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# Space use and relative habitat selection for immature green turtles within a Caribbean marine protected area

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## Abstract

**Background:** A better understanding of sea turtle spatial ecology is critical for the continued conservation of imperiled sea turtles and their habitats. For resource managers to develop the most effective conservation strategies, it is especially important to examine how turtles use and select for habitats within their developmental foraging grounds. Here, we examine the space use and relative habitat selection of immature green turtles (*Chelonia mydas*) using acoustic telemetry within the marine protected area, Buck Island Reef National Monument (BIRNM), St. Croix, United States Virgin Islands.

**Results:** Space use by turtles was concentrated on the southern side of Buck Island, but also extended to the northeast and northwest areas of the island, as indicated by minimum convex polygons (MCPs) and 99%, 95%, and 50% kernel density estimations (KDEs). On average space use for all categories was  $< 3 \text{ km}^2$  with mean KDE area overlap ranging from 41.9 to 67.7%. Cumulative monthly MCPs and their proportions to full MCPs began to stabilize 3 to 6 detection months after release, respectively. Resource selection functions (RSFs) were implemented using a generalized linear mixed effects model with turtle ID as the random effect. After model selection, the accuracy of the top model was 77.3% and showed relative habitat selection values were highest at shallow depths, for areas in close proximity to seagrass, and in reef zones for both day and night, and within lagoon zones at night. The top model was also extended to predict across BIRNM at both day and night.

**Conclusion:** More traditional acoustic telemetry analyses in combination with RSFs provide novel insights into animal space use and relative resource selection. Here, we demonstrated immature green turtles within the BIRNM have small, specific home ranges and core use areas with temporally varying relative selection strengths across habitat types. We conclude the BIRNM marine protected area is providing sufficient protection for immature green turtles, however, habitat protection could be focused in both areas of high space use and in locations where high relative selection values were determined. Ultimately, the methodologies and results presented here may help to design strategies to expand habitat protection for immature green turtles across their greater distribution.

**Keywords:** Acoustic telemetry, *Chelonia mydas*, Home range, Resource selection

## Background

Marine environments are vulnerable to multiple anthropogenic threats, especially nearshore coastal habitats. In these areas, human activities are increasing and often negatively impacting the ecosystem and dependent marine animals [1], including destructive land use

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practices [2], pollution [3], overexploitation [4], damaging fishing practices [5], dredging [6], and large-scale oil spills [7]. Coastal habitats can intrinsically be more difficult to manage than terrestrial systems because both stakeholder use and oceanic processes are operating at multiple, often complex temporal and spatial scales [8, 9]. In response to the increasing pressures and associated complications for effective conservation efforts, resource managers have begun to rely heavily on spatial management techniques [10] and the establishment of marine protected areas (MPAs) [8, 11–13].

MPAs have been implemented around the world and they vary widely in purpose, size, duration, enforcement, and regulation [14, 15]. In recent years, MPA effectiveness has become questioned; many fail to meet conservation and management goals because they lack local or governmental buy-in, enforcement, or are simply too small to be ecologically effective [16–19]. In addition, spatial conservation strategies often lack the formal incorporation of animal movement data to inform the size, structure, and ultimately, the effectiveness of the MPA [20, 21]. As such, it is essential to quantify the habitat and space use of marine life to ensure management plans adequately match the spatial ecology of the species they are designed to protect. Ultimately, well-designed MPAs should incorporate animal movement data to allow for resource managers to establish and implement the most efficient, appropriate, and effective management decisions to protect resources [22–24].

Sub-tropical and tropical coastal habitats are frequently utilized by immature marine turtles as developmental feeding grounds, primarily for green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles. These turtles can remain in these neritic waters, foraging in benthic habitats (e.g., seagrass, sponges) for up to multiple decades, until reaching sexual maturity [25–27]. While conservation and management efforts, such as harvest and bycatch regulations, have led to increasing trends in sea turtle populations around the world [28, 29], evidence indicates that coastal habitats are still threatened [30]. Considering turtles use these nearshore waters for a substantial period of their juvenile life stage, MPAs could be well-suited to protect turtles from direct and indirect take, but also protect their forage and shelter habitats. However, a detailed evaluation of the distribution and use of these areas by juvenile sea turtles is critical to determine the efficacy of an MPA [31] for continued conservation of their populations and essential habitats [31, 32].

Satellite telemetry has been the most commonly used technology to examine turtle movements [33], resulting in novel findings related to their spatial ecology. For

example, Scott et al. [34] demonstrated, globally, that 35% of satellite tagged green turtles aggregated within MPAs, while Hart et al. [35] highlighted 82% of satellite tagged green turtles were within local and regional MPAs in Florida. However, while satellite telemetry is effective at examining large-scale movements, this technology generally provides coarse-scale position data, thus limiting the capacity to fully understand fine-scale habitat use for immature turtles. To gain insights into fine-scale marine life movements and space use, acoustic telemetry has become a pervasive tool [33]. While researchers must address caveats unique to acoustic telemetry [36], relative to satellite telemetry, acoustic telemetry uses less expensive transmitters (i.e., allows for higher sample sizes) and provides information at both broad and fine spatial-temporal scales that is meaningful for informing local and regional management [33, 37–39]. This technology typically involves the use of stationary hydrophone receivers that can detect hundreds of transmitters enabling researchers to answer new fine-scale ecosystem level questions by tagging multiple species [40]. Further, with the increase of transmitters and receivers deployed over the last 25 years, researchers are now able to track individuals across many hundreds of kilometers through large-scale collaborative acoustic telemetry networks [33, 39, 41]. While this technology can be utilized to examine long-distance movements, the most prevalent and useful application for marine turtles is for the study of immature turtle space use within developmental grounds at a finer resolution. While this technology has proven to be valuable when providing insights on the immature turtle home range, space use, and behaviors [31, 42–47], there is still much to gain when it comes to understanding marine turtle ecology.

