * \text{CngBoats} + c$. Def Freedom = 434

Variable	Coefficient	p
$\log_{10}(\text{NoDolphins} + 1)$	1.1833	0.014
CngBoats - D	0	0.029
CngBoats - I	-1.9101	
CngBoats - N	-0.3924	

AIC analysis for behavior ‘play’

The AIC reduction selected variables (log-transformed) number of dolphins and boat presence or absence as influencing the occurrence of ‘play’ behavior (see Tables 11.1; 11.2).

Table 11.1. AIC selection process for the first part of the analyses for TwoMinPlay. AIC values for stepwise elimination presented.

Model	AIC
Start	161.73
Location	153.28
CngBoats	150.89
End	150.89

Table 11.2 Metrics for final model for the behavior ‘Play.’ $\text{TwoMinPlay} \sim a * \log(\text{No. Dolphins} + 1) + b * \text{BoatPres} + c$. Def Freedom = 434

Variable	Coefficient	p
$\log_{10}(\text{NoDolphins} + 1)$	-1.6305	0.1309
BoatPres - N	0	0.135
BoatPres - Y	-0.7443	

AIC analysis for behavior ‘wake riding’

The AIC reduction process determined that none of the variables influenced whether dolphins engaged in ‘wake riding’ behavior (see Table 12).

Table 12. AIC selection process for the first part of the analyses for TwoMinWakeRiding. AIC values for stepwise elimination presented. Final mode

Model	AIC
Start	193.01
Location	185.57
BoatPres	183.75
log10(NoDolphins + 1)	182.25
CngBoats	182.00
End	182.00

AIC analysis for behavior 'fast travel'

For the behavior 'fast travel', the number of dolphins (log-transformed) was determined to be influential (see Tables 13.1; 13.2), albeit non-significant. Dolphins tended to engage more in 'fast travel' behavior when there were fewer dolphins.

Table 13.1. AIC selection process for the first part of the analyses for TwoMinTravFast. AIC values for stepwise elimination presented.

Model	AIC
Start	187.43
Location	177.28
BoatPres	175.31
CngBoats	174.25
End	174.25

Table 13.2 Metrics for final model for the behavior 'Travel Fast.' TwoMinTravFast ~ a * log(No. Dolphins +1) + b. Def Freedom = 434

Variable	Coefficient	p
log10(NoDolphins + 1)	-1.8946	0.057

AIC analysis for 'sexual behavior'

The AIC reduction process for 'sexual behavior' selected boat presence or absence as the only influential variable (see Tables 14.1; 14.2).

Table 14.1. AIC selection process for the first part of the analyses for TwoMinSexual. AIC values for stepwise elimination presented.

Model	AIC
Start	189.17
Location	183.27
CngBoats	181.56
log10(NoDolphins + 1)	181.17
End	181.17

Table 14.2. Metrics for final model for the behavior 'Sexual.' TwoMinSexual ~ a *BoatPres + b. Def Freedom = 434

Variable	Coefficient	p
BoatPres - N	0	0.093
BoatPres - Y	-0.7443	

AIC analysis for the 'rest' behavior

AIC results selected changes in the numbers of dolphins and the presence or absence of boats as influencing variables for the occurrence of the behavior 'rest' (see Tables 15.1; 15.2). Therefore, resting behavior happened less often in the presence of boats and more often when there were many dolphins.

Table 15.1. AIC selection process for the first part of the analyses for TwoMinRest. AIC values for stepwise elimination presented.

Model	AIC
Start	354.32
Location	346.34
CngBoats	342.98
End	342.98

Table 15.2. Metrics for final model for the behavior 'Rest.' TwoMinRest ~ a * log(No. Dolphins + 1) + b*BoatPres + c. Def Freedom = 434

Variable	Coefficient	p
log10(NoDolphins + 1)	1.6443	0.005
BoatPres - N	0	0.030
BoatPres - Y	-0.617	

AIC analysis for 'milling' behavior

The AIC reduction process determined that none of the variables influenced 'milling' behavior (Table 16).

Table 16. AIC selection process for the first part of the analyses for TwoMinMilling. AIC values for stepwise elimination presented.

