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Spatial ecology of the Turks and Caicos Boa *Chilabothrus c. chrysogaster* Cope, 1871 (Serpentes: Boidae)

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Obtaining ecological and natural history data from cryptic squamates can be challenging, but is crucial to understanding species' biology, particularly in the context of conservation. In the Greater Antilles, this challenge is especially apparent, particularly among the West Indian boas (genus *Chilabothrus*). Most species have had only minimal natural history study, with a few exceptions. The Turks and Caicos boa (*C. chrysogaster*) has been studied intensively for over 16 years on the small privately owned island of Big Ambergris Cay, Turks and Caicos Islands. We conducted a multi-year radio-tracking study on the species to generate information relevant to spatial habitat use and movement that will inform conservation decision-making in the face of increasing development pressure. We tracked a total of 19 female snakes using surgically implanted transmitters, enabling us to obtain between 16 and 40 location observations per boa over the lifetime of each transmitter. We found that females have an average home range of 1.83 ha and a core space use area of 0.39 ha. We also estimated occurrence distributions, the use of space between specific time intervals, finding an average occurrence area of 0.76 ha. Several females overlapped in their spatial habitat use, with an average overlap proportion of 28 %. During this study we observed female boas using two novel habitats for the species (iron shore wrack and red mangrove). This study provides valuable information on the spatial ecology of an endangered boa and will serve to inform conservation work that is currently underway.

Keywords: conservation, movement, home range, snake, spatial ecology

INTRODUCTION

Understanding how animals such as snakes use physical space in their habitats can provide a tremendous amount of valuable natural history information, including characterisation of habitat use, population health, mortality, density, dispersion, and/or demographic dynamics, among others (Gregory et al., 2001; Collinge, 2010). Further, common techniques for measuring spatial use in terrestrial animals, such as snakes, require repeated serial observations of the same individual at different times, which can yield many important behavioural and ecological insights into how they interact with their environments (e.g. Huey et al., 1989; Madsen & Shine, 1996; Bruton, 2013). Collectively, these data can better characterise a species' natural history, but in the case of threatened species these data might also be crucial to designing conservation interventions (e.g. Newman et al., 2019; Nordberg et al., 2021). For example, human alterations to habitats can produce negative impacts on the fitness and survival rates of species that depend on specific aspects of their environment; aspects which might have been unknown prior to spatial habitat use studies (Harrison et al., 1991; Webb & Shine, 1997; Roe et al., 2004).

Snakes can be especially challenging to study, as many species are cryptic, nocturnal, and exist at relatively low densities compared to some other small squamate reptiles (Macartney et al., 1988). Despite their generally low densities, snakes are important members of local ecological communities, assuming the role of both predator and prey (Greene, 1997). As a result, the spatial ecology of a given species has strong effects in structuring the trophic ecology of a community. This means that even the largest snakes can exhibit a huge variety of spatial use patterns, ranging from nearly sedentary (Smaniotto et al., 2020) to having home ranges similar to large predators such as jaguar (8–87 km^2; Hart et al., 2015; Marshall et al., 2019).

Radiotelemetry, or radio tracking, generally uses implantable Very High Frequency (VHF) transmitter packages and has revolutionised ecological research on snakes (Ciofic & Chelazzi, 1991; McDiarmid et al., 2012). Transmitters are surgically implanted intraperitoneally,

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or subcutaneously in larger species, while the 5–10 cm antenna is most often threaded subcutaneously. Snakes are subsequently located using an antenna and receiver tuned to individual frequencies. Such techniques have resulted in a wealth of natural history information, including seasonal variation in movement, location of basking and hibernaculum sites, movement rates, home ranges, habitat use, site fidelity, and many, many more (Webb & Shine, 1997; Gregory et al., 2001; Brito, 2003; Pearson et al., 2005; Gerald et al., 2006; Zappalorti et al., 2015; Smaniotto et al., 2020).

On Caribbean Islands, snakes, particularly boas (*Chilabothrus* and *Boa*) can be the largest terrestrial predators and occupy tertiary and quaternary food chain roles (Reynolds et al., 2023). Hence, it is important to understand the amount of space and habitat they require to persist. One of the more common uses of radiotelemetry is to obtain a series of locations of an individual snake, using these data to then calculate measurements of home range and spatial use. Such studies have revealed a tremendous amount of information for the Caribbean boa species that have been studied in this way, although only three other members of the genus have been the subject of published spatial ecological research, and each of these used few focal animals.

Jamaican Boas *C. subflavus* studied near caves show sex differences in movement, homing ability over 1 km, philopatry, and a lack of strong overlap in spatial use among individuals (Miersma, 2010; Koenig, 2019). A radio tracking study of eight females and six male Jamaican Boas *C. subflavus* was conducted between 2008 and 2012 near the Windsor Research Centre in Cockpit Country, Trelawny Parish, Jamaica (Miersma, 2010; Koenig, 2019). Boas moved a mean distance of 20 m per day, with no difference in mean daily movement distance between males and females. Cave-associated boas (two males and one female) had smaller home ranges (95 % Minimum Convex Polygons [MCPs] 0.75 to 2.51 ha) than free-ranging boas; the latter ranged from 16.28 ha to 70.11 ha in males (50 % MCP 0.20 ha to 0.34 ha) and from 2.16 ha to 19.56 ha in females (50 % MCP 0.64 ha to 6.63 ha). Boas were also found to move as far away as 1 km and return to the exact point of previous capture, suggesting excellent navigation skills and some evidence for philopatry and territoriality (Miersma, 2010). Newman et al. (2019) studied short-distance translocation (SDT) in *C. subflavus* as a potential conservation tool to move animals away from dangerous situations. Translocation distances for seven females ranged from 693–3,545 m. Two boas returned to their original point of capture in the first two months following translocation; others remained 500 m to > 1,000 m from their points of capture. Thus, translocation in *C. subflavus* might be an effective conservation practice, but only at distances over several hundred metres.

The Puerto Rican Boa *Chilabothrus inornatus* has been studied using radio telemetry at four localities including intact forest and fragmented habitat, showing seasonal shifts in movement as well as home range sizes, and difference in home range size depending on habitat (Puente-Rolón, 1999; Puente-Rolón & Bird-Picó, 2004; Wunderle et al., 2004). Like the Jamaican Boa, cave-associated populations of boas tend to have smaller home ranges than "surface" populations (Puente-Rolón & Bird-Picó, 2004; Wunderle et al., 2004). In a study focused on a cave-associated population near Arecibo, Puente-Rolón & Bird-Picó (2004) found that male and female home range sizes (based on 95 % MCPs) did not differ significantly, although females did have a slightly larger mean home range size of 0.79 ha vs. male mean home range size of 0.50 ha (95 % MCP, n = 11; range 0.01–1.8 ha). In a surface population, home ranges (95 % MCPs) ranged between 0.7–44.7 ha in females and 2.6–68.1 ha in males (Wunderle et al., 2004).

A third species, the Bahamas Boa *C. strigilatus*, has been studied on Andros Island, albeit incidentally, and were found to consume novel prey and move up to 248 m in a single day (Knapp & Owens, 2004). The authors found that, while radio tracking hatchling *Cyclura cychlura*, boas consumed some of the hatchlings and so they were able to obtain spatial data on six adult snakes. Mean daily movement ranged from nine to 198.5 m over tracking periods between five and 28 days. The authors estimated a 100 % MCP range between 0.03 and 2.0 ha. A study on the same species on the island of South Bimini has been conducted (R. Potts, pers. comm. to RGR) but those data are not yet available. Similarly, a study is currently ongoing on *C. angulifer* at the Naval Station Guantanamo Bay (P. Tolson, pers. comm.).

