Using behavior indices and vital rates to determine the conservation impact of wildlife tourism: Guided sea turtle watch programs in Florida

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ABSTRACT

Recent rapid growth in wildlife tourism necessitates understanding its biologically-significant impacts on targeted species. To evaluate these effects, we studied how loggerhead sea turtles (*Caretta caretta*) responded to public sea turtle watch programs on a nesting beach in southeast Florida. We introduced two new measures of behavior in addition to other well-known behavior parameters, by which to measure behavioral responses of turtles during the nesting process. Five of ten behavior parameters we measured were significantly influenced by the presence of a turtle watch group. However, we found no relationship between observed changes in nesting behavior and measures of reproductive success (estimated clutch size, hatching success, and hatchling emergence success). We conclude that either the measured behavioral changes did not affect the outcome of reproduction, or their effect was undetectable. This study highlights the importance of pairing behavioral and demographic variables when evaluating the conservation impact of wildlife tourism programs. When wildlife tourism programs prioritize animal welfare and are periodically evaluated for their biological impact on target species, they are an effective tool for educating the general public and promoting conservation and environmental stewardship.

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1. Introduction

Wildlife tourism is broadly defined as the observation of, or interaction with, flora or fauna in their natural environments (Tapper, 2006). Non-consumptive wildlife tourism does not result in mortality or removal of wildlife from their native habitats (Duffus and Dearden, 1990; Newsome et al., 2012), and as such can be considered a desirable alternative to negative interactions that involve extractive use or incidental take of wildlife. Still, non-consumptive tourism can induce disturbance or behavioral changes in animals (Anderson and Keith, 1980; Christiansen et al., 2010). For non-consumptive wildlife tourism programs to be considered both successful and appropriate, they must satisfy three criteria: 1) they foster a conservation ethic; 2) animal participants are undisturbed and unharmed; and 3) human participants are highly satisfied

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with their experience. In the real world, these criteria may conflict, and a balance between them is often difficult to achieve (Reynolds and Braithwaite, 2001). Over the last few decades, non-consumptive wildlife tourism has significantly increased worldwide and has encouraged research that attempts to quantify the effects of wildlife tours on both individual animals and populations (Honey, 2008). A primary focus of resulting ecotourism research has concerned how the behavior of human participants is linked to behavioral changes in wildlife (Jordan and Burghardt, 1986; Gander and Ingold, 1997; Maréchal et al., 2011; Hayes et al., 2017).

Although animal behavior studies often reveal effects of wildlife tourism, these effects seldom equate to species or population-level impacts (Gill et al., 2001; Heithaus et al., 2008; Tablado and Jenni, 2017). Research that relies solely on behavioral factors, such as reactivity, could overlook effects not visible to human observers and exaggerate effects from more obvious behavioral responses (Caine, 1990; Lima and Dill, 1990; Gill et al., 2001; Coetzee and Chown, 2016). Establishing a direct link between a disturbance and subsequent behavior is not always possible, although a causal relationship is often assumed due to confirmation bias (Marsh and Hanlon, 2007). Even if a wildlife tourism program is associated with behavioral changes in wildlife, the disturbance may not necessarily impact demographic vital rates (Christiansen and Lusseau, 2015; Gallagher et al., 2015). Vital rates are a critical component of measuring population-level impacts of wildlife tourism because they affirm whether observed behavioral changes in response to tourism have biological significance for the species, which in turn is essential for recommendations of best practices for wildlife tourism programs (Geffroy et al., 2015).

Loggerhead sea turtles (*Caretta caretta*) migrate to nesting beaches every 2–3 years and build 3–6 nests in the sand each nesting season (Witherington and Witherington, 2015). Their arrival on their natal nesting grounds is predictable, as are the precise series of nesting behaviors they exhibit when constructing new nests (Hailman and Elowson, 1992). Because sea turtle nesting behavior is stereotypic and unlearned, changes in nesting behavior are easily attributed to specific disturbances during the nesting process, such as artificial beachfront lighting (Witherington, 1992; Silva et al., 2017), interactions with predators (Shoop et al., 1985), and direct human disturbance (Jacobson and Lopez, 1994). The opportunity to evaluate nest success post-hatching informs our understanding of the long-term effect of changes in nesting behavior on hatchling production. Sea turtles and their nesting beaches are an ideal system in which to 1) measure behavioral effects of wildlife tourism on target species; 2) measure how behavioral effects influence animals' interaction with their environment (nest making); and 3) understand tourism-related impacts to key demographic parameters (hatchling recruitment).

Florida's beaches host 90% of sea turtle nesting in the United States (Ceriani and Meylan, 2017). Our study area borders the Archie Carr National Wildlife Refuge in southeastern Florida, which annually supports an average of 11 556 + /- 1129 loggerhead sea turtle nests (Ehrhart et al., 2014). The predictable nesting of loggerhead sea turtles on southeast Florida beaches has created a unique wildlife tourism opportunity –guided public sea turtle watches. The public sea turtle watch program, regulated by the Florida Fish and Wildlife Conservation Commission (FWC) and operated by its marine turtle permit holders, was introduced in 1989. Participants hear an interpretive presentation covering sea turtle natural history, biology, threats to survival, and public actions that aid sea turtle conservation. Guides then escort participants to the beach to observe a female loggerhead sea turtle laying eggs, covering and camouflaging her nest, and returning to sea.

The only published study of a managed sea turtle watch program's effect on sea turtle nesting behavior and nest productivity, Johnson et al. (1996), concluded that the presence of watch groups altered loggerhead nesting behavior, but not hatchling production. Other studies have focused on the influence of poorly controlled tourist groups and have shown distinct effects on sea turtle nesting behaviors and the likelihood of nest-site abandonment (Jacobson and Lopez, 1994; Waayers et al., 2006). Turtle-watch program operating guidelines in many areas are now less intrusive than when the Johnson et al. (1996) study was conducted. Our study reevaluates the effects of public sea turtle watches on loggerhead nesting behavior and nest productivity 25 years following the first evaluation (Johnson et al. 1996), during which time several changes have been made to the operating guidelines for the program (Table 1). Because loggerhead sea turtles are a threatened species, it is imperative that turtle watch programs be periodically evaluated to ensure that they are not negatively impacting turtle nesting success. In this study, we document the behavioral responses and effort expenditure of nesting loggerhead sea turtles in response to being observed by public turtle watch groups, and evaluate the reproductive success of turtle nests after hatchlings emerge.

Table 1

Comparison of the Florida Department of Environmental Protection (FDEP) and the Florida Fish and Wildlife Conservation Commission (FWC) Marine Turtle Conservation Handbook guidelines for Sea Turtle Night Watch Programs.

