# Persistent Effects of Begging on Common Bottlenose Dolphin (*Tursiops truncatus*) Behavior in an Estuarine Population

Rebeccah A. Hazelkorn,<sup>1</sup> Bruce A. Schulte,<sup>2</sup> and Tara M. Cox<sup>3</sup>

<sup>1</sup>Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236, USA E-mail: rhazelkorn@mote.org

<sup>2</sup>Western Kentucky University, 1906 College Heights Boulevard #11080, Bowling Green, KY 42101, USA <sup>3</sup>Savannah State University, 3219 College Street, Savannah, GA 31404, USA

#### Abstract

Human interactions can have negative effects on individuals and populations of dolphins. Quantifying these effects is essential for conservation. Common bottlenose dolphins (*Tursiops truncatus*) near Savannah, Georgia, have demonstrated some of the highest rates of human interactions worldwide; thus, our aim was to determine if begging by dolphins has become a persistent foraging strategy which subsequently has altered behavioral patterns of the bottlenose dolphins in waters around Savannah. Dolphins were classified as either beggars or non-beggars based on whether they had displayed human-interactive behaviors, such as patrolling, begging, or human-interaction foraging, during their sighting history. Instantaneous and continuous observation sampling during 90-min focal follows were used to collect behavioral data on 17 individual beggars and 16 individual nonbeggars. A Pearson's chi-squared and Kruskal Wallis ANOVA were used to analyze behavioral data. In the time they were observed, beggars spent a significantly smaller percentage of time foraging (26%) compared to non-beggars (45%; p <0.0001). In contrast, beggars spent significantly more time observed traveling (53%) compared to non-beggars (40%; p < 0.0001). The amount of time they were observed at play, rest, and engaged in social behaviors were similar when comparing beggars and non-beggars (approximately 1% of all behaviors). Boat presence was not a major factor influencing behavioral differences as on average less than one boat, including the research vessel, was within either 10 or 50 m during each focal follow. Thus, the behavioral differences observed are likely indicative of a persistent behavioral shift taking place. Increased interactions with humans not only perpetuate potential further behavioral changes but raise the potential for injuries in dolphins resulting from these human interactions. Health implications for dolphins and their offspring

are also a concern as the quality of food received by begging dolphins has not been quantified to determine if a provisioned diet is calorically dense enough for their long-term health.

**Key Words:** behavioral pattern, human interactions, begging, transitory vs persistent, bottlenose dolphin, *Tursiops truncatus* 

#### Introduction

As interactions between humans and wildlife increase, unintended consequences on wildlife also increase (Hoyt, 2000; Green & Higginbottom, 2001; Orams, 2002; Madison, 2008; Ballantyne et al., 2009; Knight, 2009; de Sá Alves et al., 2013). Provisioning, or artificial feeding by humans, of many species has been documented to lead to changes in home ranges, aggression levels, and daily behavioral patterns (Wrangham, 1974; Tate & Pelton, 1983; Hill, 1999; Koganezawa & Imaki, 1999; Saj et al., 1999; De la Torre et al., 2000; Orams, 2002; Ram et al., 2003; Treves & Brandon, 2005; Berman et al., 2007; Donaldson et al., 2012; Hammerschlag et al., 2012). With additional provisioning, less time needs to be focused on foraging and more time becomes available to spend on other activities (Orams, 2002). For example, stone and tool handling behaviors by Japanese macaques (Macaca fuscata) peaked after periods of provisioning, while troops that were not provisioned sustained low levels of stone handling behaviors (Leca et al., 2008), demonstrating provisioned troops using "free" time to engage in additional and exploratory behaviors in their environment. When provisioned to the extent that caloric values were met and weight gain occurred, free-ranging meerkats (Suricata suricatta) more than doubled their rate of play compared to nonprovisioned meerkats (Sharpe et al., 2002).

Cetaceans also have exhibited behavioral changes through exposure to humans in controlled

swim with settings (Kyngdon et al., 2002; Trone et al., 2005) as well as during wild animal studies (Orams et al., 1996; Lusseau, 2003, 2004; Constantine et al., 2004; Christiansen et al., 2010). While area avoidance and decreased relative abundance in cetaceans have been documented as a persistent response to tourist activities (Lusseau, 2005; Bejder et al., 2006), many studies only report behavioral responses as transitory. For example, foraging and resting behaviors by common dolphins (Delphinus spp.) were less likely to continue once a tour boat approached (Stockin et al., 2008). Indo-Pacific bottlenose dolphins (Tursiops aduncus) also displayed similar transitory behavioral changes when in the presence of boats (Christiansen et al., 2010). Resting, foraging, and socializing behaviors all significantly decreased during tour boat interactions and transitioned to traveling behaviors for the duration of the interaction (Christiansen et al., 2010). Nonprovisioned bottlenose dolphins (Tursiops truncatus) in New Zealand progressively increased switching from traveling and milling behaviors to avoidance behaviors during swim-with-dolphin attempts (Constantine, 2001). Temporary aerial behaviors by spinner dolphins (Stenella longirostris) in Oahu increased, and swimming direction immediately changed following encounters with humans (Delfour, 2007). Behavioral transitions displayed by bottlenose dolphins in Doubtful Sound as a reaction to tour boat interaction mirrored those of the previously mentioned studies (Lusseau, 2003). Interestingly, the significant behavioral transitions outlined by Lusseau (2003) did not translate to differences in the overall behavioral budget of bottlenose dolphins, demonstrating that a permanent shift in behaviors had not yet occurred, and behavioral changes remained transitory. However, with the increasing frequency and intensity of human-wildlife interactions and tourism, longerterm activity patterns are likely to be altered and remain present even after the human stimulus has ended.