Here, we quantify the space use and relative habitat selection of immature green turtles within the waters of Buck Island Reef National Monument (BIRNM), St. Croix, United States Virgin Islands (USVI) using acoustic telemetry. Relative habitat selection was examined with respect to habitat variables such as zone type (lagoon, bank/shelf, reef, other), reef type (no reef, patch reef, continuous reef), seagrass proximity, and depth. The objectives of this study were to determine immature green turtle space use and relative habitat selection to further understand their spatial ecology within the MPA. These data and analytical methods are useful for developing spatial management strategies for immature green turtles, plus our study also provides insights on the broader use of acoustic telemetry on sea turtles that typically has limited tag retention rates [48].

## Results

Each detection log was examined individually to determine if or when a given transmitter may have fallen off a tagged turtle and, thus, resulting in many false detections. After the data were filtered and potential false detections removed, we examined the detection logs of 58 immature green turtles within the BIRNM using 68 transmitters (due to retagging) deployed across 2012 ( $n=38$ ) and 2013 ( $n=30$ ) (Additional file 1: Figs. S1, S2, Table S1). Individual size of tagged turtles ranged from 33.8 to 65.5 cm (straight line carapace nuchal [SCLn];  $46.9 \pm 7.0$  cm). Full minimum convex polygon (MCP) values for detection logs ranged from 0.0 to  $4.2 \text{ km}^2$  ( $0.9 \pm 0.9 \text{ km}^2$ ). Days at liberty (i.e., tracking duration) ranged from 1 to 505 days ( $146.3 \pm 100.1$  days) and residency values (i.e., detection days/days at liberty) ranged from 0.6 to 1 ( $0.8 \pm 0.3$ ). Tracking duration was limited, with only four transmitters remaining active 10 detection months after release. This is likely an effect of transmitter retention due to tear-outs from attachment holes failing and/or tags moving towards the edge of their scutes from growth [48] (Fig. 1). Thus, limited and variable tracking durations also led to variation in individual and overall mean cumulative monthly MCP values and the proportions to their full MCPs (Fig. 1). However, cumulative monthly MCP values began to stabilize around six detection months and proportions to their full MCPs appeared to stabilize around three detection months after release.

After removing detection logs with less than 100 centers of activity (COAs) ( $n=10$ ), we used a total of 97,065 centers of activity to examine the space use of 52 immature green turtles (with 58 transmitters due to retagging) across 2012, 2013, and 2014. Constructed 99% kernel density estimates (KDEs) ranged from 1.2 to  $5.9 \text{ km}^2$  ( $2.3 \pm 0.8 \text{ km}^2$ ) with a mean overlap of 67.7% ( $\pm 19.3\%$ ), 95% KDEs range from 0.7 to  $3.7 \text{ km}^2$  ( $1.4 \pm 0.5 \text{ km}^2$ ) with a mean overlap of 64.5% ( $\pm 21.25\%$ ), and 50% KDEs ranged from 0.1 to  $0.6 \text{ km}^2$  ( $0.3 \pm 0.0 \text{ km}^2$ ) with a mean overlap of 41.9% ( $\pm 33.6\%$ ) (Fig. 2). While 95% and 50% KDEs were largely located on the southern side of Buck Island, some individual 95% KDEs extended around to the northeast and northwest areas of the island as well (Fig. 3).

### Resource selection function (RSF) model and relative selection predictions across space

Variance inflation factors revealed reef type and zone type were highly correlated and, thus, we decided to remove reef type from the model. The top RSF generalized linear mixed model (GLMM) (using a random 60% subset of the data) was the full model, as indicated via model selection (Additional file 1: Table S2). This model included diel and depth as an interaction term, diel and

distance to seagrass as an interaction term, diel and zone type as an interaction term, and individual and transmitter as the random effects. However, summary outputs for the final model indicated the random effect, year, had a variance component equal to zero, thus was removed in further analysis.

