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A stable home: Autocorrelated Kernel Density Estimated home ranges of the critically endangered Elongated tortoise

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Home range analysis is a standard and fundamental concept in ecology used to describe animal space use over their lifetimes. Connecting home range sizes with animal characteristics, location, and habitat can be used to inform conservation decisions. Reptiles are frequently lacking robust estimates of space use, particularly reptiles in tropical regions. Here we analyse a publicly available dataset, collected by the authors of this study, describing the movements of Critically Endangered Elongated tortoises *Indotestudo elongata*. The tortoise data included the locations of 17 tortoises (12 females, 5 males) collected on average once every three days for an average duration of 353.76 SE ± 33.10 days. We use these data to estimate the home range of Elongated tortoise, and explore how tortoise size and sex influences home range size. To mitigate issues resulting from low effective sample sizes and low temporal resolution of the data, we used a modern home range estimation method – Autocorrelated Kernel Density Estimators (AKDE). We found 14 of 17 individuals appear to be occupying a stable home range (using variograms to determine range residency). The average AKDE home range for all 14 individuals with range residency was 44.81 ± 10.44 ha. Bayesian Regression Models suggest comparable size estimates between male and female home ranges, despite males being physically larger than females in both mass and carapace length. These AKDE home range estimates have the added utility of being more comparable with other studies, less susceptible to errors from a suboptimal tracking regime, and are well positioned for inclusion in future meta-analyses.

Keywords: testudine, autocorrelated kernel density estimator, spatial ecology, space use, Thailand, *Indotestudo elongata*

INTRODUCTION

Understanding an animal's lifetime space use can yield insight into many aspects of its ecology. Most importantly we can identify the spatial requirements for maintaining healthy populations (Di Franco et al., 2018). We can better optimise our limited conservation resources by using methods that quantify animal space use – which is often explored via expensive and long-term datasets – in a more efficient manner (Laver & Kelly, 2008). The most commonly used metric for quantifying an animal's lifetime space use is termed home range (Burt, 1943; Worton, 1989; Fauvelle et al., 2017). Here we follow Silva et al. (2022) and define home ranges as the lifetime space use of an animal.

Information on home range sizes and location can begin to elucidate the decision-making processes animals engage in. Decisions based upon resources (Mitchell & Powell, 2004; 2012; Powell & Mitchell, 2012), topography, and habitat can all filter down to impact animal space use (Fieberg & Kochanny, 2005), and aids in understanding an animal's spatial niche (Xirouchakis et al., 2021). Understanding these phenomena in target species can have implications for both land-use and protected area management (Linnell et al., 2001; Viggers & Hearn, 2005; Houser et al., 2009). For example, Breininger et al. (2011) calculated home ranges for Indigo snakes *Drymarchon couperi* and concluded that the species needed large land tracts with substantial corridors between sites to avoid significant sources of road mortality. However, these tools only have value if the underlying data are treated properly, and the output is interpreted in a biological context.

Traditional approaches for estimating home ranges such as Minimum Convex Polygons (MCP), which essentially draw a polygon around the outermost collected points from a spatial dataset, are still widely used in herpetological research despite serious drawbacks (Crane et al., 2021). Specifically, MCPs tend to mis-estimate true space use (Silva et al., 2020) potentially leading to false conclusions when modelling predictors of home range size (Crane et al., 2021). The MCP approach is often inappropriate for comparisons among studies because it is sensitive to the tracking regime, tracking duration, and location error; and thus may yield flawed comparisons (Silva et al., 2020). If data

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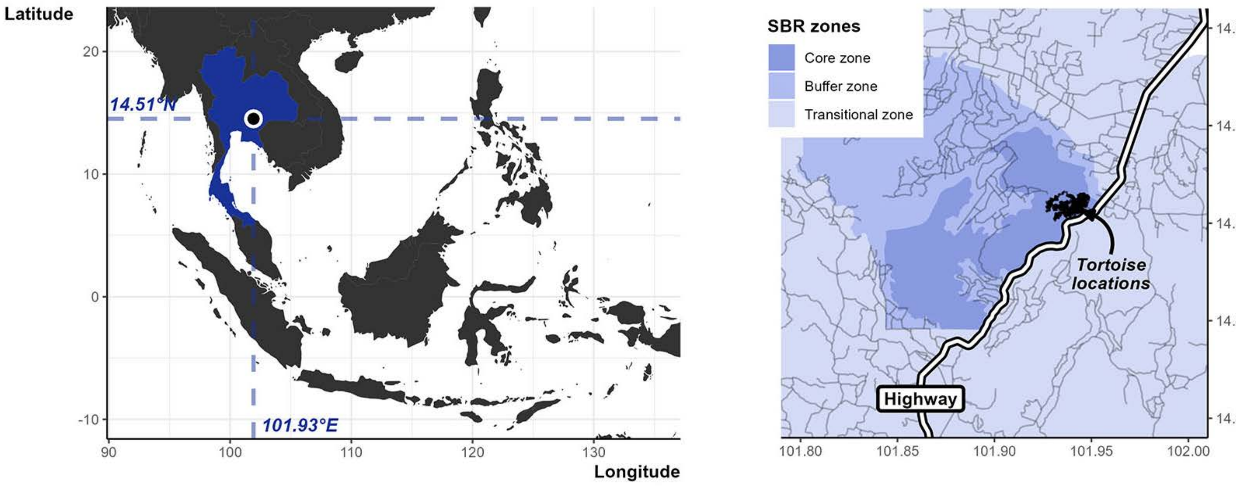