Common bottlenose dolphins near Savannah, Georgia, have demonstrated extremely high rates of human-interactive behaviors (i.e., begging behaviors) compared to other known problem areas (Perrtree et al., 2014); more bottlenose dolphins in Savannah showed begging behaviors than all bottlenose dolphins that were conditioned to interacting with humans in Cockburn Sound, Australia, or Sarasota, Florida, across multi-year studies (Finn et al., 2008; Powell & Wells, 2011; Perrtree et al., 2014). Begging also was observed across a larger geographic range around Savannah compared to other study areas (Samuels & Bejder, 2004; Finn et al., 2008; Powell & Wells, 2011; Perrtree et al., 2014).

The present study examines the occurrence of more persistent behavioral changes among dolphins of the Savannah population based on if interacting with humans and/or boats is part of their behavioral repertoire. Beggars were defined based on a sometimes brief, momentary interaction, including one or more of begging, depredation, provisioning, and patrolling behaviors. The question arose whether or not these varying, relatively short interactions were indicative of a persistent behavioral pattern change. Are begging bottlenose dolphins simply opportunists that are otherwise indistinguishable from nonbeggars? By this line of reasoning, the high interaction rates around Savannah would be linked to opportunity, predicting that all dolphins should beg when boats are around. Concentrated food patches tend to attract animals (Krebs, 1978), with shrimp trawling and dolphin-associated foraging, which is present in Savannah, being one of the best illustrated examples (Corkeron, 1990; Fertl & Leatherwood, 1997; Kovacs & Cox, 2014). However, this was not the case. Begging dolphins did not always beg or engage in human-associated foraging tactics when encountered (Perrtree, 2011). We hypothesized that begging has become a foraging strategy that has subsequently affected activity patterns, even when provisioned food is unavailable. We also hypothesized that if behavioral patterns changed, it would be most evident in foraging behaviors. In accordance with primate studies (Orams, 2002; Sharpe et al., 2002; Leca et al., 2008), we hypothesized that behaviors such as socializing, playing, and resting would be greater for beggars than non-beggars due to the possible efficiency of human-interaction foraging and the quality of the food received.

# Methods

# Study Site

Behavioral data were collected on bottlenose dolphins in the inshore waters of Savannah, Georgia, from south of the Savannah River to northern Ossabaw Sound (Figure 1). The study area covered approximately 340 km<sup>2</sup> and included the southern range of the Northern Georgia/Southern South Carolina Estuarine System stock (Waring et al., 2010). Photo-identification surveys were conducted from May through August 2011 and May through July 2012 from a vessel, either a 6.7-m Boston Whaler or a 5.8-m Carolina Skiff, both with 4-stroke outboard engines. Surveys were conducted along previously set transects in water accessible at high tide at an on-effort speed of 33 to 41 km/h.

### Behavioral Data Collection

Once bottlenose dolphins were sighted, boat speed was modified to match dolphin movement patterns. Photographs of the dorsal fin of each dolphin were taken. Sightings lasted a minimum of 5 min and continued until photo coverage of all dolphins was obtained or conditions prevented further photo coverage. Bottlenose dolphins were considered a group if they were within 100 m of each other moving in the same direction and engaged in similar behaviors (Shane, 1990). In the event that boats passed within 50 m of the dolphins, the number, speed, and type of boats were documented, including the research vessel. All attempts by dolphins to engage in patrolling, human-interaction foraging, or begging were documented, with additional photos taken of the dolphin(s) involved.

Individual focal follows lasting approximately 90 min were conducted on 33 bottlenose dolphins. Focal dolphins were determined based on 2009 through 2012 sighting data and assigned a beg or non-beg status. Begging was defined as either a dolphin surfacing head-up, with rostrum out of the water, oriented toward a boat, and within 10 m of the boat or surfacing parallel and within 2 m of a vessel with ventral surface toward the vessel (Perrtree et al., 2014). Dolphins were considered confirmed beggars (n = 17) if they were seen six or more times during surveys and begged or attempted to interact with humans or boats in any manner to receive food (excluding play or bow/ wake riding behaviors) on at least one occasion from 2009 through 2012. No dolphin that was assigned a beg status performed human-interactive behaviors on every sighting. Dolphins were considered non-beggars (n = 16) if they had been sighted six or more times between 2009 and 2012 and never displayed human-interactive behaviors. A minimum of six sightings was deemed sufficient to categorize dolphins since greater than 90% of cataloged beggars displayed begging

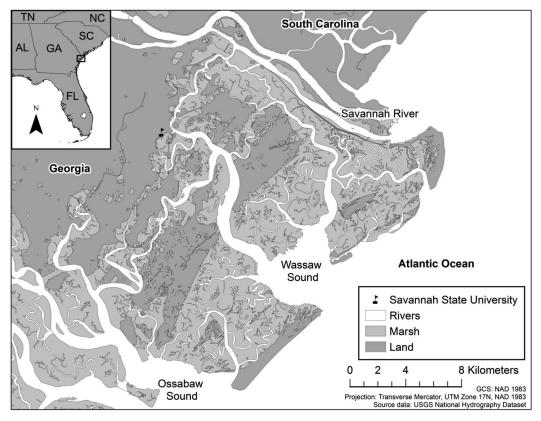


Figure 1. The study area consisted of the estuaries ranging from south of the Savannah River to northern Ossabaw Sound around Savannah, Georgia, which represents the southern portion of the common bottlenose dolphin (*Tursiops truncatus*) Northern Georgia/Southern South Carolina Estuarine System stock. *Source data:* U.S. Geological Survey National Hydrography Dataset (NHD); projection: UTM 17N NAD 1983.

behaviors by their fourth sighting (Perrtree, 2011). To avoid observer bias, the classification of the focal dolphin as a beggar or non-beggar remained unknown during all follows.