	FDEP guidelines (1989–1999)	FWC guidelines (1999-present)
Group size	25 participants per guide. 50 total participants.	20 participants per guide. 40 total participants.
Lights	Low intensity flashlights used by guides only while leading participants to beach. One flashlight used to illuminate nest cavity.	No white light flashlights. Red low intensity flashlights with a red LED light source only. One may be used to illuminate nest cavity.
Egg removal	Single egg removed and passed around group.	No egg removal permitted.
Photography	None permitted.	Non-flash photography permitted.
Contact with nesting female	Permitted after egg deposition is complete.	No contact with nesting female permitted.

2. Methods

2.1. Study system

We studied public guided sea turtle watches conducted by Disney's Animals, Science, and Environment (ASE), an FWC marine turtle permit holder which offers the program on a 2.5 km stretch of beach in Indian River County, Florida. The study area extends 0.5 km north of Disney's Vero Beach Resort's (DVBR) northern property line, and 1 km south of the DVBR southern property line (Fig. 1). Average loggerhead nesting density for the study site is 98 crawls per kilometer per year (unpublished data, Disney) and is considered high by the FWC's Fish and Wildlife Research Institute Statewide Nesting Beach Survey (FWRI, 2018). Five additional turtles were opportunistically sampled in the Archie Carr National Wildlife Refuge (~23 km north of DVBR).

Directly behind our study area was a mix of single-family homes, condominiums, resorts, and undeveloped areas. All beach areas were public, although public access was closed at night (when nesting and turtle watches took place). A sea wall extends 0.6 km south from the northern site boundary, within the area scouted for nesting turtles. Localized beach erosion and accretion varied with storm events, tidal activity, and periodic dune nourishment projects. Recreational beach use is seasonal, with highest use in the summer, coinciding with sea turtle nesting season.

2.2. Sampling effort

We conducted our observational study of loggerhead sea turtles from 2014 to 2016, and again in 2019. Data were recorded for experimental loggerheads (turtles observed by a public sea turtle watch group) and for control loggerheads (turtles observed only by a single ASE researcher). Sampling trips were scheduled when public sea turtle watch programs were offered at DVBR, 3–4 nights per week during peak nesting in June and July. Only one turtle could be observed by a watch group on each sampling trip, per FWC guidelines. Experimental turtles were encountered between 2100 h and 0000 h, while control turtles were encountered between 2100 h and 0400 h. Experimental turtles could not be encountered after 0000 h because the public turtle watch protocol stipulates that the program concludes at this time, whether a turtle has been encountered or not. We are not aware of evidence that demonstrates changes in sea turtle nesting behavior with time of night.

2.3. Sampling experimental and control turtles

To locate turtles, researchers walked along the water's edge to avoid disturbing turtles that had already begun to construct their nests. Turtles were first observed by encountering their incoming track or by seeing them emerge from the surf. We used night vision binoculars to avoid producing artificial light, which can cause turtles to become disturbed or disoriented. For both control and experimental turtles, we did not approach until digging behaviors were observed. When approaching a turtle, we quietly ascended her incoming track and remained 1 m behind the turtle's carapace, staying out of her field of vision. Observation of eggs dropping into the egg chamber confirmed oviposition.

Experimental turtles were observed by a public sea turtle watch group from oviposition to descent (Fig. 2). Turtle watch groups averaged 22 registered participants, although additional participants (range: 9–65) were asked to join the group when encountered on the beach, as required by state guidelines (FWC, 2016). Unregistered beachgoers are encouraged to join the guided group to prevent their disturbance of other nesting turtles. Registered participants were instructed to walk in single file at the water's edge and once at the turtle, remain seated and quiet until trained guides had verified the turtle had initiated oviposition. Turtle watch groups are not permitted to view a nesting loggerhead during her ascent, her nest site preparation (body pitting), and her excavation of the egg chamber (digging), due to increased likelihood of disturbance and nest abandonment (FWC, 2016; Witherington and Witherington, 2015). During oviposition (but prior to the group's approach to the turtle), program leaders removed a small amount of sand from the nest cavity to improve visibility of the eggs dropping into it. After oviposition began, turtle watch participants were led to an area 1 m behind the nesting turtle and asked to sit down and observe her quietly. Once the turtle completed nesting and initiated her descent to the surf, staff arranged participants in a line perpendicular to the water and greater than 1 m from the turtle's likely route. Participants were directed not to enter the water or move seaward of the turtle as she returned to the water.

Minimal interaction with control turtles occurred during the nesting process. A trained ASE scout used night vision binoculars to observe control turtles from a minimum distance of 5 m and approached turtles only after the digging stage was nearly complete and oviposition had started. Unlike for experimental turtles, sand was not removed from the nest cavity. During the oviposition, covering, and camouflaging stages, staff remained a minimum of 1 m behind the turtle, completely out of sight.

