

Nonchalant neighbors: Space use and overlap of the critically endangered Elongated Tortoise

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Abstract

To prevent population extirpations we need to understand species' requirements, especially for critically endangered species inhabiting biodiversity hotspots. Studying animal movement provides insights into such requirements and gauges protected area effectiveness. Southeast Asian protected areas are becoming isolated; thus, we must ensure existing areas can sustain populations. We used multi-year radio-telemetry with the critically endangered Elongated Tortoise (*Indotestudo elongata*) to assess: movements, space-use, and conspecific overlap in a small protected area –Sakaerat Biosphere Reserve, Thailand. Movements were weakly seasonal, increasing in hot and wet seasons compared to the dry season. Individuals annual space-use varied (4.24–55.57 ha), while frequently overlapping with conspecifics. Conspecific comparisons revealed males (n = 5) moved similarly to females (n = 12) but used larger areas. Explorations of temporal avoidance versus attraction reveal more instances of conspecific attraction than avoidance (20:8). Avoidance/attraction behavior appeared disconnected from carapace length or mass; therefore, that conspecific interaction patterns may potentially be a result of resources (mates or food) rather than competition (i.e., no apparent evidence of smaller individuals avoiding larger individuals). Female-female attraction suggests an absence of resource exclusion tactics at the temporal resolution of our data. Male-female attraction may indicate reproductive movements coinciding with hot season, but we failed to detect significant interactive effects linking conspecific attraction or step length to proximity to breeding activity. Our observations of annual space-use and space overlap present critical components when designing robust population assessments; assessments that will underline any successful *I. elongata* conservation effort. When considered in the context of previous work connecting space overlap with population viability, our results suggest the biosphere reserve population of *I. elongata* to be reproductive, with enough resources to be potentially viable; the findings help emphasize the importance of even relatively small protected natural areas.

Keywords

tropical, step-selection, conspecific interaction, dBMM, space-use, seasonality, Thailand, Sakaerat
Biosphere Reserve

1. INTRODUCTION

To counter increasing biodiversity loss (Ceballos et al., 2015), we must understand species requirements. The International Union for Conservation of Nature Red List provides a guide for which species need conservation efforts. But without strong foundational understanding of species requirements based on sound science (Morin, Fuller, Royle, & Sutherland, 2017), the limited conservation resources risk being misallocated (Polasky et al., 2008).

Areas and taxa with limited protected area coverage are of particular concern, especially when paired with extensive human pressure and knowledge gaps –such as in Southeast Asia (Allan et al., 2019; Felton et al., 2009; Hughes, 2017b; Lawler et al., 2006). Southeast Asia covers four biodiversity hotspots experiencing rapid forest loss and fragmentation threatening some of the rarest and richest habitats in the world (Bellard et al., 2014; Dinerstein et al., 2017; Hughes, 2017a). Under worst case scenarios, Southeast Asian forest cover could decrease by 5.2 million ha over the next 30 years (Estoque et al., 2019). Small remnant protected areas may be the final refuge for critically endangered species.

In small protected areas, habitat is often restricted by hard external barriers limiting animal movement options and resources (Fahrig, 2007). A window into how animals use and compete for limited resources can be gained through studying animal movement (Gunther & Smith, 2004; Van Moorter, Rolandsen, Basille, & Gaillard, 2016). With the boom in bio-logging technology researchers have provided unprecedented insight into animal migrations (Mueller et al., 2011), breeding (Glaudas & Rodríguez-Robles, 2011; Jellen & Aldridge, 2014; Jellen, Shepard, Dreslik, & Phillips, 2007), predator-prey interactions (Courbin et al., 2016; Vogt et al., 2018), resources (Prange, Gehrt, & Wiggers, 2004), and intraspecific competition (Antunes, Oliveira-Santos, Tomas, Forester, & Fernandez, 2016; Bauder et al., 2016). All of these possible insights positions movement ecology as a valuable asset in garnering developing conservation-relevant knowledge (Fraser et al., 2018).

Identifying conspecific interactions requires quantifying both spatial and temporal overlap between individuals. Attraction to conspecifics can affect spatial distributions (Beauchamp, Belisle, & Giraldeau, 1997; Campomizzi et al., 2008), leading to aggregations (Quinn & Graves, 1999; Stamps, 1988). Whereas, asociality and avoidance can cause more limited areas of conspecific overlap (Guy, Bohan, Powers, & Reynolds, 2008; Nilsson, 2006; Pizzatto, Child, & Shine, 2008), potentially resulting in greater areas of habitat required to sustain similar populations. Levels of intraspecific competition interact with population density, the increase of latter often being a conservation goal (Belovsky & Slade, 1995; Cooper, Dimopoulos, & Pafilis, 2015; Dumont, Crête, Ouellet, Huot, & Lamoureux, 2000; Flockhart, Martin, & Norris, 2012; Újváry, Horváth, & Szemethy, 2012). Therefore, we must be wary of unintended cascading effects, such as population declines through resource depletion, when increasing population densities, especially in small protected areas with limited resources.

We explored the spatial ecology of the critically endangered Elongated Tortoise, *Indotestudo elongata* (BLYTH, 1854) in a small (8,000 ha) protected area isolated by agriculture and a highway. The *I. elongata* is suffering the same fate as many Southeast Asian species: exploited through multiple international and local trades (food-, medicine- and pet trade), with insufficient monitoring to identify effects on their wild populations (Ihlow *et al.* 2016). Despite a distribution spanning India, Southeast Asia and Southern China, *I. elongata*'s local population sizes, demography, dietary requirements, space use, breeding behaviors and habitat needs are poorly understood. There are approximately five projects that have collected data on four populations of this species until this project, each of which gathering data either from small samples, reintroduced individuals from trade, and/or animals in anthropogenic environments (Ihlow *et al.* 2016). Research into the diet, breeding, and space use of *I. elongata* has unsurprisingly led to varied results due to the spread of study locations and varied habitats, with some studies even being held in unique and unnatural settings (Tharapoom 1996, van Dijk 1998, Sriprateep *et al.* 2013, Rahman *et al.* 2014, Ihlow *et al.* 2016); further study in natural settings is required to understand *I. elongata*'s requirements.

Here we aim to expand the knowledge of *Indotestudo elongata* by determining the annual space-use, with an examination of seasonal movements (using dynamic Brownian Bridge Movement Model derived motion variance), conspecific interactions (using Integrated Step-Selection Functions), and whether tortoise size is associated with conspecific interactions. Strong connections between attraction/avoidance behaviors and tortoise size, paired with limited space overall, could suggest high competition over resources. Exploration of these aspects of tortoise ecology will help build towards a more coherent picture of their requirements, while gaining an insight into the health of the population and presenting key prior information for undertaking future population studies required for long-term conservation monitoring.

2. METHODS

2.1 Study site

We undertook this study at the Sakaerat Biosphere Reserve (SBR; 14.44–14.55°N, 101.88–101.95°E), a patchy landscape of protected forest in southern Nakhon Ratchasima, Thailand. The biosphere reserve has varying levels of human disturbance, within three policy delineated zones (core zone, buffer zone, and transition zone). Our study took place within the core zone of the SBR; where human disturbance was minimal, limited to educational groups, ranger patrols, and researchers visiting the SBR's research station.

The biosphere reserve protected area (core zone and a portion of the buffer zone) has approximately 7,800 ha of forested or semi-natural landscapes. The two dominant forest types are dry dipterocarp forest (DDF: 20% coverage), and dry evergreen forest (DEF: 60% coverage). The remaining 20% comprises bamboo forest, forestry plantations, open grassland, and research station grounds. The DEF consists of dense evergreen trees with heterogeneous understory and multi-story connectivity. The DDF is characterized by bamboo grasslands with sparse dipterocarp deciduous trees and low canopy connectivity, and is subject to major changes in structure across the year caused by annual fires in March. The fires result in fluctuations

of bamboo grass height, from a few centimeters (post fire) to 2m (wet season). Our work was based solely within DDF and DEF –the habitats used by *I. elongata*. Thus, our effort was centered in a 400 ha stretch of habitat including DEF and DDF, bounded by a four-lane highway to the south (Figure 1).

We used previously published results on seasonality based upon daily readings of temperature and rainfall from Sakaerat Environmental Research Station (Marshall et al., 2020b, 2020a; Sakaerat Environmental Research Station, 2018b). There are three seasons: hot (16th of March to 30th of September: $\bar{x} = 33.8 \pm 2.8^\circ\text{C}$, $\bar{x} = 2.5 \pm 7.9$ mm/day rainfall), wet (1st of October to 31st of December: $\bar{x} = 29.9 \pm 2.2^\circ\text{C}$, $\bar{x} = 5.9 \pm 11.1$ mm/day rainfall) and dry (1st of January to 15th of March: $\bar{x} = 29.0 \pm 3.5^\circ\text{C}$, $\bar{x} = 0.2 \pm 0.8$ mm/day rainfall).

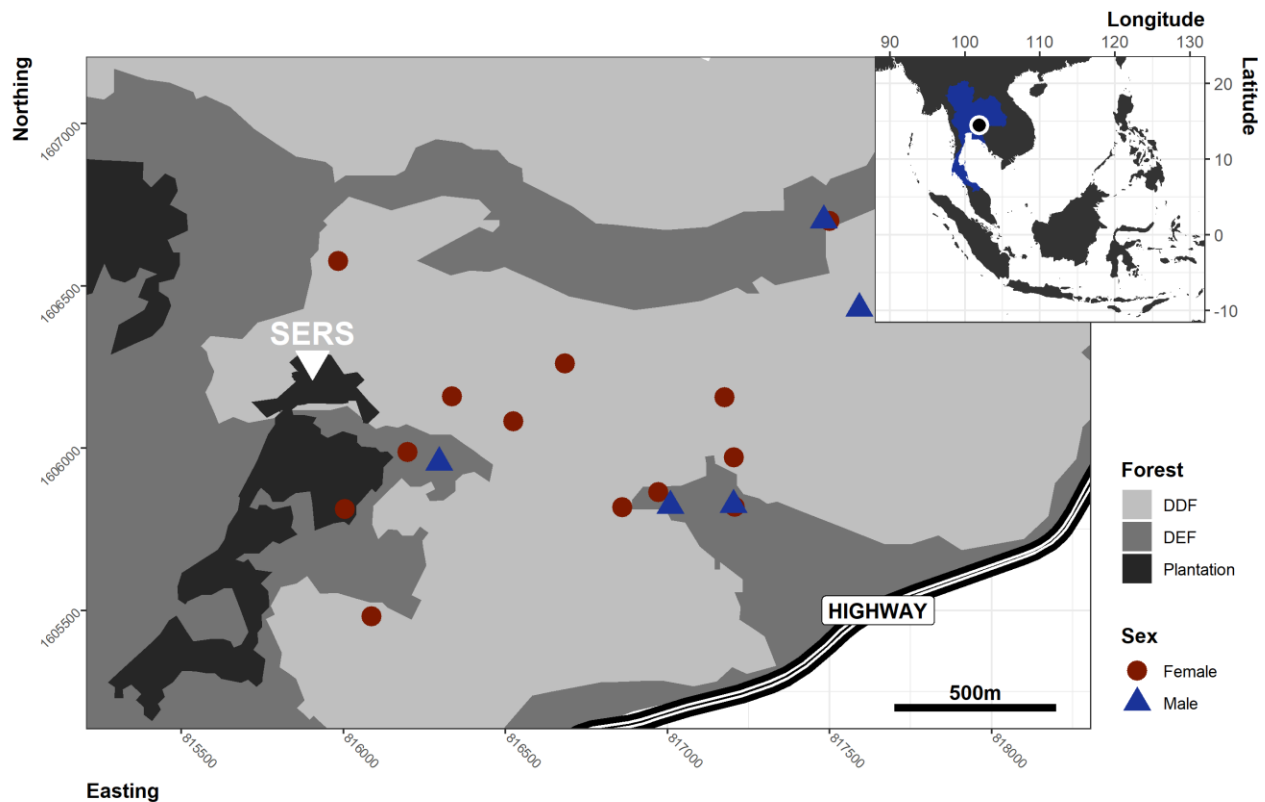


Figure 1. Study site location. Insert top right shows the Sakaerat Biosphere Reserve's location within Thailand and Southeast Asia. Larger map shows the forest types: dry dipterocarp forest (DDF), dry evergreen forest (DEF), and plantation (Sakaerat Environmental Research Station, 2018a); with the first data point locations of all tracked tortoises highlighting their sex (blue triangles = male, red circles = female). The location of the Sakaerat Environmental Research Station is highlighted with a white triangle. Highway position is illustrated by two black lines (OpenStreetMap contributors, 2017).

2.2 Study animals

We opportunistically sampled tortoises in the 400 ha target study area, supplemented by animals discovered ad-hoc during transit or via notations (detailed photographic records and/or live individuals given opportunistically to the research team). Upon capture, we recorded sex, mass (kg, to the nearest 10 grams), curved carapace length (cm, to the nearest 0.1 cm), curved carapace width, straight carapace length, and straight carapace width, of each individual. We excluded individuals under 0.8 kg mass and 11 cm straight carapace length to ensure we tracked only healthy adults. We attached transmitters (Holohil RI-2B, 10g) to the anterior carapace of the tortoise, and released them within 100m of their capture location.

We radio tracked ten individuals (five males, five females) captured between 16 March 2016 and 3 June 2016, and removed transmitters between 28 February 2017 and 21 March 2017. Between 22 October 2017 and 22 November 2017, we captured another eight females (one recapture from the previous year) and radio tracked this new set of individuals 26 August 2018 to 1 September 2018.

