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Post-release changes in the fine-scale diving behavior and activity of loggerhead sea turtles (*Caretta caretta*) from the Northeastern Gulf of Mexico

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Abstract

Biologging devices have been used to provide critical insights into the ecology of many animal taxa and are particularly valuable when studying species that are difficult to observe directly, like sea turtles. However, post-release changes in movement and behavior, likely the result of capture, handling, and tag attachment, can introduce biases that need to be accounted for when analyzing the data obtained from tag deployments. Fortunately, recent advancements in biologging devices allow not only for horizontal movements to be monitored at high resolution, but vertical movements as well, often in concert with behavioral data collected by integrated cameras. These types of data allow for rigorous assessment of post-release effects on study subjects. Here, we investigated short-term changes in loggerhead sea turtle (*Caretta caretta*) behavior following capture and release in the Northeastern Gulf of Mexico, Florida, U.S.A, using tags equipped with high-definition cameras, pressure sensors and tri-axial accelerometers to record movement and diving behavior at sub-second resolutions. We used a generalized additive model framework to identify non-linear temporal changes in sea turtle behavior following release. Longer handling times were associated with more frequent, shorter dives and more swimming. These dive characteristics were also seen immediately following release. Dive activity (dynamic body acceleration) was nearly twofold higher immediately following release relative to when it had stabilized, suggesting greater energy expenditure. However, these behavioral effects were relatively short lived. Diving frequency and activity decreased over time as dives became longer and the probability of observing individuals foraging and resting increased. However, we found that the time it took for behaviors to stabilize to what might be considered more natural varied substantially depending on the behavior considered. As such, investigators should carefully consider how behaviors of interest change after release to avoid biases in interpretation, rather than just excluding data before a pre-defined cutoff. Our data contribute to a growing literature investigating the effects of capture and handling on post-release behavior of tagged animals across a variety of taxa and highlight the need to consider behaviors separately. This will help to limit biases when interpreting tagging data and serve to fine tune tagging methods to improve animal welfare.

Keywords Animal movement, Animal-borne video, Biologging, Capture, Dive behavior, Dynamic body acceleration, Generalized linear models, Generalized additive models, Handling, Marine turtles

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Background

Behavioral and movement observations are crucial for understanding how animals interact with their environment and can provide information about the ecological roles animals play in ecosystems. This knowledge ultimately benefits both management and conservation [1, 2]. However, obtaining information on the behavior and movement of cryptic species that spend most of their time underwater can be difficult. In such cases, biologging devices have been instrumental in providing important insights into their physiology, ecology, and movement at increasingly fine spatiotemporal resolutions [3–6]. This has allowed researchers to study animal migration [7, 8], home range movements and characteristics [9–12], socially mediated spatial interactions [13], competition [14–16], foraging behavior [17], and energetics [18]. The insights gained from these studies have improved our understanding of key ecological patterns and processes, and provided invaluable information for the management and conservation of threatened species [19–21].

While tags have provided substantial insights into the behavior and ecology of animals, they also have the capacity to affect behavior, particularly when individuals must be captured and handled for tag deployment [22–25]. Handling effects can introduce biases in subject behavior that need to be considered when analyzing and interpreting data, highlighting the need to quantify post-release changes in behavior, possibly caused by capture, handling, and tag deployment on study subjects [22]. Further, such studies can inform decisions regarding best practices for minimizing those effects on the study subjects [26]. A range of effects have been observed across various taxa and include changes in movement ability, foraging ecology, activity, and social behavior [24, 27]. These effects are known to vary among taxa, emphasizing the need to consider taxa-specific effects associated with capture and release [22, 28].

Tagging, particularly satellite telemetry, has been used in sea turtle research for decades (e.g., [29]; reviewed in [30, 31]), providing insights into the large-scale migration of neonate and adult sea turtles moving between nesting and foraging areas [32–38]. At smaller spatial scales, satellite and acoustic telemetry have been used to study habitat and space use in sea turtles [39–42] while tags with pressure sensors have been used extensively to study dive behavior [43–47]. Animal-borne video cameras have been used to observe interactions associated with intra- and interspecific competition [48] and with predators [49]. Tags equipped with cameras and various sensors have also been used to infer sea turtle behavior through the application of different predictive models, where algorithms are developed to predict behaviors as observed from cameras [50, 51]. However, little effort has been devoted to determining how capture, handling, and tag deployment influence post-release behaviors in sea turtles and the time it takes for them to stabilize to what might be considered their natural levels (but see [52, 53]).

The effects of capture and handling on sea turtles have been studied in the context of fisheries bycatch (e.g., [54]). In contrast, only one study to date has rigorously investigated the effect of capture and tag deployment on sea turtle behavior. Thomson and Heithaus [52] found that the behavior of green sea turtles immediately following release (up to ~2.5 h post-release) differed markedly from behavior on the day after release, with turtles mainly being found to have higher activity budgets, more erratic dives, and less foraging activity post-release. However, because turtle behavior was not continuously monitored beyond 2.5 h after release, they were unable to determine how sea turtle behavior changed through time nor could they specify exactly when behaviors stabilized, reverting to more natural states after release. Following this study, some have adopted the procedure of discarding the first 2 h of data (e.g., [52]) to account for the effects of capture and handling on sea turtle behavior (e.g., [55]). Others have made more modest cut-offs (30 min) based on a visual return of typical behaviors (e.g., resting and foraging, [56]) obtained from animal-borne cameras. Similarly, behavioral data immediately after release has been excluded based on when specific quantifiable parameters (e.g., dive patterns) stabilize over time [57]. However, these approaches assume that specific behaviors (e.g., diving, swimming, foraging) stabilize at the same time after release, which may prove problematic. Data exclusion should be specific to the behaviors being considered by different studies, rather than a hard cut-off. As such, there is a need for a more detailed and quantifiable evaluation regarding how sea turtle dive behavior and activity change post-release. Fortunately, recent advancements in biologging devices (e.g., tri-axial accelerometers, miniaturized cameras; [58]) provide continuous, sometimes sub-second data on movement and behavior, that can provide further insights into how sea turtles might change their behavior post-release [59, 60].

We leveraged these advancements to explore changes in the dive behavior and energetics in loggerhead (*Caretta caretta*) sea turtles following capture, handling, and release. Specifically, we analyzed data collected by tri-axial accelerometers and pressure sensors to investigate changes in dive behavior, including the frequency and duration of the dives, as well as activity (dynamic body acceleration, DBA) during dives. We also extracted behavioral data from high definition (HD) video footage to investigate concurrent changes in observable behaviors (e.g., swimming, resting, and foraging). We fit a combination of generalized linear models (GLMs) and generalized additive models (GAMs) to better understand how these behaviors are affected by handling time and change following release. We then use this information to provide recommendations for the interpretation of behavioral data obtained during biologging studies.

Methods

Study site and sea turtle capture

This study was conducted in the coastal waters of the Northeastern Gulf of Mexico between Crystal Bay and Homosassa Bay (Citrus County, Florida), known to be important habitat for green turtles (*Chelonia mydas*), loggerhead turtles (*Caretta caretta*), and Kemp's ridley turtles (*Lepidochelys kempii*; [41, 61]). The study site, hereafter referred to as Crystal River, includes two management zones: the state managed St. Martins Marsh Aquatic Preserve and the federally managed Chassahowitzka National Wildlife Refuge (for map of study site, see [41]).

Surveys were conducted monthly from June to October 2023 as part of an ongoing assessment of sea turtle population structure in the Crystal River. During these surveys, *C. caretta* were opportunistically sighted and captured using the rodeo technique, consisting of pursuing healthy individuals and capturing them by hand as we jumped from our vessel (Fig. 1a, b). Active pursuit did not exceed 13 min (4.1 ± 3.9 min; Supplemental Information: Table S1) or two breaths by turtles. No more than two attempts at capture (i.e., two jumps) were made to prevent unnecessary stress to the animal. Once captured, turtles were brought onboard the vessel (Fig. 1c) to be measured with calipers and transect tape (accuracy ±0.1 cm; straight [SCL] and curved [CCL] carapace length, as measured from the anterior point at the nuchal scute to the posterior tip of the supracaudals). Mass was determined to the nearest ±0.1 kg. Turtles were tagged with two Inconel flipper tags (National Band and Tag Company, Style 681) and a passive integrated transponder (PIT tag, Biomark, GPT12; [62]). Tags (CATS, Customized Animal Tracking Solutions, QLD, Australia) were attached to 15 *C. caretta* that met the minimum standard carapace length requirements (>50 cm SCL; range = 64.0 – 94.2 cm SCL) in accordance with our permits. We tagged turtles with two different tags, a larger device (24.5 cm × 11.5 cm × 5 cm, 436.7 g) and a smaller one (22.5 cm × 7.0 cm × 3.0 cm, 332.7 g). We estimated that the large device increased drag on tagged turtles by 13.1–23.9% (89.4 and 64 cm SCL turtles, respectively), while the small tag increased drag on tagged turtles by 5.6–7.9% (82.4 and 67.7 cm SCL turtles, respectively; [63]). Handling time, including measurement and tag attachment, did not exceed 2 h (mean ± sd, 74.3 ± 12.4 min, n = 15; SI: Table S1).