Although the Turks and Caicos boa *C. chrysogaster* has been extensively and intensively studied for over 16 years (Reynolds, 2011; Reynolds & Gerber, 2012; Reynolds et al., 2011; 2020), nothing is known about how much they move, how often they move, how much space they use and what their home ranges are. These data are not only meaningful for understanding boa biology and ecology, but also are especially relevant to potential conservation measures. To understand the spatial ecology of boas on Big Ambergris Cay, we conducted a two-cohort, multi-season, multi-year study. We wanted to determine 1) the distance snakes move on the island during a given time period, 2) what size home ranges they have, and 3) does their use of space differ from their use of a core home range. We examined these questions using both traditional approaches (minimum convex polygons) as well as spatial interpolation analyses, including kernel density estimates and Brownian bridge movement models. We compare these data to what is known of congeneric spatial ecology and demonstrate the utility of using multiple spatial analysis methods to inform snake spatial ecology and conservation.

MATERIALS & METHODS

Study area and specimens

This study was conducted on the privately owned island of Big Ambergris Cay, Turks and Caicos Islands located near the south-eastern edge of the Caicos Bank (Fig. 1; latitude: 21.299, longitude: -71.633, maximum elevation 32 m), a mostly submerged carbonate platform with several larger and many smaller emergent islands. The island is 6.4 km in length, a maximum of 1.6 km in width and ~400 ha in total area. The island consists of a reduced representation of salt-tolerant coastal vegetation varieties found in the Turks

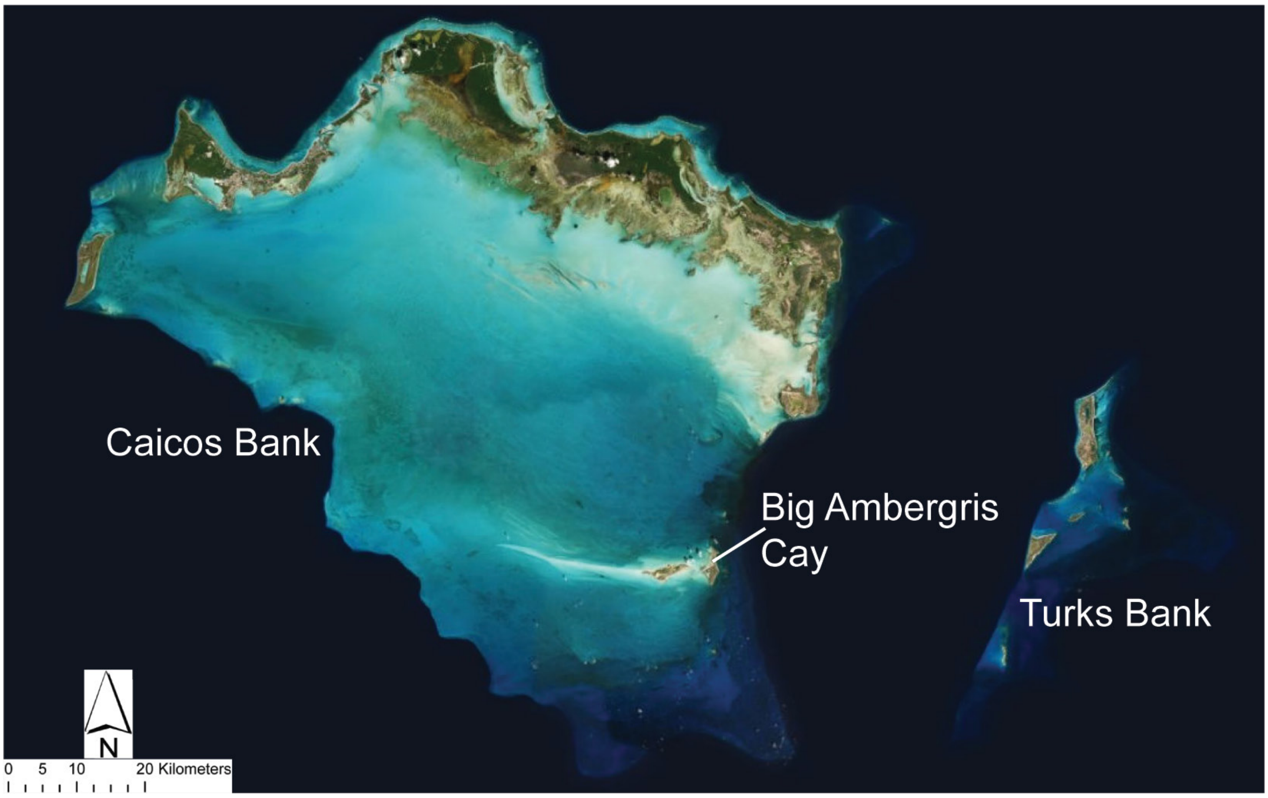

Figure 1. The Caicos and Turks banks as seen in satellite imagery (ArcGIS 2021, Redlands, CA). The Turks and Caicos are a series of seven larger islands and several hundred smaller cays and rocky islets distributed across two shallow carbonate banks at the south-eastern terminus of the Lucayan Archipelago. These islands are home to several endangered terrestrial reptile species including the Turks and Caicos boa *Chilabothrus chrysogaster* and the Turks and Caicos rock iguana *Cyclura carinata*. The study was conducted on Big Ambergris Cay, near the south-eastern margin of the Caicos Bank.

and Caicos —supporting sandy soil and palm *Cocothrinax* forest in low-lying areas, rocky cactus scrub, mangrove stands on the leeward side of the island and whiteland coppice developed over loose limestone elsewhere. This island is one of the last strongholds of Turks and Caicos boas and is an ideal place to study them for several reasons. First, no introduced predatory species, such as cats or rats, have been allowed to persist on the island. Second, the island has the highest known density of boas, with over 12 snakes per hectare (Reynolds, 2011; Reynolds & Gerber, 2012; Reynolds et al., 2020). Big Ambergris Cay has been intensively developed since 2004, now hosting the largest private air strip in the greater Caribbean, two restaurants, tennis courts and a marina that has been built into formerly natural salina salt flats (Fig. 2). The island is also criss-crossed with a network of over 20 km of unpaved roads.

Two cohorts of boas were studied over a period of 20 months between August 2018 and March 2020. The first cohort, Cohort A, was initiated between 23 July and 10 August 2018. For this cohort, 13 adult female boas were captured, and only large females that were ≧ 150 g in body mass were selected. Cohort B was initiated between 4–7 August 2019 and consisted of six adult females > 200 g in mass. All boas were collected by hand between 1800 h and 0100 h and maintained overnight at ambient temperature prior to transmitter implantation (described below).