2.3 Data collection

A maximum of two technicians followed the Very high frequency (VHF) signal using a radio receiver (AOR 8000) to a tortoise's location on average every 71.35 hours (± 1.18 , 24–792 hours; see results for distribution of tracking time lags). We aimed to visually locate individuals upon each radiotrack, but when tortoises were not visible we used triangulation to obtain the individual's location within a 5m² area. Upon determining the individual's location we collected GPS coordinates (Garmin GPS64 Map or

eTrex10) using the 47N UTM zone coordinate system. Whenever possible we observed behaviors of tracked animals and recorded 21 observations suggestive of reproductive activity; including pink coloration of the eyes, ears and nasal membranes (indicative of blood flow increases to sensory organs, referred to later as “pink nose”), cohabitation of sleeping sites and mating (Senneke 2000, Ihlow *et al.* 2016).

2.4 Data, code, and software availability

We have made all data files and full analysis scripts available on Open Science Framework (URL: <https://osf.io/6vfp9/>). Tortoise tracking data is additionally available on MoveBank (MoveBank, <https://www.movebank.org>, ID: 1128208874).

We used *R* v.3.5.3 (R Core Team, 2019) and *R Studio* v.1.2.1335 (R Studio Team, 2019) for analysis and data visualization. We used packages: *dplyr* v.0.8.4 (Wickham, François, Henry, & Müller, 2019), *lubridate* v.1.7.4 (Grolemund & Wickham, 2011), *raster* v.3.0.12 (Hijmans, 2020), *reshape2* v.1.4.3 (Wickham 2007), *rgdal* v.1.4.3 (Bivand, Keitt, & Rowlingson, 2019), *tidybayes* v.2.1.1 (Kay, 2019), and *zoo* v.1.8.8 (Zeileis & Grothendieck, 2005) during data reading and manipulation; *adehabitatHR* v.0.4.16 (Calenge, 2006), *amt* v.0.0.6 (Signer, Fieberg, & Avgar, 2018), *bestNormalize* v.1.6.1 (Peterson & Cavanaugh, 2019), *brms* v.2.13.5 (Bürkner, 2018), *move* v.3.1.0 (Kranstauber, Smolla, & Scharf, 2016), *performance* v.0.4.8 (Lüdtke, Makowski, Waggoner, & Patil, 2020), *rgeos* v.0.4.2 (Bivand & Rundel, 2018), *sf* v.0.8.2 (Pebesma, 2018), and *wiqid* v.0.3.0 (Meredith, 2020) during analysis; *bayesplot* v.1.7.2 (Gabry, Simpson, Vehtari, Betancourt, & Gelman, 2019), *cowplot* v.0.9.4 (Wilke, 2019), *ggplot2* v.3.2.1 (Wickham 2016), *ggpubr* v.0.2 (Kassambara, 2018), *ggribes* v.0.5.2 (Wilke, 2018) *ggspatial* v.1.0.3 (Dunnington, 2018), *gtable* v.0.3.0 (Wickham & Pedersen, 2019), *ggtext* v.0.1.0 (Wilke, 2020), *scales* v.1.1.0 (Wickham & Seidel, 2019), and *scico* v.1.1.0 (Pedersen & Crameri, 2018) for data visualization.

2.5 Descriptive tests

We completed basic descriptive tests on the morphometric data and space-use of the tortoises, using \pm to indicate standard error where means are reported. To decide which morphometric characteristics to compare, we used a correlation matrix to examine collinearity. We chose two morphometrics that produced the greatest overall correlation. Using the two selected metrics (mass and curved carapace length) we compared male and female size with Bayesian comparative tests. We opted for Bayesian comparative tests because of our small non-random sample size likely deviated from assumptions required for parametric tests and frequentist statistics more generally. We used 10,000 iterations with 100 burn-in and 3 chains to generate the normal distributions that we used to compare the overlap differences in male-female space-use, mass, and curved carapace length. We judged convergence using \hat{r} values < 1.1.

2.6 Space-use and motion variance

Using the *move* package (Kranstauber et al., 2016), we generated dynamic Brownian Bridge Movement Models (dBBMMs) to estimate tortoise space-use. Dynamic Brownian Bridge Movement Models use constrained Brownian walks to produce utilization distributions, while accounting for location error and serial autocorrelation (Kranstauber et al., 2012). They produce more stable estimates of space-use than traditional estimators (Minimum Convex Polygons, Kernel Density Estimation) enabling comparisons, while still being suitable for low-frequency VHF tracking data (Silva, Crane, Marshall, & Strine, 2020; Silva, Crane, Suwanwaree, Strine, & Goode, 2018).

To estimate dBBMM and detect changes in motion variance (motion variance: a measure of how diffuse random walks are between known locations, used here as a proxy for activity), we selected a window size of 31 data points and a margin of 7 data points. This selection translated into a window calculated over 91.65 ± 0.46 days, and a margin of 20.63 ± 0.16 days. Because of the coarse tracking regime, we selected a window size sufficiently large to smooth sudden changes in movement caused by infrequent tracking,

while still capable of detecting seasonal changes. There were 39 instances where we collected two data points on the same day, as they lacked a specific timestamp we had to exclude one data point on each day. We set location error to 5m, which presented a generous estimate of overall GPS error in the study site forests. Selecting the appropriate contour to represent overall space-use is largely arbitrary, without consistent observations of behavior to infer biological importance, instead we chose to report the area generated from a range to demonstrate the sensitivity of area estimates (90%, 95%, and 99% contours).

We explored how motion variation differed between seasons using a Bayesian regression model (implemented via the *brms* v.2.13.5 package; Bürkner, 2018). The Bayesian regression model allowed us to implement an autoregressive term to correct for the strong temporal structure of motion variance values (i.e., the way motion variance values are calculated on a rolling basis within the dynamic Brownian Bridge Movement Model's margin and windows). The implementation of an autoregressive term in *brms* requires the response to be Gaussian distributed. To convert the heavily skewed motion variance values, we used the *bestNormalize* v.1.6.1 package to identify and perform the optimal transformation (orderNorm; Peterson & Cavanaugh, 2019). We used the transformed motion variance as the response, with *season* (dry season coded as the intercept) and *sex* (female coded as the intercept) as population effects, *individual tortoise ID* as a group effect, and an seventh order autoregressive term based on sequential datapoint number (seventh order was selected to match the margin size used to calculate motion variance). The final model formula was *normalized motion variance* ~ *sex* + *season* + (1/*individual tortoise ID*) + *ar*(*p* = 7). We ran the model with 5 chains, 5,000 iterations, and 1,000 iterations warm-up, using trace plots, acf plots, and rhat values to determine model convergence. Because we had very little prior information, we elected to use non-informative priors (the defaults in the *brms* package): Student t distribution (*df* = 3, *mu* = 0, *sigma* = 2.5). To explore model performance and results, we calculated median highest density intervals (using the *tidybayes* v.2.1.1; Kay, 2019), generated posterior predictive plots (using *bayesplot* v.1.7.2; Gabry et al., 2019), determined conditional and marginal R^2

(using *performance* v.0.4.8; Lüdecke et al., 2020), and visualized posterior distributions (using *ggridge* v.0.5.2 Wilke, 2018).

2.7 Conspecific overlap

Traditional approaches assessing space use overlap tend to rely on metrics that quantify the overlap of utilization distributions, home range contours, or both (Bauder et al., 2016). However, these metrics can underappreciate an important aspect of use overlap time. Animals do not inhabit their range homogeneously, shifting the utilization over time. We generated utilization distributions for smaller subsets of time, while retaining information on animal movement capability derived from dBBMMs based on the entire dataset. We could then examine how an animal's movements interact with the recent movements (subsetting utilization distributions) of another, rather than the overall space-use. To achieve this we adjusted code written by Schlägel et al., (2019) who used step-selection functions to detect avoidance or attraction in bank voles (*Myodes glareolus*). While Schlägel *et al.* (2019) used the *ctmm* package function *rolling_od()* (Calabrese, Fleming, & Gurarie, 2016), we adapted code from the *moveUD* v.1.1.0 package (Collier, 2016) to generate subsetting utilization distributions from dBBMMs. We used 7 data points on a rolling basis to generate a set of utilization distributions for each individual (each utilization distribution presented the potential space-use for a 7 data point period).

We used the subset utilization distributions as the primary predictor in step selection functions. For every data point we generated 100 random unused locations, whose location was based on the step and angle (drawn from gamma and Von Mises distributions respectively), and from which we extracted the nearest utilization distribution value (NAs were used when there was no utilization distribution within the previous 7 days). Then using *amt*'s (Signer et al., 2018) step selection functionality, we ran a model that used 7-data-point-utilization distribution values (scaled 0 to 1; *opponent*) to predict use/non-use ($case_ \sim opponent + strata[step_id_]$). We ran models that compared every individual's movement against all others utilization distributions where both tracking duration and 99% dBBMM contour overlapped. For

individuals whose 99% contour only marginally overlap, the models could fail to converge. We flagged convergence failures and excluded their results from further analysis. The resulting coefficients can offer insights if compared (Thurfjell, Ciuti & Boyce, 2014). For figures and descriptions, we summarized resulting coefficients by sex. We then separately tested for correlation of the coefficients against tortoise mass and curved carapace length with Spearman's rank test. We excluded F05 in these tests because we failed to collect unique morphometric measurements for her second tracking year (F05b).

After examining the initial model results, we created a second set of models that explored the possible interactions with breeding activity –whether breeding activity impacts attraction/avoidance (relationship with opponent's utilization distribution) and movement (relationship with step length). We specified this model as $case_ \sim opponent + opponent:diffbreed + sl_:diffbreed + strata[step_id_]$. Where *diffbreed* equaled the number of calendar days until/since an observation of breeding related behavior (in any year; Figure S1), and *sl_* is step length.

To supplement the step-selection functions, we explored the cohesion of movement direction and displacement using Dynamic interaction index (DI-index; (Long and Nelson, 2013). The DI-index operates under the assumption that the movement pathways are close enough to affect each other (Long et al., 2014); the overlap in dBBMM confidence areas provided adequate evidence to use the DI-index. Further the DI-index allowed for examination of movement path cohesion overtime (i.e., local movement cohesion; Long and Nelson, 2013) that enabled us to search for seasonal patterns. We used a cut off of 71.35 hours, i.e., considering any data points collected within this time frame as simultaneous. We ran the DI-index, both globally (entire individual's movement path) and locally (each movement path between data points), for every pairing of individuals that overlapped temporally.

3. RESULTS

3.1 Study animals

We tracked 17 individuals, who weighed on average 1.75 ± 0.06 kg (range: 1.25–2.1 kg), with an average curved carapace length of 37.1 ± 0.53 cm (0.32–0.40 cm). Overall, all body measurements (mass, curved carapace length and width, straight carapace length and width) were correlated (Figure S2). In subsequent analysis we used mass and curved carapace length as they had the greatest total correlation to other metrics. Tracked males ($n = 5$) were larger than tracked females ($n = 12$), by mass (mean difference = 0.15 ± 0.00 kg, 95% CrI = -0.16 – 0.45, 86.56% probability of a positive difference; Figure S3A, S4A), and curved carapace length (mean difference = 2.19 ± 0.01 cm, 95% CrI = 0.03 – 4.44, 97.42% probability of a positive difference; Figure S3B, S4B).

*Table 1. Summary of individual results. Data points = number of data points recorded; Days = number of days tracked for; Lag time = mean \pm SE time in hours between data points; σ^2m = mean \pm SE motion variance; Con.90, Con.95 and Con.99 = area of dBBMM contours in ha; Mass (g) = mass of individual at capture; Carapace (cm) = length of curved carapace at capture. * F05b represents the second year measurements for individual F5, who was used in both year's data collection.*

ID	Data points	Days	Lag time (hrs)	σ^2m	Con.90	Con.95	Con.99	Mass (kg)	Carapace (cm)
F01	120	365	73.61 ± 4.63	5.25 ± 0.37	42.54	55.57	87.99	1.50	37.1
F02	112	342	73.95 ± 8.05	3.37 ± 0.27	24.73	41.16	102.98	1.82	37.2
F03	127	343	65.33 ± 5.11	3.39 ± 0.31	25.99	32.65	48.31	1.73	38.6
F04	127	344	65.52 ± 4.45	4.1 ± 0.22	17.96	22.19	32.99	1.72	37.9

F05	133	344	62.55 ± 4.31	3.08 ± 0.26	10.35	15.70	27.56	1.85	37.2
* F05b									
(year 2)	95	288	73.53 ± 3.8	1.84 ± 0.12	13.17	16.95	24.81	-	-
F06	98	310	76.7 ± 5.04	1.57 ± 0.15	30.57	39.81	59.64	1.53	36.2
F08	99	313	76.65 ± 4.72	1.03 ± 0.09	14.86	20.90	35.47	2.10	38.0
F09	102	303	72 ± 3.17	1.17 ± 0.1	6.77	8.54	12.53	1.67	35.9
F10	90	283	76.31 ± 4.55	0.94 ± 0.07	8.47	11.91	19.55	1.66	35.4
F12	88	287	79.17 ± 5.32	0.53 ± 0.06	3.89	5.20	8.51	2.04	39.5
F14	89	284	77.45 ± 5.27	0.59 ± 0.05	3.24	4.25	6.51	1.25	32.1
F15	90	279	75.24 ± 4.9	0.38 ± 0.02	3.30	4.24	6.20	1.60	33.0
M01	134	365	65.86 ± 4.37	2.79 ± 0.17	14.56	19.42	32.66	2.07	40.3
M03	130	352	65.49 ± 4.33	6.91 ± 0.81	21.53	32.71	55.01	1.84	38.5
M04	130	350	65.12 ± 5.17	4.88 ± 0.27	29.84	39.28	62.25	1.79	38.2
M05	137	337	59.47 ± 4.21	10.97 ± 0.87	37.56	51.36	92.31	1.54	36.8
M06	99	287	70.29 ± 6.22	9.14 ± 0.78	24.60	40.05	84.34	2.05	39.7

3.2 Tracking data

We obtained 115.35 ± 7.94 (88–227) data points per tortoise, over a period of 353.76 ± 32.01 days (279–870 days [maximum includes a gap between tracking periods for F05]; Figure S5), resulting in a between track lag times of 71.35 ± 1.18 hours (24–792 hours; Figure S6). We recorded 98.47 ± 7.73 (64–211) relocations (any datapoint > 5 m from the previous datapoint) per individual (Table 1). We split the data of one female (F05) because she was tracked in both 2016 and 2017; we report and use both periods in overlap analysis, but only use 2016 space-use estimations in relation to morphometrics.