CATS tags were equipped with cameras to record behavior in high-definition (1920 × 1080p), pressure sensors (30 bar, accuracy ±0.5% full scale, temperature range −20–85 °C) to investigate dive behavior, and tri-axial accelerometers (±4 *g* with integrated 16-bit ADC, sensitivity = 4800 LSB/g) to record fine-scale movement and activity. The tags were affixed to the midline of each turtle's carapace, just behind the nuchal scute, using three points of attachment (Fig. 1c, d). Galvanic timed-releases (International Fishing Devices, Jupiter, FL, USA) and zip-ties were used to attach the tags to mesh screen that was fixed to the carapace using a two-part epoxy (Kwik-Weld, J-B Weld, Marietta, GA, USA). Galvanic timed-releases (model A6) were used, and fully dissolved ~24-h after releasing the turtles back into the ocean. After the releases dissolved sufficiently, the tags detached from the carapace and floated to the surface where they were recovered by VHF radiotelemetry (Advanced Telemetry Systems, Isanti, MN, USA; transmitter—F183B, receiver R410 216–219.99 MHz bandwidth).

Our analyses focused on data from tag deployments on 10 individuals (mean ± sd, 75.9 ± 8.0 cm SCL and 83.2 ± 8.0 cm CCL) for which we had 18.9–24.6 h deployments (mean ± sd, 21.3 ± 2.1 h) and at least 6 consecutive hours of data during daylight hours (i.e., before sunset) immediately following release (SI: Table S1). We also used the data acquired from video analyses of footage collected during four other deployments (SI: Table S1) to assess inter-rater reliability as described below, though these deployments lacked the 6 consecutive hours of data collected during daylight hours immediately following release to be included in our primary analyses.

Accelerometer and pressure sensor data

All data processing, analysis, and visualization was done using R software and computing language (R v. 4.3.1 [64]). Our accelerometers were programmed to sample at 20 Hz. We performed bench calibrations of the triaxial accelerometers in our tags following the procedure in [65]. The acceleration data were corrected to conform to East-North-Up (ENU) axis conventions, and the calibration constants needed to calibrate these data were determined using the spherical function in the tagtools package (v. 0.1.0; [66]). The calibration constants identified in the bench calibrations were applied to correct the raw acceleration data from each deployment. Raw acceleration data consists of a static component due to gravity and a dynamic component (*dA*) that results from animal movement. The static component of acceleration was determined in each axis (*x*, *y*, and *z*) by computing a running mean of the calibrated acceleration data centered on

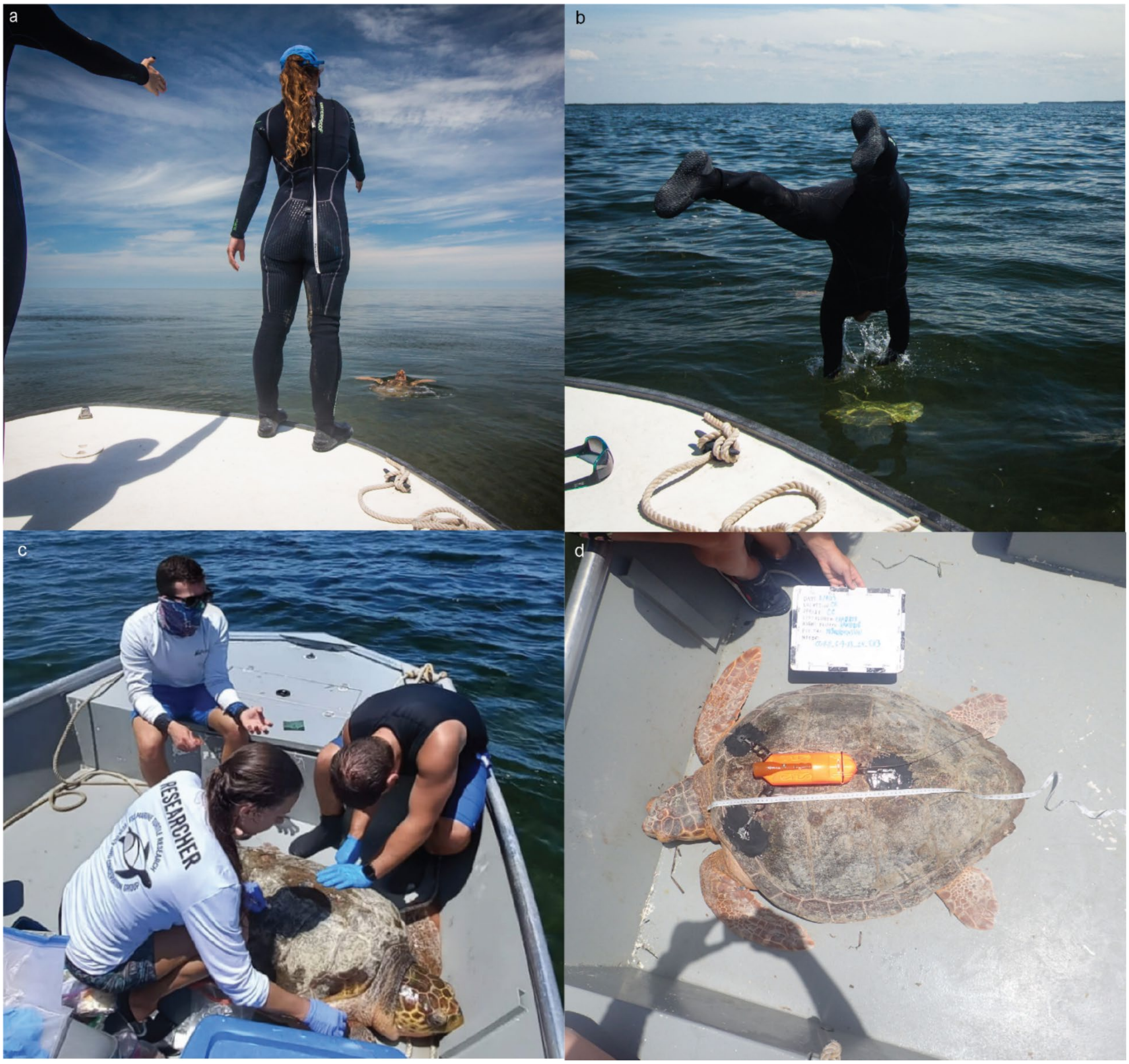

Fig. 1 Turtles were opportunistically sighted, chased (**a**), and captured using the rodeo technique (**b**). Once captured turtles were brought onboard for sampling, measurements, and tagging (**c**). CATS tags were then affixed to the carapace using epoxy and galvanic timed releases (**d**)

a 2 s window (as in [67]). Dynamic acceleration was calculated by subtracting static acceleration from raw acceleration for each axis and these values were then used to quantify dynamic body acceleration (DBA, Eq. 1; [68]). In addition to being a measure of activity level, DBA is proportional to oxygen consumption in many taxa and acts as a proxy for energetic expenditures during movement [59, 68–71]. We quantified DBA at high frequency and kept one value per 2 s.

$$DBA = \sqrt{(dA_x{}^2 + dA_y{}^2 + dA_z{}^2)} \tag{1}$$

Our pressure sensors were programmed to collect pressure (i.e., depth) data at 10 Hz. The data acquired from each tag deployment were calibrated using the diveMove package (v. 1.6.1; [72]). Specifically, zero-offset corrections of the depth data were performed by computing running quantiles (p) over different window sizes in a recursive manner (first pass: $p = 0.5$, window = 3 s; second pass: $p = 0.05$, window = 12 s) using smoothing splines [73]. Zero-offset corrections were implemented using the calibrateDepth function, which was also used to identify dives and their phases. The diveStats function was then used to compute dive statistics (e.g., dive duration) for each dive. A minimum depth of 1 m for at least 30 s was used to define dives and the diveStats output was adjusted as such. Defining dives in this way is well supported by the literature [50, 74, 75], and was necessary given the shallow nature of our study sites (1.4 ± 0.3 m depth at capture, mean ± sd for 14 turtles). Finally, we computed the mean DBA for each dive.