Two types of temperature-sensitive radio transmitters were custom ordered from Holohil Systems, Inc. (Ontario, Canada): 'button-type' transmitters (model PD-2T), and 'barrel-type' transmitters (model SB-2T) in two batches, one in June 2018 and one in November 2018. These transmitters had frequencies in the range of 172.024–172.965 MHz and a battery life of six months (button-type) or one year (barrel-type) once activated. The transmitters were sterilised by individually sealing the entire unit, including the antenna, in gas sterilisation bags and then subjecting them to human surgical-grade peroxide gas sterilisation conducted by a hospital sterile processing department. Sterilisation took place between 8–15 days prior to implantation, and transmitters were stored in a protective and cushioned case during transport to the field site.

Transmitter types were matched to female body sizes, with the smaller females receiving 3.5 g button type transmitters and the larger females receiving 5.5 g barrel type transmitters. These transmitters were matched such that they weighed ≤ 3 % of snakes' body mass (Table 1).

Surgical procedures

A brief pre-surgical health exam was conducted on all snakes the morning following their capture. The agents alfaxalone or dexmedetomidine plus ketamine were administered per standard techniques. When dexmedetomidine was administered, the antagonist (atipamezole) was administered at the conclusion of the procedure. The agents used were chosen based on the temperament of the snake and surgical approach. Local analgesia was provided in all cases by injection of lidocaine in a line along the intended surgical incisions. After completion of each procedure,

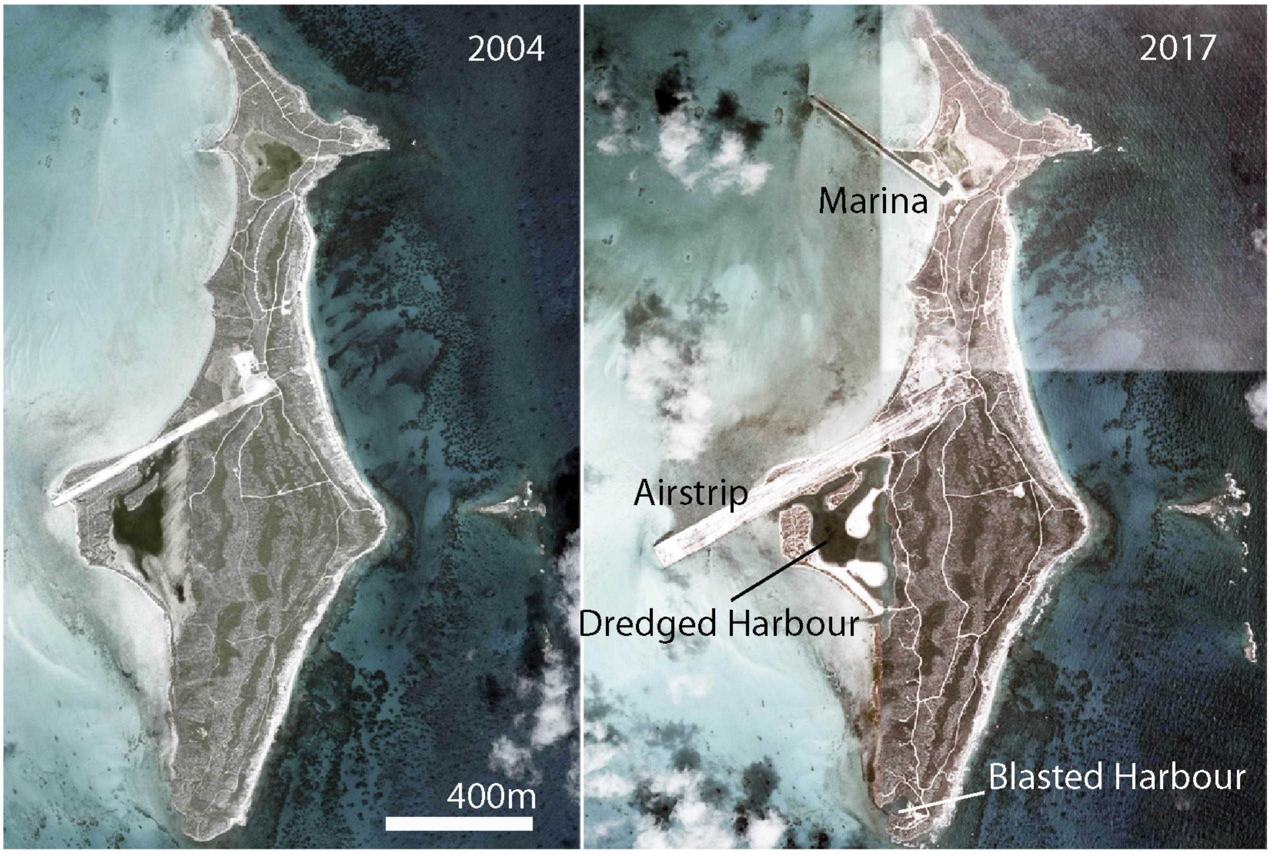

Figure 2. Development has increased dramatically on Big Ambergris Cay since 2004 (left) and 2017 (right) including the addition of private homes, a private airstrip, marina, tennis courts and restaurants. Images are from Google Earth.

each animal was given a nonsteroidal anti-inflammatory (meloxicam) as well as the antibiotic ceftiofur crystalline free acid (Excede, Zoetis, Parsippany, New Jersey).

Animals were maintained at ambient shade temperature for the duration of the procedure. Times for first effect (characterised by visual slowness), loss of righting reflex, and start and end time of surgery were recorded for each procedure. All animals underwent surgical preparation by cleansing their bodies caudal to the heart with a dilute chlorhexidine solution left in contact with the skin for 2–3 minutes. Incision areas were swabbed with alcohol and animals were placed in right lateral recumbency while the snake was held manually or taped into position with paper tape. The eyes were covered with cloth and sterile surgical drapes were placed on and around the body to establish a sterile field. Standard surgical techniques were used including sterile equipment and supplies (i.e. gloves, surgical mask, instruments, gauzes, sutures). Radio transmitters were surgically implanted using one of the two following techniques, generally following the methods of Weatherhead & Anderka (1984).

For subcutaneous implantation (n = 13), a small incision was made 2/3 of the way down the length of the snake on the dorsal-lateral left side. The transmitter was placed subcutaneously, caudal to the incision and affixed to the underlying muscle with a single absorbable suture around the neck of the transmitter. The Teflon® insulated antenna was passed subcutaneously towards the head (cranially) through a rigid polypropylene catheter or blunt surgical stylet guide.

For transmitters placed intracoelomically (n = 6), the initial skin incision was made 2–3 rows of scales above the intersection of the ventral and lateral scales. A small incision was made through the muscle below the ribs at that site. The transmitter was placed into the coelom caudal to the stomach and a suture surrounding the transmitter through the musculature was used to attach the transmitter to the body wall. The antenna was brought out through the musculature and tunnelled subcutaneously anteriorly using a polypropylene catheter or blunt surgical stylet guide. The muscle was opposed using absorbable sutures. Skin incisions were closed using skin adhesive (Nexaband®) and monofilament suture of appropriate size (3-0 to 5-0 USP).

Passive integrated transponders (PIT tags, Trovan®) were inserted subcutaneously approximately 5 cm anterior to the cloaca on the left side of each boa pre-recovery for subsequent identification. A 5 mm section of the tail tip was removed for future genetic analysis. Post-surgery, snakes were kept in 25–28 °C individual enclosures until they were fully recovered from anaesthesia and handling.