3.3 Space-use and motion variance

Dynamic Brownian Bridge Movement Models returned an average space-use estimate of 26.17 ± 4.06 ha at the 95% contour ($n = 17$, 90%, 18.87 ± 2.95 ha; 99% 45.58 ± 7.75 ha; Figure 2). The 95% areas of males ($n = 5$, 36.56 ± 5.23 , 19.42–51.36 ha) was larger than females ($n = 12$, 21.84 ± 4.89 , 4.24–55.57 ha; mean difference = 14.76 ± 0.05 ha, 95% CrI = -2.83 – 32.88, 95.17% probability of a positive difference; Figure S7).

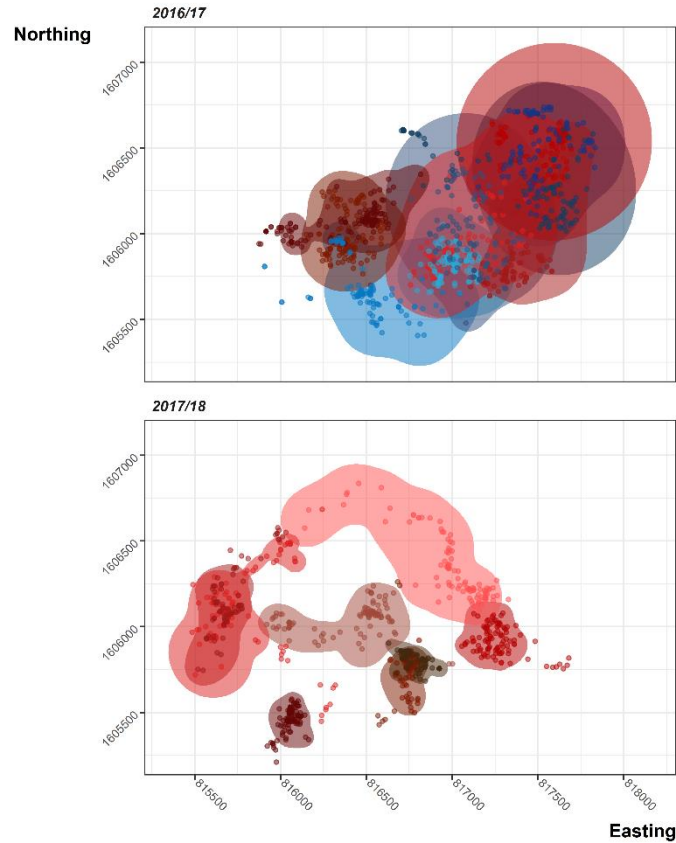


Figure 2. 95% dBBMM space-use estimates split between cohorts: 2016/17 and 2017/18. Red tones indicate female ranges, blue tones indicate male ranges. Mapped extent matches Figure 1.

Mean motion variance was $3.72 \pm 0.12 \sigma^2\text{m}$ (<0.001 – 41.21) and was over dispersed. Figure 3A (and Figure S8) suggests that tortoises activity was lower in the dry season. Females were most active in the wet season, males were most active in the hot season. Our Bayesian model converged successfully, and its results (Figure 3B) reflect the observations from Figure 3A ($n = 1727$; conditional $R^2 = 0.956 \pm 0.000$; marginal $R^2 = 0.934 \pm 0.002$, model diagnostic plots included at: <https://osf.io/6vfp9/>). However, the model shows there is considerable overlap between seasons and sexes motion variance values. The coefficients pertaining to hot and wet season's 95% credible intervals overlapped zero (hot = 0.04 ± 0.06 , 95% -0.07 – 0.15 ; wet = 0.08 ± 0.04 , 95% -0.01 – 0.17), along with the male motion variance coefficient (0.87 ± 0.90 , 95% -0.90 – 2.67). Overall seasonal and sex effects seem weak, likely driven by the consistently year-long appearance of low motion variance values. The apparent spikes in movements of

males appeared to coincide with observations of mating (Figure 3C; Figure 4), but were insufficient to clearly be detected in the model.

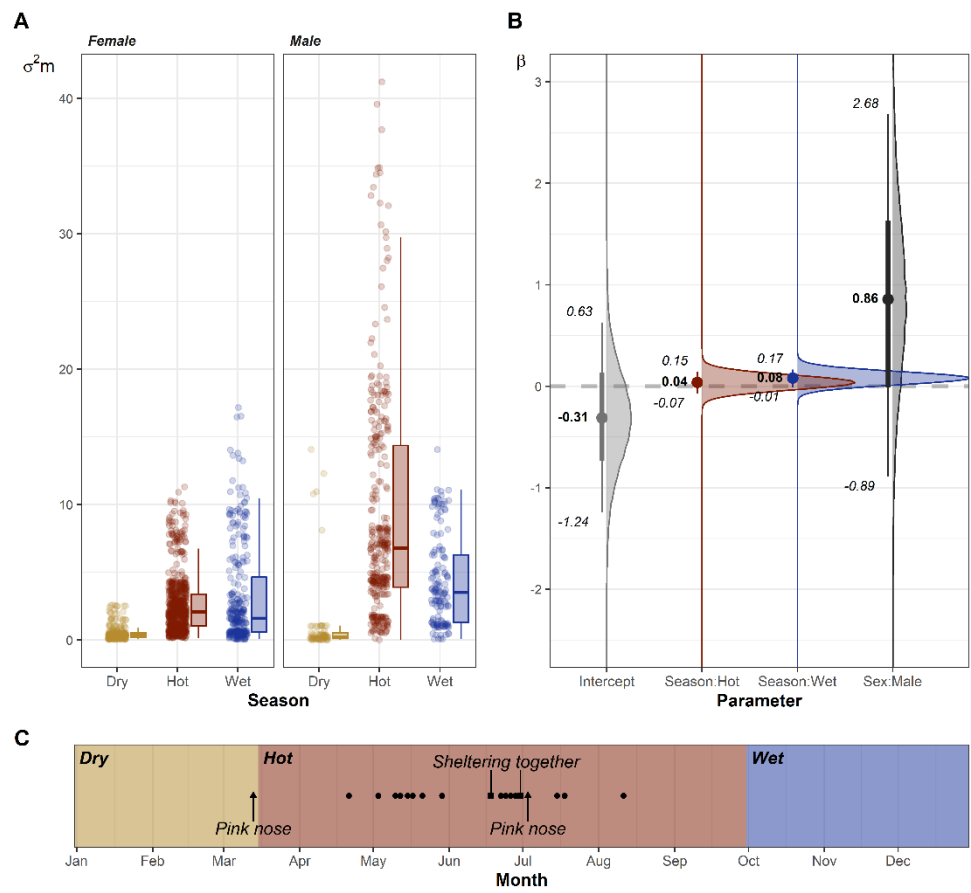


Figure 3. Seasonal differences in motion variance values and observations of mating behavior. *A) Box and jittered scatter plots of motion variance values split between female and male. B) Posterior distribution of model beta estimates, circles indicate point estimate means, thick and thin bars show the 66% and 95% credible intervals based on the median highest density interval. C) Observations of mating or mating related behavior in relation to the seasons (across both years). Circles: observed mating, Triangles: observations of individuals with pink noses, Squares: individuals sheltering together.*

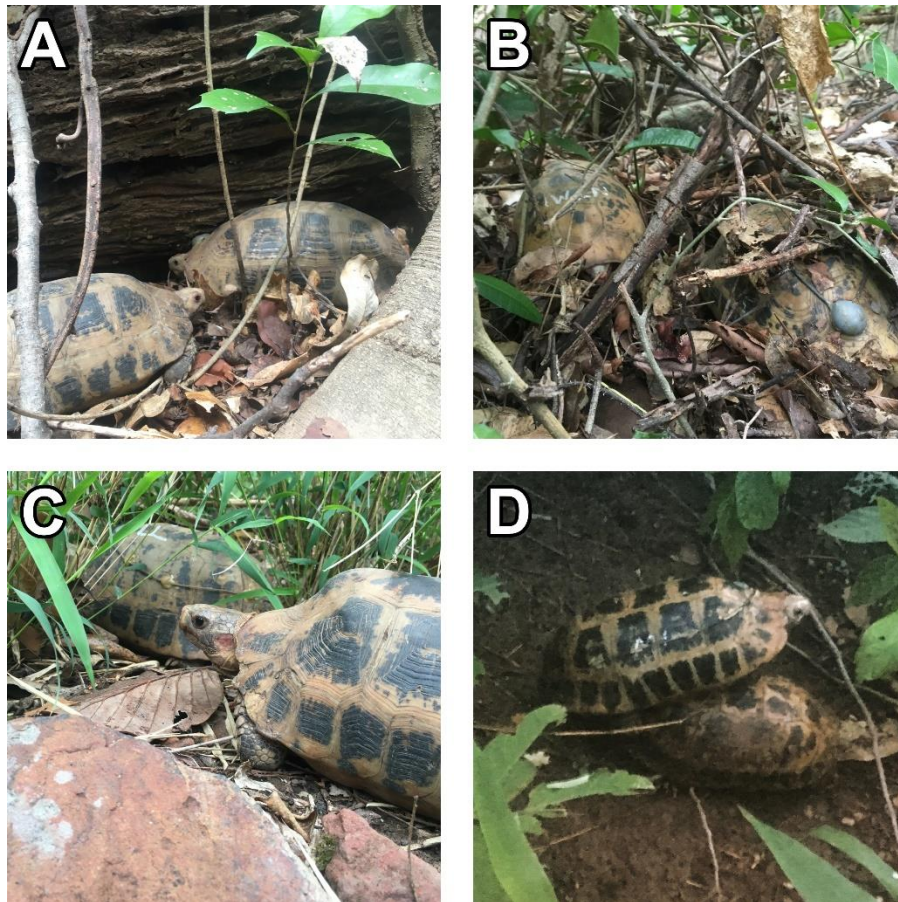


Figure 4. Photographs of observed mating-related behavior. *A) 24 June, individual F05; B) 26 June individual F03; C) 28 June individual F04; D) 18 July individual M01. Original photographs have been square cropped for display.*

3.4 Conspecific overlap

Between our 18 tracking sets (F05 was included in each year) there were 306 possible comparisons between an individual's tracking data and another individual's utilization distribution. Of those 306 pairings, 236 did not have tracking data nor 99% dBMM contours that overlapped. We modelled

seventy pairings, but excluded four models because they failed to converge. Ultimately, we were left with 66 models providing estimates of attraction versus avoidance suitable for further analysis.

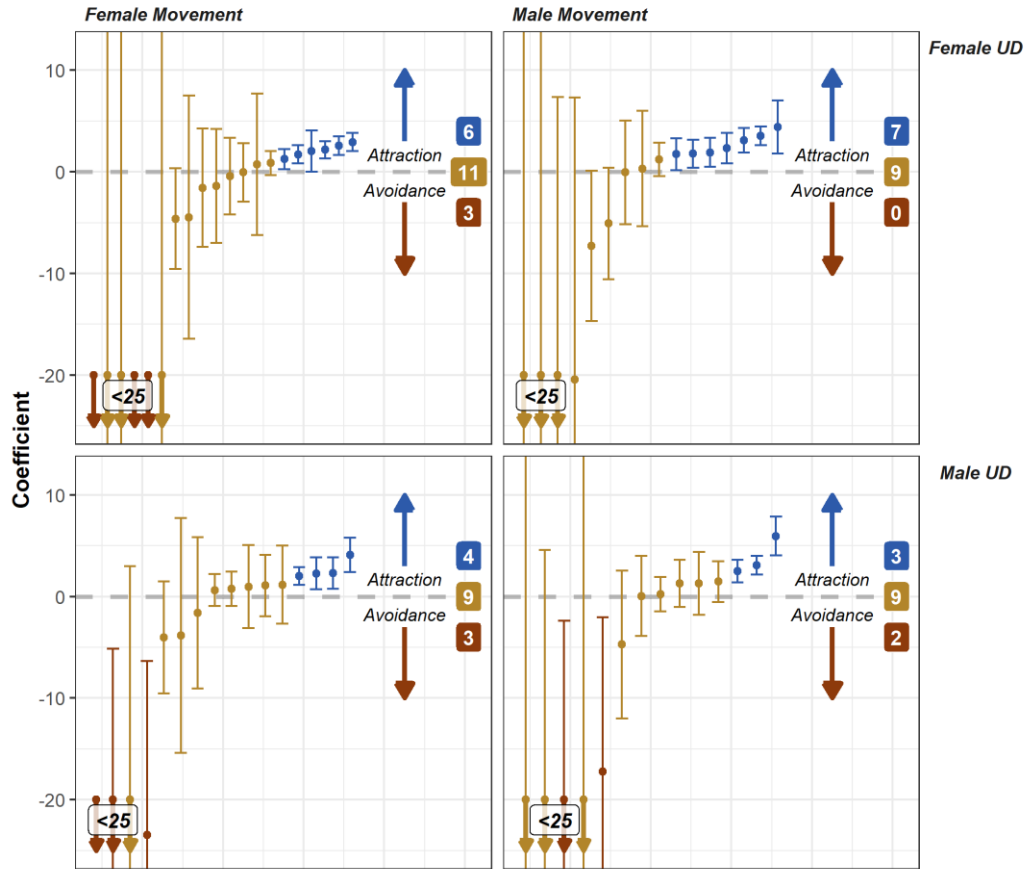


Figure 5. Model coefficients describing attraction or avoidance between individuals. Error bars represent the standard error on the coefficient estimate. Point and error bar colors indicate the direction of the effect and whether the confidence intervals overlap zero: blue = positive with no overlap, yellow = overlap therefore no clear direction, red = negative with no overlap. Right hand colored labels show the count of coefficient estimates indicating attraction (blue), overlapping zero (yellow), and avoidance (red). Colored arrows bottom left indicate instances where point estimates are extremely low and plotting would have obscured overall patterns (excluded range = -395808 – -41).