Figure 1. Study location in Thailand. Highlighted in blue is the location of the Sakaerat Biosphere Reserve (SBR) study site: 14.51° N, 101.93° E. The map is north orientated, 0.01° latitude = approx. 1.07 km. Second map shows the SBR in context, with the three zones making up the UNESCO Man & Biosphere Reserve (three levels of blue shading), the highway (black and white line), and minor roads (light grey lines).

are autocorrelated, Traditional Kernel Density Estimators (KDE) generate outputs which are not comparable between studies because KDEs are highly sensitive to changes in the duration and intensity of data collection, as well as kernel parameterisation (Averill-Murray et al., 2020; Silva et al., 2020, Noonan et al., 2019). In a simulation study, Silva et al. (2020) found that consecutive datapoints needed to be spaced multiple months apart in order to satisfy the assumption of independence required for traditional methods (e.g. KDEs). Substantial thought should therefore be put into the choice of home range estimator and the methodological approach before quantifying and comparing home range outputs (Signer & Fieberg, 2021). It is also critical to tie the biology of the target study species to the intended estimators and assess whether the tool is applicable given the nature of the animal's movement processes, the techniques used to collect the data, and the research question asked. Avoiding misestimation is particularly important given that spatial ecology research may inform conversation strategies (Fraser et al., 2018).

Tortoises are long-lived reptiles with a domed bony carapace, capable of moving substantial distances (but typically less than similar sized mammals and considerably slower) over time (Hailey, 1989; Nicholls, 2012). Numerous studies have evaluated tortoise spatial ecology using home ranges (e.g. Yager et al., 2007; McMaster & Downs, 2009; Monadjem et al., 2013; Drabik-Hamshare & Downs, 2017), but most studies have used traditional home range estimators that can impede inter-study comparisons. A review covering 20 years of reptile home range studies found that the reporting of methodological details in the majority of studies were insufficient for meaningful comparisons of home range size (Crane et al., 2021).

In Thailand, the Elongated tortoise *Indotestudo elongata* (Blyth, 1854) is listed as Critically Endangered due to its limited distribution (Rahman et al., 2019). This species is often exploited via illegal markets for local bushmeat, international/regional food, exotic pet, and medicinal trade (Ihlow et al., 2016). At present, we have limited information on home range sizes for *I. elongata*. Studies either lack details concerning range residency, which undermines assertions that the tortoises occupied a stable home range, or the studies use a mix of wild/translocated individuals where the impacts of translocation on home range size or stability are difficult to discern (Tharapoom, 1996; Ihlow et al., 2014; Ihlow et al., 2016). For our study population (Sakaerat Environmental Research Station, Nakhon Ratchasima, Thailand), we previously identified substantial individual overlap of potential movement pathways, a lack of conspecific avoidance or attraction, and potentially evidence of year-round reproductive activity (Ward et al., 2021); but have yet to explore the space requirements of this population occupying a small protected area.

Many factors can influence home range size, such as resource availability (Wasko & Sasa, 2009) or major disturbances such as fire (Drake et al., 2015). Often however, the inherent characteristics of the individual best predict home range size; for example, larger individuals can be expected to require larger areas in order to meet their energetic requirements. Alternatively, reproductively active male tortoises may cover greater distances and move more frequently to maximise access to females. In mating systems where reproductive activity is observed year-round, such as observed for Elongated tortoises (Ward et al., 2021; Ward, 2021), we would expect substantially larger male home ranges than females unless females were also to engage in mate searching behaviour.