Our CATS tags also collected temperature data at 10 Hz. We calibrated the temperature data obtained from each tag using the sea surface temperature measured at capture with a calibrated YSI (YSI Pro Plus, Ohio, USA). We first calculated the differences between temperature obtained by the tag's onboard temperature sensor between 15 – 30 min after release and the seawater temperature recorded at capture. We disregarded the first 15 min to avoid spurious values related to exposure of the camera to the sun while the turtle was on the boat. We used the mean of these differences (pooling readings from all deployments for each camera) as an offset to correct the temperature sensor data. For the final dataset, all temperature values from release to 30 min were made to reflect the corrected temperature at 30 min.

Behavioral annotation of videos

Several HD videos (range = 6–22 videos) were obtained from each deployment (n = 15, SI: Table S1). These videos were 26.5 ± 8.4 min (mean ± sd, n = 187) in duration. Two observers used the behavior analysis software BORIS [64] to analyze videos for each of the 15 turtles, and record when the following 6 behaviors occurred in those videos: breathing, swimming, resting, foraging, species interactions, and other (see SI: Table S2 for descriptions). Each observer watched approximately half of the videos from each deployment. A randomly selected subset (n = 20) of all videos (n = 187) were watched by both observers to assess inter-rater reliability (i.e., how well the observations of different observers aligned). Intra-class correlation coefficients (ICC) were calculated to determine agreement between observers for each behavior using a two-way mixed effect model implemented with the icc function in the irr package (v. 0.84.1; [76]). Inter-observer agreement was high (mean ICC >0.8; [77]) for all behaviors except 'other' (SI: Table S3). As such, we assumed that there were no significant observer biases and we moved forward with analyses, using the data from the first observation for videos that were annotated twice. We retained annotations from videos where the midpoint of the observation interval was 6 h from release, focusing analysis on the 10 turtles that we identified as having at least 6 h of sensor data during daylight following release.

Statistical analyses

We assumed that behavior would change non-linearly after release. So, we implemented a generalized additive model (GAM) approach using the mgcv package (v. 1.8.42; [78]). We initially fit time from release and temperature as smooths in our models, setting the number of basis functions, k = 5. All smoothing factors were fit with thin plate regression splines. Turtle identification was also included as a random effect (i.e., random intercept smooth) in some models (detailed below). Handling time was included in each model as a linear predictor. After fitting our initial models, we used the gam.check function in mgcv (v. 1.8.42; [78]) and the simulateResiduals function in DHARMa (v. 0.4.6; [79]) to visually assess whether residuals met model assumptions, to check that k was appropriately specified for each smooth, and to determine whether smooths were necessary for our predictors (i.e., edf >1). All models were fit using restricted maximum likelihood (REML) estimation. For our final GAM models, we analyzed the first derivative of significant smooth terms to identify periods of significant increase or decrease in our response variables using the derivatives function in the gratia package (v. 0.8.1; [80]). When none of our predictors were non-linear (i.e., edf = 1), we instead fit generalized linear models (GLM) using the glmmTMB package (v. 1.1.7; [81]) and their assumptions were visually checked using the DHARMa package (v. 0.4.6; [79]). We estimated marginal effects for variables of interest while holding all other variables as constants at their means using the predict function in the stats package (v. 4.3.1; [64]). Results were visualized using the ggplot package (v. 3.4.3; [82]).

The number of dives 30-min^{-1} was modeled with a GLM fit to a Poisson distribution that included time from release, handling time, and temperature as fixed factors (SI: Table S4). The log of dive duration was modeled with a GAM fit to a Gaussian distribution that included time from release (based on the midpoint of each dive) as a smooth (k = 5) and turtle identification as a random effect. Temperature (at the beginning of the dive) and handling time were included as linear predictors in the model (SI: Table S5). Mean DBA dive^{-1} (hereafter, dive DBA) was modeled with a GAM fit to a scaled t-distribution for heavily tailed data that included time from release and temperature as smooths (k = 5 and k = 20, respectively). We also included dive duration as a smooth (k = 5), as dive duration has been correlated with activity in past studies [44, 60]. Turtle identification was included as a random effect (SI: Table S6).

A similar approach was implemented to assess how observed behavior changed following release, focusing on swimming, resting, and foraging. Videos were the unit of replication for these analyses. The midpoint of each video (determined by the timestamp associated with each video) was used to determine time from release. The mean temperature for the entire video period was used as a predictor in these models. We fit a GAM to a Gaussian distribution for total time (s) spent swimming during each video that included time from release as a smooth (k = 5) and turtle identification as a random effect. Temperature (mean for the video period) and handling time were fit as linear predictors, and we included log of the total observation time (s) as an offset (SI: Table S7). For resting and foraging, we fit two separate GAMs using a hurdle approach. The first GAMs fitted the probability of resting or foraging (i.e., did resting or foraging occur in the video?) to binomial distributions (SI: Table S8 and S10, respectively). The second GAMs fitted the total time spent resting and the log of total time spent foraging when they occurred (i.e., excluding videos with no occurrence) to Gaussian distributions (SI: Table S9 and S11, respectively). Both GAMs for resting and foraging included time from release (midpoint of the video) as a smooth (k = 5) and turtle identification as a random effect. The models also included temperature and handling time as linear predictors in the model, and log of observation time as an offset.

Results

The behavior of two adult female (85.9 ± 4.9 cm SCL, 92.4 ± 4.5 cm CCL; mean ± sd), one adult male (85.6 cm SCL, 93.1 cm CCL), and 7 subadult (71.6 ± 4.6 cm SCL, 79.2 ± 5.4 cm CCL; mean ± sd) loggerhead turtles were analyzed (SI: Table S1). In total, 879 dives were included in our analyses.

There was a significant effect of handling time ($\beta = 0.008$, se = 0.003; z = 2.440, $p = 0.015$) and time from release ($\beta = -0.001$, se = 0.0003; z = −3.717, $p < 0.001$) on the number of dives 30-min^{-1}. For every minute increase in handling time, the expected number of dives 30-min^{-1} increased by 0.78% (Fig. 2a). Turtles dove more frequently immediately after release and the expected number of dives 30-min^{-1} decreased by 0.13% every minute following release (Fig. 2b). Dive duration (log scale) decreased significantly as a function of handling time ($\beta = -0.018$, se = 0.006; t-value = −3.008, $p = 0.003$; Fig. 3a). Additionally, there was a significantly non-linear relationship between dive duration (log scale) and time from release (edf = 3.207, k = 5, F-ratio = 32.017, $p < 0.001$). Dives were shortest immediately following release (Estimate = 53.8 s, 95% CI = 42.0–68.9 s at 1.2 min after release) and increased until 176 min post-release (Estimate = 141.5 s, 95%

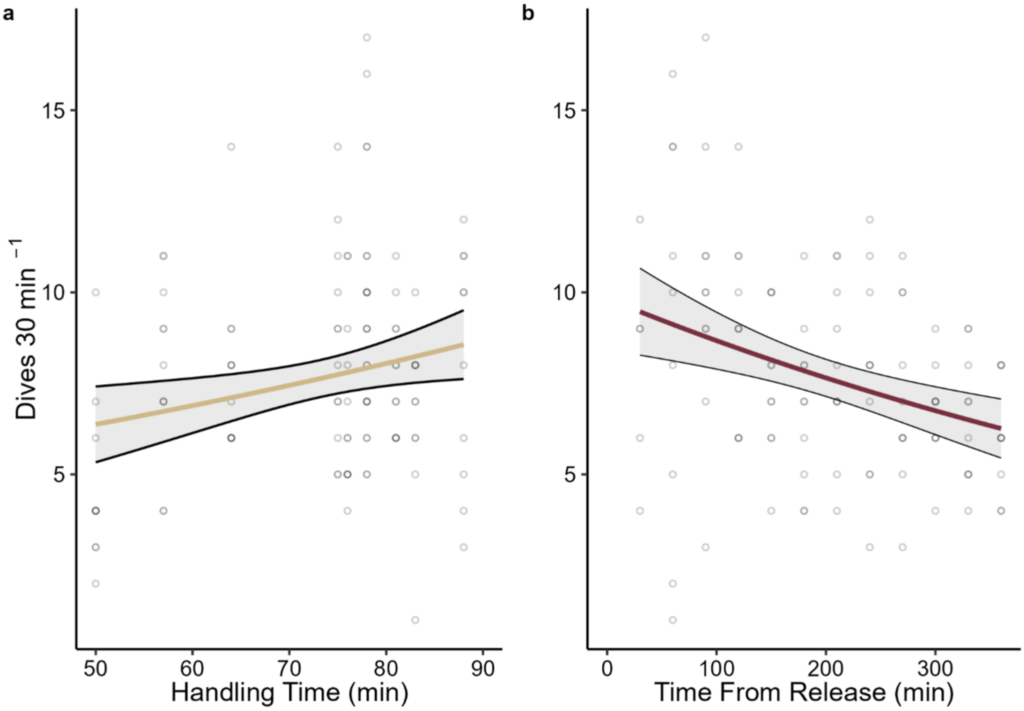

Fig. 2 a The relationship between the number of dives per 30-m bin and handling time (min). **b** The relationship between the number of dives per 30-min bin and the amount of time elapsed since release (min). For both plots, points represent raw counts per 30-min bin and the lines (with ±95% CIs) reflect the marginal effects predicted from the fitted Poisson regression model (GLM) while holding all other variables constant at their means. Garnet and gold segments denote significant decreases and increases, respectively