Overall, we saw more attraction in pairings than avoidance (34:32), and a larger number of the avoidance results were ambiguous (attraction 20:14, avoidance 8:24; Figure 5). Tortoise size did not reveal any significant association with attraction or avoidance coefficients, whether measured by mass ($n = 65$, $S =$

37588, $\rho = 0.179$, $p\text{-value} = 0.155$; Figure S9A) or carapace length ($n = 65$, $S = 37906$, $\rho = 0.172$, $p\text{-value} = 0.172$; Figure S9B).

Our second model set exploring whether attraction/avoidance behaviors were impacted by proximity to breeding activity generally performed poorer (68/70 successfully converged), identified via higher AIC values (Figure S10). The interaction effects (between proximity to breeding activity and opponents utilization distribution) failed to significantly alter predictions of avoidance/attraction (Figure S11-S12). Similarly the interaction between breeding activity and step length only revealed small unambiguous impacts in 13/68 individual pairings (7/13 decreased step length and 6/13 increased step length in closer proximity to breeding observations; Figure 4; Figure S13). Eleven of the significant relationships were associated with female movement, but the effects occurred in both directions: seven decreasing and four increasing step length nearer breeding activity.

Our explorations using the global Dynamic-interaction index (DI-index) appear largely in agreement with the step-selection results –mixed cohesion of movement paths with more frequent cohesion than avoidance (Figure S14). Similarly the local analysis fails to show any clear patterns linked to breeding season (Figure S15; S16). The only stand out pattern on the local scale is a reduction in significantly incoherent male movements in the dry season (January, February; Figure S15).

4. DISCUSSION

We found that annual space use varied highly among individuals tracked for both sexes (ranging from 4.24 to 55.57 ha). Males appeared to move more than females, with greater activity in the hot season, but models revealed considerable overlap between seasons and sexes. We did not detect any clear associations linking increased movement to observations of breeding activity at the temporal scale of the data (mean time lag between data points of 71.35 hours). Female movement mirrored male patterns, reducing in the dry season but models similarly reveal substantial overlap with other seasons. Female movement appeared to marginally decrease in relation to breeding activity observations (7 models), but

there were also instances of increased movement (4 models). Attraction/avoidance between tortoises appeared unaffected by temporal proximity to breeding activity observations (supported by step-selection models and Dynamic interaction index). Regardless of season, tortoises exhibited a lack of conspecific avoidance (only 8/66 models showed unambiguous avoidance), and a general tendency to share space.

4.1 Space use and requirements

Findings from the few past studies of tropical forest-dwelling tortoises and primarily terrestrial turtles have revealed substantial variation in space use between individuals (Ihlow et al., 2014; Lawson, 2006; Montaña et al., 2013; Moskovits & Kiester, 1987; Tharapoom, 1996; Wanchai, Stanford, Thirakhupt, & Thanhikorn, 2012), but some highlight intersexual differences in space-use, with males typically occupying larger areas than females (Lue & Chen, 1999; Montaña et al., 2013).

Our males showed greater movement than females in our study (although models show large overlap in motion variance values) that translated into larger space-use estimates. Previous work on *I. elongata* did not find differences between male and female tortoise space-use (Ihlow et al., 2014; Tharapoom, 1996), but overall space-use estimates broadly agree with our own (this study, 95% dBBMM: 26.17 ± 4.06 ha, $n = 17$; Tharapoom 1996, Minimum Convex Polygon: 19.25 ± 6.21 ha, $n = 11$; Ihlow *et al.* 2014: Minimum Convex Polygon: 16.80 ± 3.77 ha, 95% Kernel Density Estimation h_{LSCV} : 3.84 ± 0.30 ha, $n = 9$). However, we strongly caution against area comparisons between studies. Without accounting for the differences in tracking duration, tracking lag time, and estimation methods we cannot determine whether differences (or similarities) are derived from the animal movements or are artifacts of the methods (Silva et al., 2020). Further, a number of individuals in previous studies were reintroduced to the study site, impacting the interpretation of the described requirements for *I. elongata*. Any species-level summary of space-use would best be achieved by standardizing analytical methods and reanalyzing raw data. We have made all raw tracking data freely available in the hopes of enabling future broader analyses (OSF:

<https://osf.io/6vfp9/>, and MoveBank, <https://www.movebank.org>, ID: 1128208874).

Species' spatial requirements are frequently integrated into conservation plans/assessments (Fraser et al., 2018). Movement plays an important role in population dynamics (Sample et al., 2018); our ability to estimate population trends or identify threats can be improved by quantifying a species' movement capacity and tendencies (Blouin-Demers & Weatherhead, 2002; Bonnet, Naulleau, & Shine, 1999; Mueller & Fagan, 2008; Nathan et al., 2008). Our results suggest a reproducing population without apparent antagonism. Information provided here on space-use could help evaluate population health, inform future study design (e.g., via the estimation of activity centers), and provide strong priors for spatially explicit mark recapture studies.

4.2 Seasonal patterns

Tortoise activity was weakly seasonal, with our models returning small effects on motion variance indicating substantial overlap in activity levels between seasons. Tortoises reduced activity during the dry season, broadly agreeing with past work describing reduced space-use during drier periods (Ihlow et al., 2014; Tharapoom, 1996). The weaker seasonal patterns of our data may be a result of differences in analyses. Resources, such as food and water, are limited during dry periods, and likely drive a need to conserve energy and water by limiting activity (Duda, Krzysik, & Freilich, 1999; Loehr, 2012; Peterson, 1996). Lower dry season temperatures compound the limited resources, likely necessitating the reduced activity of exothermic taxa such as tortoises (Douglass & Layne, 1978; Lagarde et al., 2002; Lambert, 1981; Nussear, Esque, Haines, & Richard Tracy, 2007). The reduced frequency of incoherent movement pathways in the dry season involving males could be a result of the reduced activity or concentration of movements to more concentrated resources.

We detected most indicators of breeding activity in the hot season, including mating, sharing shelters, and presence of pink nose (Ward et al., 2018). The timing of breeding activity was unexpected: *I. elongata* in Cambodia appear to primarily mate during their rainy season (Ihlow, Dawson, Hartmann, & Som, 2016). In our study, the dry season is followed by the hot season, bringing more regular rainfall. For the tortoise

species *Homopus femoralis* in semi-arid grasslands, activity is closely associated with rain (Loehr, 2012). Rainfall likely boosts resources, thus triggering opportunistic reproductive activity (i.e., mate searching, mate competition, and copulation), as has been documented in other vertebrate species (Hau, 2001; McNamara, Barta, Klaassen, & Bauer, 2011; Tökölyi, McNamara, Houston, & Barta, 2012). The female tortoises' peak activity during the wet season is likely due to the influx in available resources (Collins et al., 2014), and potentially nesting activity (Lagarde et al., 2002; Henen, van Bloemestein, Hofmeyr, & Weatherby, 2017).

Reproductive success has been linked to increased movement and space use (Jellen et al., 2007; Kamath & Losos, 2018). Peaks in male activity (motion variance) occurred in the hot season, but failed to detect any association between step lengths and temporal proximity to breeding activity observations.

Potentially, the benefits from increases in movements (increased female encounter rates) are only visible at a finer temporal resolution, driven by more sinuous movements rather than patterns visible in step lengths recorded on average every 71.35 hours.

Encounter rates play a major role in poaching prevalence (Ciuti et al., 2012). As tortoise poaching appears to be largely opportunistic (Ihlow et al., 2016), periods of lower sheltering frequency could increase poaching vulnerability. Poaching for the Asian food markets and the international pet trade is considered a major threat to *I. elongata* (Hendrie, 1998; Ihlow et al., 2016; Jenkins, 1995; Rahman et al., 2018).

Anti-poaching activities may see greater pay-offs if they focus on the periods of heightened tortoise activity. However, we found no apparent evidence of tortoise poaching during the two-year study, which may be evidence for effective enforcement methods within the protected area (although assertions concerning the lack of poaching require more comprehensive monitoring).

4.3. Overlap and sociality

Tortoises are largely solitary, but use olfactory cues as social signals (Bulova, 1997). Several species of tortoises use olfactory cues to distinguish the identity, sex and reproduction status of conspecifics

(Alberts, Rostal, & Lance, 1994; Bulova, 1997; Galeotti, Sacchi, Rosa, & Fasola, 2007), likely modifying movements accordingly (Bulova, 1997).

Telemetered *I. elongata* were largely apathetic to conspecifics, with several even showing attraction to conspecifics. Female to female attraction, which was relatively strong, is likely resource driven; frequent random encounters resulting from shared resources (Drabik-Hamshare & Downs, 2017; Frazier, 1988; Josseume, 2002). However, male to male attraction was more ambiguous, possibly suggesting greater avoidance, as there were lower attraction levels than seen in other pairings (i.e., male-female, female-male, female-female). Small amounts of male to male attraction are likely resource driven, and may even be due to mate competition (e.g., combat; Ward et al., 2018) –the latter supported by several instances of positive interactions between attraction and breeding activity observations (4/13 models). Male to female attraction was the most evident, with male movements being the most strongly influenced by the presence of female tortoises. The stronger attraction may be a combination of mate searching behaviors and indirect attraction to shared resources. However, there appears to be no temporal change in this attraction (in relation to proximity to breeding observations), thus weakening the argument for breeding season driving attraction patterns. Despite a course tracking regime, we suggest that the nonuniversal attraction and dissociation with tortoise size indicative of sufficient resources such as shelter, food, and water in the protected area. Higher resolution movement data would be required to test whether the patterns we observed exist at finer temporal or spatial scales.

Tortoises are long-lived animals meaning that declining populations can persist in areas for decades before becoming extirpated (McCoy, Mushinsky, & Lindzey, 2006; McGowan et al., 2017). Occurrence in a habitat is not necessarily an adequate indicator of success or population viability. Space use overlap and nearest neighboring conspecific can be density dependent as seen in gopher tortoises (*Gopherus polyphemus*) from North America (Guyer, Johnson, & Hermann, 2012). Tortoise populations may become unviable once densities decrease to levels that preclude conspecific encounters for reproduction (Guyer et al., 2012; McGowan, Allan, Servoss, Hedwall, & Wooldridge, 2017). Higher densities of

tortoises increase males' chances of locating mates, facilitating reproduction. Therefore, shared space-use of *I. elongata* indicates frequent mating opportunities and likely a sufficient density of tortoises without an apparent need to significantly increase movements (at the tracking scale of this study) to encounter mates. Our findings appear to suggest that the Sakaerat Biosphere Reserve is serving as a refuge for this critically endangered species. Potentially the reserve is providing adequate resources, space, and protection from anthropogenic threats (namely poaching) to sustain a reproducing population, demonstrating the importance of even small protected areas for the conservation of endangered species. However, reproductive success and survival rates for *I. elongata* are unknown. We suggest future studies examine population densities, resource needs, and recruitment of *I. elongata* within the Sakaerat Biosphere Reserve in order to better evaluate the effectiveness of this reserve. Population studies of other *I. elongata* can be enhanced with the space-use details provided here, boosting the potential for evaluation and protection.

Declarations

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Ethics and permits

We had ethical approval from the Suranaree University of Technology Ethics Committee, Thailand Institute of Scientific and Technological Research, Site Access from Sakaerat Environmental Research Station, National Research Council of Thailand (Permit Number: 0002/3589), Department of National Parks Plant and Wildlife Conservation

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Conflicts of Interest

We declare that there are no conflicts of interest.

Author contributions

Conceptualization, M.W., Y.M., T.A., and C.T.S.; Methodology, M.W., Y.M., C.T.S., and B.M.M.; Formal Analysis, B.M.M.; Investigation, M.W., and Y.M.; Resources, M.W., Y.M., C.T.S., S.W., and T.A.; Writing – Original Draft, B.M.M., C.W.H., and C.T.S.; Writing – Review & Editing, B.M.M.,

C.W.H., C.T.S., M.W.; Visualization, B.M.M.; Supervision, C.T.S., S.W., and T.A.; Funding Acquisition, M.W., and Y.M.