Here we investigate home range sizes for the Elongated tortoises in Sakaerat Environmental Research Station, Nakhon Ratchasima, Thailand. To account for the irregular sampling of our data, we use Autocorrelated Kernel Density Estimators (AKDE) as suggested by Averill-Murray et al. (2020) and Silva et al. (2022). We assess radio-tracked male and female Elongated tortoises movements for range residency (to determine if home range estimation is viable) and provide baseline estimates of home range size. Finally, we attempt to ascertain if individual differences in home range sizes are related to body size or sex.

METHODS

Study site

The study took place within the core area of Sakaerat Biosphere Reserve (SBR), a UNESCO Man and Biosphere site. The site is split into three zones of varying levels of human impact: a transitional zone where agriculture and settlement are permitted, the buffer zone that is predominantly reforestation efforts, and the core zone that consists of primary forest. The protected core area is managed by Sakaerat Environmental Research Station which covers an area of approximately 80 km^2 (Fig. 1). The site primarily consists of seasonal dry evergreen forest and dry dipterocarp forest with patches of mixed deciduous forest and bamboo stands scattered throughout the landscape (Trisurat, 2010). We tracked all tortoises in the core area of the SBR where dry evergreen and dry dipterocarp forest merge to form an ecotone area (Ward et al., 2021). The study site also includes a small single-lane paved access road bisecting the dry dipterocarp forest to the main station grounds which are consistently occupied by staff and visitors but represent less than 1 % of the overall protected area. The protected area of the reserve is adjacent to the major four lane highway that connects Bangkok (south) and Nakhon Ratchasima (north).

Capture and radio-telemetry

We set out to select animals using random encounter surveys, with a total of 10 individuals being sought for a telemetry period of 12 months (n = 10; 2016/17, and n = 8, 2017/18, but one individual appeared in both years). We had great difficulty finding animals during the random surveys, so we supplemented this method with opportunistic findings through road encounters and through other observers who encountered individuals whilst in the reserve conducting other studies. After collecting individuals, we recorded tortoise biometric data (weight, straight carapace length, domed carapace length), took identification photos of the carapace, plastron, and face, and marked the individual with an ID number (M01 - Male 1, F01 - Female 1, etc.) using a white paint pen. After measuring and marking, we attached radio transmitters (Holohil RI-2B 9g glue mount transmitter; Holohil Systems Ltd, 2021; https://www.holohil.com/) using a non-toxic industrial epoxy (Gurit industries Ltd). Using the epoxy resin with a hardening solution (50/50 mix), we coated the underside of the transmitter and placed it firmly to the anterior scute of the animal's carapace above the head and nuchal scute. We then placed globules of the resin mix on the 20 cm long antenna and affixed it to the lateral scutes of the tortoise toward the posterior. The following day we released the animal at the same location they were caught and resumed tracking the individual the day after. We aimed to track 10 individuals, locating each individual once every two days. We undertook tracking in pairs, using one tracking radio receiver. The tracking regime was not always strictly adhered to due to team turnover, weather, and other external factors. During our second telemetry period (2017/18), we focused on female tortoises.

Home range estimates

We used Autocorrelated Kernel Density Estimators (AKDE) to calculate tortoise home ranges (Fleming & Calabrese, 2017; Fleming et al., 2015). The manual collection of radio-tracking data, compared to regimented or automated GPS collection methods, makes AKDE an excellent analysis method to help address unforeseen lapses in data collection (e.g. due to staffing limitations, equipment failure, or inclement weather) particularly with the weighted AKDE function in the ctmm package (Calabrese et al., 2016; Silva et al., 2022; Fleming et al., 2018), which corrects for unrepresentative sampling in time.

We used the ctmm package (Calabrese et al., 2016; Fleming & Calabrese, 2021) to generate variograms for each individual, which visualise the average square distance travelled by the individual within given time lags (termed semi-variance). Using the variograms, we visually determined whether an individual's movements suggested range residency (a flattening of the semi-variance values), which is an assumption required for estimating home ranges with AKDEs (i.e. tortoises tend to remain within their home range areas, and do not exhibit nomadic or migratory behaviours). In further analyses we only included those ranges determined to be stable (n = 14). Via the ctmm package we fit a number of movement models (ctmm's default range of models) using several processes: Ornstein-Uhlenbeck (OU), Ornstein–Uhlenbeck Foraging (OUF), and Independent Identically Distributed (IID). While the IID process is analogous to a traditional KDE approach assuming independent points, the OU process accounts for a central tendency in the animal movement (i.e. range residency or home range). The OUF process is largely similar to OU but also accounts for autocorrelative structures in the velocity of movement. We fit each of these processes in two forms: isotropic and anisotropic, to cover instances where the home range may be more circular or elliptical, respectively.