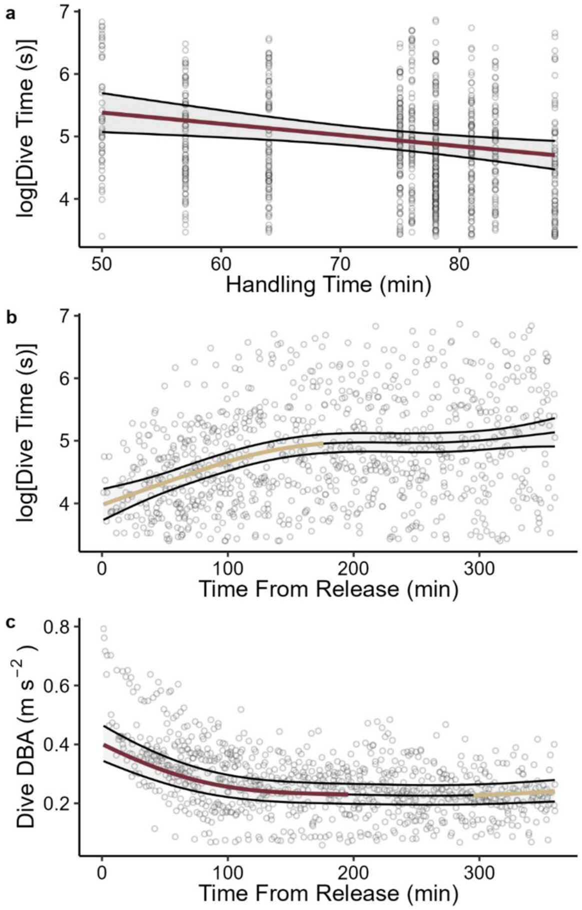

Fig. 3 **a** The relationship between the log of dive duration (s) and handling time (min). **b** The relationship between the log of dive duration (s) and the amount of time elapsed since release (min). **c** The relationship between dive DBA (m s^{-2}) and the amount of time elapsed since release (min). For all plots, points represent the raw data and the lines (±95% CIs) reflect the marginal effects predicted from the fitted GAMs while holding all other variables constant at their means. Garnet and gold segments denote significant decreases and increases, respectively

CI = 121.7–164.4 s), after which the relationship plateaued (Fig. 3b). Neither the frequency nor duration of dives were significantly affected by temperature.

Activity (dive DBA) during dives was not significantly affected by handling time, but there were significant non-linear effects of time elapsed since release ($k = 5$, $edf = 3.881$, $\chi^2 = 890.7$, $p < 0.001$) and dive duration ($k = 5$, $edf = 3.807$, $\chi^2 = 708.8$, $p < 0.001$) on dive DBA. Dive DBA was highest during dives immediately following release (Estimate = 0.399 ms^{-2}, 95% CI = 0.344–0.463 ms^{-2} at 1.2 min after release) but decreased significantly until 196 min after release (Estimate = 0.230 ms^{-2}, 95% CI = 0.199–0.266 ms^{-2}; Fig. 3c). Dive DBA was then relatively constant before significantly increasing from 295 min post-release (Estimate = 0.228 ms^{-2}, 95% CI = 0.197–0.264 ms^{-2}) until 360 min after release (Estimate = 0.240 ms^{-2}, 95% CI = 0.206–0.279 ms^{-2}; Fig. 3c). Dive DBA was highest during the shortest dives (Estimate = 0.300 ms^{-2}, 95% CI = 0.259–0.347 ms^{-2} for 30 s dives) and decreased significantly until dives reached 684 s in duration (Estimate = 0.119 ms^{-2}, 95% CI = 0.100–0.142 ms^{-2}), after which the relationship flattened out (SI: Figure S1). The relationship between dive DBA and temperature was significantly non-linear ($k = 20$, $edf = 16.776$, $\chi^2 = 151.3$, $p < 0.001$) but showed no clear pattern (SI: Figure S2).

The amount of time *C. caretta* spent swimming increased significantly as a function of handling time ($\beta = 16.332$, $se = 7.968$, t-value = 2.050, $p = 0.044$; SI: Figure S3). Conversely, the total time spent swimming decreased as a function of temperature ($\beta = -97.178$, $se = 36.513$, t-value = −2.661, $p = 0.010$; SI: Figure S4). There was a significant, non-linear effect of time elapsed since release ($k = 5$, $edf = 3.281$, F-ratio = 6.735, $p < 0.001$) on the time *C. caretta* spent swimming. The time spent swimming peaked 76 min post-release (Estimate = 1452.676 s, 95% CI = 1233.464–1671.887 s for a 1683.976 s mean observation period) and remained high for 102 min after release before declining throughout the remainder of the 6-h period, with significant declines between 102–177 min and 267–353 min (Fig. 4a).

Handling time did not have a significant effect on resting probability, but was negatively associated with the total time *C. caretta* spent resting ($\beta = -19.827$, $se = 5.432$, t-value = −3.650, $p < 0.001$; SI: Figure S5). There was also a significant, non-linear effect of time from release on resting probability ($k = 5$, $edf = 2.832$, $\chi^2 = 14.237$, $p = 0.003$), but not on the total time spent resting. The probability of resting was lowest immediately after release and increased significantly from release until 121 min post-release (Figure S6). The probability of resting was not affected by temperature, but temperature did have a significant, positive linear effect on the total time spent resting when it occurred ($\beta = 72.793$, $se = 31.022$, t-value = 2.346, $p = 0.025$; SI: Figure S7).

Handling time negatively affected the probability for foraging to occur in *C. caretta* ($\beta = -0.088$, $se = 0.032$, $z = -2.801$, $p = 0.005$; SI: Figure S8), but had no effect on the log of total time spent foraging when it occurred. We found a significant, non-linear effect of time from release on both the probability of foraging occurring ($k = 5$, $edf = 1.436$, $\chi^2 = 12.525$, $p = 0.001$) and on the log of the total time spent foraging when it occurred ($k = 5$, $edf = 2.166$, $F = 3.441$, $p = 0.031$). The foraging probability increased significantly from release to 264 min after release, after which it remained elevated (Fig. 4b). Total time spent foraging was very low immediately following

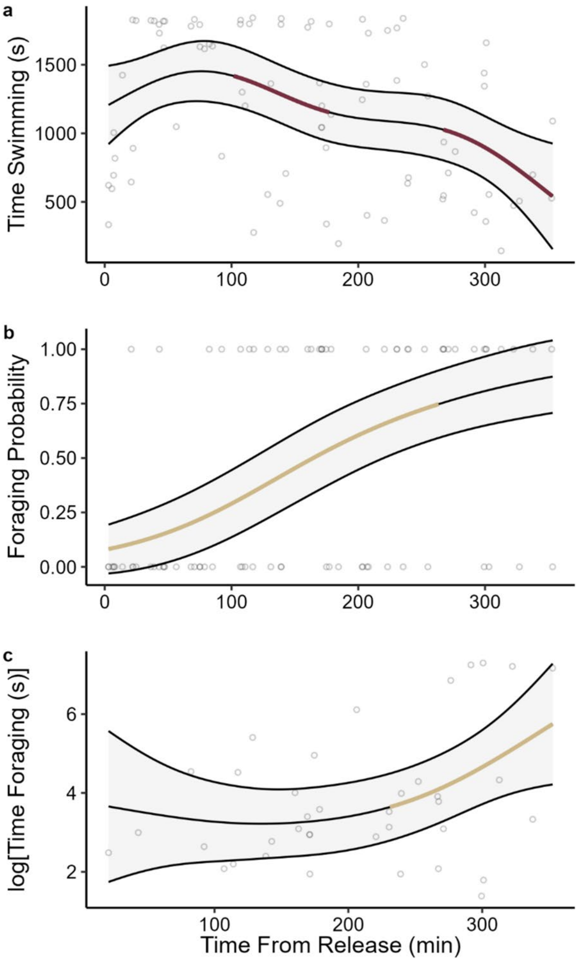

Fig. 4 **a** The relationship between the total time spent swimming (s) during an observation period (mean = 1683.976 s observation, n = 82 videos) and the amount of time elapsed since release (min). **b** The relationship between foraging probability for an observation period (mean = 1683.976 s observation, n = 82 videos) and the time elapsed since release (min). **c** The relationship between the log of total time spent foraging (s) during an observation period (mean = 1771.842 s observation, n = 38 videos) and the time elapsed since release (min). For all plots, points represent the raw data extracted from the annotated videos and the lines (±95% CIs) reflect the marginal effects predicted from the fitted GAMs while holding all other variables constant at their means. Garnet and gold segments denote significant decreases and increases, respectively

release (Estimate = 38.745 s, 95% CI = 5.720–262.434 s for a 1771.842 s mean observation period at 20.9 min after release; estimate back-transformed from the log-scale) and remained low until 231 min after release, but then significantly increased the remainder of the time (Fig. 4c). There was a significant negative effect of increasing temperature on foraging probability ($\beta = -0.306$, se = 0.135, $z = -2.274$, $p = 0.023$; SI: Figure S9), but not on the log of the total time spent foraging.