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Supplementary Material

Supplementary Figures: S1-S16

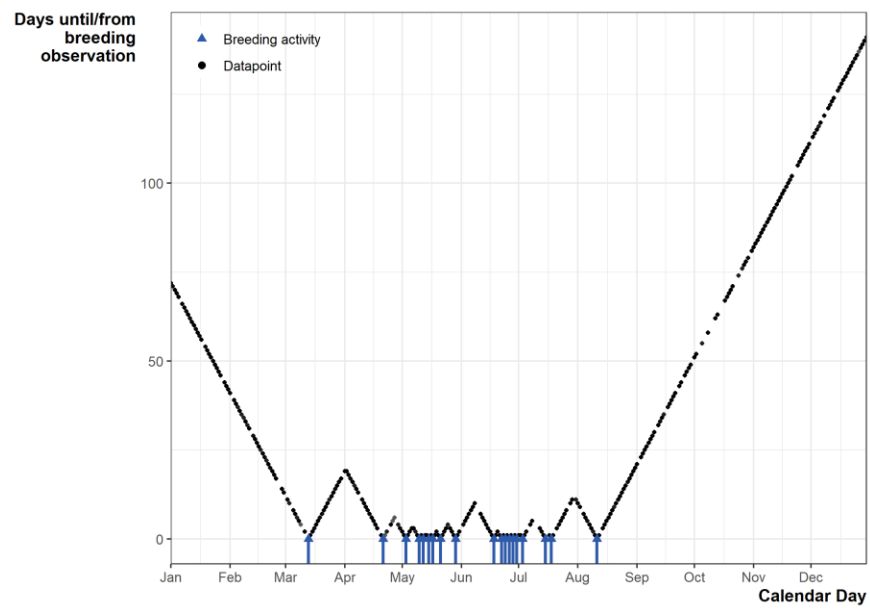


Figure S1. Data point proximity to a calendar date that a breeding activity observation was made across any year. Black circles are the data point, blue triangles and lines show when activity was observed

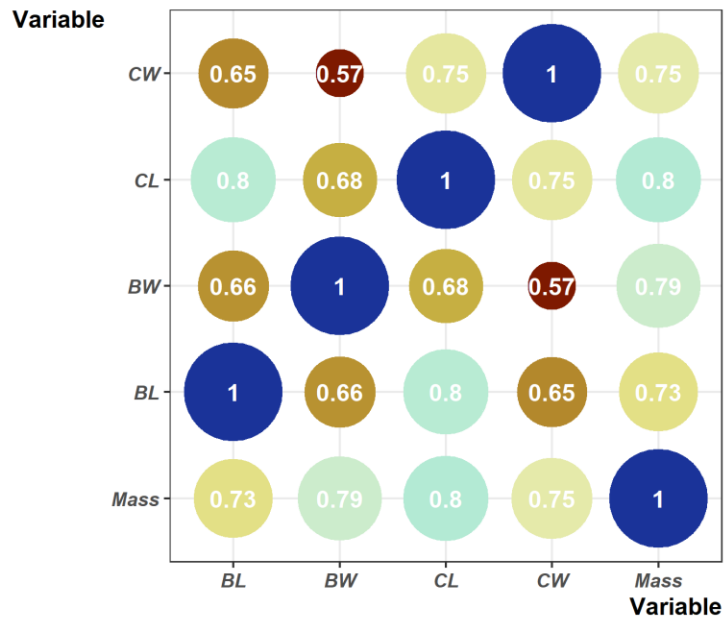


Figure S2. Correlation matrix comparing: mass, carapace width (CW), carapace length (CL), body width (BW), and body length (BL). Values displayed are Spearman's rho, where size and color of the circles reflect the strength of correlation.

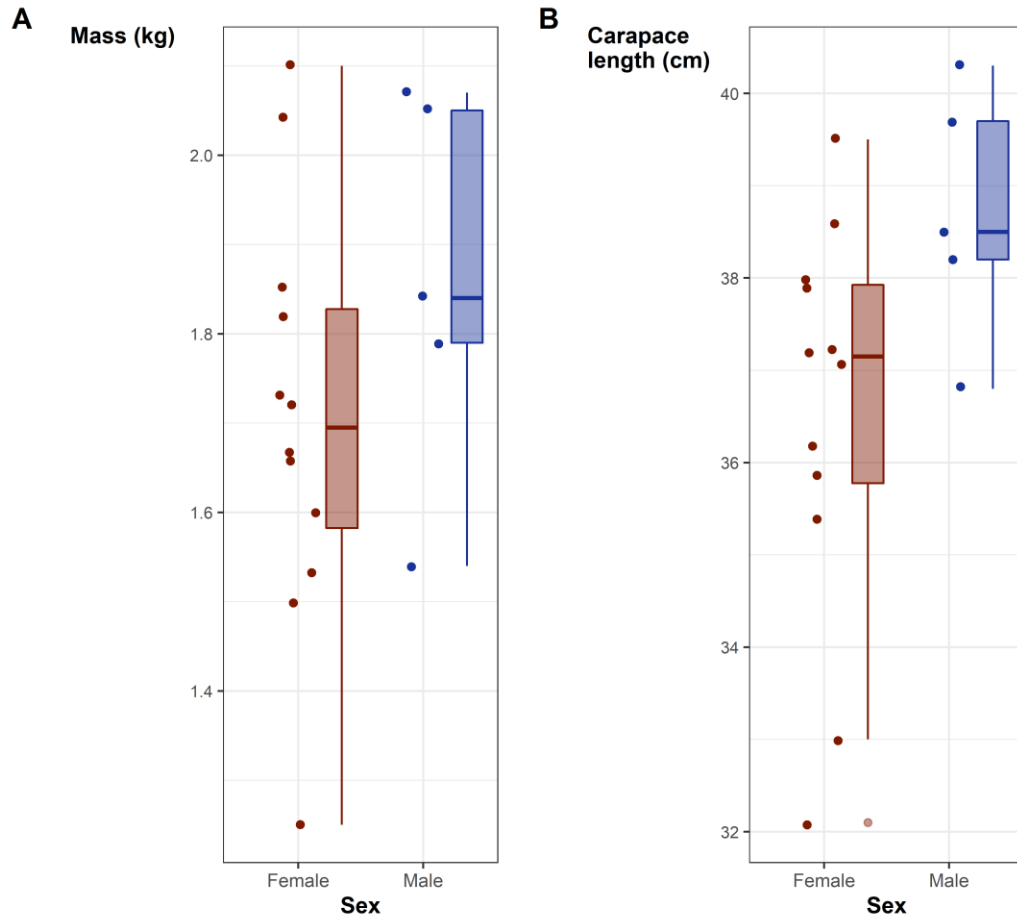


Figure S3. Boxplots alongside jittered points illustrating the values of female and male, A) mass (kg), and B) curved carapace length (cm).

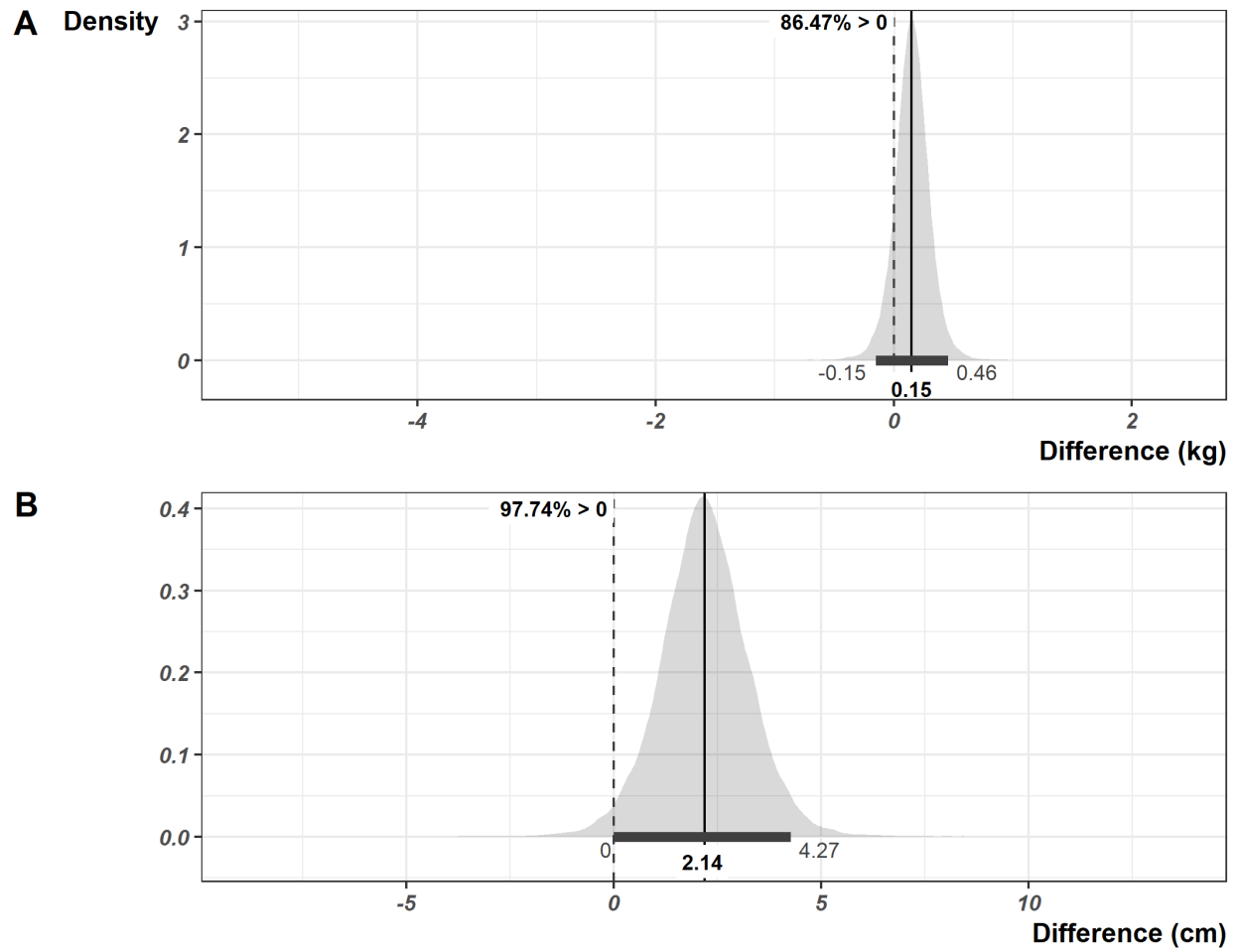


Figure S4. Distribution of the difference between male and female A) mass and B) curved carapace length. Thick line shows the 95% Highest Density Interval, with values either end showing the extent. Central label indicates the overall estimated mean difference. Top label shows the probability that the difference was larger than zero.

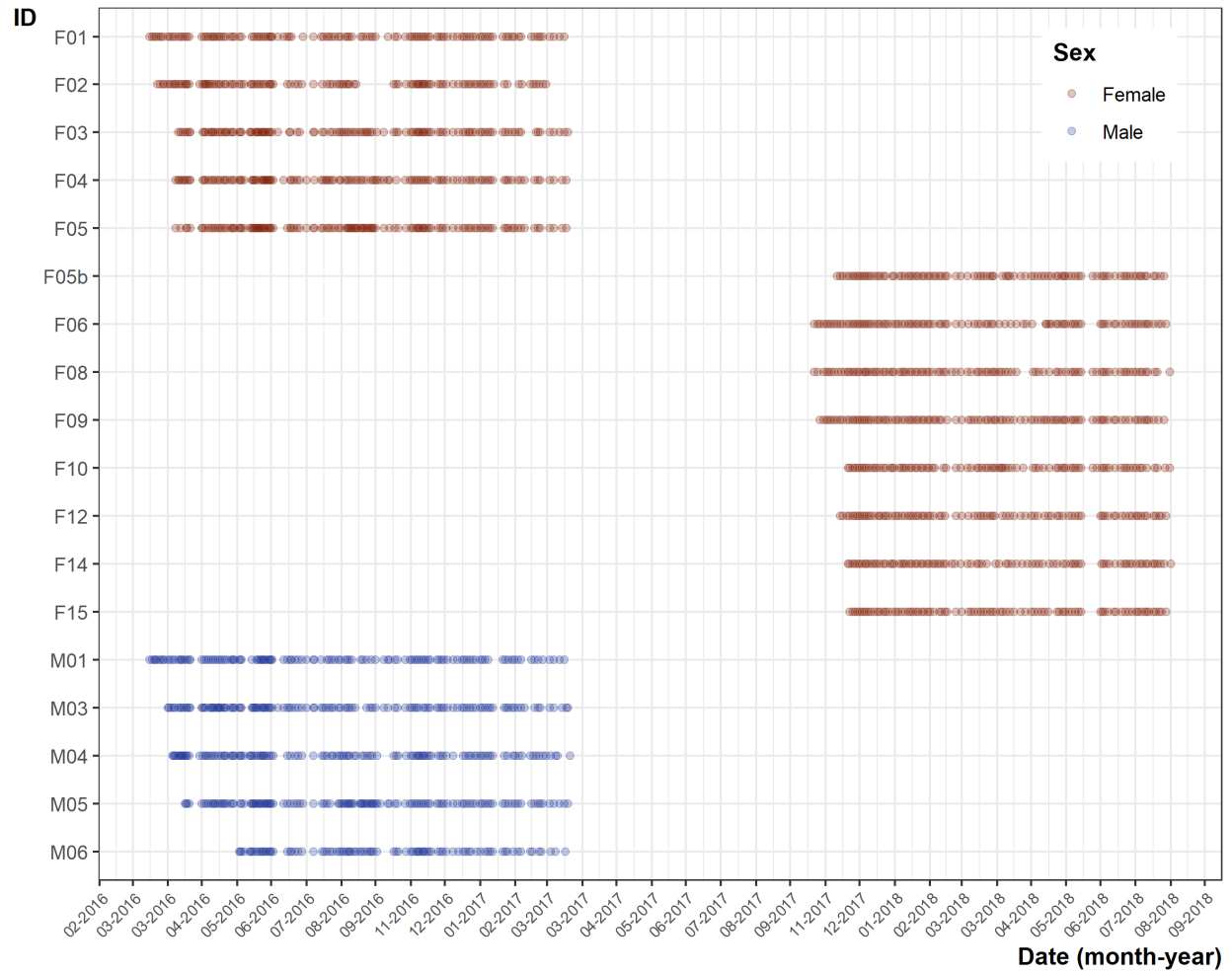


Figure S5. Dates on which a datapoint was recorded, split across all tracked individuals. Red points are females, blue points are males.