We fit the movement models (using all of the aforementioned processes) using the perturbative hybrid residual maximum likelihood method (pHREML; Fleming et al., 2019) and used AICc to select the best fitting movement model for each individual. We also recovered the home range crossing time and effective sample sizes (approximately the tracking duration divided by average home range crossing time; Silva et al., 2022). Effective

Table 1. Tracking summary by individual. ± indicate standard error associated with means

ID	Data points	Start date	End date	Days tracked	Tracking time lag (hour)	Moves
F01	119	16-03-2016	16-03-2017	365	74.24 ± 4.63	94
F02	111	23-03-2016	28-02-2017	342	74.62 ± 8.1	86
F03	121	10-04-2016	19-03-2017	343	68.6 ± 5.19	108
F04	122	08-04-2016	18-03-2017	344	68.23 ± 4.46	115
F05	227	08-04-2016	26-08-2018	870	92.39 ± 25.15	211
F06	98	22-10-2017	28-08-2018	310	76.7 ± 5.04	94
F08	99	22-10-2017	31-08-2018	313	76.65 ± 4.72	95
F09	102	27-10-2017	26-08-2018	303	72 ± 3.17	99
F10	90	21-11-2017	31-08-2018	283	76.31 ± 4.55	76
F12	88	14-11-2017	28-08-2018	287	79.17 ± 5.32	78
F14	89	21-11-2017	01-09-2018	284	77.45 ± 5.27	80
F15	90	22-11-2017	28-08-2018	279	75.24 ± 4.9	64
M01	128	16-03-2016	16-03-2017	365	68.98 ± 4.39	101
M03	129	01-04-2016	19-03-2017	352	66 ± 4.33	84
M04	124	05-04-2016	21-03-2017	350	68.29 ± 5.26	103
M05	130	16-04-2016	19-03-2017	337	62.7 ± 4.26	105
M06	94	03-06-2016	17-03-2017	287	74.06 ± 6.32	81

sample size highlights the amount of information available to the home range estimator once redundant location information resulting from autocorrelation is accounted for. Finally, we estimate weighted AKDE home range areas (Silva et al., 2022), selecting the 95 % contour to represent their home range area and using the point estimate of the 95 % contour for comparisons.

Comparisons

Due to the small sample size, and lack of a priori hypotheses, we elected to use Bayesian tests of difference to explore how home range size differed between sexes, and in relation to mass (Ellison, 2004). We used the same Bayesian methods to describe differences in mass and carapace length between the sexes. We used a student t-distribution as the response distribution, and the three model formulae were:

1. AKDE 95 % contour point estimate ~ 0 + sex, sigma ~ sex
2. Mass ~ 0 + sex, sigma ~ sex
3. Carapace length ~ 0 + sex, sigma ~ sex

We used weakly informative priors for the three models, based upon means and spreads reported in a previous publication concerning these tortoises (Ward et al., 2021). For a prior describing the home range estimates, we used the previously reported dynamic Brownian Bridge Movement Model (dBBMM) 95 % confidence areas – mean of 26.17 ha, standard deviation (SD) of 33.48 ha (Ward et al., 2021). Although dBBMM estimates do not target home ranges like AKDEs, the way dBBMM confidence areas describe the uncertainty associated with the animal's movement path (calibrated by the animal's movement capacity) can help infer an animal's overall space requirements. We set the carapace length prior to a mean of 37.1 cm and SD of 4.37 cm; and we set the mass prior to a mean of 1.75 kg and SD of 0.5 kg. All three priors were normally distributed with a lower bound limit of 0. For the spread we used two standard deviations to weaken the strength of the prior.

We ran the models with the following setting: 4 chains, 2000 iterations, and 1000 iterations of warmup. Due to convergence issues, we modified two MCMC settings: we increased the adaptive delta to 0.90, and the maximum tree depth to 15.