A curved carapace length measurement was taken for all turtles sampled in 2015 and 2016 using a soft measuring tape. From 2014–2016, turtles were checked for passive integrative transponders (PIT tags) during oviposition by scanning all four flippers with a universal PIT tag reader for the presence of a tag. We did not apply PIT tags or flipper tags to control or experimental turtles during this study, as these activities are more intrusive and have been shown to significantly affect post-nesting behavior of loggerhead sea turtles (Broderick and Godley, 1999).
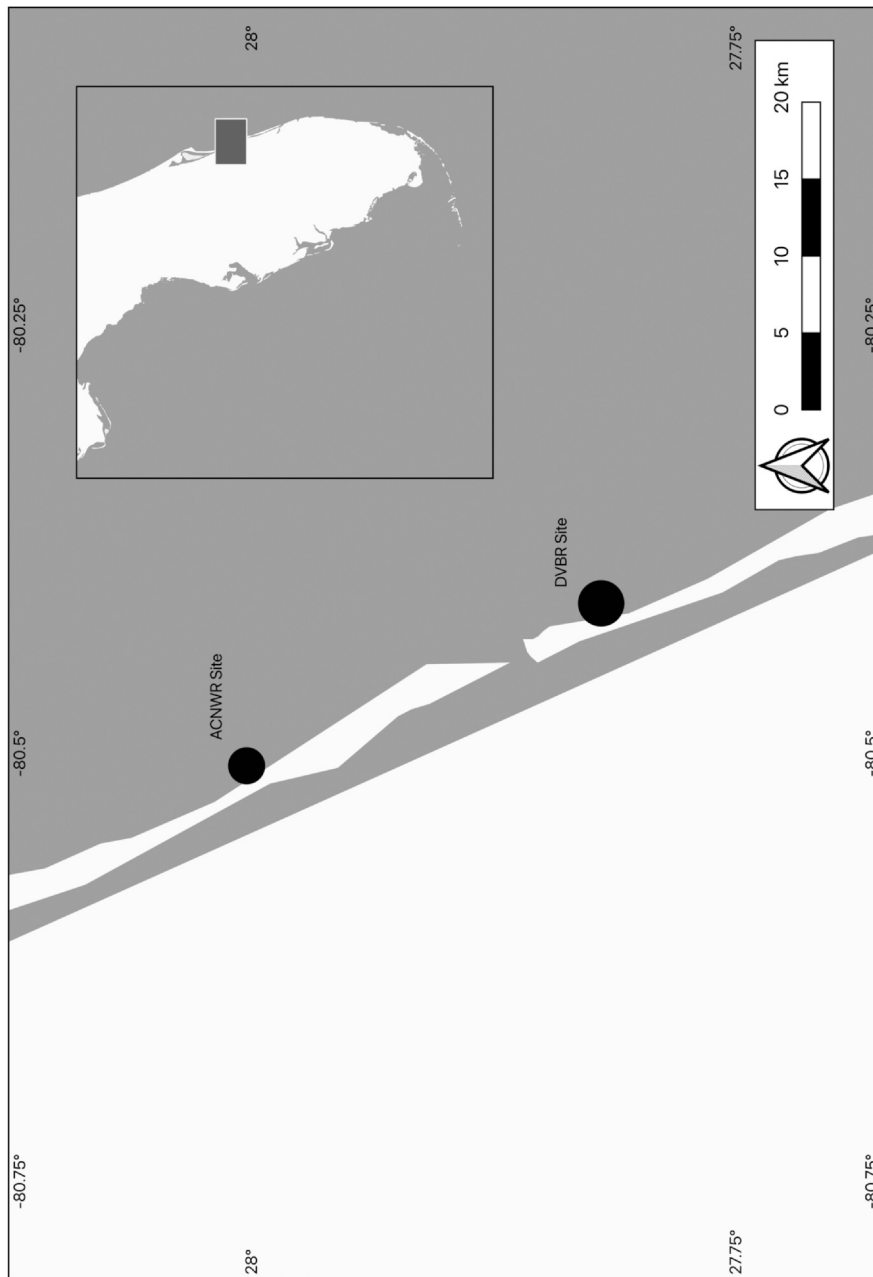
Fig. 1. The two sites where turtles were observed for this study: Disney's Vero Beach Resort (DVBR; n (control = 62, experimental = 58), and Archie Carr National Wildlife Refuge (ACNWR; n (control = 5).
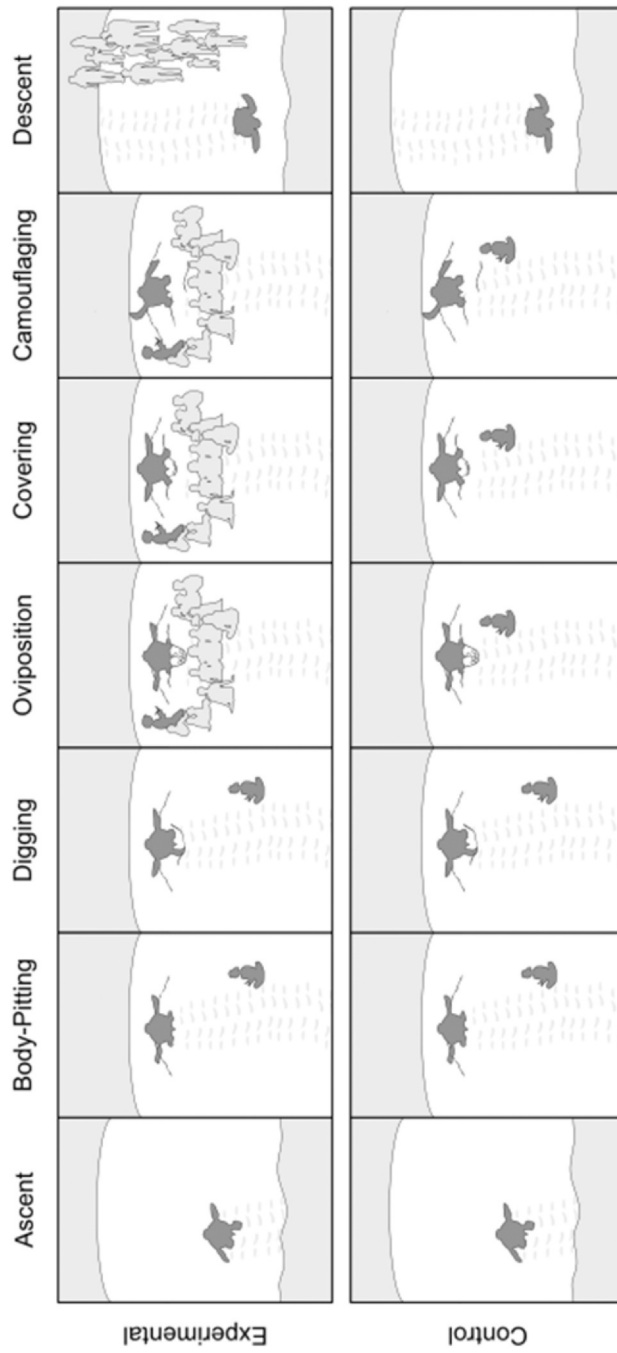
Fig. 2. Depiction of the locations of researchers (single person) and the turtle watch group in relation to the nesting turtle during the seven known nesting stages. The upper portion of each pictorial represents the toe of the primary sand dune, and the water line is below the turtle.

Table 2

The seven distinct nesting stages for loggerhead sea turtles, as described in Johnson et al. (1996).

Nesting stage	Definition
Ascent	Time elapsed between first sighting on sand at water's edge and first sand-sweeping motion of a front or rear flipper.
Body pitting	Time elapsed between first sand-sweeping motion of a flipper and the first anterior flick of a rear flipper.
Digging	Time elapsed between first anterior flick of a rear flipper and first egg dropping.
Oviposition	Time elapsed between first egg dropping and rear flipper making a sweeping movement.
Covering	Time elapsed between rear flipper making a sweeping movement and a front flipper making a sand-sweeping movement.
Camouflaging	Time elapsed between front flipper making a sand-sweeping movement and an obvious push away from nest site.
Descent	Time elapsed between first push away from nest site and crossing of reference line.

2.4. Data collection

2.4.1. Nesting stage duration

For both control and experimental turtles, durations of seven distinct nesting stages were recorded based on nesting stage definitions described in Johnson et al. (1996) (Table 2). Start and end times for each nesting stage were recorded using a handheld stopwatch (hh:mm:ss). Only nesting stage durations observed in their entirety were included in analyses.