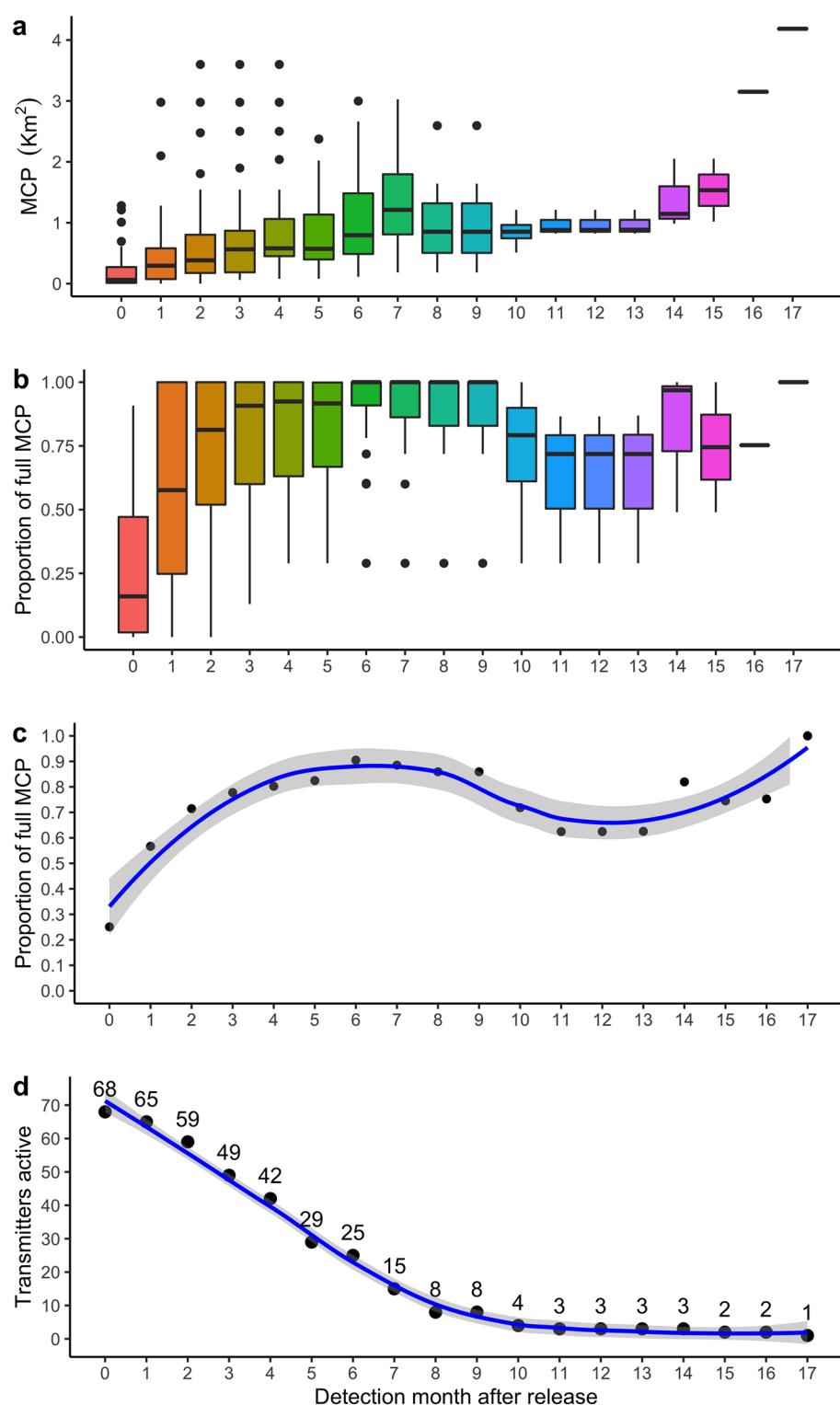
Using the trained RSF GLMM and the holdout dataset (i.e., the random 40% subset of the original data frame), overall model accuracy was 77.3% with predictions of 1 s at 72.2%. While 0 s are considered background points and represent the area that was available (not absences), our model predicted 0 s at 85.2% accuracy. Model performance across the three categorical variables (diel period, and zone type) and their levels ranged from 71.7 to 100% ( $77.1 \pm 11.3$ , Additional file 1: Table S3).

We examined the relative habitat selection of turtles via marginal effects plots as generated from our top model (Fig. 4a). Relative selection by turtles was high in areas 200 m or closer to seagrass in both day and night (Fig. 4a). Shallower depths (less than 10 m) were found to have higher relative selection probabilities both day and night, however, there were higher relative selection probabilities in the day (Fig. 4a). For zone type, turtles had the three highest relative selection probabilities within reef zones at day, reef zones at night, and within lagoon zones at night (Fig. 4a).

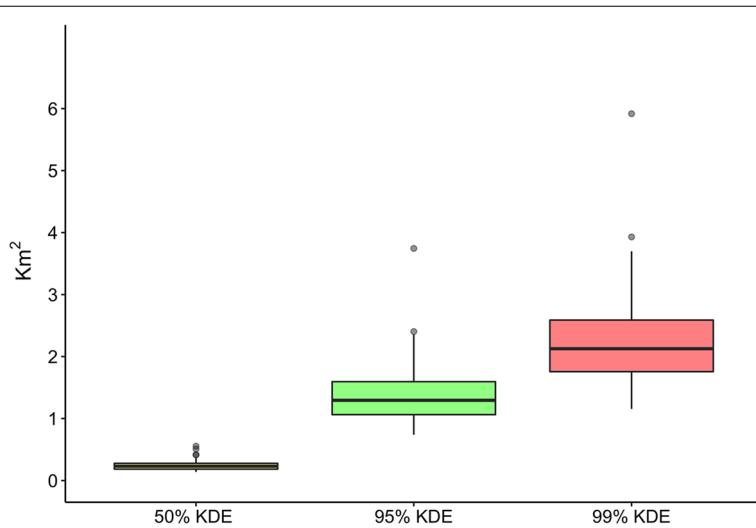
Using the top model to predict across BIRNM (including areas with no detection coverage), the greatest relative selection probabilities for immature green turtles were located within shallow depths near Buck Island and generally decreased farther away from the island at deeper depths (Fig. 5). While turtle KDEs did not perfectly match predicted relative selection probabilities, higher probabilities were located directly adjacent to the island and off the northwestern end the island where lagoon and reef zones exist. Areas in close proximity to seagrass coverage, and lagoon and reef zone habitats produced higher probabilities of relative selection than areas farther away or outside, respectively (Fig. 5).

