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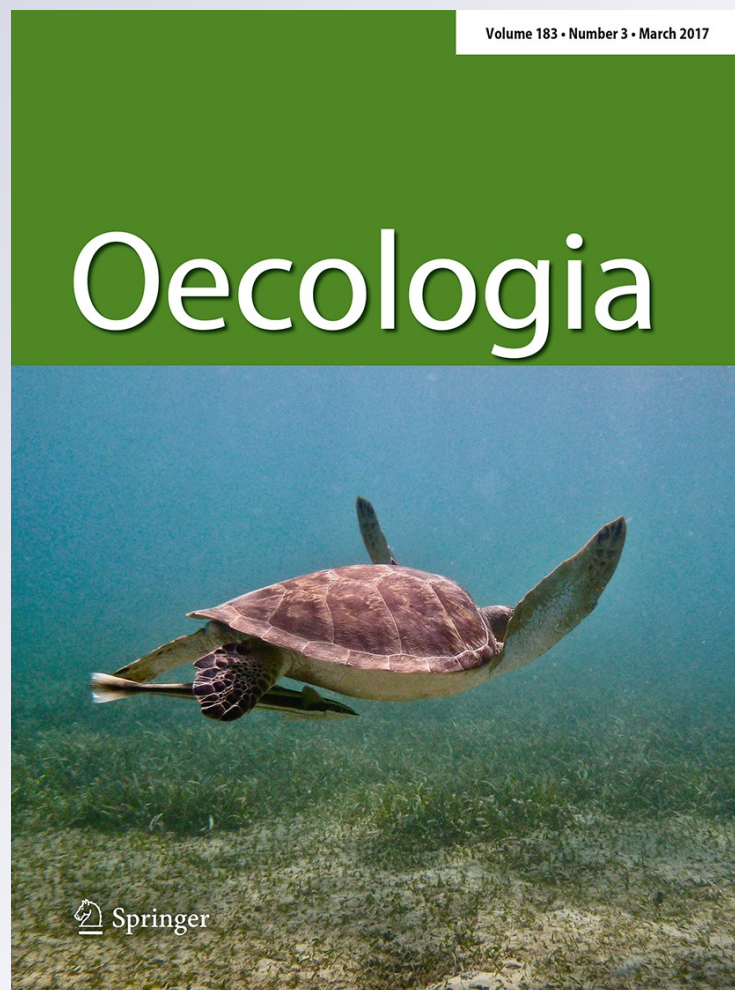
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Individual-level behavioral responses of immature green turtles to snorkeler disturbance

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Abstract Despite many positive benefits of ecotourism, increased human encounters with wildlife may have detrimental effects on wild animals. As charismatic megafauna, nesting and foraging sea turtles are increasingly the focus of ecotourism activities. The purpose of our study was to quantify the behavioral responses of immature green turtles (*Chelonia mydas*) to disturbance by snorkelers, and to investigate whether turtles have individual-level responses to snorkeler disturbance. Using a standardized disturbance stimulus in the field, we recorded turtle behaviors pre- and post-disturbance by snorkelers. Ninety percent of turtles disturbed by snorkeler ($n = 192$) initiated their flights at distances of ≤ 3 m. Using principal component analysis, we identified two distinct turtle personality types, ‘bold’ and ‘timid’, based upon 145 encounters of 19 individually identified turtles and five disturbance response variables. There was significant intra-individual repeatability in behavioral

responses to disturbance, but bolder turtles had more behavioral plasticity and less consistent responses than more timid individuals. Bolder individuals with reduced evasion responses might be at a higher risk of shark predation, while more timid turtles might have greater energetic consequences due to non-lethal predator effects and repeated snorkeler disturbance. Over the longer term, a turtle population with a mix of bold and timid individuals may promote more resilient populations. We recommend that snorkelers maintain >3 m distance from immature green turtles when snorkeling, and that ecotourism activities be temporally and spatially stratified. Further, turtle watching guidelines need to be communicated to both tour operators and independent snorkelers to reduce the disturbance of turtles.