The objective of the present study did not include examining the effect that boat presence had on dolphin behavior; therefore, focal follows were conducted on days with the least number of boats on the water (i.e., Tuesday through Thursday; Hazelkorn, 2012). These days also coincided with having the least variability in number of boats on the water based on 2009 and 2010 data, reducing the effect of boat number on bottlenose dolphin behavior. However, any boat that did pass within 10 or 50 m of the focal dolphin (including the research vessel) was recorded. Any attempt by the focal dolphin to approach a vessel and beg was documented as an instantaneous point sample.

Continuous sampling as described by Altmann (1974) was used throughout each 90-min follow to obtain behavioral state durations. The time of every surfacing bout was documented as well as the current behavioral state of the focal dolphin. Behavioral states were forage, human-interaction forage, nondirectional, patrolling, play, rest, social, travel, and unknown (Table 1). The research vessel attempted to remain 30 to 50 m from the focal dolphin during a follow. This

distance functioned to limit the research vessel's direct influence on behavior yet still allowed observers to be in range to identify behaviors. Dolphins were still able to approach the research vessel to beg.

## Analyses

Total time spent in each behavior was combined for all focal follows of individuals of similar beg status to create percentages of time in each behavior. To determine any significant differences in the percentages of the behavioral pattern between beggars and non-beggars, a Pearson's chi-squared was used. However, combining the behaviors of all follows did not account for individual variability by each focal dolphin. To account for the variability in focal animal behavior, the average proportion of time spent in each of the behaviors was calculated. Because these data were not normally distributed, they were arcsin transformed. A Kruskal-Wallis one-way analysis of variance (ANOVA) was used to determine if there were significant differences in the proportion of time spent foraging and traveling between beggars and non-beggars. A Kruskal-Wallis ANOVA also was used to determine if these transformed proportions differed across behaviors for both beggars and non-beggars. If there was a significant difference, a Tukey's HSD post-hoc test was used ( $\alpha = 0.05$ ).

 Table 1. Ethogram of behavioral states for dolphins (adapted from Lusseau, 2003)

Behavioral state	Definition
Foraging	Direction of movement varies; synchronous dives for long intervals; individual performs steep dives, arching its back at the surface to increase speed of descent; category includes kerplunking, fish whacking, strand feeding, circling, hardstops, headstands, and fish in mouth behaviors (Bowen, 2011).
Human-interaction foraging	Depredation or successful provisioning (Powell & Wells, 2011); associating with a shrimp trawler, either actively trawling or eating catch being discarded from the dock (Chilvers & Corkeron, 2001).
Non-directional	No net movement; individuals surfacing facing different directions; group often changes direction; dive intervals variable but short; group spacing varies.
Patrolling	Traveling in repeated movements or moving non-directionally within 20 m of a stationary vessel.
Play	Diverse, interactive behavioral events observed involving the use of an object such as wrack, marine debris, or non-prey items.
Resting	Moving slowly in a constant direction; swimming with short, relatively constant, synchronous dive intervals; individuals tightly grouped.
Socializing	Diverse, interactive behavioral events observed such as body contacts, pouncing, and genital inspections; individuals often change position in the group; dive intervals vary.
Traveling	Moving steadily in a constant direction; swimming with short, relatively constant dive inter- vals; group spacing varies.
Unknown	Behaviors are not known or indicative of losing the animal for a 3-min time interval.

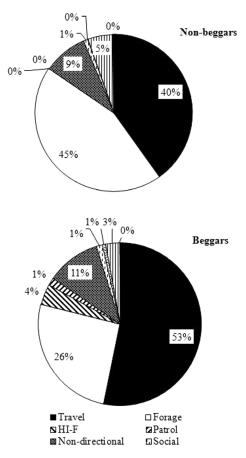
Additionally, a Kruskal-Wallis ANOVA was used to determine if there were any significant differences in the number of boats present across behavioral states for beggars and non-beggars. A Tukey's HSD post-hoc test was used to determine significant differences between specific behaviors.

#### Results

Seventeen dolphins classified as beggars were observed over a total of 1,456 min, while 16 nonbegging dolphins were observed for a total of 1,258 min. Focal follows took place on a total of 20 d between May and August in 2011 and 2012. Nonbeggars engaged in natural foraging behaviors 45% of the time observed, while beggars only displayed natural foraging behaviors 26% of that time ( $\chi^{2_1}$  = 104.01, p < 0.0001; Figure 2). Beggars engaged in human-interaction foraging and patrolling behaviors for a total of 5% of the time observed. Beggars still spent significantly less time engaged in all foraging tactics (e.g., natural foraging, human-interaction foraging, and patrolling) than non-beggars (31 vs 45%, respectively;  $\chi^{2_1} = 48.82$ , *p* < 0.0001). Conversely, begging bottlenose dolphins spent significantly more of their time traveling (53%;  $\chi^{2}_{1} = 46.62$ , p < 0.0001), while non-beggars only traveled 40% of the time they were observed. Both beggars and non-beggars spent the least amount of time observed (<1%) engaged in social, rest, and play behaviors. A comparable amount of time spent engaged in nondirectional and unknown behaviors was observed for beggars and non-beggars (Figure 2).