## Discussion

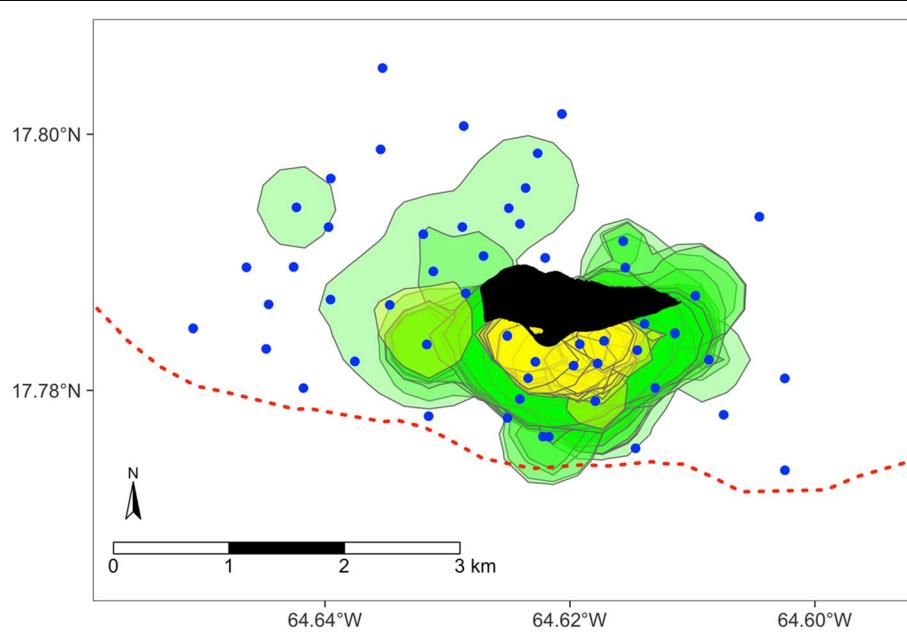
The combination of acoustic telemetry and RSFs demonstrated that immature green turtles within the BIRNM have small, specific home ranges and core use areas, primarily associated with shallow depths, reef and lagoon zones, and areas of seagrass coverage or areas in close proximity to seagrass. Cumulative space use generally increased with each month passing after release and stabilized around six detection months, while proportions to their full MCPs appeared to stabilize around three detection months following release. Overall, tracking duration times varied among individuals likely due to transmitter retention issues [48], yet our MCP metrics



**Fig. 1** **a** Cumulative minimum convex polygon (MCP  $\text{km}^2$ ) boxplots, median shown by black horizontal bar, for turtle detection datasets each detection month after release, **b** boxplots, median shown by black horizontal bar, showing proportion of monthly cumulative MCPs to full MCPs for each individual and each detection month after release, **c** mean overall proportion of monthly cumulative MCPs to full MCPs for each detection month after release (loess regression with 95% confidence interval (CI)), **d** number of transmitters active (i.e., producing MCP values) for each detection month after release (loess regression with 95% CI)



**Fig. 2** Boxplots representing the area of turtle kernel density estimations (KDEs) across 50% (yellow), 95% (green), and 99% (red). Original kernel utilization distributions (KUDs) were constructed using a 200-m smoothing parameter. Note, median shown by black horizontal bar