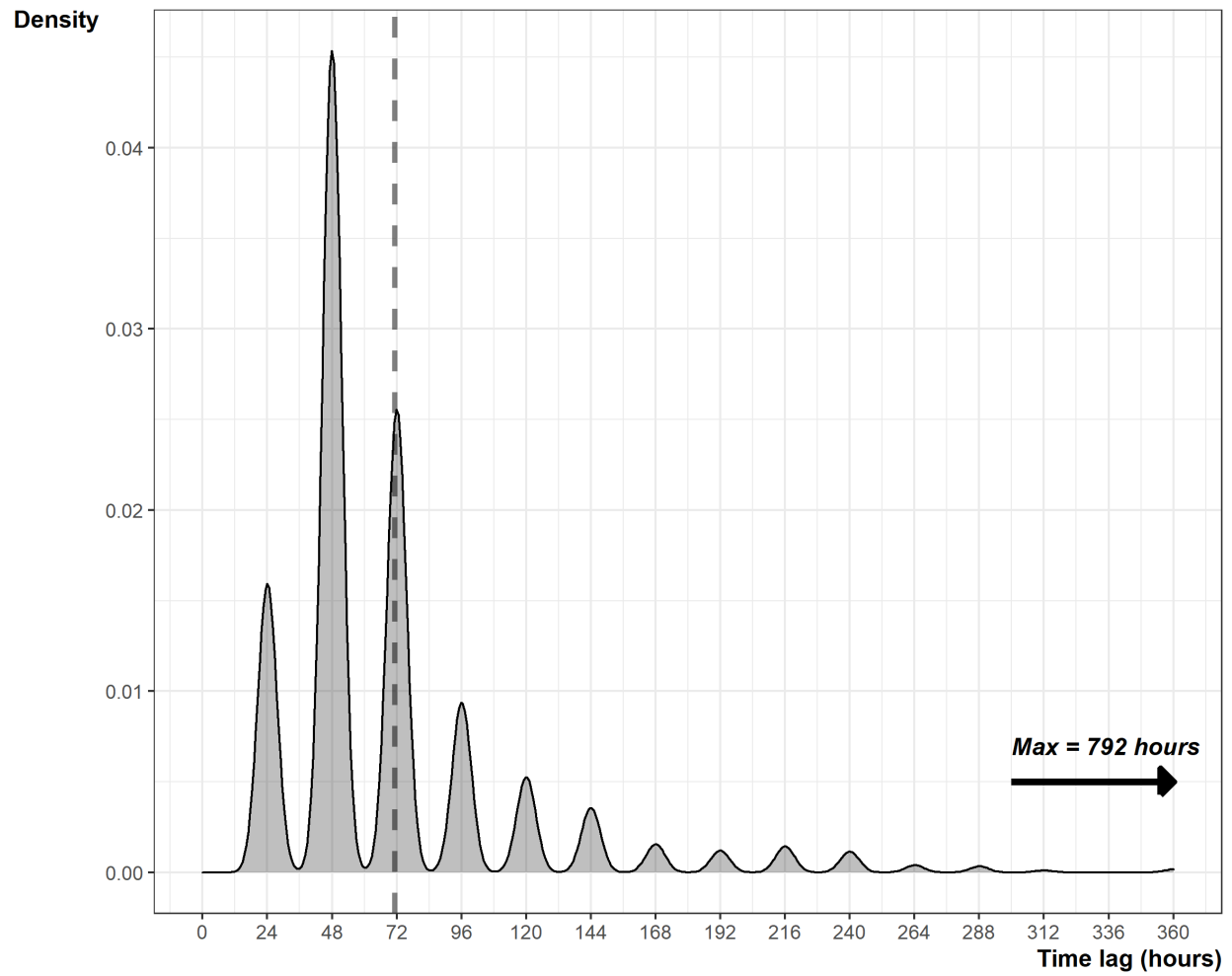


Figure S6. Distribution of the time lag between subsequent tracks. The dashed line indicates the mean time lag. The x axis has been truncated at 360 hours to aid with visualization.

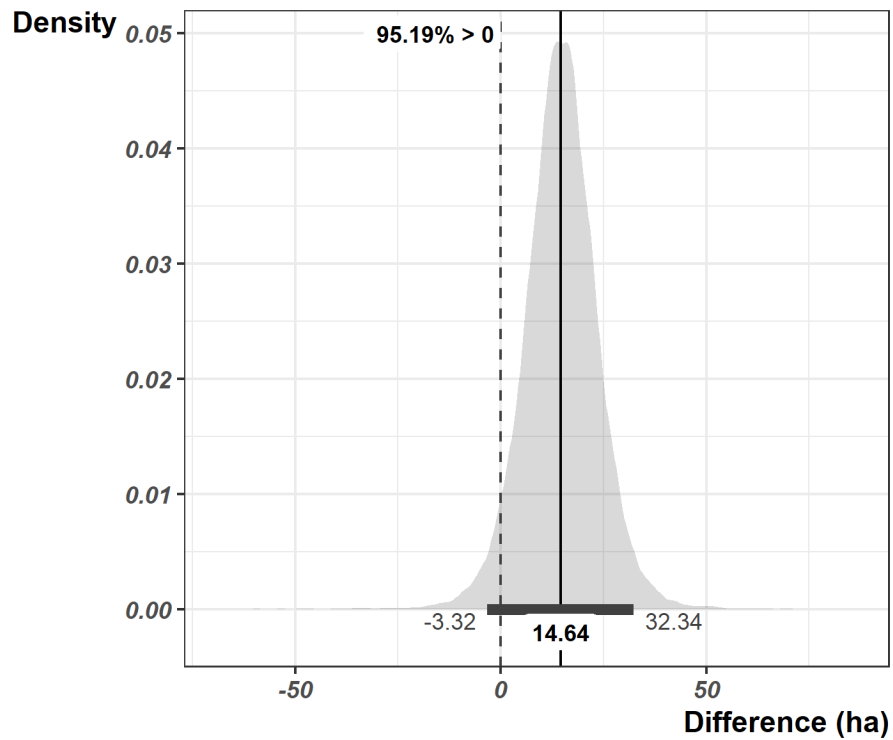


Figure S7. Distribution of the difference between male and female space-use estimates. Thick line shows the 95% Highest Density Interval, with values either end showing the extent. Central label indicates the overall estimated mean difference. Top label shows the probability that the difference was larger than zero.

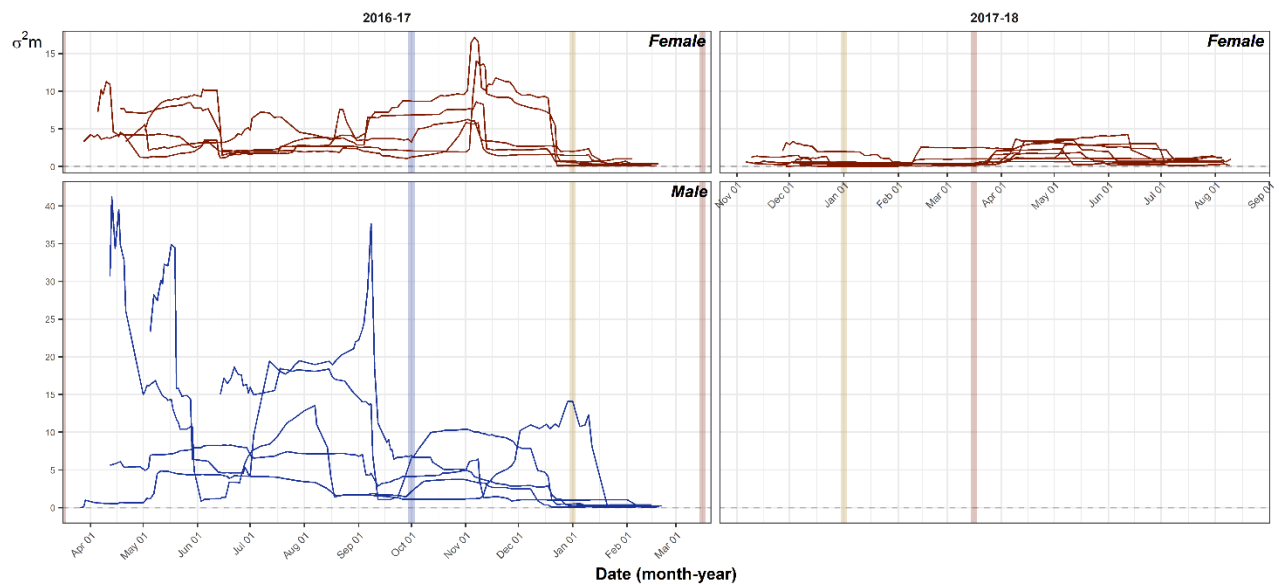


Figure S8. Motion variance over time, split between sexes and cohorts. Red, blue and yellow vertical lines indicate the beginning of hot, wet, and dry seasons respectively.

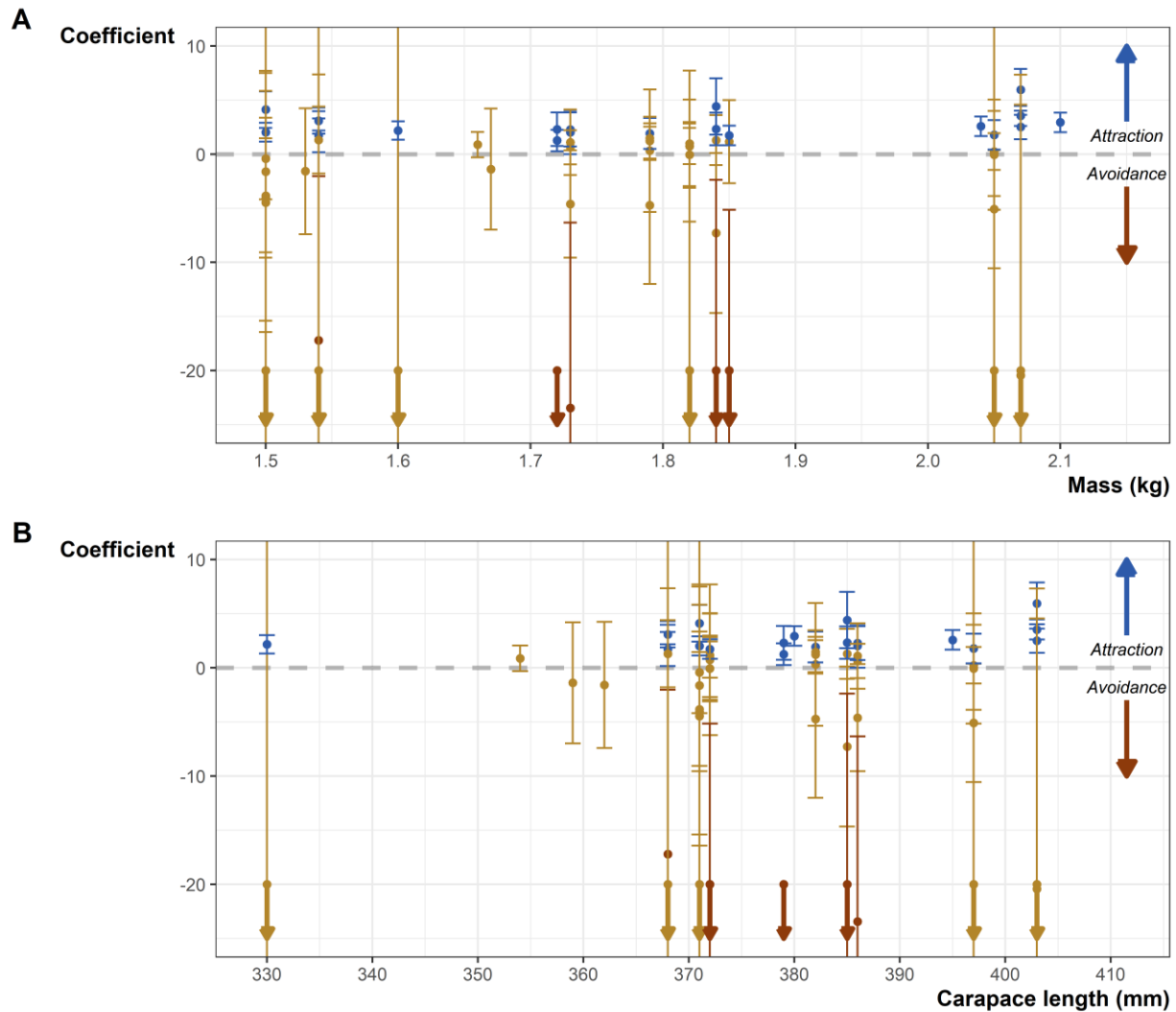


Figure S9. Step-selection model coefficients plotted against tortoise size. A) mass (kg). B) carapace length (mm). Error bars represent the standard error on the coefficient estimate. Point and error bar colors indicate the direction of the effect and whether the confidence intervals overlap zero: blue = positive with no overlap, yellow = overlap therefore no clear direction, red = negative with no overlap. Colored arrows bottom left indicate instances where point estimates are extremely low and plotting would have obscured overall patterns (excluded range = -395808 – -41).