Discussion

The combination of HD video footage of sea turtle behavior and fine-scale movement and dive data acquired from triaxial accelerometers and pressure sensors allowed us to explore how loggerhead dive behavior and activity were affected by handling and how those behaviors changed after release. Longer handling times were associated with more frequent shorter dives, increased swimming activity, and decreased resting and foraging activity. Behavior immediately following release seemed to reflect these handling effects. Dives were shorter and more frequent immediately following release, corresponding with more active dives (higher dive DBA). Specifically, dives were ~2.6-fold shorter and dive DBA was ~1.7-fold higher immediately following release than after they had stabilized. These findings suggest a possible increase in energy expenditure and oxygen consumption as a result of handling and tagging [59, 68–71]. Total time spent swimming peaked at 76 min after release and remained high for 102 min, before beginning to decline. The probability of resting and foraging were low immediately following release and increased until 121 and 264 min, respectively. Sea turtle behaviors eventually stabilized after release, likely returning to more natural states. Dives became longer and energy expenditure during dives declined (lower dive DBA), while resting and foraging behaviors became more likely as time increased from turtle release. This is consistent with findings that longer dives, particularly U-shaped dives, are often associated with resting and/or foraging behavior in sea turtles [74].

Previous work by Thomson and Heithaus [52] found comparable results to ours when exploring the effects of capture of green sea turtles on post-release behavior. Specifically, they found that swimming was more prevalent at the beginning of their deployments; while foraging and resting were more common at the end of their deployments. They also suggested that it took at least 2.5 h post release for turtles to return to more stable behavior, though they did not continuously observe turtle behavior beyond 2.5 h [52]. Although our work focused on a different species, it indicates that the time it takes for behaviors to return to a more natural state may be behavior-dependent. For example, resting probabilities stabilized 121 min after release, while the foraging probabilities stabilized 264 min after release. Conversely, the total time spent foraging was still increasing at the end of the 6 h period. Energy expenditure during dives decreased by ~58% before stabilizing 196 min after release, while dive duration increased by ~38% before stabilizing 176 min after release. The expected number of dives within a 30-min period continually decreased throughout the 6-h period. Therefore, rather than discarding data before a predetermined cut-off, it may be necessary to impose behavior-specific cutoffs to avoid biases in inference when analyzing biologging data. Additionally, the difference in the time it took for loggerhead sea turtle foraging behavior to stabilize following release in our study relative to the green sea turtles in [52] suggests that that there may be species- and/or site-specific differences in post-release behavioral effects of tagging. Regardless, understanding post-release changes in behavior is crucial for making informed inferences from biologging data.

The effects of capture and handling associated with the deployment of biologging devices has been demonstrated in many taxa, including birds [83–85], mammals [25, 86, 87], and elasmobranchs [88, 89]. Consistent with our findings, some of these studies found that individuals increased their energy expenditure and locomotion after release [75, 79], whereas other taxa (e.g., terrestrial omnivores and carnivores) were initially less active and mobile, with effects lasting hours to weeks [87]. Long-term post-release effects, potentially from tag deployment, have also been observed to impact reproductive success and migration of different animals [84]. These effects can have critical implications for individual fitness and populations dynamics. Tagging in our study appeared to have relatively short-term effects on behavior, though not all behaviors (e.g., dive frequency) fully stabilized during our 6 h observation period. Capture, handling, and tagging are also known to cause physiological changes in different taxa [90–92]. In sea turtles, studies exploring the sublethal impacts of bycatch and associated capture, indicated that capture can also induce stress and metabolic responses (e.g., increase in blood cortisol, and lactate concentrations, increased lactate, respiratory acidosis; [93–95]). As such, future studies exploring the effects of handling and tag deployments on sea turtles might also consider effects on these parameters. Additionally, understanding how responses to capture, handling, and tagging vary within (life-stage and sex) and among species will allow for better interpretation of biologging data, providing a stronger basis for answering fundamental questions related to the behavior of sea turtles [22, 52]. We were limited in our ability to conduct a thorough analysis of the effects of life stage and sex on post release behavior due to the small sample size of adult sea turtles we were able to capture. However, we have included information on life stage and sex in the supplement (SI: Table S1) as a catalyst for future work.

To broaden our understanding of how different aspects of capture and handling affect individuals, studies should also collect and report information on how individuals where captured (e.g., dip net, soak net, rodeo), as this can influence the responses of captured animals [96]. Studies should also report associated chase or soak times, as well as the duration that individuals were restrained for data collection and deployment of tags (included in SI: Table S1 for this study). Tag size and attachment methods can also affect animal behavior and energetics [97]. For example, tag shape and size relative to animal body size can affect the drag experienced by the animal [63]. As such, these factors should also be considered and reported in studies deploying tags and in the analysis of the effects of tag deployment and associated effects from handling and capture [85, 98–100]. Based on the frontal areas of our tags and the sizes of tagged turtles, our tags increased drag by 5.6–23.9%, which is within an acceptable range based on previous studies and best practices for attachment procedures for sea turtle biotelemetry [63, 101]. Our larger tag was teardrop shaped, which may further reduce drag and associated energetic costs relative to square shaped tags [101]. As such, our drag estimates for this tag may have been somewhat overestimated. The effects of the tags themselves on the yearly energy budgets of our turtles were likely to be negligible due to the short duration of our study (<25 h).

A simple way to minimize the effects of tagging on post-release behavior is to deploy tags in a way that does not require capture and handling of animals. Unlike other taxa (e.g., marine mammals), sea turtles are often captured or restrained for tag deployment, which could elicit capture related stress and changes in behavior. To our knowledge, only one study to date has used a pole to deploy tags on turtles, deploying a TurtleCam system with suction cups on leatherback sea turtles from a boat [102]. Although the deployment of tags with suction cups is becoming more common on sea turtles (see [49, 103]), the majority of studies are still capturing and handling turtles, since capture also allows for a plethora of other information (e.g., on body size, body condition, health) and samples (e.g., for genetic and stable isotope analyses) to be collected. Additionally, the suction cup method only works well if suction can be maintained. This is not always possible when the carapace is fouled or uneven, as was the case with the loggerhead sea turtles captured in this study.

Other factors may impact the behavior of released animals, including whether they are held for a period of time in an acclimating environment before release (i.e., a soft release) or released immediately after being held in captivity (i.e., a hard release), as per our study. Soft releases, including in terrestrial reptiles, have been shown to improve the success of conservation translocation programs, including reducing movement away from the release site [104]. However, soft releases would be logistically challenging for sea turtles, as it would require taking them into captivity, where conditions differ to the wild and can cause other adverse effects. Environmental factors, namely temperature, may also affect animal behavior, especially of ectotherms [105]. Indeed, in our study, increased temperature resulted in reductions in swimming and foraging behavior, and increases in the time spent resting by our tagged sea turtles. However, these effects are likely the result of temperature variability across deployments (i.e., seasonal changes in temperature; range = 21.0–33.2 °C) rather than within a single deployment. Seasonally, dive duration is expected to be negatively correlated with temperature because of metabolic depression and reduced oxygen consumption at lower temperatures [106–111]. Neither dive frequency nor dive duration were significantly affected by temperature in the present study, and there was no clear effect of temperature on dive DBA. The lack of a strong relationship between temperature and dive behavior may be the result of variability driven by the relatively shallow depth range the turtles were experiencing and its effects on within dive variation in temperature.

While our study focuses on the effects of handling on sea turtles, our main findings and conclusions should be applicable across taxa. The trade-offs between the benefits of capturing animals and the associated effects of capture and handling on behavior need to be considered when planning research to ensure that sufficient data are collected to avoid biases and allow for meaningful inferences to be drawn from them. The effects of capture and handling may be behavior-specific, and the time it takes for different behaviors to stabilize following release may vary substantially. As such, considerations made when processing data from tag deployments will depend on the questions and behaviors of interest. As biologging becomes more accessible, these kinds of studies will be increasingly important. We recognize that video tags and, therefore, direct observation of behavior may not be widely available at present. However, substantial insights can be obtained from the analysis of movement data (both vertical and horizontal) obtained from inertial measurement units within tags. The data collected by accelerometers, for instance, can be used to infer behavior through changes in body orientation and motion, and allow for the estimation of energy expenditure (i.e., DBA; [112–114]). In marine animals, substantial insights can also be gained from the analysis of dive profiles [45, 109]. These data can and should be used to inform how tagging affects animals, not only to improve research outcomes but also animal welfare.