Keywords Ecotourism · Flight initiation distance · Principal component analysis · Personality · Repeatability

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Introduction

Developing nations, regions, and communities typically cultivate ecotourism in hopes of creating environmentally sustainable economic prosperity while supporting wildlife conservation (Scheyvens 1999; Ashley and Roe 1998; Brooks et al. 2006; Gallagher and Hammerschlag 2011; Fennell 2015). Ecotourism can also generate funding and support for conservation activities and create socioeconomic incentives to preserve and rehabilitate functioning ecosystems (Higginbottom et al. 2001; Cisneros-Montemayor et al. 2013). Despite these potential benefits, ecotourism may also increase human encounters with wildlife, causing detrimental effects such as avoidance, habituation, attraction, and cryptic responses (e.g., increased stress) (Higginbottom et al. 2001; Müllner et al.

2004; Piñeiro et al. 2012). Increased human encounters with wildlife may affect short- and long-term animal behaviors (Gabrielsen and Smith 1995; Green and Higginbottom 2001; Williams et al. 2006) and physiological responses (Knight and Cole 1995) as well as result in habitat abandonment (Lusseau and Bejder 2007) and reduced reproductive success (Bejder 2005; Constantine and Bejder 2008).

Understanding how individual animals respond to disturbance provides resource managers with tools for developing conservation strategies (Conrad et al. 2011) as well as insight into ecological and evolutionary processes (Réale et al. 2010; Wolf and Weissing 2012). Yet, there can be much variation in behavioral plasticity between individual animals across taxa including mammals (Wilson et al. 1994; David et al. 2004; Svartberg et al. 2005; Martin and Réale 2008), insects (Bonte et al. 2007; Schuett et al. 2011), birds (Carere et al. 2005; Quinn and Cresswell 2005; Dingemanse et al. 2012), fishes (Dingemanse et al. 2007; Biro et al. 2010; Cote et al. 2010; Wilson et al. 2010), and reptiles (López et al. 2005; Highcock and Carter 2014; Kuo et al. 2015). Individual animals are often described as ‘bold’ when they demonstrate either high levels of exploratory behaviors (e.g., low anti-predator vigilance and short flight initiation distances) or short startle response durations following a disturbance (e.g., time duration of hiding). For example, Briffa et al. (2008) classified individual hermit crabs (*Pagurus bernhardus*) as ‘bold’ or ‘timid’ based on the duration of their startle response (i.e., hiding within their shell) when disturbed. When such behaviors are consistent across a range of situations, or through time, they are often referred to as representing animal ‘personality’ (Gosling 2001; Réale et al. 2007) or behavioral syndromes (Sih et al. 2004). Examining intraspecific behavior differences within a population is important for recognizing the possible presence of particularly sensitive individuals and developing comprehensive management plans. Nevertheless, few studies have incorporated how individual-level responses can be incorporated into management plans to mediate human effects.

The long-lived, globally threatened green turtle (*Chelonia mydas*) frequently inhabits coastal marine areas (Bolten 2003; Seminoff et al. 2015). Following their omnivorous oceanic phase, juvenile green turtles typically recruit to neritic (less than 200 m water depth) foraging grounds and shift to primarily herbivorous benthic feeding (Bolten 2003; Heppell et al. 2003; Jones and Seminoff 2013). Turtles use these areas as developmental habitats for decades until reaching sexual maturity (Bjorndal et al. 2000), then migrate hundreds to thousands of kilometers to natal areas to forage, mate, and nest (Bowen and Karl 2007; Arthur et al. 2008). Sea turtles are relatively docile and easily located while nesting on beaches (Campbell 1999) and while foraging within neritic areas (Landry and Taggart 2010). As charismatic megafauna, ecotourism activities to

observe sea turtle nesting and foraging are increasing, and it is argued that these encounters benefit conservation by raising awareness and appreciation for sea turtles (Tisdell and Wilson 2002; Ballantyne et al. 2011). Yet, others suggest that such tourist activities may disturb turtles, potentially reducing their survivorship and fitness (Landry and Taggart 2010; Hayes et al. 2016).