Model	AIC
Start	226.18
Location	220.32
CngBoats	218.13
BoatPres	216.33
log10(NoDolphins + 1)	215.09
End	215.09

AIC analysis for the behavior ‘surfacing’

For the behavior ‘surfacing,’ location was determined to be influential (see Tables 17.1; 17.2). ‘Surfacing’ behavior was seen more in Almirante, Bahia Honda, Dolphin Bay, Isla Popa Uno, Loma Partida, Osa Perezoso, Pastores, and Shark Hole. It was less likely to occur in Basimentos, Bocas del Drago, Isla Peresosos, Punta Caracol, and Solarte.

Table 17.1. AIC selection process for the first part of the analyses for TwoMinSurfacing. AIC values for stepwise elimination presented.

Model	AIC
Start	562.9
BoatPres	561.03
CngBoats	559.42
log10(NoDolphins + 1)	558.25
End	558.25

Table 17.2. Metrics for final model for the behavior ‘Surface.’ TwoMinSurfacing ~ a * Location + b. Def Freedom = 434

Variable	Coefficient	p
Location - Almirante	0	0.002
Location - Bahia Honda	1.4702	
Location - Basimentos	-1.1325	
Location - Bocas Del Drago	-15.5014	
Location - Dolphin Bay	0.6446	
Location - Isla Peresosos	-15.5014	
Location - Isla Popa Uno	0.5051	
Location - Loma Partida	0.6592	
Location - Osa Perezoso	0.1484	
Location - Pastores	0.2915	
Location - Punta Caracol	-15.5014	
Location - San Cristobal	1.4702	
Location - Shark Hole	0.1484	
Location - Solarte	-15.5014	
Location - T. Oscura	-0.8812	

AIC analysis for ‘aggression’

The variable ‘change in the number of boats’ was selected as influencing the presence of ‘aggression’ (See Tables 18.1: 18.2), with the likelihood of occurrence higher when vessel numbers had recently declined.

Table 18.1 AIC selection process for the first part of the analyses for TwoMinAggression. AIC values for stepwise elimination presented.

Model	AIC
Start	214.08
Location	204.48
log10(NoDolphins + 1)	202.52
BoatPres	201.10
End	201.10

Table 18.2 Metrics for final model for the behavior ‘Aggression.’ TwoMinAggression ~ a *CngBoats + b.
Def Freedom = 434

Variable	Coefficient	p
CngBoats - D	0	0.026
CngBoats - I	-17.0079	
CngBoats - N	-1.1897	

Discussion

This study demonstrates that dolphinwatching in Bocas del Toro causes short-term behavioral disruption to the resident dolphins. There is most concern about anthropogenic disruption to the vital behaviors of socializing (that may include important reproductive behavior), foraging, and resting because the disturbance of these behaviors may have significant impacts on the health or the vitality of the population. In this study, foraging was found, perhaps unsurprisingly, to be highly dependent on location (see Table 9.2). It was also found to occur less frequently when boats were present. Given this combination, it would be difficult to assess from these results alone which areas may be important foraging areas, as vessel presence may be altering the natural behavior of the animals. Nevertheless, as foraging is disrupted by boat presence, this is a concern for the sustainability and conservation of the population.

More generally, this study demonstrates the applicability of this new survey method and statistical procedures to the task at hand. Focal Group Scanning in combination with statistical model reduction using AIC has produced comparable results to many other

studies (see below for more details), but with several notable advantages. For example, it is not limited to the use of fairly generalized categories of behavior and largely descriptive assessments of effect (e.g., Steckenreuter et al., 2012). At the other extreme, this approach requires less statistical expertise than many more elaborate analyses while also not restricting data collection to prevailing behavior (e.g., Lusseau 2003). The result is a flexible, yet rigorous methodology that does not exclude occasional or rare behaviors, provided there is enough data to support the analyses.

In terms of specific results obtained in this study, it was determined through the AIC process that social behavior is related to the number of dolphins and changes in boat numbers (see Table 10.2). Unsurprisingly, greater numbers of dolphins seem to make social behaviour more probable. However, it was also more probable when the number of vessels around the dolphins decreased. This may represent some sort of effort to re-establish bonds or social order following a disturbance event, but more detailed study would be needed to assess this.

Sexual behavior was found only to be related to boat presence or absence and to occur less when there were boats present, albeit non-significantly (see Table 14.2). This may suggest that more important factors were missing from the analysis. Vessel presence also seemed to be related to a lower resting rate (see Table 15.2). For resting behavior, the number of dolphins was also important suggesting that the dolphins in this area may gather in larger groups to rest. Again, this is an important consideration for the conservation and viability of the population. Boat activity in Bocas Del Toro is linked to a decrease in reproductive, resting and foraging behavior, and thus, the trifecta of biologically important behaviors were all affected by dolphinwatching for this population.