During the week of 4–10 January 2019 each snake with a functioning transmitter was collected for a health exam or surgical repair (if needed). Due to the shorter lifespan of the button transmitters, one healthy animal with a button transmitter underwent a second surgical procedure to remove the subcutaneous button transmitter and replace it with a new barrel transmitter intracoelomically (snake T13; Table 1). Health exams consisted of a weight comparison, brief overview of site of incision and

Table 1. Transmitter type, mass, and snout-vent lengths (SVL in mm) of 19 female *Chilabothrus chrysogaster* individuals that underwent implantation for tracking via radiotelemetry (mean SVL = 1040.2 ± 60.8 mm, mean mass = 438.7 g ± 98.2 g). Prop. Mass represents the proportional mass of the transmitter relative to the snake capture weight. Cohorts are described in the text.

ID	Cohort	Transmitter Type	Mass (g)	SVL (mm)	Prop. Mass	Notes
T1	A	button	162	820	2.1%	Removed from study
T2	A	barrel	182	815	3.0%	—
T3	A	button	166	830	2.1%	—
T4	A	barrel	900	1,355	0.6%	—
T5	A	barrel	855	1,315	0.6%	—
T6	A	button	227	900	1.5%	—
T7	A	barrel	320	1,030	1.7%	—
T8	A	button	259	949	1.3%	—
T9	A	button	276	953	1.3%	—
T10	A	barrel	505	1,170	1.1%	—
T11	A	button	271	920	1.3%	—
T12	A	barrel	330	990	1.7%	—
T13	A	button, then barrel	1,675	1,475	0.2%; 0.3%	Transmitter replaced
B23	B	barrel	1,135	1,500	0.5%	—
C42	B	barrel	234	1,001	2.3%	—
D45	B	barrel	580	1,190	0.9%	—
D51	B	barrel	280	1,025	1.9%	—
E9	B	barrel	256	940	2.1%	—
E40	B	barrel	278	1,005	2.0%	—

Table 2. Initiation dates and tracking dates for each cohort of boas

Cohort	Tracking Dates
A	25 July–10 August 2018
A	17–20 December 2018
A	04–10 January 2019
B	04–15 August 2019
B	06–12 March 2020

ID	Cohort	Initiated	Last Day Located	Total # Tracking Days	Total # Locations
T1	A	25/07/18	31/07/18	7	7
T2	A	27/07/18	08/08/19	25	40
T3	A	25/07/18	06/08/18	11	16
T4	A	28/07/18	06/01/19	20	35
T5	A	29/07/18	10/01/19	21	34
T6	A	29/07/18	08/09/18	12	20
T7	A	29/07/18	01/06/19	17	28
T8	A	30/07/18	07/08/19	17	19
T9	A	30/07/18	09/08/19	10	18
T10	A	30/07/18	10/01/19	21	36
T11	A	31/07/18	09/08/18	10	18
T12	A	31/07/18	10/01/19	20	36
T13	A	02/08/18	15/03/19	18	32
B23	B	04/08/19	13/03/20	16	27
C42	B	05/08/19	12/03/20	16	27
D45	B	06/08/19	12/03/20	15	26
D51	B	06/08/19	13/03/20	16	27
E9	B	07/08/19	09/03/20	11	19
E40	B	07/08/19	13/03/20	14	25

transmitter placement, and overall behaviour (whether the animal actively resisted restraint and had good muscle and skin tone or was listless with loose skin tone).

Telemetry Data Collection

Animals were released at the site of original capture a minimum of six hours after completion of the surgery once total recovery from anaesthesia was confirmed, but no animal required observation longer than 48 h to recover. A series of tracking sessions commenced (Table 2), during which we attempted to locate every boa twice per day, once at mid-day and once after dark with a minimum interval of five hours between consecutive locations. Animals were located using R1000 VHF telemetry receivers (Telonics Inc., Mesa, Arizona) in conjunction with a hand-held Yagi three-element antenna connected via a coaxial cable. Once the animal was located (either visually or within < 2 m if underground), the latitudinal and longitudinal co-ordinates of the site were recorded in decimal degrees (WGS 84, 3 m accuracy) using a Garmin eTrex10® handheld GPS (Olathe, Kansas).

Spatial Analyses

All data were analysed using R v 4.2.3 (R Core Team, 2023) implemented in RStudio v 2023.3.0 (RStudio Team, 2023). Data for most analyses consisted of .csv formatted data matrices which included columns of snake identity as well as the latitude and longitude for each telemetric location and the time/date when the location was obtained. Decimal degree WGS 84 spatial points were converted to a Universal Transverse Mercator (UTM) projection (zone = 19N, datum = NAD83) using the SpatialPoints(), CRS(), and spTransform() functions in the package sp (Bivand et al., 2013). Total distances travelled were then calculated for each boa using the SpatialLines() function in the package sp, which allowed for the comparison of the total movement distances of all females in the study, but does not allow for estimates of distances travelled per day.

When calculating spatial characteristics, it is important to differentiate between space use, or the use of all space documented during the study, and occurrence area, the movement of an animal over a period of time (Crane et al., 2021). We chose to calculate space use as 1) the home range, constituting the 95 % contour of locations the animal used, and 2) the core area, the 50 % contour of space use. Occurrence area was calculated using the 50 % contour of the movement path over the sampling period. Two types of space use estimates were used (sensu Crane et al., 2021), range distributions (RDs) and occurrence distributions (ODs). Range distributions correspond to the traditional definition of a home range, which is the spatial extent of an animal's use of area throughout its lifetime (Burt, 1943; Crane et al., 2021), although we note that home range has been defined numerous ways, including the use of space during a sampling period (Gregory et al., 2001). Methods to estimate RDs use known location data to extrapolate areas-of-use (including future use) and are best suited for calculating traditional lifetime spatial use models; but we note that RDs are less ideally suited (although still commonly used) to estimate sampling period bounded home ranges (Crane et al., 2021). Occurrence distribution models are interpolations developed specifically for investigating the movement of an animal during the period of a study, and hence do not explicitly refer to a home range (although, in practice they might closely represent a home range depending on study design and species). Occurrence distribution models use known spatial points paired with time between sampling intervals to estimate the occurrence area between sampling points. Further, it is important to note that most RDs and ODs in practice represent spatial use in two dimensions, rarely incorporating elevational data to calculate three-dimensional space use. Hence, landscape topography would be a separate factor to consider (although it is not relevant to our study given the low topography of the island).

RDs were calculated using autocorrelated kernel density estimates (AKDEs; Fleming et al., 2015; Fleming & Calabrese, 2017). Kernel density estimates represent the utilisation distribution, or the probability of 2-dimensional space the individual uses, indicating a home range in the context of an RD (although many studies have improperly interpreted it in the context of an OD). Until recently, few studies using KDE accounted for any effect of autocorrelation, even though radio telemetry data violate an assumption of data independence (Fleming et al., 2015; Silva et al., 2022). Traditional KDE has been implicated as being strongly influenced by autocorrelated data, which might dramatically underestimate space use and space use uncertainty (Fleming et al., 2015). However, AKDEs are robust to small sample size, heterogeneous sampling intervals and autocorrelation in datasets (Fleming et al., 2019; Silva et al., 2022). Both 50 % and 95 % AKDEs were estimated for each boa in the dataset using a weighted AKDE method (wAKDE; Silva et al., 2022) using the R package ctmm (Calabrese et al., 2016; Fleming & Calabrese, 2017). The perturbative hybrid REML method and AICc were used to select the best fitting model, and resulting 95 % range isopleths were visualised in R, inclusive of confidence intervals. We then calculated range overlap among boas that crossed ranges during the study using the overlap() function in ctmm, which estimates a Bhattacharyya coefficient to quantify proportional overlap on a scale of 0–1 from AKDE ranges (Winner et al., 2018).