There are several reports of tourist activities adversely affecting green turtle behavior. Jacobson and Lopez (1994) reported that tourist activities (i.e., flashlights, flash cameras, physical blocking, touching) disturbed nesting green turtles on Costa Rican beaches, decreasing nesting success. Balazs et al. (1987) suggested that some green turtles in Hawaii shifted their feeding to evening periods in areas with high human activity during the day. In Hawaii, Meadows (2004) observed green turtles that were chased and touched by snorkelers exhibited changes in foraging activities and increased energy expenditures. Similarly, the presence of snorkel (Slater 2014; Kostas 2015) and SCUBA (Hayes et al. 2016) activity altered sea turtle behaviors when approached. Taquet et al. (2006) and Landry and Taggart (2010) cautioned against high ecotourism activities in neritic zones where sea turtles congregate. With increasing ecotourism worldwide (TIES 2006), there is a need to better understand the effects of ecotourism activities on sea turtles.

The primary goal of this study was to quantify the response of free-ranging wild immature green turtles to disturbance by snorkelers in the field using a standardized disturbance stimulus meant to mimic a tourist diving down to approach a turtle. The second aim of this study was to determine whether turtles exhibit consistent individual-level responses using their behavioral responses as a measure of boldness and by defining personality as repeatable individual differences in a single context that are consistent over time. These data may offer a measure of the sensitivity of immature green turtles to disturbance by tourists and provide the foundation for management guidelines while simultaneously providing insight into ecological processes.

Methods

Study site

We conducted the study in Tamarindo Bay (18°19'04" N 65°19'02" W), located within the Luis Peña Channel Natural Reserve on the western side of Culebra Island, Puerto Rico. Tamarindo is a shallow bay (1–10 m in depth) with expansive turtle grass (*Thalassia testudinum*) beds and is subject to high levels of ecotourism. Upward of 30 000 tourists visit the bay each year, and four tour operators offer guided kayak and snorkel tours to view green turtles as they forage (Diego Morell Parea, Culebra Adventures,

pers. comm. 2015). “High” and “low” tourist seasons are difficult to determine on Culebra Island, especially in regard to snorkel activity. While Culebra Island attracts non-Puerto Rico mainland residents during the winters, the summers attract primarily Puerto Rico mainland residents on vacation. Based on input from local snorkel guides (Diego Morell Parea, Culebra Adventures, pers. comm. 2015) it is also difficult to parse out tourist seasons because local Puerto Rico tourists independently swim with turtles but engage less with local tour operators as non-residents would.

Typically, all green turtles observed are immature (estimated straight-line carapace length ranged between 40 and 60 cm); adults are rarely reported (Carlos Diez, Department of Natural and Environmental Resources, Commonwealth of Puerto Rico, pers. comm. 2014). Collectively, tour companies guide an average of 65 kayak/snorkel clients per day (Diego Morell Parea, Culebra Adventures, pers. comm. 2015), and we observed up to 30 tourists viewing a single turtle during a snorkel tour. In addition to tour groups, tourists often snorkel independently to search for foraging green turtles. A main road leading from town easily accesses this beach and provides numerous public-parking options for high tourist days. There are no tourist accommodations at the beach, and beach access is never restricted.

Encounter and disturbance

To locate turtles, four snorkelers swam four 300 m-long transects parallel to the beach at approximately 7 m/min. Snorkelers were spaced evenly at 10, 40, 70, and 100 m from shore and snorkelers were rotated randomly throughout the study to avoid individual biases. Transects were swum twice a day between 0700–1000 and 1600–1800 h, four days a week, from 25 June 2014 to 27 July 2014. Transects were performed twice a day to investigate if disturbance responses differed across diel phases. To limit tourist encounters, which could interfere with data collection, transect times were chosen in the morning and late afternoon. Upon encountering a green turtle, the observer maintained a 7–10 m distance from the turtle to record (1) time, (2) if turtle was alone or with one or more additional turtles within a 5 m radius (Y/N), (3) type of movement (sedentary/mobile), and (4) foraging rate (number of bites min^{-1} during a 1-min observation period). All observers had undergone in-water distance estimation practices for accuracy, precision, and standardization purposes.