We also ran a model to explore the relationship between home range area and mass. We included a group effect to account for the possible non-independence of home range sizes within each sex. Our final formula was: AKDE 95 % contour point estimate ~ 1 + Mass + (1|sex). As we had less prior knowledge concerning the home range~mass relationship, we elected to use a very

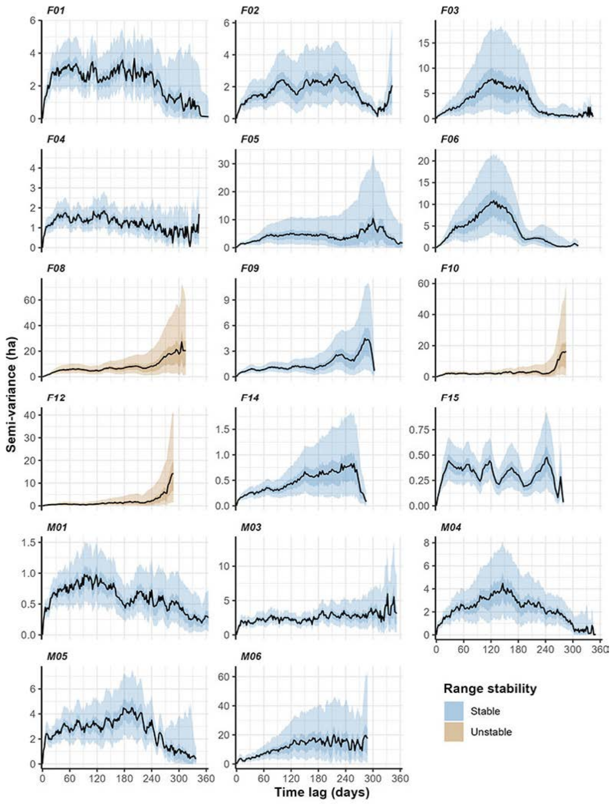

Figure 2. Variograms displaying semi-variance of home range area estimates with x-axis starting at the beginning of each individual's tracking period. Shaded areas display the 50 % (dark shading) and 95 % (light shading) confidence intervals. Blue coloured areas are ranges considered stable; orange coloured areas are ranges considered unstable.

weakly informative prior to constrain the beta coefficient describing the effect of mass (Lemoine, 2019): a Cauchy prior with location 0.1 and scale 5. We ran this model using different settings due to the increased difficulty for the model to satisfactorily converge: 4 chains, 8000 iterations, 2500 warmup iterations, and adaptive delta of 0.95, and a maximum tree depth of 15.

For all models, we used $\hat{R}$ values (~1), trace plots, acf plots, and posterior predictive check plots to check model convergence (see https://osf.io/rxu6f/).

RESULTS

Tracking summary

We tracked 17 individuals (12 females, 5 males) for a mean of 353.76 ± 33.10 days (range 279–870; Fig. S1). We found tortoises frequently relocated between subsequent data points, with a mean of 98.47 ± 7.73 moves (range 64–211) compared to a mean of 115.35 ± 7.94 data points (range 88–227; Table 1). The gap between each data point was approximately 74.25 ± 3.13 hours (range 24–5712; the largest gap was the lag between F05 tracking in 2016/17 and 2017/18; Fig. S2).