To account for the individual variability in focal animals, the average proportion of observed time spent in each behavior was calculated. There was a significant difference in observed time spent across behaviors for both beggars (df = 8, 144; F = 29.32;p < 0.001) and non-beggars (df = 8, 135; F = 27.97; p < 0.001; Figure 3). Beggars spent a greater proportion traveling and foraging than they did in other behaviors, with traveling as the dominant behavior. Non-beggars spent a significantly greater proportion of time both traveling and foraging than they did in other behaviors, but there was no difference between the proportion of time traveling and foraging for non-beggars (Figure 3). When comparing beggars and non-beggars, the proportion of time spent foraging (df = 1, 32; F = 3.20; p = 0.08) or traveling (df = 1, 32; F = 1.93; p = 0.17; Figure 3) did not differ significantly.

The average number of boats present within 50 m during the most frequent behaviors—foraging, nondirectional, and traveling—was similar at approximately one boat for both beggars ( $0.98 \pm 0.45$ ) and non-beggars ( $0.79 \pm 0.30$ ; Figure 4), indicating only the research vessel was present. The average numbers of boats present within 10 m during all

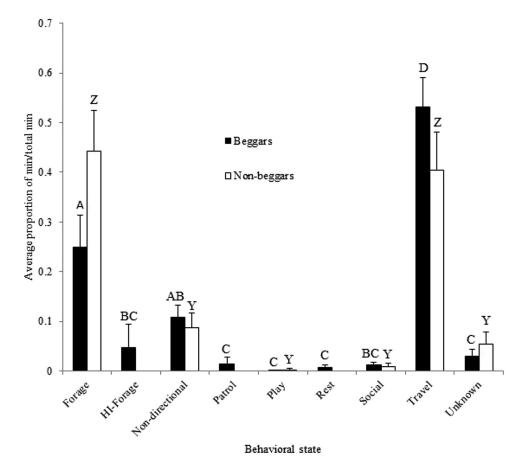


**Figure 2.** Percentage of total time common bottlenose dolphins spent engaged in various behaviors in Savannah, Georgia, from May through August 2011 and May through July 2012. Beggars traveled significantly more than non-beggars ( $\chi^{2_1} = 46.62$ , p < 0.0001), and non-beggars naturally foraged significantly more than beggars ( $\chi^{2_1} = 104.01$ , p < 0.0001). When all foraging tactics for beggars were combined, there was still a significant difference in time spent foraging between beggars and non-beggars ( $\chi^{2_1} = 48.82$ , p < 0.0001). HI-F indicates the one incident of human-interaction foraging.

behaviors during both beggar and non-beggar follows was less than one (Figure 5). Begging behavior toward the research vessel was displayed less than 0.2% of the time all beggars were followed.

#### Discussion

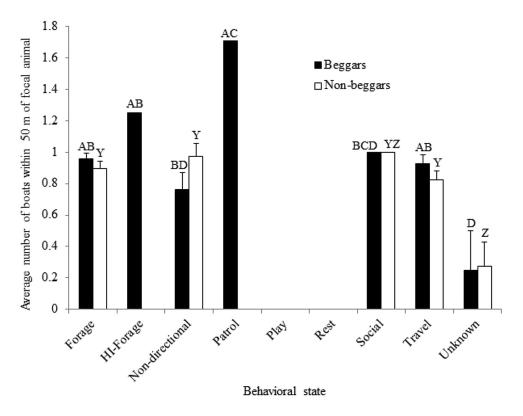
Bottlenose dolphins that were classified as beggars traveled more and foraged less than dolphins classified as non-beggars. In this study, behavioral differences were not just a transitory response to boat



**Figure 3.** Proportion (average  $\pm$  SE) of time (min/total min) spent in each behavioral state for begging and non-begging common bottlenose dolphins around Savannah, Georgia, from May through August 2011 and May through July 2012. There was a significant difference in proportion of time spent in each behavior for beggars (df = 8, 144; F = 29.32; p < 0.001) as there was for non-beggars (df = 8, 135; F = 27.97; p < 0.001). Within each behavior, letters indicate group classes; the same letter above a subset of bars denotes lack of statistical difference, whereas different letters represent statistical difference according to Tukey's HSD post-hoc. Beggars are denoted by the letters "A" through "D," while non-beggars are denoted by the letters "Y" and "Z." HI-Forage indicates the one incident of human-interaction foraging. There was no difference in proportion of time foraging between beggars and non-beggars (df = 1, 32; F = 3.20; p = 0.08), nor was there for traveling (df = 1, 32; F = 1.93; p = 0.17).

presence and interaction, unlike other studies that demonstrated behavioral changes as a direct result of human interaction (Lusseau, 2003; Stockin et al., 2008; Christiansen et al., 2010). Rather, this study was conducted mostly in the absence of boats, and behavioral changes were persistent and were reflected in the different behaviors displayed by beggars and non-beggars during the time observed. The change in the behaviors of the dolphins indicates that begging from boats is a long-lasting foraging tactic adopted by some dolphins.

Begging dolphins spent a significantly smaller proportion of the observed activity budget foraging compared to non-begging dolphins. We posit that these dolphins have adopted a permanent tactic of begging and searching for boats from which they would beg or receive bycatch. This tactic may increase the chance of encountering prey and be a more energetically beneficial way to detect, capture, and consume prey (Heithaus & Dill, 2002). If obtaining human-provided food is quicker and energetically more beneficial than natural foraging, these animals may have an advantage. A foraging strategy of receiving handouts and bycatch closely aligns with the optimal foraging theory in which predators should seek prey that is more calorically



**Figure 4.** Average number of boats  $\pm$  SE present within 50 m of begging and non-begging common bottlenose dolphins from May through August 2011 and May through July 2012 in Savannah, Georgia. There was a significant difference in the average number of boats across all behaviors for beggars (df = 8, 38; F = 5.23; p < 0.001) and non-beggars (df = 8, 40; F = 8.88; p < 0.001). Within each behavior, letters indicate group classes; the same letter above a subset of bars denotes lack of statistical difference, whereas different letters represent statistical difference according to Tukey's HSD post-hoc. Beggars are denoted by the letters "A" through "D," while non-beggars are denoted by the letters "Y" and "Z." HI-Forage indicates the one incident of human-interaction foraging.

beneficial than the energy expended to obtain it (Stephens & Krebs, 1986; Sih & Christensen, 2001; Spitz et al., 2012). However, we have not evaluated the quality and quantity of food received by dolphins nor the caloric costs associated with this behavior to determine if begging is a superior strategy energetically.