Conclusion

Our study contributes to the growing literature regarding the effects of capture, handling, and tagging on animal behavior. We found that capture and handling associated with tagging affects the post-release behavior of sea turtles. Additionally, the time it takes for sea turtle behavior to stabilize following release was highly behavior-dependent. We recommend careful consideration be given to the biases introduced by the capture and tagging, which will be partly determined by the questions and behaviors of interest. Fortunately, tags themselves offer a means of doing so in a rigorous fashion.

Abbreviations

ADC	Analog to digital converter
CATS	Customized Animal Tracking Solutions
CCL	Curved carapace length
dA	Dynamic acceleration
DBA	Dynamic body acceleration
GAM	Generalized additive model
GLM	Generalized linear model
HD	High definition
ICC	Intra-class correlation coefficients
LSB	Least significant bit
PIT	Passive integrated transponder
SCL	Straight carapace length
VHF	Very high frequency

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-025-00406-4.

Additional file 1.

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Author contributions

JCM, MMPBF, SR, and CH conceptualized the manuscript and were involved in data collection and processing. JCM performed statistical analyses and data visualization. JCM, MMPBF, SR, and CH contributed to the original draft and subsequent revisions. MMPBF secured the funding for this research.

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Availability of data and materials

The data sets generated and analyzed in this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

All research activities conducted herein were authorized by National Marine Fisheries Service Permit #19496, Florida Fish and Wildlife Conservation Commission Permit # 243 and FSU IACUC PROTO202100042.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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References

1. Santos AJB, Cullen J, Vieira DHG, Lima EHSM, Quennessen V, dos Santos EAP, et al. Decoding the internesting movements of marine turtles using a fine-scale behavioral state approach. Front Ecol Evol. 2023;11:1–19.
2. Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, et al. Ecosystem engineering in space and time. Ecol Lett. 2007;10:153–64.
3. Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, et al. Aquatic animal telemetry: a panoramic window into the underwater world. Science. 2015;348:1255642.
4. Kays R, Crofoot MC, Jetz W, Wikelski M. Terrestrial animal tracking as an eye on life and planet. Science. 2015;348:aaa2478.
5. Cagnacci F, Boitani L, Powell RA, Boyce MS. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philos Trans R Soc B Biol Sci. 2010;365:2157–62.
6. Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, et al. Biotelemetry: a mechanistic approach to ecology. Trends Ecol Evol. 2004;19:334–43.
7. Byholm P, Beal M, Isaksson N, Lötberg U, Åkesson S. Paternal transmission of migration knowledge in a long-distance bird migrant. Nat Commun. 2022;13:1–7.
8. Merkle JA, Sawyer H, Monteith KL, Dwinnell SPH, Fralick GL, Kauffman MJ. Spatial memory shapes migration and its benefits: evidence from a large herbivore. Ecol Lett. 2019;22:1797–805.
9. Davis K, Carlson PM, Lowe CG, Warner RR, Caselle JE. Parrotfish movement patterns vary with spatiotemporal scale. Mar Ecol Prog Ser. 2017;577:149–64.
10. Howard KG, Claisse JT, Clark TB, Boyle K, Parrish JD. Home range and movement patterns of the Redlip Parrotfish (*Scarus rubroviolaceus*) in Hawaii. Mar Biol. 2013;160:1583–95.
11. Relyea RA, Lawrence RK, Demarais S. Home range of desert mule deer: testing the body-size and habitat-productivity hypotheses. J Wildl Manage. 2000;64:146–53.
12. Donovan TM, Freeman M, Abouelezz H, Royar K, Howard A, Mickey R. Quantifying home range habitat requirements for bobcats (*Lynx rufus*) in Vermont, USA. Biol Conserv. 2011;144:2799–809. https://doi.org/10.1016/j.biocon.2011.06.026.
13. Benhamou S, Valeix M, Chamaillé-Jammes S, Macdonald DW, Loveridge AJ. Movement-based analysis of interactions in African lions. Anim Behav. 2014;90:171–80. https://doi.org/10.1016/j.anbehav.2014.01.030.
14. Macandza VA, Owen-Smith N, Cain JW. Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. Oikos. 2012;121:891–8.
15. Berger KM, Gese EM. Does interference competition with wolves limit the distribution and abundance of coyotes? J Anim Ecol. 2007;76:1075–85.
16. Papastamatiou YP, Bodey TW, Friedlander AM, Lowe CG, Bradley D, Weng K, et al. Spatial separation without territoriality in shark communities. Oikos. 2018;127:767–79.
17. Naito Y, Costa DP, Adachi T, Robinson PW, Fowler M, Takahashi A. Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. Funct Ecol. 2013;27:710–7.
18. Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, et al. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. J Anim Ecol. 2006;75:1081–90.
19. Fuentes MMPB, Gillis AJ, Ceriani SA, Guttridge TL, Van Zinnicq Bergmann MPM, Smukall M, et al. Informing marine protected areas in Bimini, Bahamas by considering hotspots for green turtles (*Chelonia mydas*). Biodivers Conserv. 2019;28:197–211. https://doi.org/10.1007/s10531-018-1647-2.
20. Grémillet D, Chevallier D, Guinet C. Big data approaches to the spatial ecology and conservation of marine megafauna. ICES J Mar Sci. 2022;79:975–86.
21. Kot CY, Åkesson S, Fernando D, Llanos A, Antonopoulou M, Balazs GH, et al. Network analysis of sea turtle movements and connectivity: a tool for conservation prioritization. Divers Distrib. 2022;28:810–29.
22. Gillies N, Fayet AL, Padget O, Syposz M, Wynn J, Bond S, et al. Short-term behavioural impact contrasts with long-term fitness consequences of biologging in a long-lived seabird. Sci Rep. 2020;10:1–10. https://doi.org/10.1038/s41598-020-72199-w.
23. Jepsen N, Thorstad EB, Havn T, Lucas MC. The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. Anim Biotelemetry. 2015;3.
24. Robert M, Drolet B, Savard J-PL. Effects of backpack radio-transmitters on female Barrow's Goldeneyes. Waterbirds. 2006;29:115–20.
25. van der Hoop JM, Fahlman A, Hurst T, Rocho-Levine J, Shorter KA, Petrov V, et al. Bottlenose dolphins modify behavior to reduce metabolic effect of tag attachment. J Exp Biol. 2014;217:4229–36.
26. Wilson RP, McMahon CR. Measuring devices on wild animals: what constitutes acceptable practice? Front Ecol Environ. 2006;4:147–54.
27. Puehringer-Sturmayr V, Loretto MCA, Hemetsberger J, Czerny T, Gschwandegger J, Leitsberger M, et al. Effects of bio-loggers on behaviour and corticosterone metabolites of Northern Bald Ibises (*Geronticus eremita*) in the field and in captivity. Anim Biotelemetry. 2020;8:1–13. https://doi.org/10.1186/s40317-019-0191-5.
28. Hoolihan JP, Luo J, Abascal FJ, Campana SE, De Metrio G, Dewar H, et al. Evaluating post-release behaviour modification in large pelagic fish deployed with pop-up satellite archival tags. ICES J Mar Sci. 2011;68:880–9.
29. Stoneburner DL. Satellite telemetry of loggerhead sea turtle movement on the Georgia Bight. Copeia. 1982;1982:400–8.
30. Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, et al. Satellite tracking of sea turtles: where have we been and where do we go next? Endanger Species Res. 2008;4:3–22.
31. Hays GC, Hawkes LA. Satellite tracking sea turtles: opportunities and challenges to address key questions. Front Mar Sci. 2018;5:1–12.
32. Hawkes LA, Tomás J, Revuelta O, León YM, Blumenthal JM, Broderick AC, et al. Migratory patterns in hawksbill turtles described by satellite tracking. Mar Ecol Prog Ser. 2012;461:223–32.
33. Godley BJ, Richardson S, Broderick AC, Coyne MS, Glen F, Hays GC. Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. Ecography. 2002;25:352–62.
34. Luschi P, Papi F, Liew HC, Chan EH, Bonadonna F. Long-distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study. J Comp Physiol A Sensory Neural Behav Physiol. 1996;178:447–52.
35. Evans DR, Carthy RR, Ceriani SA. Migration routes, foraging behavior, and site fidelity of loggerhead sea turtles (*Caretta caretta*) satellite tracked from a globally important rookery. Mar Biol. 2019;166:1–19. https://doi.org/10.1007/s00227-019-3583-4.
36. Benson SR, Eguchi T, Foley DG, Forney KA, Bailey H, Hitipeuw C, et al. Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. Ecosphere. 2011;2:1–27.
37. Mansfield KL, Wyneken J, Porter WP, Luo J. First satellite tracks of neonate sea turtles redefine the "lost years" oceanic niche. Proc R Soc B Biol Sci. 2014;281.
38. Okuyama J, Watabe A, Takuma S, Tanaka K, Shirai K, Murakami-Sugihara N, et al. Latitudinal cline in the foraging dichotomy of loggerhead sea turtles reveals the importance of East China Sea for priority conservation. Divers Distrib. 2022;28:1568–81.
39. Gaos AR, Lewison RR, Wallace BP, Yañez IL, Liles MJ, Baquero A, et al. Dive behaviour of adult hawksbills (*Eretmochelys imbricata*, Linnaeus 1766) in the eastern Pacific Ocean highlights shallow depth use by the species. J Exp Mar Bio Ecol. 2012;432–433:171–8. https://doi.org/10.1016/j.jembe.2012.07.006.