2.4.2. Directness and stroke rate

An index of directness for the turtle's outgoing track was calculated by dividing the length of the most direct path by the length of her actual path back to the ocean. We considered the portion of the turtle's outgoing track that began at the camouflaging mound and extended just landward of the water line. While the turtle was covering her nest, a track end reference line was drawn in the sand, parallel to the water line. The intercept of the track end reference line and the turtle's outgoing track was defined as the track end point. When the turtle began her descent, we documented the time that she crossed the track end reference line. After the turtle returned to the water, we determined the length of her outgoing track by measuring the distance between the camouflaging mound and the track end point. We also measured the length of the most direct path the turtle could have taken. 1.0 on the index of directness indicates the most direct path.

To determine the turtle's gait during descent, we measured flipper stroke rate using a continuous 3 m section of the turtle's outgoing track. Using a surveyor's rope, we selected the section of the track with the most discrete flipper strokes. We inferred flipper stroke rate per meter within the 3 m section by counting the number of strokes and dividing them by three.

2.4.3. Covering and camouflaging mounds

To estimate effort during covering and camouflaging, we measured the height of displaced sand during both nesting stages. During oviposition for control and experimental turtles, an L-beam was used to aid measuring the depth of the sand (mounds) moved by the turtle during different nesting stages (Fig. 3). The L-beam was inserted into the sand just beyond the back flippers with the end of the extended arm positioned above the turtle, over the egg chamber. During camouflaging, a reference marker was placed directly underneath the extended arm of the L-beam to indicate the bottom of the camouflaging mound.

We measured height of the mound after the turtle returned to the surf. For these measurements, we pounded the L-beam into the sand until the extended arm made contact with the surface of the camouflaging mound. We dug directly below the extended arm of the metal L-beam to locate the reference marker placed at the onset of camouflaging. We then measured the depth of the camouflaging mound from the extended arm of the L-beam (the top of the camouflaging mound), to the reference marker (the top of the covering mound). Investigators reburied the clutch with the same sand immediately after depth measurements were collected. Depth of the covering mound was calculated by subtracting the depth of the camouflaging mound from the depth of the L-beam to the top of the egg chamber.

2.4.4. Nest productivity

Clutch size, hatching success, and emergence success were calculated for control and experimental nests from 2014 to 2016. We observed nests daily throughout incubation, and first and subsequent hatchling emergence events were confirmed by a depression in the sand and hatchling tracks leaving the nest site. Three days following the final emergence event (or if signs of emergence were not observed, 70 days following nest building), we performed nest excavations to inventory the number of empty eggshells (E), unhatched eggs (U), and deceased or living hatchlings (H) in the egg chamber. The nest contents allowed determination of estimated clutch size (CS; E + H), hatching success (HS; [E / CS] x 100), and emergence success (ES; [E – H] / CS x 100).

2.5. Data analysis

We used normal probability (Q-Q) plots to test the assumptions of normality (see Online Appendix A). Nesting stage durations (excluding descent), height of covering and camouflaging mounds, return stroke rate, hatching success, emergence success, and clutch size met assumptions for normality. We used a generalized linear mixed model (GLMM) to compare differences in nesting behavior and reproductive success between control and experimental turtles, combining data from all years of observation. To control for effects of inter-annual variation, the random effect of year was accounted for in the GLMM. A
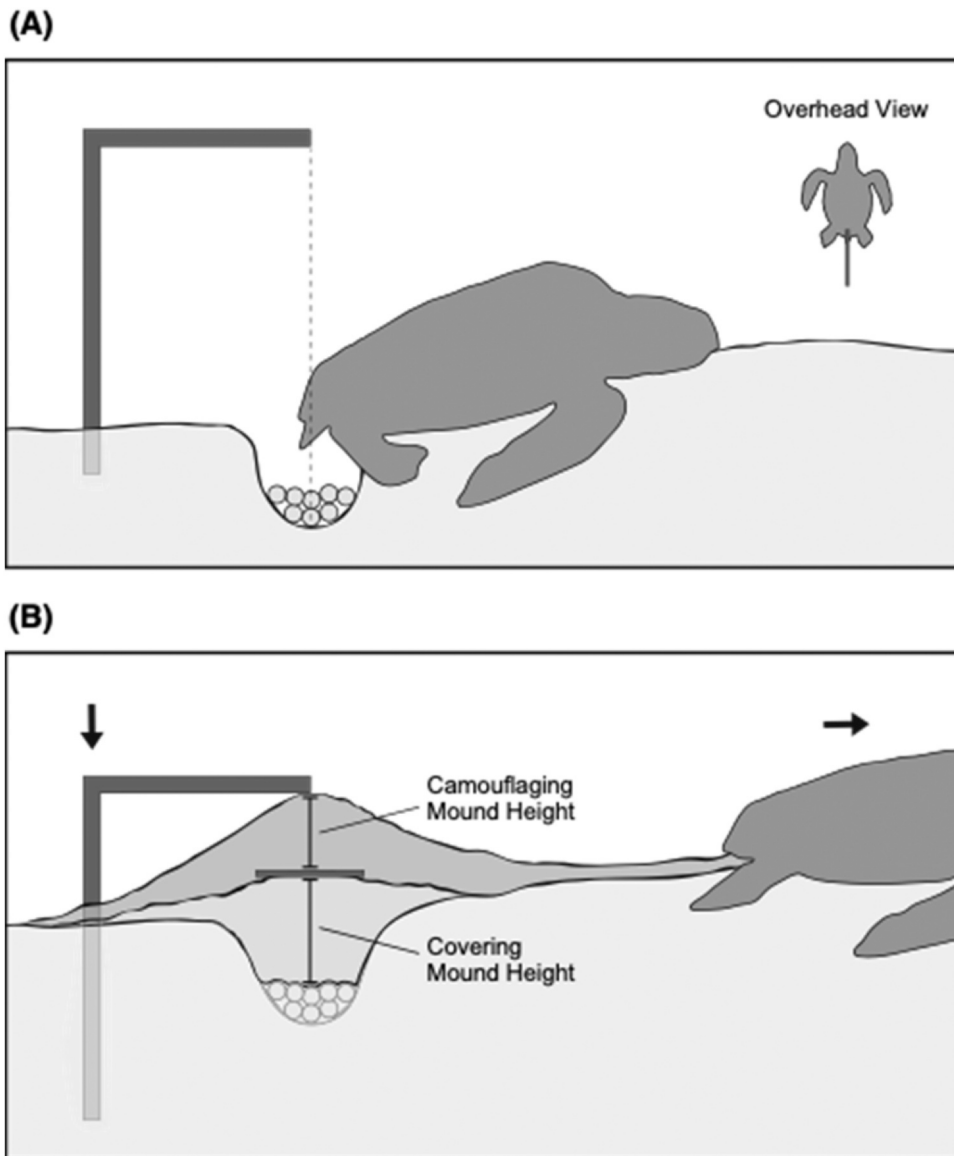
Fig. 3. Using the L-beam to measure the height of the covering and camouflaging mounds left by the nesting female loggerhead. In (A), the L-beam is placed over the center of the egg clutch during oviposition. In (B), the L-beam is lowered to calculate both mound measurements after the turtle had departed the nest site.

log +1 transformation was used on camouflaging mound height data to fit the normality assumptions of the GLMM. Descent duration and index of directness were analyzed using Mann-Whitney U non-parametric tests because the data were not normally distributed.