Range residency was further estimated using effective sampling size and variograms calculated in the package ctmm. Range residency is established when tracking data suggest that the animal has crossed its range at least once and can be indicated by effective sampling size > 5.0, which is the tracking duration divided by the number of home range crossings (Silva et al., 2022). Further, variograms allow visualisation of home range stability, when an asymptotic curve is apparent in a plot of duration versus range. While range residency is an assumption of AKDE methods, we elected to retain boas that did not fit this assumption for some analyses, identifying them as appropriate. However, summary statistics are not reported from boas that do not fit these assumptions.

Because so many previous studies of snakes have used two traditional estimators: minimum convex polygons (MCPs) and kernel density estimates (KDEs), these were calculated as well, with the caveat that autocorrelation, range residency and small sample size will cause significant bias (e.g. Row & Blouin-Demers, 2006). Minimum convex polygons connect spatial points such that a resulting polygon incorporates all the location fixes and are perhaps the most commonly used way to represent both RDs and ODs (although unfortunately most studies rarely diagnose which models they are using; Crane et al., 2021). The mcp() function was used in the adehabitatHR package (Calenge, 2006) to calculate MCPs for each boa in the study and visualised using ArcGIS Pro v 2.7.1 (Esri Inc., Redlands, California). Estimates for both 50 % and 95 % KDEs were calculated using the ctmm package.

Neither of these traditional approaches (MCP and KDE) to estimating RDs and ODs are without flaws, particularly as they are both technically suited for RD and not OD (despite their frequent use for the latter; Crane et al., 2021). Therefore, an explicit OD approach using Brownian bridge movement models (BBMMs) was selected, which incorporates different weights for spatial habitat use by accounting for time steps between observations (Horne et al., 2007; Silva et al., 2020). Brownian bridge movement models are OD estimations that focus on using movement between location points to build a model that measures the probability of space use between each location (Horne et al., 2007; Silva et al., 2018). Time steps between each data point were calculated to the nearest hour, then the functions in the R package BBMM 3.0 (Nielson et al., 2015) were used to construct 50 % BBMMs for each boa. A 50 % cut-off was chosen, as generating higher cut-offs would have required more spatial points per boa than we had available. Output files with spatial grid information in a polyline format were created that we could then import into ArcGIS Pro. Areas for the BBMMs were calculated by transforming the polyline data into an area polygon using the construct polygon tool in ArcGIS Pro v. 2.7.1 and vertices edited to join lines where needed. Areas of the resulting polygons are then available in the layer attributes table.

RESULTS

Radio Transmitter Implantation

A total of 20 radio transmitters were implanted in 19 female snakes (Table 1). The mean SVL of snakes was 1,107 mm (range 815–1,500 mm), with a mean mass of 524 g (range 160–1,675 g; Table 1). Of the 19 snakes, seven received button transmitters and 12 received barrel transmitters, with one individual (T13) receiving both types following a replacement of one (Table 1). The mass of boas receiving barrel transmitters was 182–1,290 g and 160–1,675 g

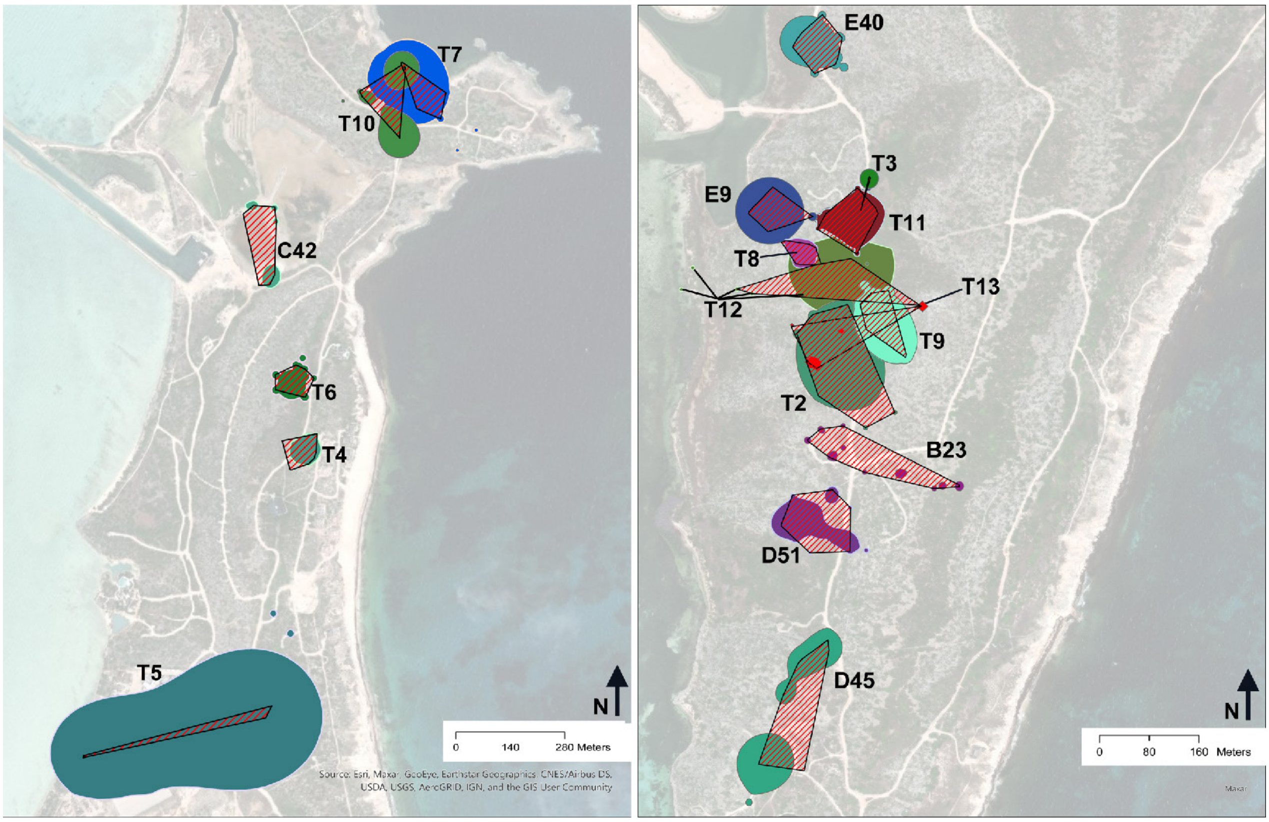

Figure 3. Spatial use models for boas in the study, with boas on the north of the island to the left, and boas from the south of the island to the right. Coloured polygons represent 50 % BBMMs for each boa. Striped polygons represent MCPs for each boa, overlaid on the BBMMs for comparison. Note that BBMMs can have more than one polygon for an individual, and that some MCPs and BBMMs are very different from each other, for example boa T13. Small circles outside the main BBMM polygons are single location observations of an individual.

for those receiving button transmitters, while the mean transmitter to mass ratio proportion was 2.0 % (range 0.2–3.0 %). One boa (T13) was confirmed to be heavily gravid in August 2018 via handheld ultrasound.