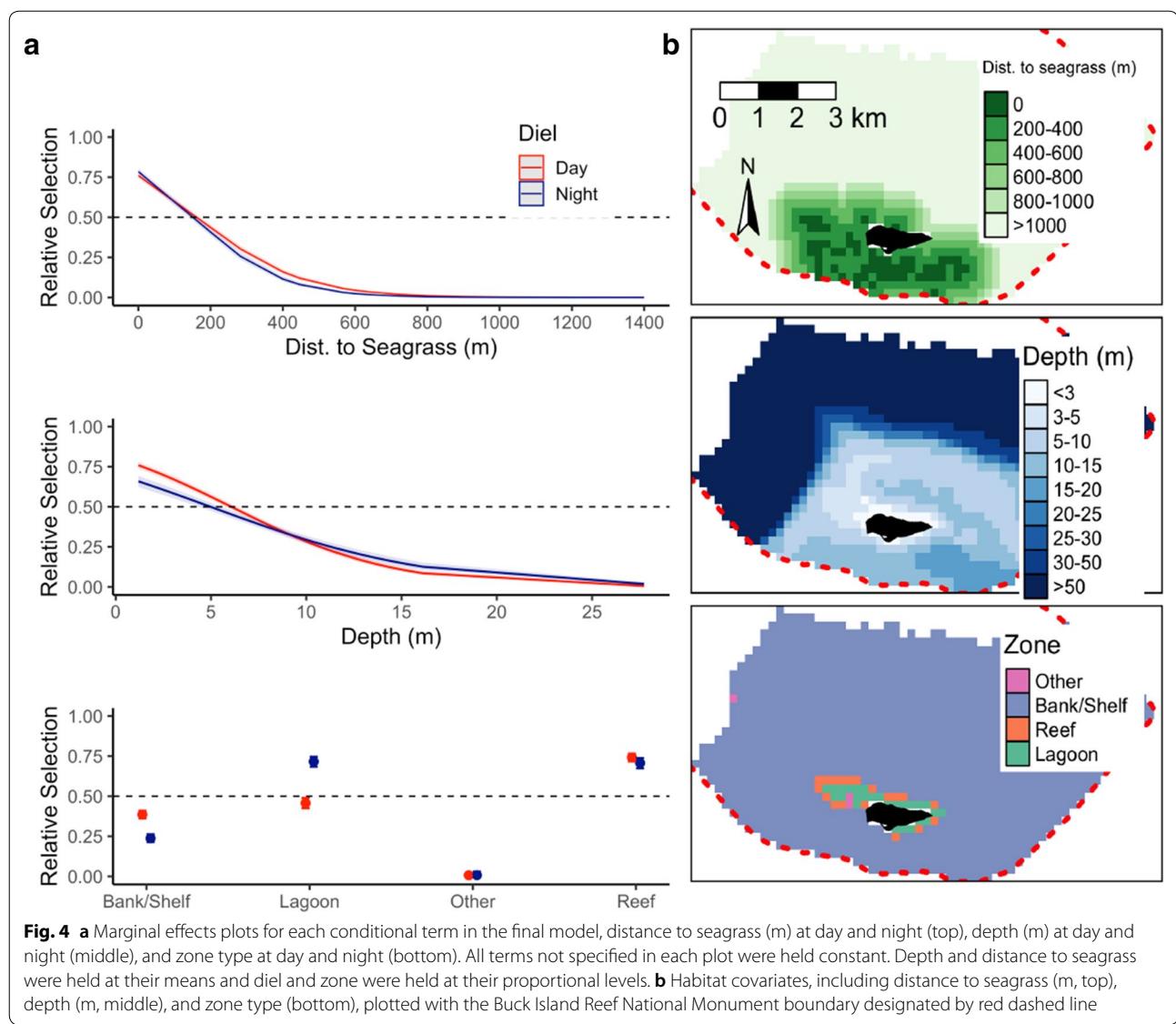


**Fig. 3** Receivers represented by blue dots, 50% and 95% turtle kernel density estimations represented by yellow and green, respectively. Darker shades of yellow or green indicate higher levels of overlap. Original kernel utilization distributions were constructed using a 200-m smoothing parameter

suggested 3 to 6 months of tracking for turtles may provide sufficient amount of data for inferences. RSFs indicated relative habitat selection (i.e., relative to the other habitats available) was high at night and day within reef zones, but only increased within lagoon habitats at night. The highest rates of predicted relative selection were in shallow depths near the island where access to shelter

habitats (i.e., reef and lagoon areas) were available. In addition, areas with, or in close proximity to, seagrass had increased relative selection propensities compared to areas farther away from seagrass.

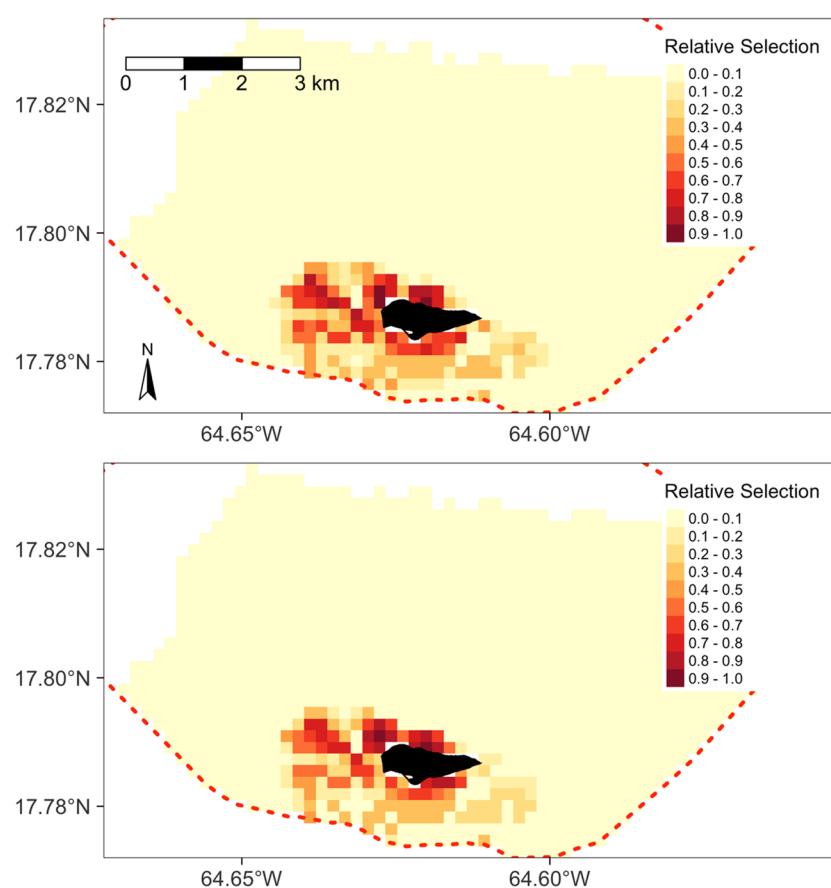
Vulnerable to predation, such as from tiger sharks (*Galeocerdo cuvier*), immature green turtles must balance foraging opportunities and risk avoidance tactics [49].



**Fig. 4** **a** Marginal effects plots for each conditional term in the final model, distance to seagrass (m) at day and night (top), depth (m) at day and night (middle), and zone type at day and night (bottom). All terms not specified in each plot were held constant. Depth and distance to seagrass were held at their means and diel and zone were held at their proportional levels. **b** Habitat covariates, including distance to seagrass (m, top), depth (m, middle), and zone type (bottom), plotted with the Buck Island Reef National Monument boundary designated by red dashed line