To test the effect of group size on nesting behavior and reproductive success of experimental turtles (all years combined), we used a parametric GLMM for data that met the normality assumption. These data included nesting stage durations (excluding descent), covering and camouflaging mound heights, return stroke rate, and clutch size. For clutch size, one data point was dropped because while the clutch size value was near the average, the high group size value of the point made it an extreme and influential outlier (see the Online Appendix B for results with the influential outlier included). Descent duration, index of directness, hatching success, and emergence success were analyzed using Spearman correlation coefficients to determine the effect of group size on the behavior and reproductive success of experimental turtles.

To test for potential inter-annual variation, we measured the effect of year on nesting behaviors (nesting stage durations, covering and camouflaging mound heights, return stroke rate, and index of directness) and reproductive success (hatching success, emergence success, and clutch size). Due to the limitation of having only four years in this study, we took a conservative

Table 3

Summary statistics for duration of six nesting stage behaviors (in minutes), four additional measures of effort, and three measures of reproductive success of control (unwatched) and experimental (watched) loggerhead sea turtles.

Parameter	Control					Experimental				
	n	Mean	SD	Min	Max	n	Mean	SD	Min	Max
Body pitting duration	17	4.031	1.764	2.220	6.800	14	5.023	3.209	0.430	13.820
Digging duration	27	16.930	4.338	6.480	28.630	30	18.190	6.477	6.300	34.330
Laying duration	40	17.090	6.469	4.130	33.080	55	16.770	5.087	8.020	31.120
Covering duration	56	13.530	4.110	5.470	25.100	62	11.354	3.870	3.720	20.420
Camouflaging duration	58	14.131	8.917	1.330	52.400	62	13.395	6.208	1.530	36.150
Descent duration	57	1.975	1.809	0.220	8.180	60	2.595	2.283	0.230	14.250
Covering mound height (cm)	58	26.530	7.213	12.250	41.500	61	22.860	6.505	6.000	34.500
Camouflaging mound height (cm)	57	11.320	7.514	0.000	39.800	61	13.310	5.763	4.750	28.000
Stroke rate of descent (m/min)	54	5.784	1.238	4.000	8.670	52	5.904	1.266	3.670	8.670
Index of directness	54	0.949	0.084	0.484	1.000	52	0.876	0.112	0.525	1.000
Hatching success (%)	26	63.160	28.367	0	97.100	40	68.530	28.892	0	97.100
Emergence success (%)	26	61.811	28.671	0	97.100	40	66.810	28.519	0	97.100
Clutch size	26	97.620	37.517	9.000	154.000	40	101.830	20.314	68.000	138.000

approach and used a non-parametric Spearman correlation to measure the effect of year on nesting behaviors and reproductive success.

All analyses were completed using R Core Team (2019) open source statistical software.

3. Results

3.1. Sampling effort

We conducted 82 sampling trips and collected behavioral data for 62 control turtles and 58 experimental turtles from 2014 to 2016 and 2019. Typically, one control turtle and one experimental turtle were sampled, with up to four turtles sampled per trip. We were unable to determine durations for all seven nesting stages each time we sampled a turtle because our first encounter with a turtle could occur during different nesting stages. We did not sample turtles that were camouflaging when we encountered them.

3.2. Nesting behavior

There were no significant differences in nesting stage duration between control (unwatched) and experimental (watched) turtles for body pitting, digging, oviposition, or camouflaging (GLMM, $p > 0.3$; Tables 3 and 4). We did not include the ascent stage because we were able to observe only three turtles complete this stage in its entirety. Watched turtles spent significantly less time covering their nests than unwatched turtles (GLMM, $t_{114.6}$ = −2.908, $p = 0.004$) and took significantly longer on the descent from their nest to the surf (Mann-Whitney U test, w = 1337.5, $p = 0.043$; Table 4). The height of the covering mound was significantly less for watched turtles (GLMM, t_{117} = −2.919, $p = 0.004$). In contrast, the camouflaging mound height was significantly higher for watched turtles than unwatched turtles (GLMM, t_{116} = 2.507, $p = 0.014$).

Watched turtles and unwatched turtles maintained a similar gait (strokes/m) during descent (GLMM, $t_{102.5}$ = 0.994, $p = 0.322$), but watched turtles took a significantly less direct path from their nest site to the sea (Mann-Whitney U test, w = 2130.5, $p < 0.001$; Table 4).

The final number of people in the turtle watch group (which varied from 9 to 65, after including unregistered beachgoers) did not significantly affect any nesting stage duration, the covering or camouflaging mound heights, return stroke rate, or index of directness in watched turtles (GLMM & Spearman rank tests, $p > 0.2$; Table 4). A yearly effect was observed on all nesting stage durations (excluding body pitting), return stroke rate, and index of directness when comparing treatment groups (Spearman correlation test, $p < 0.05$; Table 5). We did not observe a year effect on body pitting, covering or camouflaging mound heights (Spearman correlation test, $p > 0.1$).

3.3. Nest productivity

Significant differences were not observed between reproductive output (clutch size), hatching success, and hatchling emergence success in nests of control and experimental loggerhead sea turtles (GLMM, $p > 0.1$; Table 4). The number of people in the public sea turtle watch group did not affect hatching success, emergence success, or clutch size in watched turtles (GLMM & Spearman correlation tests, $p > 0.1$; Table 4). We observed a yearly effect on hatching and emergence success when comparing control and experimental groups (Spearman correlation test, $p < 0.05$) but did not observe an effect on clutch size (Spearman correlation test, $\chi^2_2 = 4.2742$, $p = 0.118$; Table 5).

Table 4

Results of Generalized Linear Mixed Models (t-values), Spearman Correlations (s-values), and Mann-Whitney U (w-values) analyses to test the effect of treatment (watched vs. unwatched turtles) and group size (for watched turtles only) on the loggerhead sea turtle nesting behaviors and reproductive success. Significant results (p < 0.05) are indicated by bold text.