After the initial pre-disturbance observation, the observer applied a standardized stimulus meant to mimic a tourist diving down to approach a turtle. This disturbance involved the observer diving to the seafloor approximately 4 m from

the turtle and approaching the turtle from the right posterior. A GoPro HERO 3+ Black Edition camera (GoPro, Inc. San Mateo, CA, USA) was used to document the disturbance event and obtain an image of the right lateral facial scale pattern on the head for later individual identification (Schofield et al. 2008). Observers, without a recognition program, processed images of right lateral facial scale patterns to identify individual turtles. Turtles were monitored for 2 min or until the observer had moved with the turtle a linear distance of 50 m (visually estimated), and as the turtle moved away the observer recorded post-disturbance behaviors. We selected our disturbance behavior metrics based upon reported natural responses of sea turtles and other animals to predators and predator stimuli. Heithaus (2013) reported anti-predator behaviors by sea turtles when they encountered sharks. We are aware of no studies of flight initiation distance (FID) in sea turtles; however, Wang et al. (2010) and Bostwick et al. (2014) documented a flight response when a shark stimulus was introduced to captive-bred sea turtles. Yet, fleeing from a predator (FID) is a cost–benefit action. If an animal flees too soon, foraging and mating opportunities may be lost along with unnecessary energy expenditure. If an animal flees too late or not at all, mortality may occur (Ydenberg and Dill 1986; Lima and Dill 1990). Consequently, we chose metrics that we associated with an animal's tendency to flee from a predator. Although sea turtles are not often categorized as social animals, grouping behavior or “foraging herds” has been documented for green turtles (Bresette et al. 2010; Heithaus 2013), which may potentially reduce predation risk as reported for other taxa (Pulliam and Caraco 1984).

FID (m) in 0.5 m increments was visually estimated and recorded as the distance when the turtle began to move away from the observer's approach. An abrupt burst-response (Y/N) was noted if a turtle exhibited a sudden and severe startled response. The distance fled (m) was visually estimated as the linear distance the turtle swam away up to a maximum of 50 m. Latency to forage (s) was measured as the time between the disturbance event and when the turtle resumed foraging up to a maximum of 120 s. Flight to nearest neighbor (Y/N) was noted if the turtle ceased fleeing within a visually estimated 5 m radius of another individual or group of turtles following the disturbance. Breached the surface to breathe (Y/N) was noted if the turtle went to the surface to breathe following the disturbance.

Statistical analyses

All statistical analyses were conducted using R 3.1.3 (R Development Core Team 2015). Quantiles (0.90) and confidence intervals (0.95) were calculated for FID. The

confidence intervals were calculated using the adjusted bootstrap method ($N = 1000$) with replacement. To show how traits vary with one another and to avoid autocorrelation issues associated with modeling individual response variables alone, we performed principal component analysis. We used the *prcomp* function to reduce five behavior response variables for each individually identified turtle (FID, distance fled, latency to forage, abrupt burst response, flight to a nearest neighbor) into one principal component (PC1). Breached the surface to breathe response variable was excluded because we could not determine when a turtle had last surfaced to breathe prior to disturbance. The PC1 was based on the correlation matrix of the five disturbance responses. The p values were calculated from randomization tests, and variables with weights >0.5 were considered major contributors to explaining the overall variability in the model. The total collection of PC1 scores was repeatedly regressed to examine the linear relationships with four pre-disturbance variables, including: session (AM/PM), if the turtle was in a group prior to disturbance, movement type, and foraging rate.

Using the PC1 scores of each encounter and individual identities as the random effect, we assessed temporal stability of post-disturbance behavior tendencies of 19 identified individual turtles from 145 encounters. Due to the approximate Gaussian distribution of the PC1 scores, we fitted a linear mixed-effects model (LMM) to the distribution with individual turtle as the random effect to estimate repeatability (*rptR* package in R, Nakagawa and Schielzeth 2010). Repeatability (r) was defined by the proportion of total variation in a behavior trait within and between individuals, and calculated as ($r = \sigma_{\alpha}^2 / (\sigma_{\alpha}^2 + \sigma_{\epsilon}^2)$) where σ_{α}^2 was the between-group variance and σ_{ϵ}^2 the within-group variance (Bell et al. 2009; Nakagawa and Schielzeth 2010). If an individual's behavior is consistent across all repeated measurements, then $r = 1$. Conversely, if the behavior of an individual is random across all measurements, then $r = 0$ (Sokal and Rohlf 1981; Lessells and Boag 1987). Variance components in the LMM were estimated using restricted maximum likelihood (REML), and 95% confidence intervals and statistical significance (p values) were estimated using a parametric bootstrap method ($N = 1000$) with replacement.