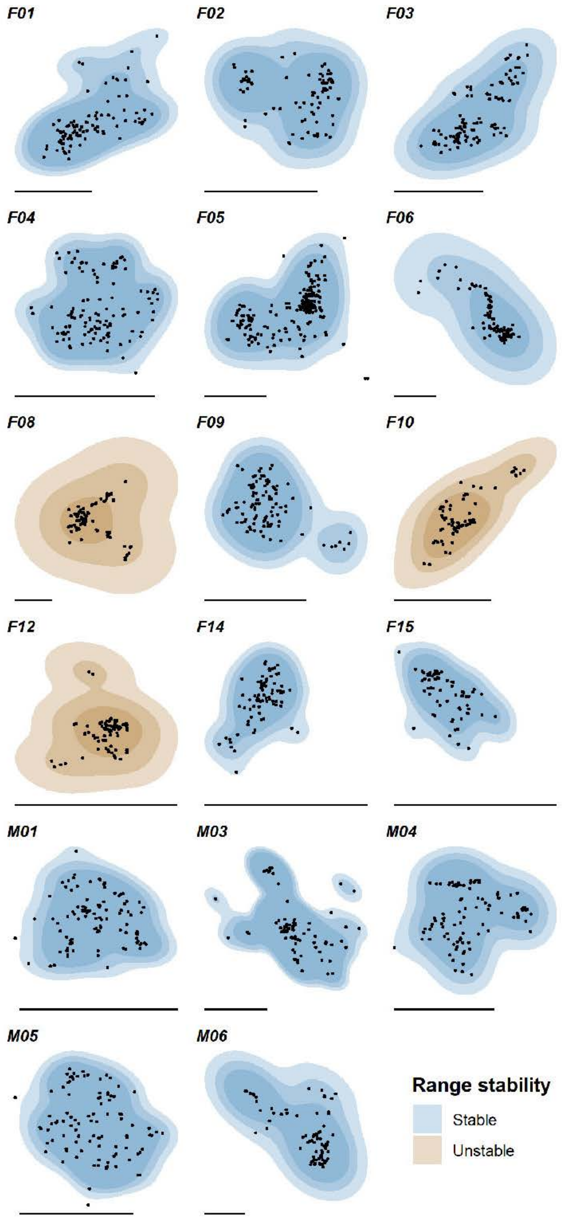

Figure 3. The 95 % contour AKDE area estimates mapped. Upper 95 % confidence level is shown with the darkest shading, the mean point estimate is shown with a medium level of shading, and the lower 95% confidence interval is shown with the lightest shading. Scale bars represent 500 m. Blue coloured areas are ranges considered stable; orange coloured areas are ranges considered unstable.

Home range

Despite the mean lag time between tracks being over three days (74.25 hours) and high uncertainty associated with semi-variance (e.g. F03 and F06 variograms), we found that 14 out of 17 individuals' ranges appear to be stable – therefore, meeting the range residency assumption required for AKDE home range estimation (Fig. 2). On average the home range crossing time was 17.24 ± 4.37 days, with considerable individual variation (2.71–72.25 days). Males had lower home range crossing times (6.51 ± 1.48 days) than females (21.70 ± 5.73 days). Effective sample size for home range estimation was on average 29.48 ± 4.97, justifying the use of pHREML fitting method and weighting the AKDE areas (Silva et al., 2022). Effective sample size ranged from 3.39 to 75.06, and four individuals had exceptionally low effective sample sizes

Table 2. Autocorrelated Kernel Density Estimate (AKDE) results per range resident individual and the movement model used to produce the estimate. Also included are the morphometric data (mass and carapace length). Lower and upper confidence intervals are 95 %. AKDE estimates are in hectares.

ID	Mass (kg)	Carapace length (cm)	AKDE lower CI	AKDE estimate	AKDE upper CI	Movement Model
F01	1.5	37.1	30.31	45.66	64.1	OU anisotropic
F02	1.82	37.2	17.35	25.3	34.72	OU isotropic
F03	1.73	38.6	29.4	48.77	72.97	OU anisotropic
F04	1.72	37.9	16.3	21.61	27.65	OU anisotropic
F05	1.85	37.2	24.75	34.74	46.4	OU anisotropic
F06	1.53	36.2	32.05	86.85	168.49	OU anisotropic
F09	1.67	35.9	11.73	18.81	27.54	OU isotropic
F14	1.25	32.1	4.2	6.56	9.45	OU isotropic
F15	1.6	33	2.99	4.67	6.7	OU anisotropic
M01	2.07	40.3	9.47	12.84	16.72	OU anisotropic
M03	1.84	38.5	31.16	40.94	52.03	OU anisotropic
M04	1.79	38.2	28.07	40.63	55.48	OU anisotropic
M05	1.54	36.8	31.2	39.66	49.12	OU anisotropic
M06	2.05	39.7	61.47	101.12	150.49	OU anisotropic

(<10: F06, F08, F10, F12; Table S2). The low effective sample sizes mirror the lack of stability displayed in the variograms of F08, F10, and F12, and supported our exclusion of these individuals for further analysis.

The 14 individuals who met the range residency assumption suggest a mean 95 % contour home range of 44.81 ± 10.44 ha (varying between the lowest CI of 2.99 ha and a maximum CI 415.36 ha; Fig. 3; Table 2). The top performing movement models selected were either Ornstein-Uhlenbeck (OU) or Ornstein-Uhlenbeck foraging process (OUF), which correspond to correlated positions but uncorrelated velocities, or correlated positions and correlated velocities, respectively (Table S3). Both movement models incorporate restricted space use. Five of the 17 individuals had multiple models within 2 delta AICc (Table S3), but three of these were the non-range resident individuals. The remaining two were F06 where OU AICc was 1.3 lower than OUF, and F09 where both models were OU, and only differed in reflecting more isotropic (more circular) versus anisotropic (more elliptical; delta AICc of 1.5) home ranges. Models that relied on assumptions of Independent Identically Distributed data (IID; i.e., traditional KDE approach) consistently produced the highest dAICc values (Table S2).

Comparisons

The AKDE area estimates did not differ substantially between males and females. Although female ranges were on average 11.09 ± 16.62 ha smaller, the 95 % Highest Density Interval (HDI) suggest that male ranges could be up to 43.66 ha larger, or up to 21.84 ha smaller than female ranges. The wide HDI can be summarised as a 75.23 % chance that males have a larger range (Fig. 4).