Effect of Treatment						
Variable	Parameter Estimate	SE	t-value	w-value	df	p-value
Body Pitting Duration	0.993	0.985	1.007		29.000	0.322
Digging Duration	1.015	1.336	0.760		52.815	0.451
Laying Duration	0.174	1.159	0.150		92.248	0.881
Covering Duration	-2.045	0.703	-2.980		114.643	**0.004**
Camouflaging Duration	-0.712	1.372	-0.519		117.475	0.605
Descent Duration		0.189		1337.5		**0.043**
Covering Mound (cm)	-3.672	1.258	-2.919		117.000	**0.004**
Camouflaging Mound (cm)	0.243	0.097	2.507		116.000	**0.014**
Stroke Rate of Descent (m/min)	0.228	0.229	0.994		102.511	0.322
Index of Directness		0.009		2130.5		**<0.001**
Hatching Success	0.036	0.067	0.531		63.080	0.597
Emergence Success	0.032	0.067	0.479		63.067	0.634
Clutch Size	4.951	7.126	0.695		63.991	0.490
Effect of Group Size						
Variable	Parameter Estimate	SE	t-value	s-value	rho	df	p-value
Body Pitting Duration	0.070	0.144	0.484			16.000	0.635
Digging Duration	-0.033	0.169	-0.197			28.262	0.846
Laying Duration	-0.093	0.078	-1.184			50.903	0.242
Covering Duration	-0.041	0.053	-0.785			57.091	0.436
Camouflaging Duration	0.002	0.091	0.026			57.763	0.979
Descent Duration		0.180		35,537	0.072		0.586
Covering Mound (cm)	-0.087	0.097	-0.897			58.000	0.373
Camouflaging Mound (cm)	0.009	0.086	0.108			58.000	0.914
Stroke Rate of Descent (m/min)	0.015	0.020	0.744			48.279	0.461
Index of Directness		0.009		22,511	0.039		0.783
Hatching Success		0.035		7878.1	0.203		0.216
Emergence Success		0.035		7319.3	0.259		0.111
Clutch Size	-0.806	0.517	-1.561			35.786	0.127

4. Discussion

4.1. Nesting behavior

We examined six nesting stage durations and only the covering stage differed significantly between watched and unwatched turtles. These results differ from Johnson et al. (1996), who found that the camouflaging stage was the only differentiator between watched and unwatched turtles. The new behavior parameters introduced in this study (heights of covering and camouflaging mounds constructed by the nesting turtle) help to explain these differences.

Watched turtles produced a shallower covering mound than unwatched turtles, which supports our observation that they spent less time covering their nests. However, the inverse is true for camouflaging; watched turtles produced a higher camouflaging mound than unwatched turtles, despite no observed difference in the time spent camouflaging the nest. A higher

Table 5

Results of Spearman correlations to test the effect of year on nesting behaviors and reproductive success in treatment groups. Significant results (p < 0.05) are shown in bold text.

Effect of Year			
Variable	χ^2	df	p-value
Body pitting duration	0.983	3	0.805
Digging duration	17.063	3	**0.001**
Laying duration	11.552	3	**0.009**
Covering duration	14.446	3	**0.002**
Camouflaging duration	12.035	3	**0.007**
Descent duration	9.577	3	**0.023**
Covering mound (cm)	1.430	3	0.699
Camouflaging mound (cm)	6.003	3	0.111
Stroke rate of descent (m/min)	13.882	2	**0.001**
Index of directness	10.588	2	**0.005**
Hatching success	12.497	2	**0.002**
Emergence success	12.305	2	**0.002**
Clutch size	4.274	2	0.118

camouflaging mound without more time for construction suggests that watched turtles were reacting to the group's presence. This suggests that the watched turtles were camouflaging in place, rather than the stereotypic behavior of continually moving forward and throwing sand behind them across the nesting site. Though nesting turtles (if encountered after oviposition is underway or completed) may not appear to be reacting to the presence of a group of human observers, camouflaging in place is a behavioral change that suggests that turtles were reacting to the presence of such a group. This possibility warrants further study, which could be accomplished by measuring the surface area of the nest site as well as physiological responses (e.g. increase in cortisol production) during each nesting stage. As the former Florida Department of Environmental Protection (FDEP) guidelines at the time of the Johnson et al. (1996) public turtle watch study allowed participants to physically interact with the nesting turtle (e.g. physical touch) once she had concluded egg laying, these interactions could have affected both the amount of time and the manner in which the turtle camouflaged her nest.

The other notable difference in behavior between the two treatment groups was directness of the turtle's return to sea. Watched turtles meandered back to the water on a less direct path from their nest site, an observation also confirmed by Johnson et al. (1996). This is important because extended time on the beach can interfere with sea finding capabilities in nesting turtles, causing them to disorient (Witherington, 1992).

While a year effect was observed on most of the nesting behaviors recorded, there are many confounding factors with inter-annual variation that could explain this effect, such as sand nourishment projects and variations in beach characteristics (e.g., slope) resulting from storm events.

4.2. Nest productivity

Recruitment, as measured by three parameters of reproductive success, did not differ between watched and unwatched turtles. We conclude that either the behavioral differences between the two groups did not affect eggs produced, hatching rate, or hatchlings emerged from the nest, or these effects were so small as to be undetectable given the power of our tests. This finding reinforces the care that must be taken when interpreting the results of behavior studies that aim to assess the impacts of wildlife tourism.

Although we did observe a yearly effect on hatching and emergence success between control and experimental groups, inter-annual seasonal variation could explain this observation. In addition to the construction of the nest by the nesting female turtle, many other factors can influence hatchling production and emergence. These include mammalian and ghost crab depredation (Brost et al., 2015), tidal overwash and storm activity (Brost et al., 2015; Lindborg et al., 2016), nest temperature (Tapilatu and Tiwari, 2007), and root invasion of eggs (Brost et al., 2015), among others. It can be challenging to interpret which factors most influence the reproductive success of a nest, and the relative importance of factors may vary spatially and temporally. Though we did not observe differences in reproductive output between control and experimental nests over the course of the study, it is important to recognize other factors influencing egg mortality and hatchling sex ratios.

4.3. Conservation impact of wildlife tourism

In addition to studies on the potentially deleterious effects of wildlife tourism on animal behavior and demography, many programs have also been evaluated for the positive conservation impact they may provide by changing attitudes, knowledge, or the intention of program participants to engage in pro-conservation behaviors (Beaumont, 2001; Zeppel and Muloin, 2008). Some programs have followed up with participants to evaluate the sustainment of these behaviors after participating in a wildlife tourism program (Hughes, 2013; Smith et al., 2019).

We recommend that wildlife tourism programs receive systematic evaluations, both in terms of human behavior change (conservation benefits) and wildlife impact (conservation costs). Management and operation of wildlife tourism programs is fluid; guidelines may change, personnel may change, and political or economic pressures may influence how programs are conducted. In our study of the public turtle watch program in Florida, we found different results (at least, behaviorally) from what Johnson et al. (1996) originally found. We might also expect our results to be different from any program conducted under different regulations to moderate the behavior of watch participants and their number near the nesting turtle. We can easily imagine higher numbers of participants and increased interaction with a turtle that produce important negative effects. Program-specific monitoring of impacts from wildlife programs on target species will allow tour operators to adaptively manage their programs in informed ways.