Our results support previous findings that turtles forage in productive seagrass habitats and likely utilize physical structure, e.g., lagoon and reef-type structures, for protection [42, 47, 50–52]. Furthermore, Casselberry et al. [53] found acoustically tagged tiger sharks within BIRNM were more likely to inhabit depths > 10 m, at which point, relative habitat selection for turtles was very low (< 0.25). The spatial distribution of individual MCPs and 99%, 95%, and 50% KDEs around BIRNM was relatively small and on average < 3 km<sup>2</sup>. Prior studies have reported similar home range sizes, with the estimated home ranges for immature green turtles in Hawaii being < 3 km<sup>2</sup> [54] and in Florida were 3 km<sup>2</sup> [42]. Further, turtle core use areas, defined by 50% KDEs, within BIRNM were small (0.3 ± 0.0 km<sup>2</sup>), similar to that reported by Makowski

et al. [42] (0.5 ± 0.4 km<sup>2</sup>) and Chambault et al. [55] (0.2 ± 0.3 km<sup>2</sup>). When resource distributions (i.e., food and shelter) were tightly clustered, space use for immature green turtles was constrained [42, 47, 54]. Alternatively, when resources were dispersed, turtles have been shown to have a much larger distribution [56]. For immature green turtles within the BIRNM, the required habitats, food, and shelter are tightly clustered within the shallow waters surrounding Buck Island itself, suggesting this MPA provides all the resources immature green turtles require. In addition, these areas are surrounded by less preferred, more exposed, and potentially more dangerous habitats (depths > 10 m), further suggesting constrained turtle space use. Similarly, immature green turtle space use on the neighboring island, Culebra



**Fig. 5** Predicted relative selection across Buck Island Reef National Monument (BIRNM) during day (above) and night (below) using the top model and its covariates (distance to seagrass, zone, and depth) while taking into account the random effect (turtle ID) variances. The BIRNM boundary designated by red dashed line

Island, Puerto Rico (<100 km), also remained in well-defined areas [47]. However, uncharacteristic of Buck Island, Culebra Island has larger protective embayments that immature turtles use almost entirely, even while suitable reef habitats exist directly adjacent to the bays. In both locations, turtles appear to be selecting for lagoon-type habitats at night, potentially for protection, however, absent of the larger protective embayments characteristic of Culebra, turtles within the BIRNM appear to also utilize reef habitats for possible protection and shelter. Blumenthal et al. [52] noted immature green turtles in the Cayman Islands exhibited a similar pattern of space use across lagoon and reef type habitats at night. While both habitat types within the BIRNM may be providing protection and shelter at night, if some immature green turtles forage at night [51], lagoon-type habitats may also provide low risk (i.e., from predation) foraging opportunities as well.

Considering immature green turtles use and have the highest predicted relative selection values near Buck

Island, the BIRNM MPA is providing sufficient protection for developmental grounds. Turtle MCPs and KDEs demonstrated space use was largely located directly south of the island and to the east and west, thus, space use did not perfectly match the predicted relative selection probabilities that were observed across a much broader spatial extent. This may be due to tagging effort being generally located south of the island where green turtle abundances were highest, thus, if immature green turtles exhibit small home ranges as demonstrated here and by Brill et al. [54], Makowski et al. [42], Griffin et al. [47], and Chambault et al. [55], we would expect tagged individuals to remain near their capture locations. Further, the RSF model could have been improved with additional covariates that capture additional environmental characteristics (e.g., fetch, wave energy, seagrass total area), ecological processes (e.g., density dependence, predator landscape metrics, [57]), and green turtle foraging strategies. These additional covariates would likely provide further insight into why relative selection values vary across

habitat zones and diel periods (e.g., higher selection values in lagoon zones just at night vs. higher selection values in reef zones at both night and day). Ultimately, RSFs are inherently phenomenological and not mechanistic, meaning while space use is an interaction between movement and habitat selection, these RSF predictions are solely focused on observed habitat selection patterns and do not take into account movement processes (e.g., home ranging behavior). These predicted relative selection probabilities are indicative of important habitats in locations that turtles would theoretically select for. Thus, detailed habitat protection (e.g., no anchor, motor and idle only zones, invasive seagrass control) could be focused in areas of space use and in locations with high relative selection probabilities, as indicated by the RSF model.

Consistent with methods provided by Selby et al. [58], we reveal a framework for examining relative habitat selection of animals using acoustic telemetry and RSFs. This analytical approach includes inferring initial space use with calculated COAs, overlaying both COAs and random points onto aggregated habitat information, and using RSF GLMMs to examine resource selection. We then used the trained RSF GLMM model to determine model accuracy and predict relative selection across the greater study area. While this methodology is useful for acoustic telemetry users that wish to examine relative selection and space use beyond areas of detection coverage, it is critical that acoustic arrays are designed to initially capture the representative habitats to reduce biases. In addition, the scaling and selection of habitat classifications are important and should be considered prior to developing models. Important animal space use-habitat relationships may be lost if cell sizes are set too large since the aggregation process selects the dominant habitat type within a cell for classification. One solution is to use a priori ecological knowledge (in our case, using seagrass proximity) to ensure appropriate habitat variables are included in analyses. Further, these analyses focus on relative selection rather than probability of occurrence, meaning that there may be additional variables to explore to improve the accuracy of interpolated space use across an entire area other than RSFs (e.g., integrated step selection functions). Ultimately, RSFs in combination with more traditional analyses (e.g., KDEs) are useful tools to understand habitat selection, space use, and to develop conservation strategies for a given species.

## Conclusion

MPAs are on the forefront of spatial management, however, it is critical to formally incorporate information on animal movements to more effectively implement, evaluate, and improve the use of this conservation tool

[20, 59–61]. Combined with the appropriate analytical methods, acoustic telemetry has become an increasingly important method for resource managers [33]. This technology combined with RSF GLMMs provides new insights in predicting relative habitat selection and space use of a given species, with this application, resource managers within and outside MPAs can refocus enforcement, habitat protection and restoration in areas of need to reach conservation endpoints.