PC1 scores were averaged for individual turtles and also grouped into two personality types—timid (negative mean PC1 scores) or bold (positive mean PC1 scores). To examine if timid and bold turtles exhibited similar degrees of variation, we calculated from the PC1 scores the mean standard deviation for each individual and conducted a one-way ANOVA with residuals weighted by number of encounters to compare the effect of personality type on the amount of variation in an individual turtle.

Results

Turtle encounters

We had 306 encounters with green turtles during our study, with 226 encounters occurring during morning surveys and 80 during late afternoon surveys. Prior to the disturbance, 78% of the turtle encounters were described as sedentary ($n = 306$) and 47% as group formation ($n = 306$). The mean foraging rate prior to disturbance was 25.1 bites/min (± 9.86 bites/min SD, $n = 254$). Following the disturbance, 12% of turtles responded with abrupt burst swimming ($n = 192$, representing the total number of disturbance events when this behavior was recorded), 66% of turtles breached the surface to breathe ($n = 256$), and 13% of turtles fled to the nearest neighbor post-disturbance ($n = 237$). FID averaged 1.7 m (± 1.02 m SD, $n = 192$). Turtles fled an average of 24.2 m (± 18.84 m SD, $n = 253$), while latency to forage averaged 61.9 s (± 43.74 s SD, $n = 242$). Using the FID observations ($n = 192$), we bootstrapped with replacement and estimated 1.6–1.8 m as the 95% confidence interval of the mean minimum approaching distance of the population. Ninety percent of turtles disturbed by a snorkeler initiated their flights at distances of ≤ 3 m (Fig. 1).

Individual-level behavioral response to disturbance

Using 145 turtle encounters with complete records, we were able to use video footage to identify 19 individual turtles from their unique facial scale patterns. A turtle encounter was considered a complete record when the individual turtle was identifiable (i.e., able to obtain an image of the right lateral facial scale pattern on the head) and when the observer was able to record all five disturbance response

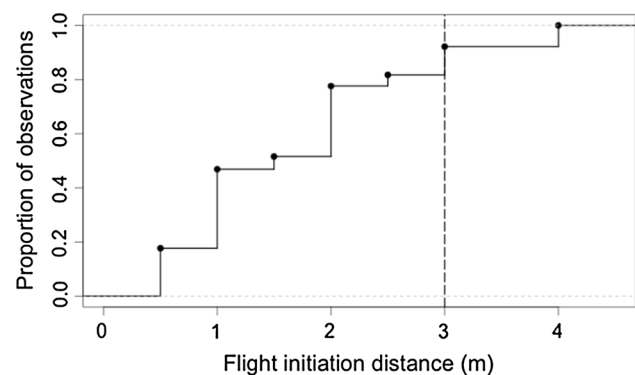


Fig. 1 Minimum green turtle flight initiation distance (FID) ($n = 192$ observations) expressed as cumulative proportion of observations, showing that 90% of flight initiations occurred at ≤ 3 m

variables (FID, distance fled, latency to forage, abrupt burst response, and flight to nearest neighbor) during the encounter. Encounters of individual turtles ranged from 3 to 14 encounters per turtle ($\bar{X} = 7.6, \pm 2.93$ SD). The principal component analysis reduced the five disturbance response variables into one significant component and explained 41.4% of the variance ($p = 0.00$). Structure correlations were all positively correlated and were highest for distance fled (factor loading = 0.86) and latency to forage (factor loading = 0.86), followed by FID (factor loading = 0.54), abrupt burst response (factor loading = 0.48), and flight to nearest neighbor (factor loading = 0.27). PC1 (Fig. 2) indicated a gradient of personality types (i.e., timid and bold) between individuals in response to disturbance. Negative PC1 scores were attributed to levels of “lower boldness” and positive PC1 scores were attributed to levels of “higher boldness”. Overall, 53% ($n = 10$) of the identified turtles were considered bold (i.e., levels of higher boldness), showing short flight initiation distance, lower frequency to exhibit an abrupt burst response, short distances fled, short latency to forage, and lower frequency to take flight to the nearest neighbor. Conversely, 47% ($n = 9$) of the identified turtles were considered timid (i.e., levels of lower boldness), showing the opposite behavior responses. There were no significant effects on PC1 scores by variables measured prior to disturbance (time of day, if the turtle was in a group, movement type, and foraging rate) (Table 1).