Carapace length was considerably more different, with females on average having a 2.34 ± 1.13cm shorter carapace (95 % HDI 0.21–4.60) and a 97.95 % chance that males have a longer carapace. Mass showed a similar pattern. On average females weighed 0.22 ± 0.14 kg less (95 % HDI 0.5 lighter–0.04 heavier), resulting in a 94.63 % chance for males to weigh more (Fig. 4).

The exploration of mass and AKDE area reveal a minor positive relationship between mass and AKDE area ($\beta = 2.88$). However, the credible intervals were wide (95 % CRI -19.74–37.05; Fig. 5) and the R^2 values were exceptionally low (Conditional R^2: 0.022, Marginal R^2: 0.001) suggesting the model fails to capture any important variation in home range sizes.

DISCUSSION

We described the home range of a Critically Endangered tortoise species *Indotestudo elongata* using a modern home range estimation method (Autocorrelated Kernel Density Estimators [AKDE]) that is capable of mitigating the biases stemming from low-resolution (and low effective sample size) telemetry data. We found that variograms indicated range residency for 14 of 17

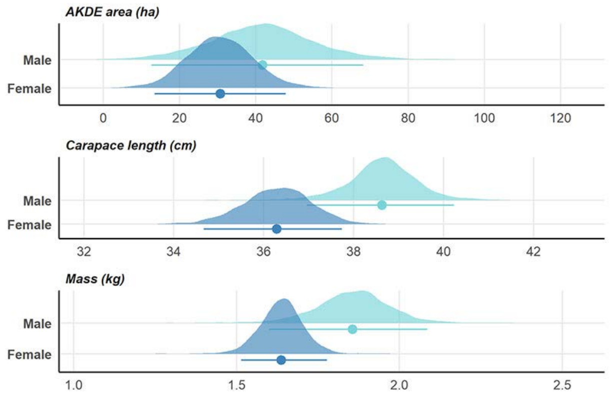

Figure 4. Bayesian comparisons between Female and Male tortoises with stabilised ranges. Point estimates are displayed with 95 % mean Highest Density Continuous Intervals.

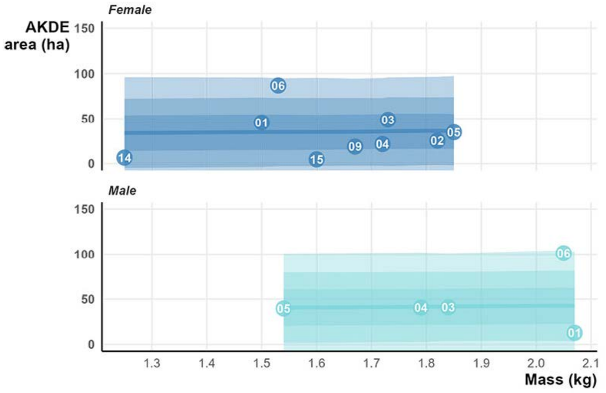

Figure 5. 95 % contour AKDE area in relation to the mass (kg) of female (dark blue) and male (light blue) tortoises. Points are the recorded mass and areas of all individuals with their ID number. Shaded areas indicate the 95 % (lightest shading), 80 % (medium shading), 50 % credible intervals (darkest shading).

tracked tortoises. While Bayesian Regression Models revealed that both mass and carapace length were larger for male tortoises, the AKDE ranges appeared on average only slightly larger for males and are broadly comparable with female tortoise ranges.

Generally, in testudines, there is a slight dimorphism in body size with males being larger than females. This size difference is more apparent in giant tortoise clades, such as the Galapagos and Aldabra tortoises (Chiari et al., 2009; Turnbull et al., 2015), but less apparent in mid-sized forest dwelling species of the tropics including *I.elongata*. Our evidence suggests tracked male individuals were larger than females, which is in line with an earlier study on the same species (Ihlow et al., 2016). However, given the lack of published information on *I. elongata* and due to potential impacts of harvesting, quantifying the size and age ratio (and observable dimorphism from that) within a population remains challenging. In some areas there is no difference between the sizes in adult males or females; however, without accurate age measurement it is impossible to discern whether individuals are still growing adults or at full size (Sriprateep et al., 2013).