## Methods

### Study site

BIRNM, managed by the United States National Park Service, was established in 1961 and expanded in 2001. This protected area, located on the northeastern shelf of St. Croix, is a 73.4-km<sup>2</sup> no-take marine reserve with small restricted anchoring zone (Additional file 1: Fig. S3). This MPA is one of the few no-take reserves in the Caribbean and one of the oldest [62]. Uninhabited, Buck Island (0.7 km<sup>2</sup>) is in the center of BIRNM and 2.5 km northeast of St. Croix, USVI. Buck Island and its surrounding waters serve as foraging and/or nesting areas for green, hawksbill, loggerhead (*Caretta caretta*), and leatherback (*Dermochelys coriacea*) sea turtles [63]. Within BIRNM, habitats range widely from shallower water to deeper water habitats. From west to east, a high rugosity linear reef surrounds the south side of the island and wraps around Buck Island towards the northwest corner [58]. This reef system encompasses a 50- to 150-m-wide lagoon. Further, the northwest corner and north of the island are characterized by many patch reefs while the south and southwest areas of Buck Island are characterized by low rugosity sea grass patches intermixed with sand flats [64]. Sea grass beds comprised *Thalassia* sp., *Syringodium* sp., *Halophila* sp.

A passive acoustic receiver array, designed to study multiple species [53, 61, 65–68], at BIRNM was expanded from six to 141 Vemco VR2W receivers (Vemco Amix Systems, NS, Canada) between 2011 and 2018. Receivers were strategically placed on sand screws and some on cement block anchors around the island and its various habitats with the majority being deployed in < 15 m. Receiver data downloads and maintenance were performed twice a year.

### Turtle capture and tagging

Following established protocols [69], green turtles were captured by hand while freediving or by “turtle jumping” rodeo method (Additional file 1: Fig. S2). After capture, turtles were brought aboard the research vessel, where curved (CCL) and straight carapace nuchal (SCLn) and total (SCLt) lengths, width, height, biological samples, were also taken along with photographs to document

any anomalies. Each acoustic transmitter, either V16-4L (16 × 88 mm, 24 g in air, 69 kHz, 152 dB, with 30–90 s delay interval, Vemco Amirix Systems, NS, Canada) or V13-1L (13 × 36 mm, 11 g in air, 60–84 kHz, 147 dB, with 30–90 s delay interval, Vemco Amirix Systems, NS, Canada), was attached to individual turtles via a coated wire secured through the right or left marginal carapace scute and by using half a tube of West Marine epoxy [48]. To reduce tagging effects on turtles (e.g., non-normal swimming behavior due to transmitter package), epoxy around the transmitters were molded for optimal hydrodynamics. Here, we also note V16-4Ls are more powerful than V13-1Ls and, theoretically, are able to be detected at greater distances.

## Data analysis

### *Data filtering and organization*

We exported turtle detection data from VUE database (Vemco) and analyzed it in the R statistical environment (R Development Core Team 2018). Data were first filtered for background detections using the `background_detections` function (time threshold set at 2700 s) in the `glatos` package (see <https://gitlab.oceantrack.org/GreatLakes/glatos>). Subsequently, detections of an individual were removed if the rate of movement exceeded 10 m/s or had a time difference of less than 30 s from its last detection. Tagged turtles often lose their transmitters prior to the expiration of the transmitter's battery life [48], thus, if a transmitter falls in vicinity of one or more receivers, many background positive detections may occur. Using the `detection_events` function, from the `glatos` package, we identified the last “event” in each turtle's detection log, in this case, a new event was defined as when two consecutive detections are logged across two different receivers. We also modified this function to incorporate distance, for example, we identified events when turtles exceeded 400 m. By examining event abacus detection plots for each individual, we were able to generate conservative cut-off periods to ensure tag failure was not resulting in background positive detections.

For each individual transmitter dataset, we filtered raw detection data and then transformed it into COAs using the mean position algorithm with 60-min bins [70]. COAs were generated with the VTRACK R package [71]; this algorithm calculates the average receiver location for a specified time (e.g., 60-min bins) to obtain fine resolution movement data while minimizing temporal autocorrelation [43, 46]. Using the calculated COAs, full and cumulative monthly MCPs were constructed for each individual transmitter with an adequate amount of tracking data. To generate cumulative monthly MCPs for each individual, an MCP would first be calculated for the first detection month after release. Calculated

MCPs for subsequent detection months would be cumulatively added to the first MCP calculated, thus cumulative monthly MCPs. For example, cumulative monthly MCP values only increase when the subsequent detection month's MCP also increases. Further, the last cumulative monthly MCP in an individual's detection log will always be equal to the observed full MCP. We also examined the proportion of monthly cumulative MCPs to full MCPs at the individual level and across all individuals for each detection month after release. MCPs were generated with the VTRACK R package [71]. Further, we examined how many transmitters remained active across detection months after release. Here, monthly MCPs were generated at the detection month level, thus, detection months after release refers to the subsequent months an individual was detected excluding any monthly gaps in detection history. For additional analyses, to ensure enough data to model individual turtle as a random effect and following Selby et al. [58], we eliminated individual transmitter datasets with less than 100 COAs. For each individual transmitter dataset, we used KDEs to represent space use. To do this, we first fitted fixed kernel utilization distributions (KUDs) to the COAs, and subsequently estimated the 99%, 95%, and 50% KDEs from each KUD. The KUD represents a bivariate probability density function of use [72, 73], while the KDE is the vectorized polygon that results from drawing isopleths around a percentage of the cumulative utilization distribution. All KUDs and KDEs were derived using the `adehabitatHR` package [74] and with a 200 m smoothing parameter. Further, for each KDE, the area and the percent overlap to other KDEs were calculated. Here, percent overlap is defined by the proportion of individual *i*s KDE that is overlapped by individual *j*'s KDE [75].