Repeatability measures

Using the 145 PC1 scores and individual turtle as the random effect, we calculated an overall significant repeatability value ($r = 0.132$, 95% CI 0.001–0.253, $p = 0.007$), indicating that repeatable tendencies exist at the individual

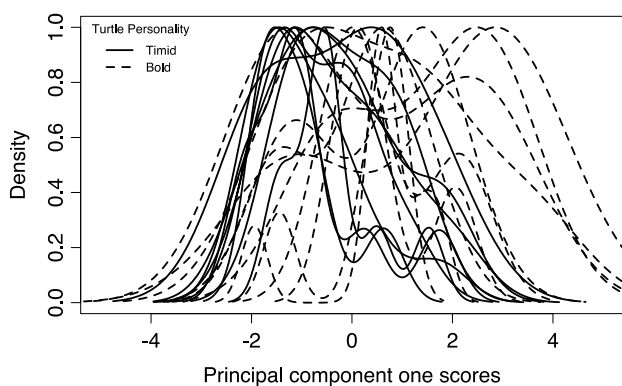


Fig. 2 Individual kernel densities (normalized) of PC1 scores of turtle disturbance responses (flight initiation distance, distance fled, latency to forage, exhibit abrupt burst response, and take flight to a nearest neighbor) of 19 turtles with timid turtles ($n = 9$) associated with negative means and bold turtles ($n = 10$) associated with positive means

level when responding to a snorkeler disturbance (Fig. 3). However, the repeatability value itself ($r = 0.132$) was low, indicating that while individuals display repeatable tendencies ($p = 0.007$), behavioral plasticity (variation) exists to some degree within individuals when responding to a snorkeler disturbance.

The two personality types, timid and bold, had a significant effect on the amount of variation in PC1 scores for an individual turtle [$F(1, 17) = 7.01, p = 0.02$]. Individual turtles that were timid had a lower mean standard deviation score ($\bar{X} = 1.14, \pm 0.19$ SD) than bold individual turtles ($\bar{X} = 1.45, \pm 0.41$ SD) (Fig. 4).

Discussion

Viable sea turtle ecotourism operations depend on the opportunity for tourists to easily observe sea turtles; however, frequent disturbance of turtles by snorkelers has the potential to shift diurnal patterns in foraging behaviors as well as habitat use (Taquet et al. 2006; Landry and Taggart 2010). Our study suggests that immature green turtles in the Luis Peña Channel Natural Reserve displayed consistent individual-level behavioral responses to tourist disturbances. Specifically, we were able to classify individual immature green turtles on a continuum from timid to bold based on their responses to snorkeler disturbance. The significant relationships between the mean standard deviation scores and behavioral type assigned to individual turtles suggest that timid turtles had more consistent disturbance responses compared to bold turtles that displayed higher variability in disturbance responses across encounters. Further, the non-significant relationships between the PC1 scores and the variables measured prior to disturbance also suggest that extrinsic factors (i.e., time of day, if the turtle was in a group, movement type, and foraging rate) had no influence on disturbance response types.

Evidence of personality in immature green turtles

Defining personality as repeatable individual differences in a single context that are consistent over time (Réale et al. 2007) and using turtles' behavioral responses to disturbance as a measure of boldness, this study was able to demonstrate that turtles exhibit consistent individual-level responses or personality. While repeatability in turtle behaviors was overall statistically significant within the context of disturbance response, the repeatability value was low which implies plasticity existed to some degree in how individual immature green turtles react to snorkelers. As Nakagawa and Schielzeth (2010) suggest, a repeatability value (r) may be low for two reasons: (1) high within-individual variation or (2) low between-individual variation. For example,