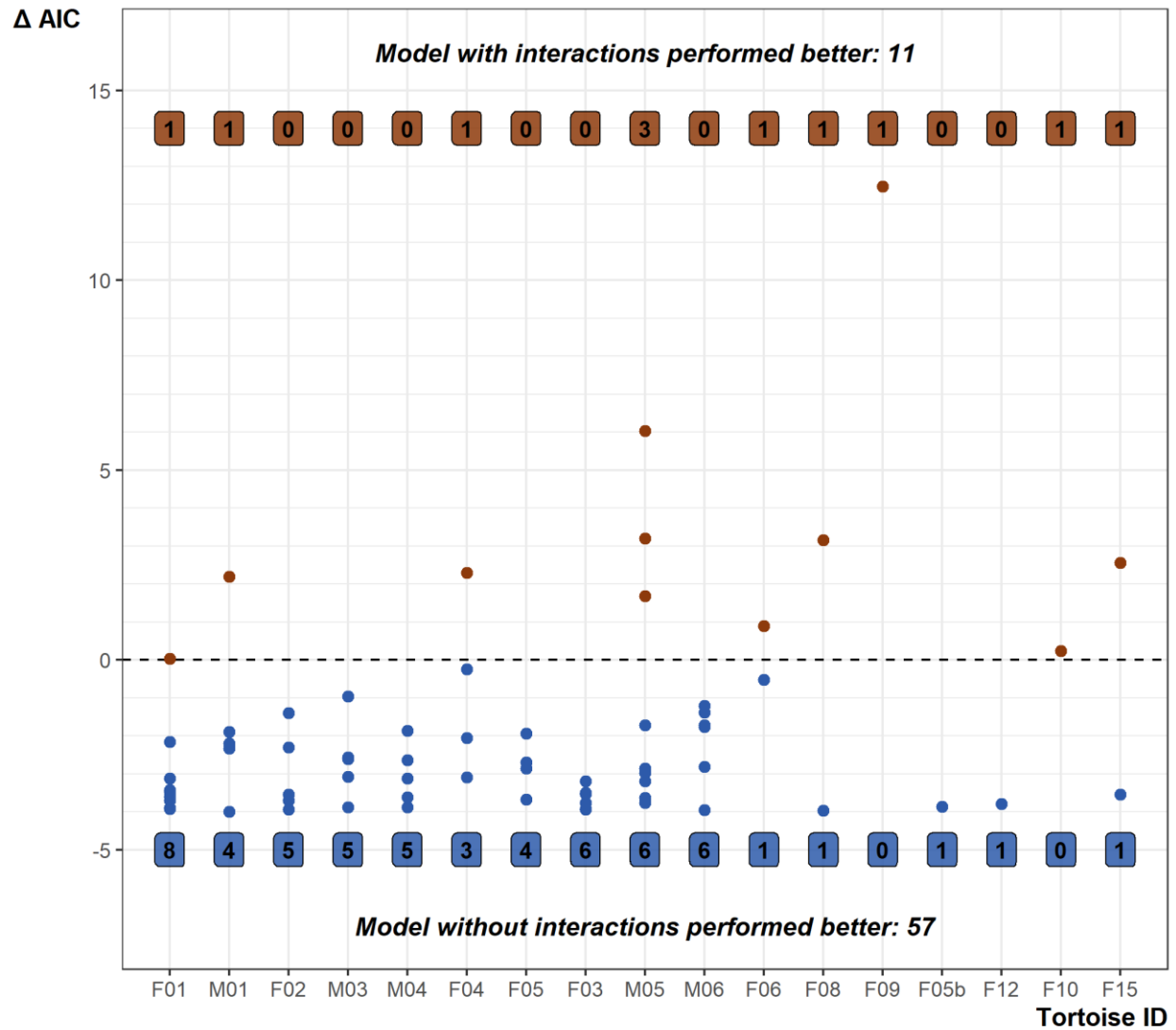


Figure S10. Delta AIC values between models excluding interactive effects and those including interactive effects. Blue points indicate models where the simpler non-interactive model had lower AIC values, whereas red points show when models with interactive effects performed better. Colored labels show the counts of which model set performed better per individual tortoise ID. Text labels provide the overall count.

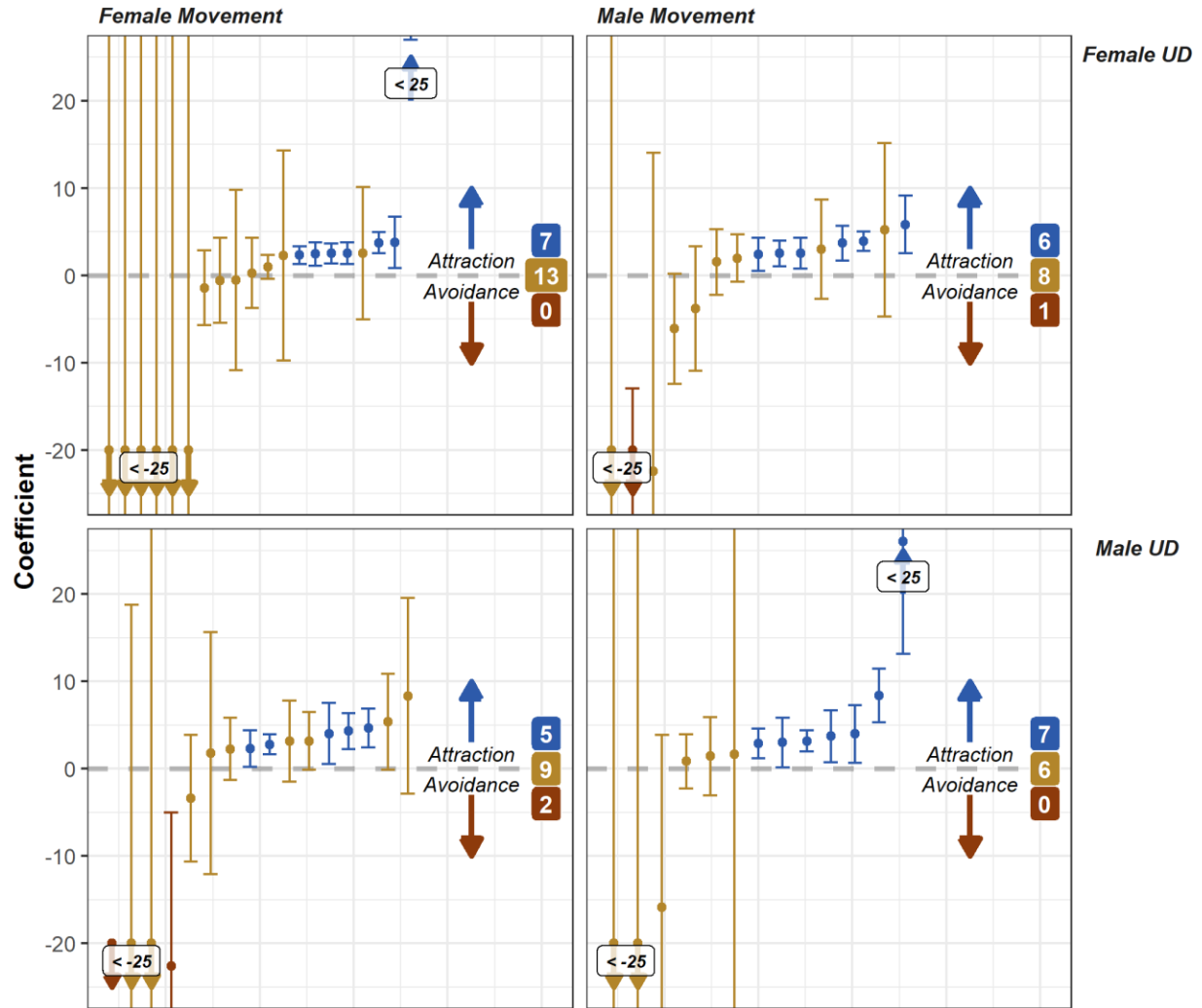


Figure S11. Model coefficients describing attraction or avoidance between individuals in the model with interactive effects.

Error bars represent the standard error on the coefficient estimate. Point and error bar colors indicate the direction of the effect and whether the confidence intervals overlap zero: blue = positive with no overlap, yellow = overlap therefore no clear direction, red = negative with no overlap. Right hand colored labels show the count of coefficient estimates indicating attraction (blue), overlapping zero (yellow), and avoidance (red). Colored arrows bottom left and top right indicate instances where point estimates and SE are extremely low or high and plotting would have obscured overall patterns (low excluded range = -3719 - 34; high excluded range = 26 - 42).

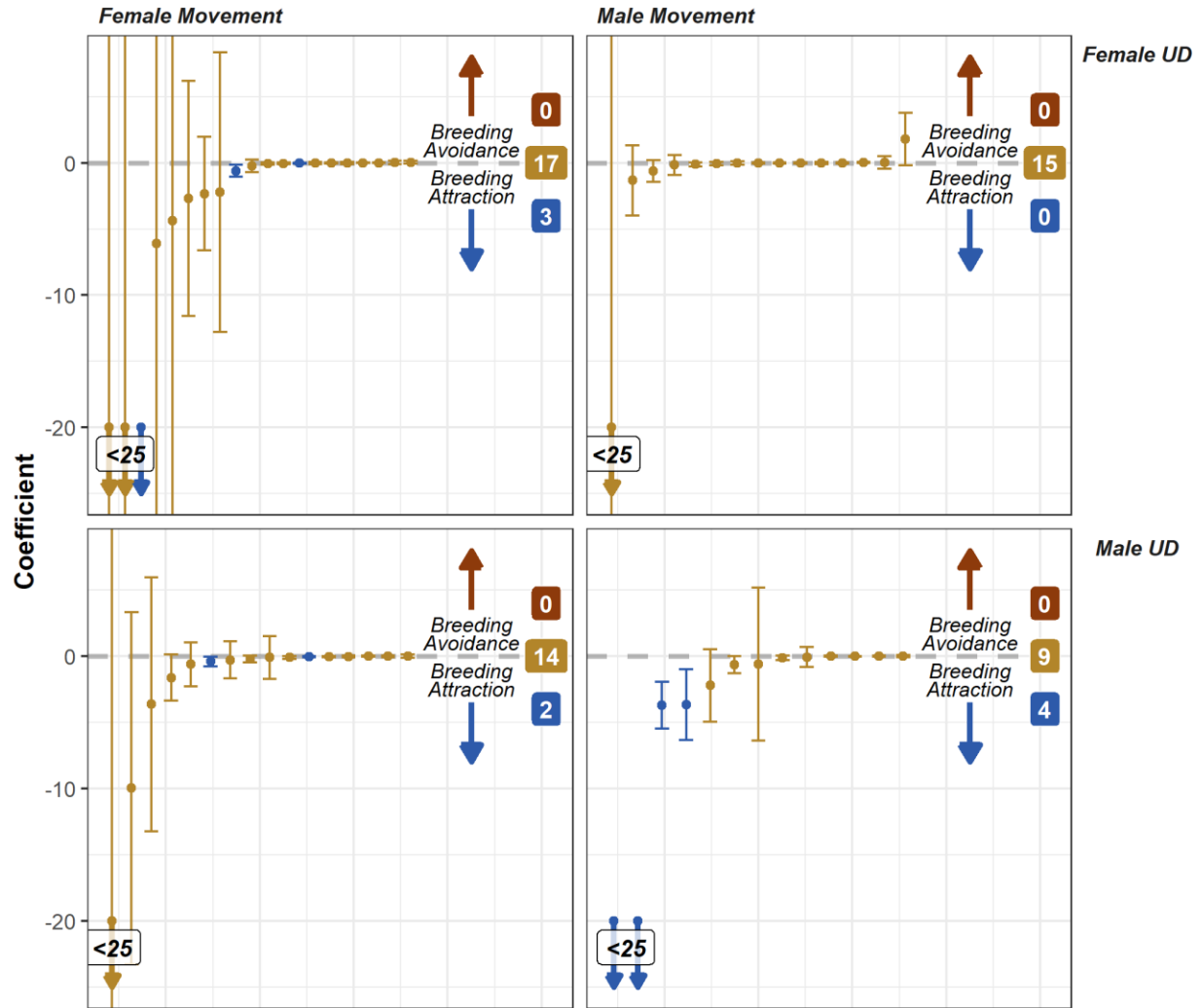


Figure S12. Model coefficients describing the interaction between attraction or avoidance and number of days until/since an observation of breeding activity. Error bars represent the standard error on the coefficient estimate. Point and error bar colors indicate the direction of the effect and whether the confidence intervals overlap zero: blue = negative with no overlap, yellow = overlap therefore no clear direction, red = positive with no overlap. Right hand colored labels show the count of coefficient estimates indicating greater attraction closer to breeding activity (blue), overlapping zero (yellow), and greater avoidance closer to breeding activity (red). Colored arrows bottom left indicate instances where point estimates and SE are extremely low and plotting would have obscured overall patterns (excluded range = -8670 – -54).