Implantation surgeries resulted in zero attributable deaths throughout the experiment, although we suspect (but were unable to verify) that boas T5 and T10 were killed by vehicular traffic during the study. Of the 20 surgeries performed, 15 were without any complications nor health concerns during subsequent observations. Three individuals (T1, T3, and T4) showed signs of minor health concern (details below) that resulted in the transmitter and individual being removed earlier than desired from the study. A further two individuals (T7 and E40) were found to have lost their transmitters, presumably through pressure necrosis, and the wounds had healed when the snakes were relocated by happenstance.

Boa T1 was recaptured 31 July 2018 showing signs of pressure necrosis from its subcutaneous button-type transmitter 16 days post-surgery. Nevertheless, the fascia and muscle underneath the transmitter appeared healthy, so the transmitter was removed, the necrotic tissue was trimmed, and the wound was cleaned and sutured. Boa T3 was recaptured on 8 August 2018 and was also exhibiting signs of pressure necrosis, so the transmitter was similarly removed. Boa T4 appeared healthy throughout August 2018, but when located on 6 January 2019 the antenna was found to be protruding from the skin and the snake had lost 10 % of its mass. The transmitter was removed, the surgical site was lavaged with sterile saline, the necrotic tissue debrided, the site re-sutured, and the animal was given a dose of ceftiofur crystalline free acid intra-muscularly (IM). Boa T5 was initiated on 29 July 2018 and, apparently unaffected by the surgery, was found to have consumed a 350 g female *Cyclura carinata* iguana on 4 August 2018. The distention caused by this meal, constituting 41 % of the mass of the snake, caused suture rupture, which was easily cleaned and repaired.

The button-type and barrel-type transmitters were expected to have battery life of six months or one year respectively. Nevertheless, transmitter signals for boas T6, T8, T9, and T11 could not be located 4–5 months after implantation. As the island is easily traversed in its entirety, the boas were likely not lost, and instead the transmitters most likely failed early.

Spatial Analyses

One boa (T1) was not included in further analyses owing to the short tracking duration (seven locations) prior to transmitter removal. The remaining 18 boas were tracked between 10 and 25 days each (mean = 16 days), with a maximum of 204 days between tracking sessions. Between 16 and 40 location recordings were obtained for each boa (mean = 26.8, total = 483). Boas moved on average a total of 1,361 m while being tracked (median = 732 m; range = 192–9,419 m; Table 3). Eight boas (within the same cohort) were observed to overlap each other's home ranges both spatially and temporally (Fig. 3). Overlap calculations

Figure 4. Many boas were observed actively foraging or resting in the open during tracking. Clockwise from top left: a large female rests at night underneath a *Cocothrinax* palm; boas were observed using coastal ironshore wrack habitat for the first time, a female observed crawling just before sunset.

ranged from 0.07–0.74 (on a scale of 0–1), with a mean overlap proportion of 0.28 (Table 4).

Data from eight of the 18 boas suggested that range residency had been observed, as evidenced by effective sample sizes (Table 3) and variograms (Supplementary material Appendix I). RD calculation using wAKDEs for boas that had established range residency (Table 3, Supplementary material Appendix II) resulted in an average 50 % RD of 0.39 ha per boa (range 0.18–0.82 ha) and an average 95 % RD of 1.83 ha per boa (range 0.88–3.99 ha). For our BBMMs, we found an average 50 % OD of 0.76 ha per boa (range 0.41–1.97 ha).

Our calculation using MCPs (Supplementary material Appendix III) yielded an average RD of 0.70 ha per boa (range 0.01–1.74 ha). We found similar values for our KDE calculations (Supplementary material Appendix III), with an average 50 % RD of 1.17 ha per boa (range 0.18–2.73 ha) and an average 95 % RD of 5.30 ha per boa (range 0.26–13.11 ha).

No correlation was found between the number of locations obtained per boa and the distance a boa travelled (Spearman rank correlation ρ = -0.15, P = 0.54) nor the OD measure using BBMM (ρ = 0.35, P = 0.15). Similarly, our RD measures were not correlated with the number of locations per boa for 50 % wAKDE (ρ = 0.04, P = 0.88) nor 95 % wAKDE (ρ = 1.88, P = 0.45). But our measures of RD were significantly positively correlated with the number of observations per boa for MCP (Pearson correlation coefficient = 0.71, P = 0.0008), 50 % KDE (ρ = 0.48, P = 0.04), and 95 % KDE (ρ = 0.59, P = 0.01). When restricting these correlations to just the eight range resident boas, none of the RD nor OD estimates were significantly correlated with the number of locations obtained (ρ = 0.12–0.69, P = 0.06–0.78).

DISCUSSION

Over the course of 20 months, space use estimates were generated by radio tracking 19 female *C. chrysogaster*. Taken together, boa home range (RD sensu lato) is likely between 0.7 and 1.2 ha. Our measures of RDs are strongly influenced by the number of locations obtained, suggesting that we could likely improve these estimates with more data. But, reassuringly, our estimates of total distance moved, as well as our ODs, were not correlated with the number of locations obtained. We were not able to generate enough location fixes in both winter and summer to make comparisons between seasons, despite this being an original component of the study design.

Our RD (wAKDE) and OD (BBMM) models yielded complimentary results for space use, with each model

Table 3. Spatial use data obtained for *Chilabothrus chrysogaster* females on Big Ambergris Cay, Turks and Caicos Islands. Data for weighted autocorrelated kernel density estimates (wAKDEs) are shown, which are estimates of home range (RD). Both 95 % (home range) and 50 % (core area) estimates, with confidence intervals (CI) are shown. Brownian bridge movement model (BBMM) is an estimate of OD. One boa (T1) of the original 19 was excluded owing to the small number of tracking observations (n = 7). All areas are in hectares. DOF area is the degrees of freedom area, equivalent to the effective sampling size. Values less than 5 indicate range instability. Bold indicates boas that were found to have range residency (stability). Xbar is the average of values from boas exhibiting range residency.

ID	DOF area	95% wAKDE	95% CI	50% wAKDE	50% CI	BBMM 50%
T2	**34.4**	**3.99**	**2.77, 5.43**	**0.73**	**0.64, 0.81**	**1.97**
T3	0.50	32.47	0.03, 163.79	7.61	0.75, 14.93	0.07
T4	**17.6**	**1.15**	**0.68, 1.75**	**0.23**	**0.19, 0.27**	**0.41**
T5	2.65	166.43	29.74, 418.5	42.33	23.21, 59.9	15.42
T6	**11.8**	**1.23**	**0.63, 2.02**	**0.33**	**0.26, 0.39**	**0.61**
T7	4.37	6.37	1.87, 13.58	1.47	0.96, 1.95	2.55
T8	**18.0**	**0.88**	**0.52, 1.32**	**0.18**	**0.15, 0.21**	**0.19**
T9	2.49	5.71	0.94, 14.68	1.35	0.72, 1.93	0.94
T10	4.32	6.07	1.76, 12.98	1.52	0.98, 2.01	1.51
T11	**17.0**	**1.32**	**0.77, 2.01**	**0.37**	**0.31, 0.43**	**0.71**
T12	**35**	**1.84**	**1.28, 2.49**	**0.19**	**0.17, 0.21**	**0.75**
T13	3.93	6.09	1.63, 13.42	1.62	1.02, 2.17	0.06
B23	2.27	5.13	0.75, 13.66	1.28	0.66, 1.86	0.11
C42	1.99	9.35	1.28, 26.07	2.38	1.14, 3.52	0.27
D45	2.90	6.20	1.23, 15.12	1.60	0.91, 2.24	1.28
D51	**7.28**	**3.03**	**1.25, 5.60**	**0.82**	**0.60, 1.02**	**0.71**
E9	3.68	2.15	0.54, 4.84	0.58	0.36, 0.78	0.97
E40	**11.94**	**1.22**	**0.63, 2.01**	**0.30**	**0.24, 0.36**	**0.71**
$\bar{x}$	19.13	1.83	—	0.39	—	0.76