Many cetacean studies have had similar findings (Lusseau 2003; Williams et al. 2006; Dans et al. 2008; Stockin et al. 2008; Christiansen et al. 2010; Steckenreuter et al. 2012). Christiansen et al. (2010) found that when tourist boats were present in Zanzibar, Tanzania, Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) behaviors such as socializing, resting and foraging were less likely to continue when boats were present.

Lusseau (2003) noted in his study that socializing reduced by half when boats were present, and resting reduced by 10%. Additionally, these findings reinforce past studies in Bocas Del Toro. May-Collado et al. (2014) who found a negative correlation between foraging and socializing with increasing boat presence.

Travelling and changes in dive frequency have also been associated with the presence of boats. May-Collado et al. (2014) found that dolphins in Bocas del Toro were seen travelling and diving more when calves were present. To give just two other examples, Christiansen et al. (2010) found travelling was more likely to start when boats were present, and Lusseau (2003) found that travel and diving were both more frequent with boat presence as well.

In this study, location was found to have a significant effect on shallow dives (see Table 2.7.1, 2.7.2). Shallow dives were more likely to occur in Almirante, Basimentos, Osa Perezoso, and San Cristibal, and less likely to occur in the other locations (see Table 2.7.1, 2.7.2). Non-significant influences were also seen by location for deep diving (a deep dive with flukes out of the water) (see Table 6.2). However, deep diving was also selected to be related to (and increased by) the numbers of dolphins present and a lack of whalewatching vessels (see Table 6.2).

Similarly to May-Collado (2013), Christiansen et al. (2010) and Lusseau (2003) this study found that ‘slow travel’ behavior was related to the presence of boats and changes in boat numbers. Boat presence was found to increase the likelihood of slow travel, although this was marginally non-significant (see Table 8.2). Smaller groups were also associated with ‘fast travel’ (see Table 13.2), although this was again marginally non-significant. It has been suggested by others, that such behavior could represent a stress response related to predation (Howland 1974; Weihs & Webb 1984; Kruse 1991). It has also been noted in other studies that cetaceans increased their swimming speeds as a response to boat disturbance and when boats approached closely (e.g., Baker et al. 1983; Richardson et al. 1985; Kruse 1991; Williams & Bain 2002b)

The number of dolphins (log-transformed) and boat presence were found to influence dolphin ‘disappearance’ (staying underwater for at least a minute) (see Table 3.2).

Disappearance was recorded less when more dolphins were present, although this may simply be an artifact of the visibility of larger numbers of animals. In contrast, the presence of whalewatching boats was associated with a greater occurrence of ‘disappearance’ behavior. This study suggests that this behavior is another indication of avoidance and is likely an indication of a stress response.

Some aerial behavior is considered to be a form of non-vocal communication (Norris & Dohl 1980; Slooten 1994; Herzing 2000; Lusseau 2006a; Lusseau 2006b). Norris and Dohl (1980) suggested aerial behaviors could be used socially for foraging. According to Wursig and Wursig (1980) Argentinean dusky dolphins (*Lagenorhynchus obscurus*) jump to catch prey at the surface, so jumping in this situation is not a form of communication. In this study, aerial behavior was more likely to occur with greater numbers of dolphins (see Table 4.2). Accordingly, it seems likely that aerial behavior in this population could be a form of communication. However, this does not rule out the possibility that aerial behavior could be involved in cooperative foraging activities. Both situations would explain aerial behavior being seen more frequently with larger numbers of dolphins.

‘Tail slaps’ were found to be more likely when vessel numbers decreased (see Table 5.2), however, this relationship was non-significant. This type of behavior was often observed when dolphinwatching vessels were departing rapidly. Perhaps the behavior might represent (at least on occasion) an aggression response to these vessels that can suddenly alter the soundscape via an increase in underwater noise (pers. obs.). This is supported by the fact that the behavior ‘aggression’ shows a similar pattern of occurrence (see Table 18.2).