40. Gaos AR, Lewison RL, Yañez IL, Wallace BP, Liles MJ, Nichols WJ, et al. Shifting the life-history paradigm: discovery of novel habitat use by hawksbill turtles. Biol Lett. 2012;8:54–6.
41. Wildermann NE, Sasso CR, Stokes LW, Snodgrass D, Fuentes MMPB, Godley BJ. Habitat use and behavior of multiple species of marine turtles at a foraging area in the Northeastern Gulf of Mexico. Front Mar Sci. 2019;6:1–13.
42. Hardin EE, Fuentes MMPB. A systematic review of acoustic telemetry as a tool to gain insights into marine turtle ecology and aid their conservation. Front Mar Sci. 2021;8:1–14.
43. Matley JK, Jossart J, Johansen L, Jobsis PD. Environmental drivers of diving behavior and space-use of juvenile endangered Caribbean hawksbill sea turtles identified using acoustic telemetry. Mar Ecol Prog Ser. 2020;652:157–71. https://doi.org/10.3354/meps13466.
44. Hays GC, Hochscheid S, Broderick AC, Godley BJ, Metcalfe JD. Diving behaviour of green turtles: dive depth, dive duration and activity levels. Mar Ecol Prog Ser. 2000;208:297–8.
45. Migneault A, Bennison A, Doyle TK, James MC. High-resolution diving data collected from foraging area reveal that leatherback turtles dive faster to forage longer. Ecosphere. 2023;14:e4576.
46. Blumenthal JM, Austin TJ, Bothwell JB, Broderick AC, Ebanks-Petrie G, Olynik JR, et al. Diving behavior and movements of juvenile hawksbill turtles *Eretmochelys imbricata* on a Caribbean coral reef. Coral Reefs. 2009;28:55–65.
47. Fujita K, Nishizawa H, Okuyama J, Arita M, Takuma S, Narazaki T, et al. Polymorphic foraging tactics in a marine reptile: insight from horizontal movement and dive behavior analyses. Mar Ecol Prog Ser. 2023;707:115–29. https://doi.org/10.3354/meps14258.
48. Lamont MM, Alday J, Alday C. Interspecific interactions among three species of sea turtle using a common resting area. Ecology. 2023;104:1–5.
49. Hounslow JL, Jewell OJD, Fossette S, Whiting S, Tucker AD, Richardson A, et al. Animal-borne video from a sea turtle reveals novel anti-predator behaviors. Ecology. 2021;102:e03251.
50. Hounslow JL, Fossette S, Byrnes EE, Whiting SD, Lambourne RN, Armstrong NJ, et al. Multivariate analysis of biologging data reveals the environmental determinants of diving behaviour in a marine reptile. R Soc Open Sci. 2022;9.
51. Jeantet L, Dell'Amico F, Forin-Wiart MA, Coutant M, Bonola M, Etienne D, et al. Combined use of two supervised learning algorithms to model sea turtle behaviours from tri-axial acceleration data. J Exp Biol. 2018;221.
52. Thomson JA, Heithaus MR. Animal-borne video reveals seasonal activity patterns of green sea turtles and the importance of accounting for capture stress in short-term biologging. J Exp Mar Bio Ecol. 2014;450:15–20. https://doi.org/10.1016/j.jembe.2013.10.020.
53. Robinson NJ, Doñate-Ordóñez R, Chatzievangelou D, Brooks AML, Cuffley J, Fields CYA, Hoefer S, Pinou T, Smith A, Mills S. Short-term effects of attaching animal-borne devices on the behavior of Juvenile Green Turtles. Ecol Evol. 2024;14(12):e70707. https://doi.org/10.1002/ece3.70707
54. Snoddy JE, Landon M, Blanvillain G, Southwood A. Blood biochemistry of sea turtles captured in gillnets in the Lower Cape Fear River, North Carolina, USA. J Wildl Manage. 2009;73:1394–401.
55. Hounslow JL, Fossette S, Chong W, Bali R, Tucker AD, Whiting SD, et al. Behaviour-specific spatiotemporal patterns of habitat use by sea turtles revealed using biologging and supervised machine learning. J Appl Ecol. 2023;60:1828–40.
56. Smulders FO, O'Shea OR, Christianen MJ. Animal-borne video reveals atypical behaviour in provisioned green turtles: a global perspective of a widespread tourist activity. Glob Ecol Conserv. 2021;25:e01417. https://doi.org/10.1016/j.gecco.2020.e01417.
57. Okuyama J, Nakajima K, Noda T, Kimura S, Kamihata H, Kobayashi M, et al. Ethogram of immature green turtles: behavioral strategies for somatic growth in large marine herbivores. PLoS ONE. 2013;8:e65783.
58. Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology. 2015;96:1741–53.
59. Okuyama J, Tabata R, Nakajima K, Arai N, Kobayashi M, Kagawa S. Surfacers change their dive tactics depending on the aim of the dive: evidence from simultaneous measurements of breaths and energy expenditure. Proc R Soc B Biol Sci. 2014;281:20140040.
60. Okuyama J, Kataoka K, Kobayashi M, Abe O, Yoseda K, Arai N. The regularity of dive performance in sea turtles: a new perspective from precise activity data. Anim Behav. 2012;84:349–59. https://doi.org/10.1016/j.anbehav.2012.04.033.
61. Wildermann N, Sasso C, Gredzens C, Fuentes MMPB. Assessing the effect of recreational scallop harvest on the distribution and behaviour of foraging marine turtles. Oryx. 2020;54:307–14.
62. Balazs et al. Factors to consider in the tagging of sea turtles. Res Manag Tech Conserv Sea Turtles. 1999;101–9.
63. Jones TT, Van Houtan KS, Bostrom BL, Ostafichuk P, Mikkelsen J, Tezcan E, et al. Calculating the ecological impacts of animal-borne instruments on aquatic organisms. Methods Ecol Evol. 2013;4:1178–86.
64. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2023. https://www.r-project.org/.
65. Cade DE, Gough WT, Czapanskiy MF, Fahlbusch JA, Rapport SRK, Linsky JMJ, et al. Tools for integrating inertial sensor data with video bio-loggers, including estimation of animal orientation, motion, and position. Anim Biotelemetry. 2021;1–21. https://doi.org/10.1186/s40317-021-00256-w.
66. DeRuiter S, Johnson M, Sweeney D, McNamara-Oh YJ, Fynewever S, Tejevbo (Oghenkevwe) Racheal, et al. tagtools: Work with data from high-resolution biologging tags. 2023. https://animaltags.github.io/tagtools_r/index.html.
67. Jeantet L, Planas-Bielsa V, Benhamou S, Geiger S, Martin J, Siegwalt F, et al. Behavioural inference from signal processing using animal-borne multi-sensor loggers: a novel solution to extend the knowledge of sea turtle ecology. R Soc Open Sci. 2020;7.
68. Qasem L, Cardew A, Wilson A, Griffiths I, Halsey LG, Shepard ELC, et al. Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? PLoS One. 2012;7.
69. Gleiss AC, Wilson RP, Shepard ELC. Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. Methods Ecol Evol. 2011;2:23–33.
70. Wilson RP, Börger L, Holton MD, Scantlebury DM, Gómez-Laich A, Quintana F, et al. Estimates for energy expenditure in free-living animals using acceleration proxies: a reappraisal. J Anim Ecol. 2020;89:161–72.
71. Enstipp MR, Ballorain K, Ciccione S, Narazaki T, Sato K, Georges JY. Energy expenditure of adult green turtles (*Chelonia mydas*) at their foraging grounds and during simulated oceanic migration. Funct Ecol. 2016;30:1810–25.
72. Luque SP. Diving behaviour analysis in R. R News. 2007;7:8–14.
73. Luque SP, Fried R. Recursive filtering for zero offset correction of diving depth time series with GNU R package diveMove. PLoS ONE. 2011;6:1–9.
74. Thomson JA, Heithaus MR, Dill LM. Informing the interpretation of dive profiles using animal-borne video: a marine turtle case study. J Exp Mar Bio Ecol. 2011;410:12–20. https://doi.org/10.1016/j.jembe.2011.10.002.
75. Houghton JDR, Broderick AC, Godley BJ, Metcalfe JD, Hays GC. Diving behaviour during the internesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. Mar Ecol Prog Ser. 2002;227:63–70.
76. Gamer M, Lemon J, Fellows I, Singh P. irr: various coefficients of interrater reliability and agreement. 2019. https://cran.r-project.org/package=irr.
77. Koo TK, Li MY. A guideline of selecting and reporting intraclass correlation coefficients for reliability research. J Chiropr Med. 2016;15:155–63. https://doi.org/10.1016/j.jcm.2016.02.012.
78. Wood SN. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc Ser B Stat Methodol. 2011;73:3–36.
79. Hartig F. DHARMa: residual diagnostics for hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.3.3.0. 2020. https://CRAN.R-project.org/package=DHARMa.
80. Simpson GL. *gratia*: Graceful ggplot-Based Graphics and Other Functions for GAMs Fitted using *mgcv*. R package version 0.8.1. 2023. https://gavinsimpson.github.io/gratia/.
81. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, et al. glmmTMB balances speed and flexibility among