Table 4. Proportions of overlap between pairwise AKDE RDs of boas observed to cross ranges during the study period. Overlap is the Bhattacharyya coefficient, which is a measure of the closeness of two samples, on a scale of 0 (no overlap) to 1 (complete overlap). Individuals in bold were found to be range-resident. Dof is the degrees of freedom, with values < 5.0 indicating insufficient sample sizes, which are also shown.

Boa 1	Boa 2	Dof	95 % CI low	Overlap	95 % CI high
2	9	24.8	0.02	0.09	0.28
12	**9**	8.9	0.04	0.23	0.64
13	**2**	5.53	0.48	0.74	0.94
13	9	4.96	0.001	0.07	0.64
$\bar{x}_i$	$\bar{x}_i$	—	—	0.28	—
Insufficient sample					
7	10	0.44	0.40	0.88	1.0
12	**2**	< 0.001	—	—	—
12	**8**	< 0.001	—	—	—
12	**11**	< 0.001	—	—	—
13	**8**	2.52	0.001	0.13	0.9
13	**12**	< 0.001	—	—	—

producing a mean space use between 0.39 (core area, 50 % wAKDE) and 1.83 (home range, 95 % wAKDE) ha per range-resident boa (Table 3). Boas that were not found to be range resident produced considerably larger estimates of RD and OD, which is expected from the lack of precision given the data for those boas. Our OD estimates (50 % BBMM) tended to be in-between range sizes of the 50 % and 95 % wAKDEs (Table 3).

More traditional measurements of RD, such as MCP, resulted in a similar mean estimate of home range (0.70 ha); albeit with a broader range of estimates among boas (0.01–1.74 ha; Supplementary material Appendix III). Whereas KDE estimates tended to be somewhat larger (mean home range size 0.57–2.51; Supplementary material Appendix III). Instructively, the difference we calculated for our MCP versus KDE estimates captures the sensitivity of traditional geometric (i.e. MCPs) versus probabilistic approaches (KDE) in estimating features of spatial ecology. Though slight in our dataset, this disparity serves as a reminder that these different methods shed light on different biological questions (also see Fig. 3). For example, KDE is the weighted probability distribution of the total space that an animal uses. Hence, when animals move between disjunct locations along a narrow corridor, KDE captures the distance in between these locations as part of the distribution estimation. MCP can yield a similar outcome if there are point locations that widen a corridor between disjunct locations, but if the polygon is narrow, then the total estimate of space use is much lower. Further, it is clear that approaches which are explicit in first estimating range residency as well as correcting for small sample size and autocorrelation (Fleming et al., 2019; Silva et al., 2022) yield very different estimates of RD. Our weighted AKDE using range-resident boas suggested that the actual RD was much smaller than what would be found using traditional KDE (Table 3). This is the opposite of what has been suggested in the literature (Fleming et al., 2015), that autocorrelation might underestimate space use, but it nevertheless is an important result that shows the value of accounting for sample size, range residency and autocorrelation.

Novel Habitat Use

Habitats on Big Ambergris Cay vary from marshy salina to mangrove to open cactus scrub to nearly closed-canopy coppiced forest. *Chilabothrus chrysogaster* have been observed using all available habitat types on the island except for mangroves (Reynolds & Gerber, 2012; Reynolds et al., 2020). Most radio-tracked boas stayed exclusively in one type of habitat (coastal scrub), which is the most dominant habitat on the island (Fig. 3). But, during this study some novel natural history insights were observed, including regular discovery of boas in habitats not previously known to be used (Fig. 4). For example, several boas were located foraging out in the wrack line along the rocky limestone coastal shore (Fig. 4), an area we

Table 5. Comparison of spatial use among species of the genus *Chilabothrus*. Note that these data are not directly comparable, as different methods were used. Data for *C. chrysogaster* are reported only for range-resident individuals. AK = 2-dimensional Adaptive Kernel.

Species	OD (method)	RDM (method)	Reference
C. chrysogaster (n = 8)	0.76 ha (BBMM)	1.83 ha (95% AKDE) 0.39 ha (50% AKDE)	This study
C. inornatus (n = 11)	—	0.01–1.8 ha (95% MCP) 0.0006–0.664 (50% MCP)	Puente-Rolón& Bird-Picó, 2004
C. inornatus (females, n = 9)		0.02–9.7 ha (50% MCP) 0.7–44.7 ha (95% MCP) 0.1–4.7 ha (50% AK) 2.0–66.8 ha (95% AK)	Wunderle et al., 2004
C. inornatus (males, n = 9)		1.2–8.5 ha (50% MCP) 2.6–68.1 ha (95% MCP) 0.3–3.8 ha (50% AK) 3.6–105.5 ha (95% AK)	Wunderle et al., 2004
C. strigilatus (n = 6)	—	0.03–2.0 ha (100% MCP)	Knapp & Owens, 2004
C. subflavus (cave, female, n = 1)	—	1.12 ha (50% MCP) 2.51 ha (95% MCP) 0.81 ha (50% AK) 4.78 ha (95% AK)	Miersma, 2010; Koenig, 2019
C. subflavus (cave, male, n = 2)		0.20–0.34 ha (50% MCP) 0.75–2.25 ha (95% MCP) 0.16–0.63 ha (50% AK) 1.10–5.92 ha (95% AK)	Miersma, 2010; Koenig, 2019
C. subflavus (surface, female, n = 7)	—	0.64–6.63 (50% MCP) 2.16–19.56 ha (95% MCP) 0.57–4.09 ha (50% AK) 3.12–22.04 ha (95% AK)	Miersma, 2010; Koenig, 2019
C. subflavus (surface, male, n = 4)	—	0.20–0.34 (50% MCP) 16.28–70.11 ha (95% MCP) 0.02–2.81 ha (50% AK) 0.59–64.95 ha (95% AK)	Miersma, 2010; Koenig, 2019

had not previously looked for boas under the assumption they would not use this habitat. While two other members of this genus (*C. exsul* and *C. strigilatus*) have been found resting under wrack debris lying on sand in the Bahamas (Sheplan & Schwartz, 1974; Tolson & Henderson, 1993), no other boa in the Caribbean has been noted to forage nor actively move along rocky wrack lines. Further, some boas were observed heading out into the red mangrove forest for days at a time and were found actively foraging (although no predation events were recorded). One boa (T12; Fig. 3) moved so far out into the red mangroves *Rhizophora mangle* that it was over 20 m from shore, entirely over water. When located, RGR had to avoid a blacktip shark *Carcharhinus limbatus* that was swimming just beneath the boa. Five other members of the genus (*C. angulifer*, *C. gracilis*, *C. striatus*, *C. inornatus*, *C. strigilatus*) are known to regularly use mangrove (*Avicennia* and/or *Rhizophora*) habitats (Sheplan & Schwartz, 1974; Henderson & Powell, 2009; Rodríguez-Cabrera et al., 2020; Reynolds et al., 2023).