These findings support the findings of Noren et al. (2009), who reported that surfacing behavior (such as spy hops, breaches, tail slaps and pectoral fin slaps) in southern resident killer whales was more frequent when boats approached closer than the recommended distance for whalewatching. Noren and colleagues (2009) suggested that these behaviors may be more frequent with moving vessels than with stationary boats. Therefore, as this study suggested, the response to rapid movement of the boats (often

associated with vessel departures) could be related to aggression, tail slap (see Table 5.2; 18.2). Herzog (2000) suggests that tail slapping could be performed for communication purposes as a means to get the attention of dolphins in the pod. This compliments this study's finding and the Noren et al. (2009) hypothesis. The tail slaps seen in Bocas del Toro could well be caused by the sudden change in noise from boat activity. Since dolphins' calls could be masked by the noise of boat engines, a tail slap may be a way of communicating or locating each other.

Other findings from this study were that 'play' behavior decreased with greater number of dolphins and in the presence of vessels, although both relationships were non-significant (see Table 11.2). It may thus be that play occurs outside periods of whalewatching disturbance. Surfacing behavior was found to be related to location (see Table 17.2) and was seen more in locations, Almirante, Bahia Honda, Dolphin Bay, Isla Popa Uno, Loma Partida, Osa Perezoso, Pastores and Shark Hole. It was less likely to occur in Basimentos, Bocas del Drago, Isla Peresosos, Punta Caracol and Solarte. This is most likely simply reflecting the selective use of different habitats, for different behaviors, due to their different properties.

Finally, no explanatory variables (location, number of dolphins, change in boats and boat presence) were found to influence the behaviors "wake riding" and "milling". However, given that wake riding requires the presence of a vessel, there may be some issues with independence affecting this result.

Similarly, lack of full independence among the explanatory variables may have influenced the significance (or lack thereof) of their relationship with the different dependent variables in various ways. For example, certain locations might be related to different activities that are also associated with different group sizes. Similarly, whalewatching vessels may more easily spot larger groups of dolphins, leading to a relationship between the two. Despite these interactions, it was not possible to further reduce the variables included in the analyses as each contained distinct and important information for consideration. Similarly in Costa Rica, Montero-Cordero (2010) found little evidence that milling behavior in spotted dolphins (*Stenella attenuata*) was

influenced by boat presence.

It is evident from this study's results that dolphinwatching in Bocas del Toro is influencing dolphin behavior. This evidence supports the previous findings of May-Collado et al. (2014). Because dolphinwatching is unmanaged in Bocas del Toro it is necessary to promote teach and enforce Panama's whalewatching guidelines.

Recommendation

The Focal Group Scanning methodology used here has been demonstrated to be a viable alternative to other less flexible data collection and analysis methods. We recommend that others explore the utility of this methodology to their studies in order to seek insight into the origins of more specific behaviors that has been possible to date.

In this particular study, sailboats had to be analyzed as a whalewatching boat or traveling transport because there were less than ten occurrences of sailboats. However, comparing whalewatching sailboats to high-powered motorized vessels is suggested as a future study as it would be interesting to see if different types of whalewatching boats have different effects on dolphin behavior. For example, sailboats may have less impact as a type of whalewatching vessel.

The unmanaged dolphin tourism in Bocas del Toro is causing behavioral change and decreasing important behaviors such as foraging, socializing and resting. Another serious concern is potential avoidance by the dolphins of their assumed feeding and breeding area, Dolphin Bay. Management is urgently required, and it can be recommended that at least some areas important to foraging and resting be designated as off-limits to whalewatching vessels as their presence seems to disrupt these activities, i.e. refuge areas.

Concern about the impact of dolphinwatching in Bocas Del Toro on the dolphins, has attracted international attention. When the status of the dolphin population was raised at the 2012 meeting of the International Whaling Commission (IWC) (which incidentally was held in Panama), the IWC Scientific Committee stated that:

*“The Committee **strongly recommends** that Panamanian authorities enforce the relevant whalewatching regulation (ADM/ARAP No. 01) and in particular promote adherence to requirements regarding boat number and approach speed and distances... The Committee **recommends** continued research to monitor this dolphin population and the impacts of tourism on it” (p.80; IWC 2013).*

Panama has official whalewatching guidelines as noted above, and it is highly recommended that whalewatching activity and compliance with these guidelines be continuously and carefully monitored in Bocas del Toro and that the existing Panamanian regulations be strictly enforced.

Acknowledgements

We wish to thank The Pacific Whale Foundation, Humane Society International, Cetacean society International and the Department of Environmental Science & Policy, George Mason University for sponsoring this research and the staff of Panacetacea.

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