Reduced foraging costs may allow more time for rest and to strengthen social bonds through play and mating behaviors (Stephens & Krebs, 1986; Hill, 1999; Koganezawa & Imaki, 1999; Sih & Christensen, 2001; Sharpe et al., 2002; Leca et al., 2008; Spitz et al., 2012). Previous studies on primates and other terrestrial animals have shown that when provisioning occurred, time spent engaged in socializing and resting behaviors was greater than the time spent foraging (Altmann & Muruthi, 1988; Saj et al., 1999; Sharpe et al., 2002; Leca et al., 2008). Interestingly, beggars increased their traveling time but showed no significant difference in time spent socializing, resting, or playing compared to non-beggars.

The difference between the begging dolphins in this study and the provisioned primates of previous studies may be in the efficiency of receiving provisioned food as there are differences in the delivery factor. Primate studies conducted provisioning sessions consistently at a designated place and time (Altmann & Muruthi, 1988; Saj et al., 1999; Sharpe et al., 2002; Leca et al., 2008); whereas, bottlenose dolphins around Savannah are likely receiving food in a more haphazard distribution in both space and time. There are no data available to suggest that beggars have learned when recreational and commercial boats are available from which to beg and receive bycatch and provisioned food.

Follows also were conducted at varying times during the day. Therefore, it is highly unlikely that

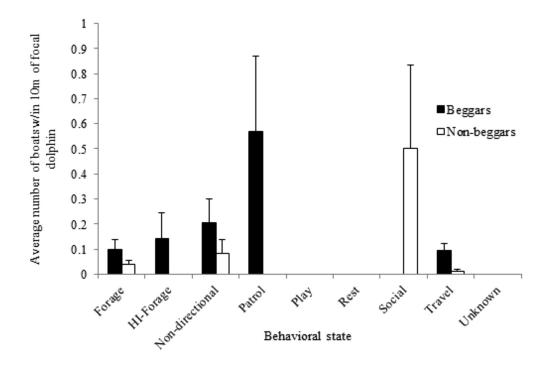


Figure 5. Average number of boats  $\pm$  SE present within 10 m of begging and non-begging common bottlenose dolphins from May through August 2011 and May through July 2012 in Savannah, Georgia. On average through all behaviors, beggars had  $0.15 \pm 0.07$  boats within 10 m of them, while non-beggars had  $0.12 \pm 0.09$  boats within 10 m of them.

behaviors, such as social and rest behaviors, took place at times in which they were unobserved. It is possible that the time begging dolphins could be putting toward socializing and resting is in reality going toward traveling to find successful begging and provisioning opportunities. Due to the high productivity in the estuarine waters, the possibility of a methodological bias is present but low. By following well-accepted and widely used behavioral definitions, it is improbable that behaviors such as socializing and play were confused with other behaviors such as traveling or foraging when viewed from the surface. A bias remains that socializing and play behaviors that take place underneath the surface may have been missed in their entirety; however, it is highly unlikely that these behaviors were not captured at all during bouts due to the behavioral definitions outlined by Lusseau (2003) (see Table 1).

Begging bottlenose dolphins around Savannah can be compared to the long-studied bottlenose dolphins in Sarasota, Florida, that interact with humans, referred to as Human Interaction (HI) dolphins. In Sarasota, HI dolphins foraged significantly less than non-HI dolphins (Powell & Wells, 2011). Similarly, in Savannah, beggars foraged less often than non-beggars. Interestingly, when foraging behaviors and human-interactive behaviors by HI dolphins were combined into a single foraging category, the difference in foraging was no longer significant between HI and non-HI dolphins (Powell & Wells, 2011). Thus, regardless of strategy employed, HI and non-HI dolphins spent approximately the same amount of time engaged in foraging behaviors, implying that the humaninteractive behaviors have become part of the foraging behavior repertoire (Powell & Wells, 2011).

In this scenario, neither group of dolphin has an advantage since the two tactics are approximately even across time observed, although energetic intake is unknown, which would reveal whether rates of intake differ. However, similar analyses on the behavioral patterns of beggars and nonbeggars around Savannah showed that beggars spent less time in all forms of foraging than nonbeggars. If this tactic of foraging was advantageous, it could be indicated by increases in other energetically costly behaviors such as socializing, play, and mating. Since these behaviors were not increased, it is possible that traveling is in actuality searching, therefore making it part of a beggar's foraging strategy. Still, these two types of dolphins are engaging in significantly different amounts of time in different behaviors.

Persistent behavioral changes in foraging can lead to subsequent fitness changes and to larger conservation implications that should be closely monitored. The sustainability of a population favors strategies that maximize fitness, and marine mammals may sometimes take the trade-off of less energetically beneficial prey to forage in a safer habitat (Heithaus & Dill, 2002; Wirsing et al., 2008). However, dolphins that forage regularly in close association with boats are at greater risk of boat strikes and injuries from propellers as well as being more susceptible to entanglement, ingesting trash, and, in extreme cases intentional harm by anglers (Wells & Scott, 1994; Wells et al., 1998, 2008; Durden, 2005; Donaldson et al., 2010). This risk of injury to bottlenose dolphins (*Tursiops* sp.) has been shown in Sarasota, Florida (Powell & Wells, 2011), and Cockburn Sound, Australia (Finn et al., 2008), both of which have a lower rate of interactions between dolphins and humans than Savannah (Perrtree, 2011).