packages for zero-inflated generalized linear mixed modeling. R J. 2017;9:378–400. https://journal.r-project.org/archive/2017/RJ-2017-066/index.html.
82. Wickham H. ggplot2: elegant graphics for data analysis. New York: Springer-Verlag; 2016. https://ggplot2.tidyverse.org.
83. Culik BM, Bannasch R, Wilson RP. External devices on penguins: how important is shape? Mar Biol. 1994;118:353–7.
84. Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, et al. A phylogenetically controlled meta-analysis of biologging device effects on birds: deleterious effects and a call for more standardized reporting of study data. Methods Ecol Evol. 2018;9:946–55.
85. Barron DG, Brawn JD, Weatherhead PJ. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods Ecol Evol. 2010;1:180–7.
86. Irvine AB, Wells RS, Scott MD. An evaluation of techniques for tagging small odontocete cetaceans. Fish Bull. 1982;80:135–43.
87. Stiegler J, Gallagher CA, Hering R, Müller T, Tucker M, Apollonio M, et al. Mammals show faster recovery from capture and tagging in human-disturbed landscapes. Nat Commun. 2024;15:1–13. https://www.nature.com/articles/s41467-024-52381-8.
88. Hammerschlag N, Gallagher AJ, Lazarre DM. A review of shark satellite tagging studies. J Exp Mar Bio Ecol. 2011;398:1–8. https://doi.org/10.1016/j.jembe.2010.12.012.
89. Bouyoucos IA, Suski CD, Mandelman JW, Brooks EJ. Effect of weight and frontal area of external telemetry packages on the kinematics, activity levels and swimming performance of small-bodied sharks. J Fish Biol. 2017;90:2097–110.
90. Wilson SM, Raby GD, Burnett NJ, Hinch SG, Cooke SJ. Looking beyond the mortality of bycatch: sublethal effects of incidental capture on marine animals. Biol Conserv. 2014;171:61–72. https://doi.org/10.1016/j.biocon.2014.01.020.
91. Jessop TS, Hamann M. Interplay between age class, sex and stress response in green turtles (*Chelonia mydas*). Aust J Zool. 2005;53:131–6.
92. Elliott KH, McFarlane-Tranquilla L, Burke CM, Hedd A, Montevecchi WA, Anderson WG. Year-long deployments of small geolocators increase corticosterone levels in murres. Mar Ecol Prog Ser. 2012;466:1–7.
93. Jessop TS, Knapp R, Whittier JM, Limpus CJ. Dynamic endocrine responses to stress: evidence for energetic constraints and status dependence in breeding male green turtles. Gen Comp Endocrinol. 2002;126:59–67.
94. Harms CA, Mallo KM, Ross PM, Segars A. Venous blood gases and lactates of wild loggerhead sea turtles (*Caretta caretta*) following two capture techniques. J Wildl Dis. 2003;39:366–74.
95. Stabenau EK, Heming TA, Mitchell JF. Respiratory, acid-base and ionic status of kemp's ridley sea turtles (*Lepidochelys kempi*) subjected to trawling. Comp Biochem Physiol Part A Physiol. 1991;99:107–11.
96. Gregory LF, Gross TS, Bolten AB, Bjorndal KA, Guillette LJ Jr. Plasma corticosterone concentrations associated with acute captivity stress in wild loggerhead sea turtles (*Caretta caretta*). Gen Comp Endocrinol. 1996;104:312–20.
97. Piacenza J, Piacenza S, Mayoral S, Kenney A, Shields N. Design opportunities for sea turtle satellite tracking devices. Proc ASME Des Eng Tech Conf. 2018;4.
98. Watson KP, Granger RA. Hydrodynamic effect of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). J Exp Biol. 1998;201:2497–505.
99. Omeyer LCM, Fuller WJ, Godley BJ, Snape RTE, Broderick AC. The effect of biologging systems on reproduction, growth and survival of adult sea turtles. Mov Ecol. 2019;7:1–12.
100. Geen GR, Robinson RA, Baillie SR. Effects of tracking devices on individual birds—a review of the evidence. J Avian Biol. 2019;50:e01823.
101. Jones TT, Bostrom B, Carey M, Imlach B, Mikkelsen J, Ostafichuk P, et al. Determining transmitter drag and best-practice attachment procedures for sea turtle biotelemetry. NOAA Tech Memo NMFS-SWFCS-480. 2011;58. http://swfsc.noaa.gov/publications/TM/SWFSC/NOAA-TM-NMFS-SWFSC-480.pdf.
102. Dodge KL, Kukulya AL, Burke E, Baumgartner MF. TurtleCam: a "smart" autonomous underwater vehicle for investigating behaviors and habitats of sea turtles. Front Mar Sci. 2018;5:1–10.
103. Charrier I, Jeantet L, Maucourt L, Régis S, Lecerf N, Benhalilou A, et al. First evidence of underwater vocalizations in green sea turtles *Chelonia mydas*. Endanger Species Res. 2022;48:31–41. https://doi.org/10.3354/esr01185.
104. Resende PS, Viana-Junior AB, Young RJ, Azevedo CS. What is better for animal conservation translocation programmes: soft- or hard-release? A phylogenetic meta-analytical approach. J Appl Ecol. 2021;58:1122–32.
105. Abram PK, Boivin G, Moiroux J, Brodeur J. Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biol Rev. 2017;92:1859–76.
106. Lutz PL, Bergey A, Bergey M. Effects of temperature on gas exchange and acid-base balance in the sea turtle *Caretta caretta* at rest and during routine activity. J Exp Biol. 1989;144:155–69.
107. Southwood AL, Reina RD, Jones VS, Speakman JR, Jones DR. Seasonal metabolism of juvenile green turtles (*Chelonia mydas*) at Heron Island. Australia Can J Zool. 2006;84:125–35.
108. Davenport J, Ingle G, Hughes AK. Oxygen uptake and heart rate in young Green turtles (*Chelonia mydas*). J Zool. 1982;198:399–412.
109. Hochscheid S. Why we mind sea turtles' underwater business: a review on the study of diving behavior. J Exp Mar Bio Ecol. 2014;450:118–36. https://doi.org/10.1016/j.jembe.2013.10.016.
110. Hochscheid S, Bentivegna F, Hays GC. First records of dive durations for a hibernating sea turtle. Biol Lett. 2005;1:82–6.
111. Hochscheid S, Bentivegna F, Speakman JR. Long-term cold acclimation leads to high Q_{10} effects on oxygen consumption of loggerhead sea turtles *Caretta caretta*. Physiol Biochem Zool. 2004;77:209–22.
112. Shepard ELC, Wilson RP, Quintana F, Laich AG, Liebsch N, Albareda DA, et al. Identification of animal movement patterns using tri-axial accelerometry. Endanger Species Res. 2010;10:47–60.
113. Wilson RP, Shepard ELC, Liebsch N. Prying into the intimate details of animal lives: use of a daily diary on animals. Endanger Species Res. 2008;4:123–37.
114. Nathan R, Spiegel O, Fortmann-Roe S, Harel R, Wikelski M, Getz WM. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. J Exp Biol. 2012;215:986–96.

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