The wildlife tourism industry also provides measurable economic benefits to local communities which often facilitates species conservation efforts (Wilson and Tisdell, 2003). But such conservation benefits are successful only when tourism activities do not significantly affect target species. We have demonstrated that, apart from biologically non-significant behavioral changes, the public sea turtle watch program in Florida does not appear to influence the reproductive success of nesting loggerhead sea turtles. This is a critical element in conducting a cost/benefit analysis for the conservation value of educational wildlife tours. To return to the three criteria for successful wildlife tourism that we introduced earlier, this program fosters a conservation ethic (Smith et al., 2019), provides a highly satisfying experience to participants, and does not harm the target species.

4.4. Study limitations

We were unable to create a scenario in which unwatched turtles were truly "unwatched," as a researcher was present to conduct the behavioral observations. The researcher remained at least 5 m away from the turtle during ascent and body pitting but approached the turtle near the end of the digging phase to confirm the start of oviposition. All researchers on our team have conducted turtle watch programs for at least two years, and every effort was made to minimize interactions as much as possible as compared to experimental turtles. Because turtles do not exhibit obvious reactivity, it is difficult to be sure that they were unaware of our presence. However, we did not find significant differences between our two treatment groups in the first stages of nesting, as we did for later stages when the turtle watch group was present for experimental turtles (Table 4). It is possible that collecting the carapace length measurement and scanning the flippers for PIT tags affected the behavioral response of both watched and unwatched turtles, but to mitigate potential effects we performed these tasks during oviposition when the turtles are the least likely to respond to external stimuli (Miller et al., 2003).

We did not track comparable sets of watched and unwatched turtles at sea following their visit to the nesting beach. We see this as an opportunity for future work, however, given the current state of telemetry-attachment methods, one could not rule out effects from these methods on observed behavior. That is, delaying each turtle's return to the sea, and stimuli associated with restraint, might easily exceed effects from turtle watch groups. Nevertheless, we consider post-nesting effects from watch groups as an important but challenging avenue of study.

Finally, we were only able to estimate final clutch size to conduct our comparisons of reproductive output. We do not know if eggs were taken from the nest (for example, from ghost crab predation) over the course of incubation. The process for counting hatched eggshells during a nest inventory produces only an approximate estimate, as many eggshells are broken into small fragments.

5. Conclusion

Wildlife tourism programs, such as public sea turtle watches, have become wildly popular in recent years. Participants in the public sea turtle watch program at DVBR were highly satisfied with their experience, and we have previously shown that participants who attend this program demonstrate lasting positive effects on their conservation-oriented attitudes and behaviors (Smith et al., 2019). In this study we demonstrate that, despite changes in loggerhead sea turtle nesting behavior associated with the presence of a group of human observers, clutch size, hatching success, and hatchling emergence success from nests were not significantly affected.

Public turtle watch programs, currently offered by 17 permitted organizations in Florida, significantly contribute to the development of a conservation ethic in the public without adversely affecting the reproductive success of nesting loggerhead sea turtles. We draw this conclusion with the assumption that groups in Florida follow the FWC guidelines governing the watch groups in our study. With rigorous and consistent evaluation of conservation benefits and impacts, well-designed wildlife tourism programs will retain their value in educating the public about wildlife conservation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01537.

References

Anderson, D.W., Keith, J.O., 1980. The human influence on seabird nesting success: conservation implications. Biol. Conserv. 18 (1), 65–80.
Beaumont, N., 2001. Ecotourism and the conservation ethic: Recruiting the uninitiated or preaching to the converted? Journal of Sustainable Tourism 9 (4), 317–341.

Broderick, A.C., Godley, B.J., 1999. Effect of tagging marine turtles on nesting behaviour and reproductive success. Anim. Behav. 58 (3), 587–591. https://doi.org/10.1006/anbe.1999.1183

Brost, B., Witherington, B., Meylan, A., Leone, E., Ehrhart, L., Bagley, D., 2015. Sea turtle hatchling production from Florida (USA) beaches, 2002-2012, with recommendations for analyzing hatching success. Endanger. Species Res. 27 (1), 53–68. https://doi.org/10.3354/esr00653

Caine, N.G., 1990. Unrecognized anti-predator behaviour can bias observational data. Anim. Behav. 39 (1), 195–197. https://doi.org/10.1016/S0003-3472(05)80741-9

Ceriani, S.A. , Meylan, A.B. , 2017. Caretta caretta (North West Atlantic subpopulation) (amended version of 2015 assessment). The IUCN Red List of Threatened Species 2017: e.T84131194A119339029. ⟨https://dx.doi.org/10.2305/IUCN.UK.2017–2.RLTS.T84131194A119339029.en⟩. (Accessed on 29 March 2020).

Christiansen, F., Lusseau, D., 2015. Linking behavior to vital rates to measure the effects of non-lethal disturbance on wildlife. Conserv. Lett. 8 (6), 424–431. https://doi.org/10.1111/conl.12166

Christiansen, F., Lusseau, D., Stensland, E., Berggren, P., 2010. Effects of tourist boats on the behaviour of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar. Endanger. Species Res. 11 (1), 91–99.

Coetzee, B.W., Chown, S.L., 2016. A meta-analysis of human disturbance impacts on Antarctic wildlife. Biol. Rev. 91 (3), 578–596.

Duffus, D.A., Dearden, P., 1990. Non-consumptive wildlife-oriented recreation: a conceptual framework. Biol. Conserv. 53 (3), 213–231. https://doi.org/10.1016/0006-3207(90)90087-6

Florida Fish and Wildlife Conservation Commission, 2016. Marine Turtle Conservation Handbook. ⟨https://myfwc.com/media/3133/fwc-mtconservationhandbook.pdf⟩. Accessed March 22, 2020.

Ehrhart, L., Redfoot, W., Bagley, D., Mansfield, K., 2014. Long-term trends in loggerhead (Caretta caretta) nesting and reproductive success at an important western Atlantic rookery. Chelonian Conservation and Biology 13 (2), 173–181.

Gallagher, A.J., Vianna, G.M., Papastamatiou, Y.P., Macdonald, C., Guttridge, T.L., Hammerschlag, N., 2015. Biological effects, conservation potential, and research priorities of shark diving tourism. Biol. Conserv. 184, 365–379. https://doi.org/10.1016/j.biocon.2015.02.007

Gander, H., Ingold, P., 1997. Reactions of male alpine chamois Rupicapra r. rupicapra to hikers, joggers and mountainbikers. Biol. Conserv. 79 (1), 107–109. https://doi.org/10.1016/S0006-3207(96)00102-4

Geffroy, B, Samia, D. S, Bessa, E, Blumstein, D. T, 2015. How nature-based tourism might increase prey vulnerability to predators. Trends in Ecology & Evolution 30 (12), 755–765.

Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biol. Conserv. 97 (2), 265–268. https://doi.org/10.1016/S0006-3207(00)00002-1

Hailman, J.P., Elowson, A.M., 1992. Ethogram of the nesting female loggerhead (Caretta caretta). Herpetologica 1–30.⟨https://www.jstor.org/stable/3892915⟩.

Hayes, C.T., Baumbach, D.S., Juma, D., Dunbar, S.G., 2017. Impacts of recreational diving on hawksbill sea turtle (Eretmochelys imbricata) behaviour in a marine protected area. J. Sustain. Tour. 25 (1), 79–95. https://doi.org/10.1080/09669582.2016.1174246

Heithaus, M.R., Wirsing, A.J., Thomson, J.A., Burkholder, D.A., 2008. A review of lethal and non-lethal effects of predators on adult marine turtles. J. Exp. Mar. Biol. Ecol. 356 (1–2), 43–51. https://doi.org/10.1016/j.jembe.2007.12.013

Honey, M., 2008. Setting standards: certification programmes for ecotourism and sustainable tourism. Ecotourism Conserv. Am. 234–261. https://doi.org/10.1079/9781845934002.0234

Hughes, K., 2013. Measuring the impact of viewing wildlife: do positive intentions equate to long-term changes in conservation behaviour? J. Sustain. Tour. 21 (1), 42–59. https://doi.org/10.1080/09669582.2012.681788

Jacobson, S.K., Lopez, A.F., 1994. Biological impacts of ecotourism: tourists and nesting turtles in Tortuguero National Park, Costa Rica. Wildl. Soc. Bull. 22 (3), 414–419.

Johnson, S.A., Bjorndal, K.A., Bolten, A.B., 1996. Effects of organized turtle watches on loggerhead (Caretta caretta) nesting behavior and hatchling production in Florida. Conserv. Biol. 10 (2), 570–577. https://doi.org/10.1046/j.1523-1739.1996.10020570.x

Jordan, R.H., Burghardt, G.M., 1986. Employing an ethogram to detect reactivity of black bears (Ursus americanus) to the presence of humans. Ethology 73 (2), 89–115. https://doi.org/10.1111/j.1439-0310.1986.tb01002.x

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68 (4), 619–640. https://doi.org/10.1139/z90-092

Lindborg, R., Neidhardt, E., Witherington, B., Smith, J.R., Savage, A., 2016. Factors influencing loggerhead (Caretta caretta) and green turtle (Chelonia mydas) reproductive success on a mixed use beach in Florida. Chelonian Conserv. Biol. 15 (2), 238–248. https://doi.org/10.2744/CCB-1206.1

Maréchal, L, Semple, S., Majolo, B., Qarro, M., Heistermann, M., MacLarnon, A., 2011. Impacts of tourism on anxiety and physiological stress levels in wild male Barbary macaques. Biol. Conserv. 144 (9), 2188–2193. https://doi.org/10.1016/j.biocon.2011.05.010

Marsh, D.M., Hanlon, T.J., 2007. Seeing what we want to see: confirmation bias in animal behavior research. Ethology 113 (11), 1089–1098. https://doi.org/10.1111/j.1439-0310.2007.01406.x

Miller, J.D., Limpus, C.J., Godfrey, M.H., 2003. Nest site selection, oviposition, eggs, development, hatching, and emergence of loggerhead turtles. Logger Sea Turt. 12.

Newsome, D., Moore, S.A., Dowling, R.K., 2012. Natural area Tourism: Ecology, Impacts and Management. Channel View Publications.

R Core Team, 2019. R. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://R-project.org/⟩.

Reynolds, P.C., Braithwaite, D., 2001. Towards a conceptual framework for wildlife tourism. Tour. Manag. 22 (1), 31–42. https://doi.org/10.1016/S0261-5177(00)00018-2

Shoop, C.R., Ruckdeschel, C.A., Thompson, N.B., 1985. Sea turtles in the southeast United States: nesting activity as derived from aerial and ground surveys, 1982. Herpetologica 252–259. ⟨https://www.jstor.org/stable/3892270⟩.

Silva, E., Marco, A., da Graça, J., Pérez, H., Abella, E., Patino-Martinez, J., Almeida, C., 2017. Light pollution affects nesting behavior of loggerhead turtles and predation risk of nests and hatchlings. J. Photochem. Photobiol. B Biol. 173, 240–249. https://doi.org/10.1016/j.jphotobiol.2017.06.006

Smith, J.R., Witherington, B., Heimlich, J.E., Lindborg, R.J., Neidhardt, E., Savage, A., 2019. Public sea turtle watches serve as effective environmental education. Environ. Educ. Res. 25 (2), 292–308. https://doi.org/10.1080/13504622.2018.1509300

Tablado, Z., Jenni, L., 2017. Determinants of uncertainty in wildlife responses to human disturbance. Biol. Rev. 92 (1), 216–233. https://doi.org/10.1111/brv.12224

Tapilatu, R.F., Tiwari, M., 2007. Leatherback turtle, dermochelys coriacea, hatching success at Jamursba-Medi and Wermon beaches in Papua, Indonesia. Chelonian Conserv. Biol. 6 (1), 154–158. https://doi.org/10.2744/1071-8443(2007)6[154:LTDCHS]2.0.CO;2

Tapper, R. , 2006. Wildlife watching and tourism. In "A study on the benefits and risks of a fast growing tourism activity and its impacts on species." United Nations Environment Program/Convention on Migratory Species Secretariat, Bonn, Germany.

Waayers, D., Newsome, D., Lee, D., 2006. Research note observations of non-compliance behaviour by tourists to a voluntary code of conduct: a pilot study of turtle tourism in the Exmouth region. West. Aust. J. Ecotourism 5 (3), 211–222.

Wilson, C., Tisdell, C., 2003. Conservation and economic benefits of wildlife-based marine tourism: Sea turtles and whales as case studies. Human Dimensions of Wildlife 8 (1), 49–58.

Witherington, B.E., 1992. Behavioral responses of nesting sea turtles to artificial lighting. Herpetologica 31–39. ⟨https://www.jstor.org/stable/3892916⟩.

Witherington, B.E., Witherington, D., 2015. Our sea turtles: a practical guide for the Atlantic and Gulf, from Canada to Mexico. Pineapple Press, Incorporated.

Zeppel, H., Muloin, S., 2008. Conservation and education benefits of interpretation on marine wildlife tours. Tourism in Marine Environments 5 (2–3), 215–227.