As observed in the present study, differential foraging tactics and activity budgets delineate two categories of dolphins, beggars and non-beggars, in the waters around Savannah, Georgia. Beggars spend less time foraging but more time traveling than non-beggars, regardless of boat presence. If the increased traveling time is related to the pursuit of food (i.e., provisioning off boats), then the overall activity budgets of beggars and non-beggars would be similar. Nevertheless, a difference in the foraging tactics of the two types of dolphins remains, although whether one tactic is superior has yet to be determined. If beggars obtain higher quality food, fitness benefits such as larger young or shorter inter-birth intervals could develop. However, the susceptibility to injury and death from boat injuries or fishing line entanglement may negate or even outweigh such benefits. Lower quality food may also result in a fitness decrease over time such as calf mortality (Mann et al., 2000). Thus, it is important to continue to observe the ongoing behavioral changes and any possible subsequent health changes to monitor the sustainability of the population.

## Acknowledgments

We thank the Savannah State University Dolphin Science Lab researchers, volunteers, and interns for contributions to the ongoing research, especially R. Perrtree, S. Bowen, and C. Kovacs. Boat time was provided by the Marine Sciences Program at Savannah State University. We appreciate comments and edits from E. Montie and M. C. Curran on previous versions. We are grateful for the additional boat time provided by the Skidaway Institute of Oceanography. We thank J. Mitchler and A. Sapp for providing assistance as boat captains as well as Captains Mike and Harry. This research was supported by many grants: Title VII Grant P382G090003: thank you to Dr. C. Curran; EDGE (Enhancing Diversity in Geosciences Education) NSF Award GEO-0194680: thank you to Dr. C. Pride; and NOAA Living Marine Resources and Cooperative Sciences Center NA11SEC4810002: thank you to Dr. D. Hoskins. Photographs and data were collected in accordance with the Marine Mammal Protection Act under National Marine Fisheries Service Letter of Confirmation Number 14219 issued to Dr. T. M. Cox.

#### Literature Cited

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49(3/4), 227-267. http:// dx.doi.org/10.1163/156853974X00534
- Altmann, J., & Muruthi, P. (1988). Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology*, *3*, 213-221. http:// dx.doi.org/10.1002/ajp.1350150304
- Ballantyne, R., Packer, J., & Hughes, K. (2009). Tourists' support for conservation messages and sustainable management practices in wildlife tourism experiences. *Tourism Management*, 30(5), 658-664. http://dx.doi. org/10.1016/j.tourman.2008.11.003
- Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., . . . Krützen, M. (2006). Decline in relative abundance of bottlenose dolphins exposed to long-term disturbances. *Conservation Biology*, 20(6), 1791-1798. http://dx.doi.org/10.1111/j.1523-1739.2006.00540.x
- Berman, C. M., Li, J., Ogawa, H., Ionica, C., & Yin, H. (2007). Primate tourism, range restriction, and infant risk among *Macaca thibetana* at Mt. Huangshan, China. *International Journal of Primatology*, 28(5), 1123-1141. http://dx.doi.org/10.1007/s10764-007-9199-4
- Bowen, S. R. (2011). Diet of bottlenose dolphins Tursiops truncatus in the northwest Florida panhandle and foraging behavior near Savannah, Georgia (Unpub. Master's thesis). Savannah State University, Savannah, GA.
- Chilvers, B. L., & Corkeron, P. J. (2001). Trawling and bottlenose dolphins' social structure. *Proceedings of the Royal Society B: Biological Sciences*, 268(1479), 1901-1905. http://dx.doi.org/10.1098/rspb.2001.1732
- Christiansen, F., Lusseau, D., Stensland, E., & Berggren, P. (2010). Effects of tourist boats on the behavior of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar. *Endangered Species Research*, 11, 91-99. http://dx.doi.org/10.3354/esr00265
- Constantine, R. (2001). Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science*, 17(4), 689-702. http://dx.doi. org/10.1111/j.1748-7692.2001.tb01293.x