### *RSFs and GLMMs*

An RSF is a statistical model that is proportional to the probability of use by an animal [76]. Relative selection strength and, thus, space use of an animal can often be defined by RSFs [77, 78], making them valuable to developing effective conservation strategies [79–81]. RSFs allow us to examine the relative selection of individuals based on a given set of covariates. Subsequently, RSFs can be used to help predict habitat selection probabilities outside the observable area based on the selected covariates. To understand relative habitat selection and space use of immature green turtles in the BIRNM, we applied RSFs using GLMMs with a binomial distribution similar to the approach presented by Selby et al. [58].

The response variable included turtle presence locations (COAs), coded as 1 s, and random background points, coded as 0 s. All COAs and random background points were constrained within the available observable

area (i.e., where acoustic receivers provided detection coverage). Random background points were randomly placed at an equal number of random locations per individual's COAs within the available observable area matching the same number of observed diel periods (day vs. night) and observed points per year. To define our available habitat, i.e., detection coverage, across the study area, we generated a 400-m buffer, at any given receiver at a given year (i.e., 2012, 2013, 2014, Additional file 1: Fig. S3). Following Selby et al. [58], we chose a 400-m buffer based on both previous range-testing of the BIRNM array [82] and to retain higher numbers of calculated COAs. All spatial data management and construction were performed using the raster [83], and sp [84] packages.

The calculated COAs (presences) and random background points were collapsed into  $200 \times 200$  m raster cells, along with habitat and depth. Habitat data were provided by and adapted from the National Oceanic and Atmospheric Administration (NOAA) [64]. Benthic habitat classifications were derived using aerial photographs, light detection ranging imagery, and four types of multibeam echosounder imagery [64]. Using the NOAA-derived habitat classifications and their attributes, we generated three variables of interest, distance to seagrass (seagrass defined as > 50% coverage, Fig. 4b), reef type (no reef, patch reef, continuous reef, Additional file 1: Fig. S4), and zone type (lagoon, bank/shelf, reef, other, Fig. 4b). We used the nearest neighbor technique to recalculate depth (Fig. 4b) into  $200 \times 200$  m raster cells, cells with no data available were replaced with the mean values of adjacent cells. All habitat information (factors) and depth (m) values were assigned to each raster cell, using the rasterize function from the raster package [83], and the corresponding COAs and random background points. In addition, diel period (day and night) were assigned to all points using civil dawn and civil dusk times within the maptools package [85]. Variance inflation factors were assessed to determine if variables were too correlated to include in models.

GLMMs were implemented using random subsets of 60% of the dataset. The remaining 40% of the dataset (holdout dataset) was later used to test model accuracy. The full model included diel and depth as an interaction term, diel and distance to seagrass as an interaction term, diel and zone type as an interaction term, and individual and year as random effects. All continuous variables were standardized (z-standardization). Datasets from individuals that had multiple transmitters attached (due to tag loss and subsequent recapture and retagging) were grouped together, respectively. We fit the full model using the glmmTMB package [86] and used the MuMIn package [87] to run all possible subsets, i.e., combination of coefficients. All models

included individual and year as random effects. We then used the Akaike information criteria (AIC) to select the top model. Variance components of random effects (year and individual) were also examined in model selection procedures. Using the proportion of data that was not used in the final model (i.e., the random subset of 40%), we assessed the model's accuracy. Model accuracy was defined as the top model's ability to correctly predict the probability of 1 s and 0 s using the 40% data subset. Further, model accuracy was assessed across all categorical variables. Marginal effects plots were generated for each conditional term in the final model using the sjPlot package [88]. All other model terms not specified in the given plot were held constant, the continuous variables, depth and distance to seagrass, were held at their means and all other factor variables were held constant at their proportional level rather than at their reference levels.

To predict the relative selection and space use of turtles across BIRNM, we first aggregated all habitat classifications and depth data from the entire study area into multiple raster layers. Subsequently, using the aggregated raster layers, we used the top model to predict and plot the relative selection probabilities across the entire study area for both day and night.

## Supplementary information

**Supplementary information** accompanies this paper at <https://doi.org/10.1186/s40317-020-00209-9>.

**Additional file 1.** Additional figures and tables.

## Abbreviations

AIC: Akaike information criteria; BIRNM: Buck Island Reef National Monument; CCL: Curved carapace length; GLMM: Generalized linear mixed model; KDE: Kernel density estimation; KUD: Kernel utilization distribution; MPA: Marine protected area; NOAA: National Oceanic and Atmospheric Administration; RSF: Resource selection function; SCLn: Straight carapace nuchal length; SCLt: Straight carapace total length; MCPs: Minimum convex polygons.

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## Authors' contributions

KH secured funding for and designed the study. LG and BS analyzed the data. LG, KH, and BS interpreted the data and wrote the manuscript. KH and BS provided analytical, interpretation, writing, and editorial oversight. KH, CP, ZHS, MC, AC performed the field work, designed the study, and provided editorial input, and AD, MC, and AC provided writing and editorial input on the manuscript. All authors were major contributors and contributed to writing and editing the final manuscript. All authors read and approved the final manuscript.

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## Availability of data and materials

The dataset contains sensitive data containing locations for a protected species. Data are available from corresponding author on reasonable request.

## Ethics approval and consent to participate

Fieldwork was permitted under NMFS permits 16146 and 20315, issued to K. Hart, National Park IACUC USGS-SESC2014-02 and USGS IACUC WARC\GNV 2017-04. Additional permits issued to K. Hart BUIS-2011-SCI-0012; BUIS-2014-SCI-0009; BUIS-2016-SCI-0009.

## Consent for publication

Not applicable.

## Competing interests

The authors declare that they have no competing interests.

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