Table 1 (a) One-way analysis of variance examining the effects of session (AM/PM), if the turtle was in a group (Y/N), and movement type (sedentary/mobile) on the PC1 scores, representing turtle behavioral responses to snorkeler disturbance, and (b) linear regression of the PC1 scores with foraging rate (bites/min) as a predictor

Model	<i>df</i>	SS	MS	<i>F</i>	<i>p</i>
a					
Session (AM/PM)	1	1.05	1.051	0.506	0.478
Residuals	143	296.98	2.077		
Total	144	298.03	3.128		
Group (Y/N)	1	7.17	7.17	3.525	0.0625
Residuals	143	290.86	2.034		
Total	144	298.03			
Movement type (sed./mob.)	1	0.56	0.5564	0.267	0.606
Residuals	143	297.47	2.0802		
Total	144	298.03			
Response variable	Parameter	Estimate	SE	<i>t</i> value	<i>p</i> value
b					
PC1 scores	Intercept	0.45	0.37	1.17	0.25
	Forage rate	−0.02	0.01	−1.23	0.22

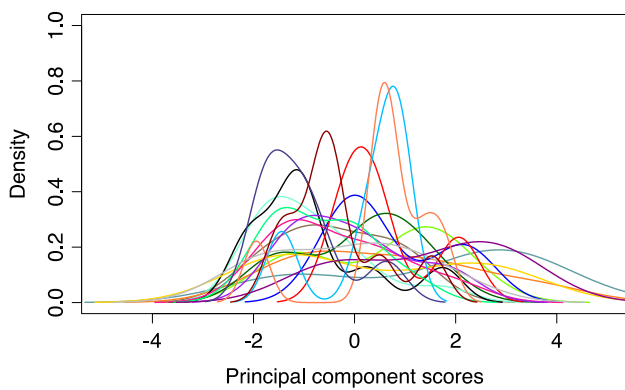


Fig. 3 Individual kernel densities (non-normalized) of PC1 scores of turtle disturbance responses (flight initiation distance, distance fled, latency to forage, exhibit abrupt burst response, and take flight to a nearest neighbor) of 19 turtles. Each kernel represents an individual turtle and the shape of kernels represents a measure of behavioral plasticity with wide, flat kernels associated with highly variable behavioral responses and narrower, peaked kernels associated with less variable responses of individual turtles to disturbance by snorkelers. Timid turtles ($n = 9$) had lower variable responses compared to bold turtles ($n = 10$)

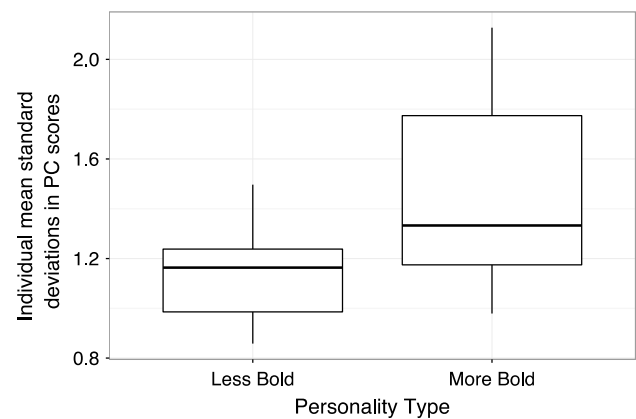


Fig. 4 Box plots of mean standard deviations of PC1 scores of disturbance responses of 19 turtles classified as timid ($n = 9$) or bold ($n = 10$), showing more consistent behavioral responses by timid turtles compared to bold turtles

between-individual differences may be low if turtles do not act drastically different from one another in general, which might be true if a spectrum or continuum of responses exists as we suggest. Deriving a low repeatability value, as this study has, is likely due to a combination of the two. In addition, since individual turtles did not always respond in the same way to disturbance, this might reflect small individual

differences in cue presentation (e.g., approach angle relative to the sun, swimming behavior of snorkeler), weather-related factors (e.g., more or less light/turbidity at the time of disturbance), or perhaps the turtles' state prior to disturbance (i.e., length of time foraging or time since last breath, level of satiation). A potential confound of this study was the inability to assess energetic states through time which could influence turtles' perceived value of resources (i.e., boldness), and a turtle's energetic state likely varies at a scale of weeks to months (Heithaus et al. 2007) which was similar to the time frame in our study.