As semi-variance represents the average square distance within all given time lags, it ultimately measures the spatial variability in movement behaviour. For short time lags, upward curvature of semi-variance indicates directional persistence. When the semi-variance spikes across intermediate time lags it indicates comparatively faster diffusive behaviour (the animal is covering greater distances), whereas spikes in the furthest/longest time lags typically correlate with migration or range shifting behaviour. While we are unable to pinpoint the cause of the spikes, seasonal variation is a likely candidate. Our study site sees strong seasonal shifts in rainfall that brings forth new vegetative growth, fungal blooms, and *I. elongata* breeding activity (Ihlow et al., 2016, Ward et al., 2021). This species is said to be a water loving testudine, with many anecdotal reports of *I. elongata* frequenting bathing locations and favouring wetlands or riparian habitats where it can be semi-submerged (Ihlow et al., 2016; Ward, 2018). We did not record many areas of such habitats within the current study site, so it is possible that during the heavy rains the tortoises moved into areas of softer clay, shallow pools, or ditches where they could wallow.

As we found an exceptionally low R^2 value while attempting to predict home range sizes based on either tortoise size or sex, we suspect there are alternative, more direct drivers of home range sizes. For example, some individuals spent substantial time along dry stream beds with steep slopes that may have limited movement in certain directions. Other individuals used more complex landscape features; for example, ecotone areas between deciduous dipterocarp forests and dry evergreen forests that could have influenced movements and the resulting home range estimates (Heit et al., 2021). Other factors that may have influenced home range variation – that we were unable to capture with our models and the resolution of our tracking data – could be seasonal shifts in resource availability (e.g. water access, usually provided by depressions along rocks) that might lead tortoises to concentrate movements toward, or cease movements once arriving at, these temporary resources.

Following the suggestions of the STRANGE framework (Webster & Rutz, 2020), we highlight a number of limitations regarding the sampling. The number of animals we could feasibly work with and the absolute (and effective sample size) resulting from our achieved tracking regime limit the inferences we can draw. We conducted this study with a revolving team (of which only two individuals were consistently present) both surveying for study animals and tracking animals. The cryptic camouflage of the carapace in the target species made finding the target species purely via systematic or random surveying unfeasible. We were able to supplement these randomly encountered individuals with animals encountered on the main access road to Sakaerat Environmental Research Station or brought to us by personnel in the area. However, with a limited team and up to 10 simultaneously tracked animals we were limited in the tracking interval we could logistically implement. The initial goal of once-per-two-day tracking became more difficult over time as a result of team turnover. The training period required for new team members ultimately resulted in a team with the capacity to track three individuals per day, thereby limiting each tortoise to three tracks per week. With the inconsistencies of trackers and the occasional absences of members through sickness, conferences or vacations, we produced an inconsistent tracking regime (much like what typically occurs in other radio-tracking studies). Rainy seasons further introduced heterogeneity into our tracking regime, as we were forced to alter protocols to both protect our equipment and keep up with highly mobile animals post rain. The radio-tracking receivers, antennas and accessories are all highly susceptible to water damage, and high humidity causes interference with the radio signal – the latter led to lost animals on numerous occasions. These inconsistencies violate the assumptions of traditional Kernel Density Estimators and make Minimum Convex Polygons fraught with difficulty (due to lack of comparability with other studies that had consistent or differing tracking regimes).

Even with tracking inconsistencies, we were able to yield biologically useful results for 14 of 17 individuals using AKDEs and bias-mitigating measures (pHREML fitting and area weighting). Thereby, providing further evidence that barriers caused by logistic constraints may be overcome when the resulting heterogeneity in sampling are accounted for appropriately. The home range estimates we provide could be used to inform the space requirements for *I. elongata* in protected areas comparable to the Sakaerat Biosphere Reserve, while also providing useful priors for designing spatially explicit capture recapture studies capable of robust estimates of *I. elongata* populations.

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Data availability

Data is available via Movebank (Study ID: 1128208874, originally published as part of Ward et al., 2021; https://www.movebank.org/; Kranstauber et al., 2011; Wikelski et al., 2021), and has been additionally published alongside analysis code and model outputs on the Open Science Framework (https://osf.io/rxu6f/). We conducted all analysis and visualisation using R v.4.0.3 (R Core Team, 2020) via RStudio v.1.4.1103 (R Studio Team, 2020). We used the R packages listed in Table S1 (with citations auto-generated using the grateful v.0.0.3 package; Rodríguez-Sánchez & Hutchins, 2020).

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Author contributions

Conceptualisation - YM, MW, CTS; Methodology - YM, MW, CTS, BMM, IS; Formal analysis - BMM, IS; Visualisation - BMM; Investigation - YM, MW; Resources - TA, SW; Writing - original draft - CTS, BMM, MW; Writing - review and editing - YM, MW, CTS, BMM, IS, TA, SW; Supervision - TA, SW; Funding acquisition - YM, MW

Competing interests

The authors declare no competing interests.

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