- Constantine, R., Brunton, D. H., & Dennis, T. (2004). Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behavior. *Biological Conservation*, *117*(3), 299-307. http://dx.doi.org/10.1016/j.biocon. 2003.12.009
- Corkeron, P. J. (1990). Aspects of the behavioral ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 285-293). San Diego: Academic Press. http://dx.doi.org/10.1016/ b978-0-12-440280-5.50018-4
- De la Torre, S., Snowdon, C. T., & Bejarano, M. (2000). Effects of human activities on wild pygmy marmosets in Ecuadorian Amazonia. *Biological Conservation*, 94(2), 153-163. http://dx.doi.org/10.1016/S0006-3207 (99)00183-4
- de Sá Alves, L. C. P., Andriolo, A., Orams, M. B., & de Freitas Azevedo, A. (2013). Resource defense and dominance hierarchy in the boto (*Inia geoffrensis*) during a provisioning program. *Acta Ethologica*, 16(1), 9-19. http://dx.doi.org/10.1007/s10211-012-0132-2
- Delfour, F. (2007). Hawaiian spinner dolphins and the growing dolphin watching activity in Oahu. Journal of the Marine Biological Association of the United Kingdom, 87, 109-112. http://dx.doi.org/10.1017/ S0025315407054148
- Donaldson, R., Finn, H., & Calver, M. (2010). Illegal feeding increases risk of boat-strike and entanglement in bottlenose dolphins in Perth, Western Australia. *Pacific Conservation Biology*, 16(3), 157-161. http://dx.doi. org/10.1071/PC100157
- Donaldson, R., Finn, H., Bejder, L., Lusseau, D., & Calver, M. (2012). The social side of human–wildlife interaction: Wildlife can learn harmful behaviors from each other. *Animal Conservation*, 15, 427-435. http://dx.doi. org/10.1111/j.1469-1795.2012.00548.x
- Durden, W. N. (2005). The harmful effects of inadvertently conditioning a wild bottlenose dolphin (*Tursiops truncatus*) to interact with fishing vessels in the Indian River Lagoon, Florida, USA. *Aquatic Mammals*, 31(4), 413-419. http://dx.doi.org/10.1578/AM.31.4.2005.413
- Fertl, D., & Leatherwood, S. (1997). Cetacean interactions with trawls: A preliminary review. *Journal of Northwest Atlantic Fishery Science*, 22, 219-248. http://dx.doi. org/10.2960/J.v22.a17
- Finn, H., Donaldson, R., & Calver, M. (2008). Feeding Flipper: A case study of a human–dolphin interaction. *Pacific Conservation Biology*, 14(3), 215-225. http:// dx.doi.org/10.1071/PC080215
- Green, R., & Higginbottom, K. (2001). Negative effects of wildlife tourism on wildlife. Gold Coast, Australia: CRC for Sustainable Tourism.
- Hammerschlag, N., Gallagher, A. J., Wester, J., Luo, J., & Ault, J. S. (2012). Don't bite the hand that feeds: Assessing ecological impacts of provisioning ecotourism on an apex marine predator. *Functional Ecology*, 26(3), 567-576. http://dx.doi.org/10.1111/j.1365-2435. 2012.01973.x

- Hazelkorn, R. A. (2012). Behavioral patterns of the common bottlenose dolphin Tursiops truncatus around Savannah, Georgia (Unpub. Master's thesis). Savannah State University, Savannah, GA.
- Heithaus, M. R., & Dill, L. M. (2002). Feeding strategies and tactics. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 412-422). San Diego: Academic Press.
- Hill, D. A. (1999). Effects of provisioning on the social behavior of Japanese and Rhesus macaques: Implications for socioecology. *Primates*, 40(1), 187-198. http://dx.doi.org/10.1007/BF02557710
- Hoyt, E. (2000). Whale watching 2000: Worldwide tourism numbers, expenditures, and expanding socioeconomic benefits. Crowborough, UK: International Fund for Animal Welfare.
- Knight, J. (2009). Making wildlife viewable: Habituation and attraction. *Society and Animals*, 17(2), 167-184. http://dx.doi.org/10.1163/156853009X418091
- Koganezawa, M., & Imaki, H. (1999). The effects of food sources on Japanese monkey home range size and location, and population dynamics. *Primates*, 40(1), 177-185. http://dx.doi.org/10.1007/BF02557709
- Kovacs, C., & Cox, T. (2014). Quantification of interactions between common bottlenose dolphins (*Tursiops truncatus*) and a commercial trawler near Savannah, Georgia. *Aquatic Mammals*, 40(1), 81-94. http://dx.doi. org/10.1578/AM.40.1.2014.81
- Krebs, J. R. (1978). Optimal foraging: Decision rules for predators. In J. R. Krebs & N. B. Davies (Eds.), *Behavioral ecology: An evolutionary approach* (pp. 22-63). London: Blackwell Scientific Publications.
- Kyngdon, D. J., Minot, E. O., & Stafford, K. J. (2002). Behavioural responses of captive common dolphin *Delphinus delphis* to a "Swim-with-Dolphin" programme. *Applied Animal Behaivour Science*, 81(2), 163-170. http://dx.doi.org/10.1016/S0168-1591(02)00255-1
- Leca, J. B., Gunst, N., & Huffman, M. A. (2008). Food provisioning and stone handling tradition in Japanese macaques: A comparative study of ten troops. *American Journal of Primatology*, 70(8), 803-813. http://dx.doi. org/10.1002/ajp.20551
- Lusseau, D. (2003). Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. *Conservation Biology*, 17(6), 1785-1793.
- Lusseau, D. (2004). Hidden costs of tourism: Detecting long-term effects of tourism using behavioural information. *Ecology and Society*, 9(1), 1-20. http://dx.doi. org/10.1111/j.1523-1739.2003.00054.x
- Lusseau, D. (2005). Residency pattern of bottlenose dolphins *Tursiops* spp. in Milford Sound, New Zealand, is related to boat traffic. *Marine Ecology Progress Series*, 295, 265-272. http://dx.doi.org/10.3354/meps295265
- Madison, J. S. (2008). Yosemite National Park: The continuous evolution of human–black bear conflict management. *Human-Wildlife Conflicts*, 2(2), 160-167.