Conservation and Comparisons

Only three of the 14 species of the genus *Chilabothrus* have published spatial data using telemetry, yet these provide some valuable comparisons to our data (Table 5). Broadly defined, 95 % RD home ranges of Turks and Caicos boas (0.88–3.99 ha) were similar to cave-associated populations of Puerto Rican boas (0.01–1.8 ha) and Jamaican boas (0.75–5.92 ha), but not to other populations of these species (Puente-Rolón & Bird-Picó, 2004; Wunderle et al., 2004; Miersma, 2010; Koenig, 2019). Non cave-associated Puerto Rican boas had 95 % RD home ranges between 0.70–105.5 ha, while non cave-associated Jamaican boas had 95 % RD home ranges between 0.59–70.11 ha (Table 5). Presumably, cave-associated boas have smaller home ranges owing to a concentration of food resources near caves (bats). Lizard densities on Big Ambergris Cay are exceptionally high (authors' pers. obs.) which could suggest that Turks and Caicos boas needn't have large home ranges to find food. Similarly, Bahamas boas have RD home ranges between 0.03–2.0 ha in areas with high concentrations of iguana hatchlings (Knapp & Owens, 2004).

Radio telemetry and spatial analyses have been used to demonstrate that habitat fragmentation negatively impacts snakes, supporting the need for protected areas and low impact zones of habitat, especially for threatened species. Indigo snakes *Drymarchon couperi* were found to have reduced survival in fragmented landscapes owing to human interaction (Breininger et al., 2012), and timber rattlesnakes *Crotalus horridus* required some protected area in which to overwinter (Nordberg et al., 2021). The habitat on Big Ambergris Cay is certainly being fragmented, particularly by the many roads that now cross the island. Indeed, we suspect that some of our study animals were killed on roads and buried to hide the evidence from us, as we have seen evidence of this for non-study animals (RGR & GPG, pers. observ.). But we found two important conclusions regarding the chances for persistence of the species: 1) the home ranges of large adult females are generally small, less than 2 ha (Table 3); and 2) home ranges of these females can overlap in time and space (Table 4). Overlapping home ranges have been found in Burmese Pythons in Florida (Hart et al., 2015), and this could have important implications if it indicates that the species is not territorial. Territoriality in snakes can limit densities (Webb & Shine, 1997), and given that the island is only 400 ha territoriality would significantly curtail the number of individuals that could coexist, especially as habitat is converted to developed areas. Jamaican boas *C. subflavus* were shown to not strongly overlap in their spatial use (Miersma, 2010; Koenig, 2019), and to-date this is the only example of potential territoriality among boas.

While the use of radiotelemetry involves the assumption that the behaviour of the telemetered individual is unaltered by the technique, and that data retrieved are representative of normal behaviour, previous studies have shown that growth, reproduction, and survival of many snake species are affected by implantation either directly or indirectly. These negative effects could come from the surgical intervention or from constant human disturbance (Webb & Shine, 1997). For example, black rat snakes *Pantherophis obsoleta* with versus without transmitters showed lower annual growth in mass but not length, and females produced lighter clutches of eggs relative to their body size (Weatherhead & Blouin-Demers, 2004). Such negative effects might be explained by impaired behaviour, cost of movement and infection. That is why we attempted to take such care with our surgical techniques, as well as minimise the number of locations of each animal, and allow periods of time with no tracking, particularly during the fall when parturition occurs (Tolson & Henderson, 1993).

There have been older (e.g. Macartney et al., 1988) and more recent (Crane et al., 2021) calls for standardisation of spatial data collection on reptiles, particularly snakes, such that meta-analysis can be conducted. Nevertheless, as Macartney et al. (1988) correctly posit, studying snakes is challenging, and it can be hard to study some species at regular intervals, to study more than a dozen at a time, or to conduct precise and comparable seasonal studies. That is perhaps why most studies of snake spatial ecology have been conducted in only a few geographic regions and a few species, for example in the United States on the genera *Crotalus* and *Pituophis* (Crane et al., 2021). Well-characterised studies, such as that on the cobra *Ophiophagus* in Thailand (Silva et al., 2018) and India (Barve et al., 2013; Rao et al., 2013) used only two individuals, while another on the anaconda *Eunectes murinus* used only eight (Smaniotto et al., 2020). Perhaps acknowledging the challenges of studying snakes, researchers such as Crane et al. (2021) now suggest that as much transparency as possible be included in spatial studies, including making data open, including specific definitions of what is being calculated (e.g. RDs versus ODs), and explicitly specifying influential model parameter values (e.g. smoothing parameters; Silva et al., 2022).

Future Directions

The size of snake home range can be influenced by sex (Breininger et al., 2012; Hyslop et al., 2014) as well as seasonal trends (Brito, 2003; Heard et al., 2004; Diffendorfer et al., 2005). While we attempted to generate enough data for seasonal comparisons, we were unable to do so. Therefore, future work on *C. chrysogaster* might include a seasonal analysis of movement. Importantly, no sex differences were found in RDs for Puerto Rican boas in two separate studies (Puente-Rolón & Bird-Picó, 2004; Wunderle et al., 2004). Free-ranging male Jamaican boas showed a trend of having larger RD home ranges (16.28–70.11 ha) than females (2.16–19.56 ha), but cave-associated populations did not (Table 5).

Female versus male movement has differed on both a per-move basis (mean daily movement per move) and monthly basis (mean daily movement per month) in *C. inornatus*, where males moved farther than females and females were immobile for significantly longer average time periods (Wunderle et al., 2004). Additionally, an increase of male snake movement can be seen throughout the reproductive season (April to June for *C. inornatus* in Puerto Rico, September for *Vipera latastei* in Portugal), suggesting that males actively search for females during specific months of the year (Brito, 2003; Wunderle et al., 2004). Additional data concerning spatial ecology associated with reproductive seasons of male and female *C. chrysogaster* would strengthen the home range and spatial use analyses for this species.

Finally, new technology being developed might allow easier, more efficient, and more robust data collection. Electronic trackers using global positioning satellites are becoming smaller, such that some are suitable for use on larger snakes (Smith et al., 2018). Drone tracking is another promising area of development (Hui et al., 2021), and while we attempted to use drones during August 2019 of our study, high winds made for impossible flight with a platform similar to that used by Hui et al. (2021). We also experimented with the use of Bluetooth trackers (Tile® Pro, paired with an iPhone® 7), but we found the square tags challenging to attach to snakes, and the tags had very poor reception if the snake was under a rock or not directly in line-of-sight. Nevertheless, technologies leveraging Bluetooth or radio frequency identification (RFID) technology might hold promise under certain conditions, and automated detectors are also showing some promise in specific deployment scenarios (DeGregorio et al., 2018).

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Data Accessibility Statement

All R code and raw data are available on Dryad (Doi https://doi.org/10.5061/dryad.crjdfn390).

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