Ecological implications

Our results suggest that individual-level behavior responses of immature green turtles may be attributed to differences in personality types. This is especially pertinent considering individual personality may drive an individual's sensitivity to non-consumptive disturbances. Ultimately, variation in the behaviors of turtles and other animals could influence both individual- and population-level processes as reported by Bejder et al. (2006) for dolphins. For example, bold turtles may adapt better over short- and long-term periods than timid turtles to non-life-threatening tourist-based disturbances. In contrast, a timid turtle might have a greater long-term energetic consequence from repeated snorkeler disturbances as a result of reduced foraging opportunities and increased stress. At the population-level, snorkeler disturbance could shift the distribution of more sensitive turtles.

Sharks, a predator of sea turtles (Heithaus et al. 2007), could also potentially influence personality-dependent selection on immature green turtles through direct predation or non-lethal effects (trait-mediated or risk effects) (Preisser et al. 2005; Heithaus et al. 2008; Creel and Christianson 2008, Creel 2011). While shark predation may target risk prone bold-individuals who exhibit reduced anti-predator behaviors (Geffroy et al. 2015), non-lethal effects motivated by shark presence may also affect turtle populations. Predator presence may require high energetic investment by turtles and missed foraging opportunities, especially for turtles in the best conditional state or with timid personalities that forego optimal but risky habitats (Werner and Peacor 2003; Preisser et al. 2005; Heithaus et al. 2007). In addition, persistent tourism disturbance may favor the selection of bold turtles, which could reduce anti-predator behaviors and increase vulnerability to predators (Geffroy et al. 2015). Over the longer term, a turtle population with a mix of bold and timid individuals may promote more resilient populations as anthropogenic and predation pressures vary over time (Schindler et al. 2010).

Conclusion

Considering that 90% of turtles in our study initiated flight response at ≤ 3 m, we recommend that snorkelers maintain >3 m distance from immature green turtles when snorkeling. However, turtles at other sites may be less habituated to snorkelers than turtles at our study site, potentially requiring greater minimum approach distances. We also concur with the turtle watching guidelines proposed by Landry and Taggart (2010) that ecotourism activities be temporally and spatially stratified to reduce the effects of snorkelers on turtles. We encourage future

studies to examine responses across seasons, which may account for any seasonal changes in turtle behavior or aggregation strategies and snorkel tourism disturbances. In addition, we were unable to account for any pre-existing conditioning some turtles may have to snorkeler disturbance in our study area. Thus, we further encourage additional research on the effects of snorkelers on green turtles across a wider diversity of sites with varying levels of snorkeler activity, including reference sites where green turtles are not affected by snorkelers. Ideally, future studies should also determine if green turtles become habituated to snorkelers and if adult green turtles react differently to snorkelers than immature green turtles. In addition, measuring repeatability across multiple contexts, not just behavioral responses to disturbance, would strengthen the claim green turtles exhibit personality and provide further insight into the relationship between tourism, turtle personality, and predatory shark interactions. We suggest co-management between local government authorities, tour operators, and other stakeholder groups in the area to develop, communicate, and implement turtle watching guidelines. Effective management plans will help to ensure that economically viable sea turtle ecotourism operations persist.

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Author contribution statement LPG and AJD conceived the study. LPG, JWB, TOG, SJC, ADMW, and AJD designed the methodology. LPG, JWB, and TOG conducted the fieldwork. LPG analyzed the data and wrote the manuscript. All authors provided editorial advice and assisted with revisions.

Compliance with ethical standards

Conflict of interest The authors declare that no conflict of interest exists. Funding source had no involvement in study design collection, and analysis and interpretation of data; in the writing of the report; and in the decision to submit the article for publication. LG was partially supported by the University of Massachusetts Intercampus Marine Science Graduate Program and the Allen Family Foundation. JB is supported by the Natural Sciences and Engineering Research Council of Canada and the Berkeley Marine Conservation Fellowship from the American Fisheries Society. TG was partially supported by the University of Massachusetts Environmental Conservation Department. AD was partially supported by UPR Sea Grant.

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