- Mann, J., Connor, R. C., Barre, L. M., & Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): Life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, 11(2), 210-219. http://dx.doi.org/10.1093/beheco/11.2.210
- Orams, M. B. (2002). Feeding wildlife as a tourism attraction: A review of issues and impacts. *Tourism Management*, 23(3), 281-293. http://dx.doi.org/10.1016/ S0261-5177(01)00080-2
- Orams, M. B., Hill, G. J., & Baglioni, A. J. (1996). "Pushy" behavior in a wild dolphin feeding program at Tangalooma, Australia. *Marine Mammal Science*, 12(1), 107-117. http://dx.doi.org/10.1111/j.1748-7692.1996. tb00308.x
- Perrtree, R. M. (2011). Begging behavior by the common bottlenose dolphin Tursiops truncatus near Savannah, Georgia: Prevalence, spatial distribution, and social structure (Unpub. Master's thesis). Savannah State University, Savannah, GA.
- Perrtree, R. M., Kovacs, C. J., & Cox, T. M. (2014). Standardization and application of metrics to quantify human-interaction behaviors by the bottlenose dolphin (*Tursiops* spp.). *Marine Mammal Science*, 30(4), 1320-1334. http://dx.doi.org/10.1111/mms.12114
- Powell, J. R., & Wells, R. S. (2011). Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Mammal Science*, 27(1), 111-129. http://dx.doi.org/10.1111/j.1748-7692.2010.00401.x
- Ram, S., Venkatachalam, S., & Sinha, A. (2003). Changing social strategies of wild female bonnet macaques during natural foraging and on provisioning. *Current Science*, 84(6), 780-790.
- Saj, T., Sicotte, P., & Paterson, J. D. (1999). Influence of human food consumption on the time budget of vervets. *International Journal of Primatology*, 20(6), 977-994. http://dx.doi.org/10.1023/A:1020886820759
- Samuels, A., & Bejder, L. (2004). Chronic interaction between humans and free-ranging bottlenose dolphins near Panama City Beach, Florida, USA. *Journal of Cetacean Research and Management*, 6(1), 69-77.
- Shane, S. H. (1990). Behaviour and ecology of the bottlenose dolphin at Sanibel Island, Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 245-265). New York: Academic Press. http:// dx.doi.org/10.1016/B978-0-12-440280-5.50016-0
- Sharpe, L. L., Clutton-Brock, T. H., Brotherton, P. N. M., Cameron, E. Z., & Cherry, M. I. (2002). Experimental provisioning increases play in free-ranging meerkats. *Animal Behaviour*, 64(1), 113-121. http://dx.doi. org/10.1006/anbe.2002.3031
- Sih, A., & Christensen, B. (2001). Optimal diet theory: When does it work, and when and why does it fail? *Animal Behaviour*, 61(2), 379-390. http://dx.doi. org/10.1006/anbe.2000.1592
- Spitz, J., Trites, A. W., Becquet, V., Brind'Amour, A., Cherel, Y., Galois, R., & Ridoux, V. (2012). Cost of living dictates what whales, dolphins, and porpoises

eat: The importance of prey quality on predator foraging strategies. *PLOS ONE*, 7(11), e50096. http://dx.doi. org/10.1371/journal.pone.0050096

- Stephens, D. W., & Krebs, J. R. (1986). Foraging theory. Princeton, NJ: Princeton University Press.
- Stockin, K. A., Lusseau, D., Binedell, V., Wiseman, N., & Orams, M. B. (2008). Tourism affects the behavioral budget of the common dolphin *Delphinus* sp. in the Hauraki Gulf, New Zealand. *Marine Ecology Progress Series*, 355, 287-295. http://dx.doi.org/10.3354/meps 07386
- Tate, J., & Pelton, M. R. (1983). Human–bear interactions in Great Smoky Mountains National Park. *Bears: Their Biology and Management*, 5, 312-321. http://dx.doi. org/10.2307/3872556
- Treves, A., & Brandon, K. (2005). Tourist impacts on the behavior of black howling monkeys (*Alouatta pigra*) at Lamanai, Belize. In J. D. Paterson & J. Wallis (Eds.), *Commensalism and conflict: The human–primate interface* (Vol. 4, pp. 147-167). San Antonio, TX: American Society of Primatologists.
- Trone, M., Kuczaj III, S. A., & Solangi, M. (2005). Does participation in Dolphin-Human Interaction Programs affect bottlenose dolphin behaviour? *Applied Animal Behaviour Science*, 93(3), 363-374. http://dx.doi. org/10.1016/j.applanim.2005.01.003
- Waring, G. T., Josephson, E., Fairfield-Walsh, C. P., & Maze-Foley, K. (2010). U.S. Atlantic and Gulf of Mexico marine mammal stock assessment – 2009 (NOAA Technical Memorandum NMFS NE 210). Washington, DC: National Oceanic and Atmospheric Administration.
- Wells, R. S., & Scott, M. D. (1994). Incidence of gear entanglement for resident inshore bottlenose dolphins near Sarasota, Florida. In W. F. Perrin, G. P. Donovan, & J. Barlow (Eds.), *Gillnets and cetaceans* (p. 629). *Report of the International Whale Commission (Special Issue 15).*
- Wells, R. S., Hofmann, S., & Moors, T. L. (1998). Entanglement and mortality of bottlenose dolphins, *Tursiops truncatus*, in recreational fishing gear in Florida. *Fishery Bulletin*, 96(3), 647-650.
- Wells, R. S., Allen, J. B., Hofmann, S., Bassos-Hull, K., Fauquier, D. A., Barros, N. B., . . . Scott, M. D. (2008). Consequences of injuries on survival and reproduction of common bottlenose dolphins (*Tursiops truncatus*) along the west coast of Florida. *Marine Mammal Science*, 24(4), 774-794. http://dx.doi.org/10.1111/ j.1748-7692.2008.00212.x
- Wirsing, A. J., Heithaus, M. R., Frid, A., & Dill, L. M. (2008). Seascapes of fear: Methods for evaluation of sublethal predator effects experienced and generated by marine mammals. *Marine Mammal Science*, 24(1), 1-15. http://dx.doi.org/10.1111/j.1748-7692.2007.00167.x
- Wrangham, R. W. (1974). Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behaviour*, 22(1), 83-93. http://dx.doi.org/10.1016/ S0003-3472(74)80056-4