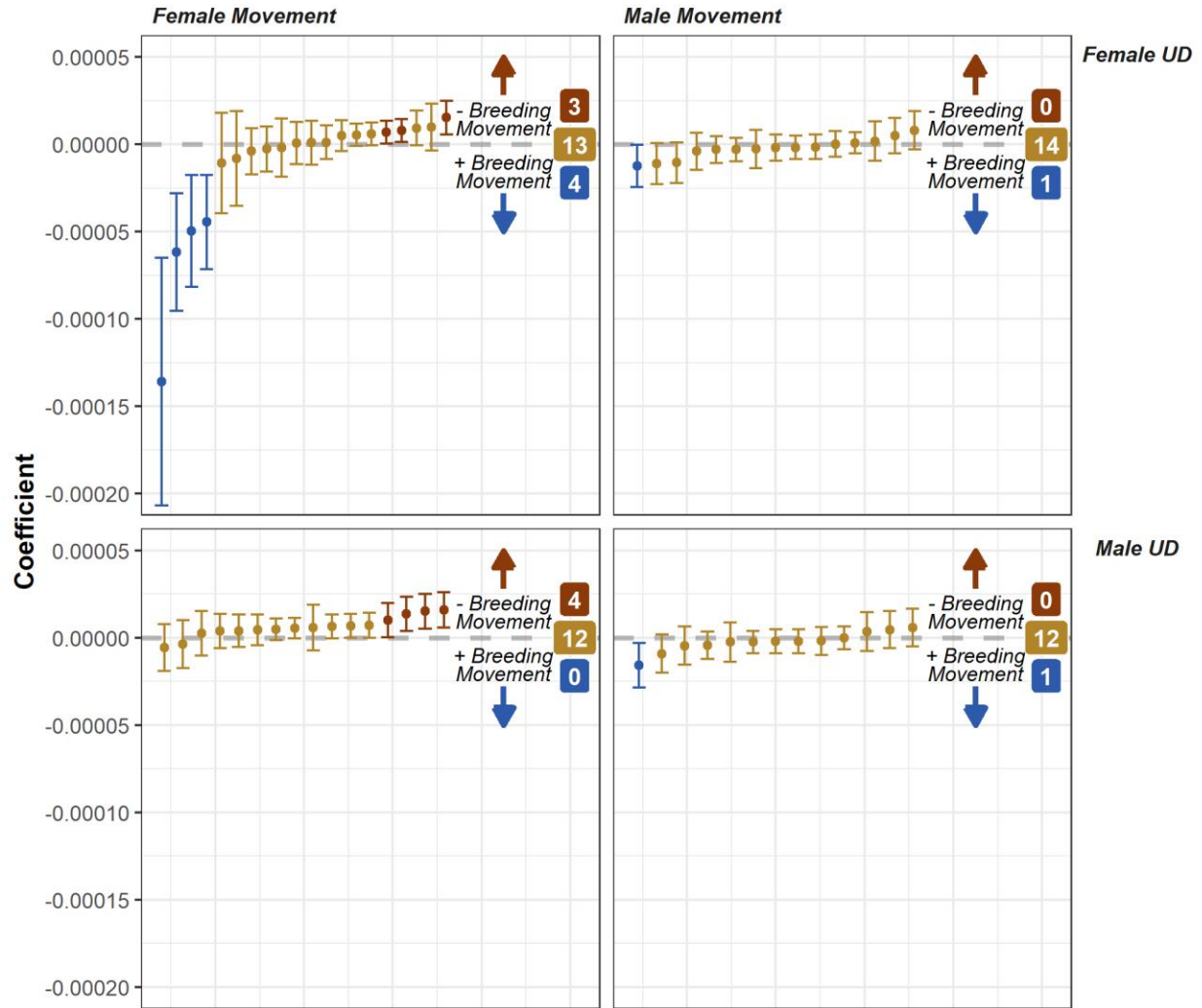


Figure S13. Model coefficients describing the interaction between step length and number of days until/since an observation of breeding activity. Error bars represent the standard error on the coefficient estimate. Point and error bar colors indicate the direction of the effect and whether the confidence intervals overlap zero: blue = negative with no overlap, yellow = overlap therefore no clear direction, red = positive with no overlap. Right hand colored labels show the count of coefficient estimates indicating larger step length closer to breeding activity (blue), overlapping zero (yellow), and smaller step lengths closer to breeding activity (red).

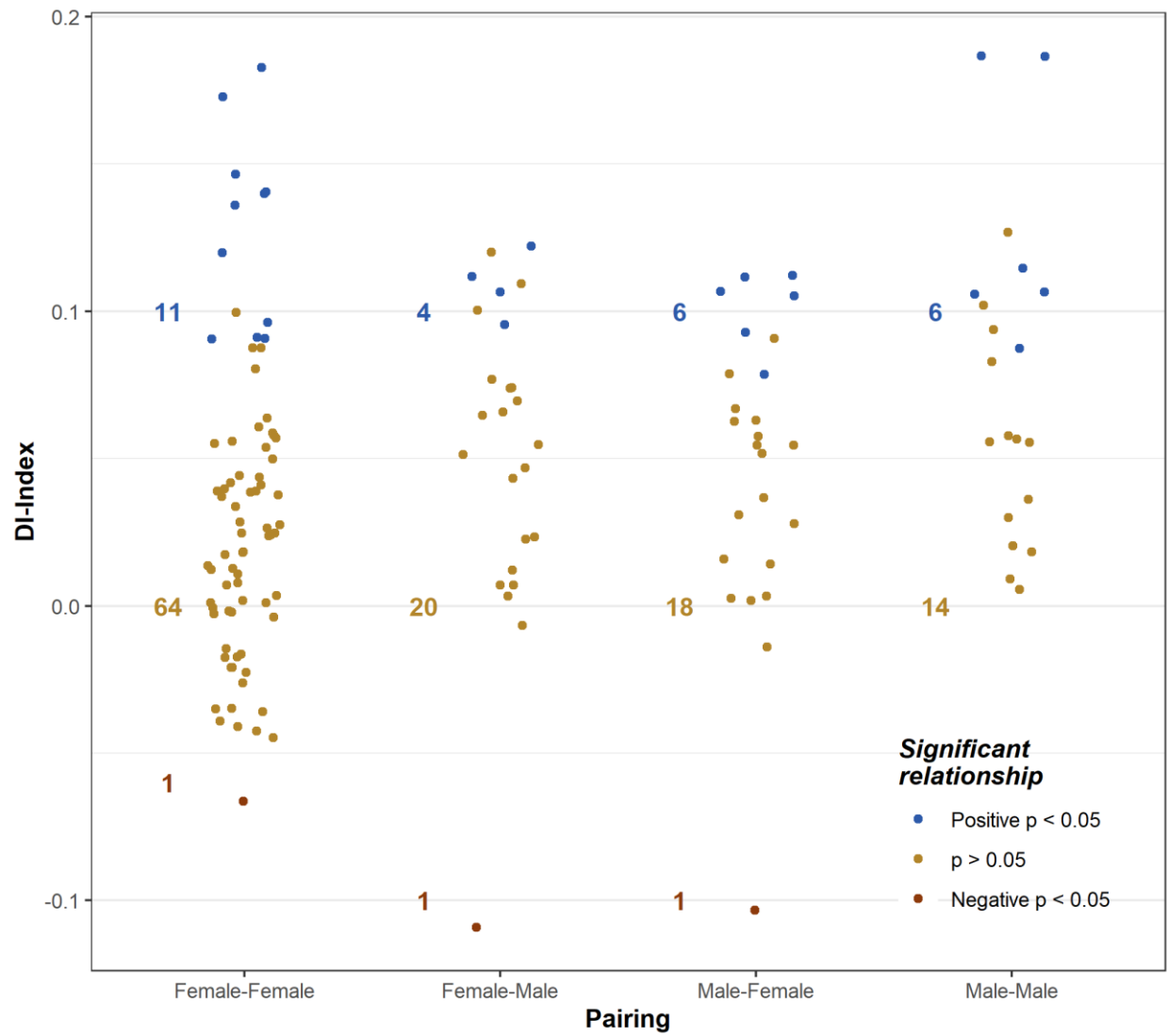


Figure S14. Global Dynamic Interaction index results for each tortoise pairing. Numbers are counts of the significantly coherent movements (blue), non-significant cohesion between movements (orange), and significantly incoherent movements (red). Nb. DI-index ranges from -1 to 1, but y-axis ranges from -0.1 to 0.2.

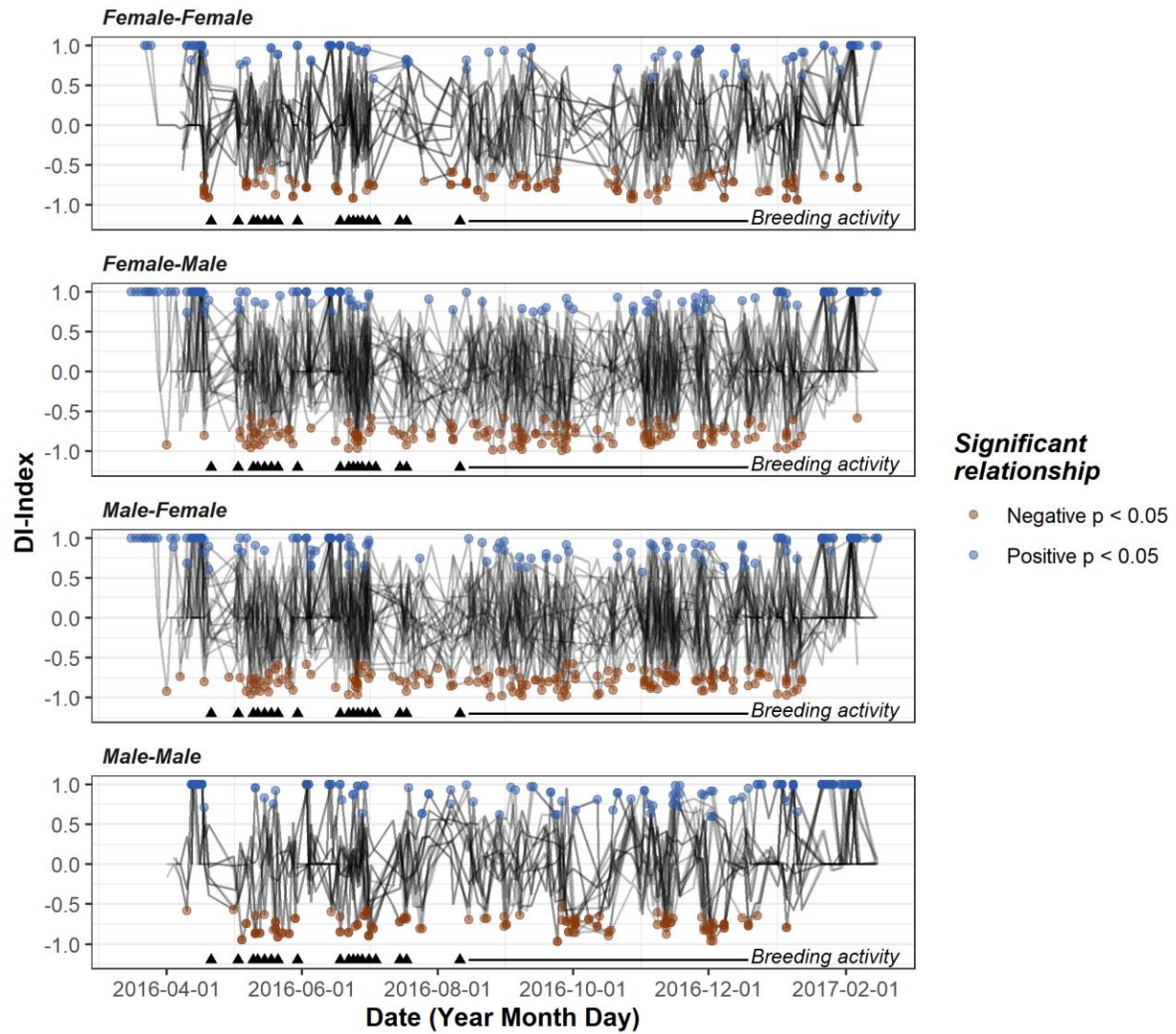


Figure S15. Local Dynamic Interaction index results for the 2016/2017 cohort. Circles indicate times of significantly cohesive (blue) or incoherent (red) movements between individuals. Triangles at the lower area of each plot show breeding activity observations (Nb. breeding observations positions are compiled from all study years). Nb. DI-index ranges from -1 to 1.

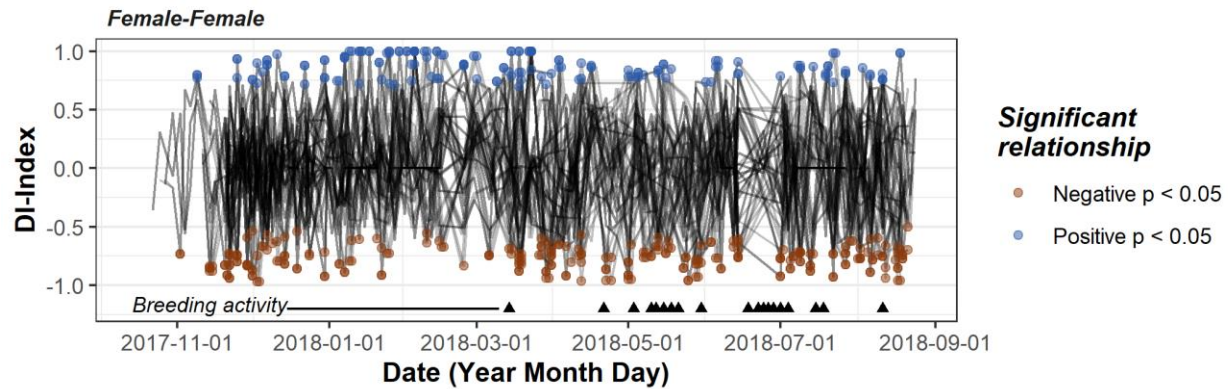


Figure S16. Local Dynamic Interaction index results for the 2017/2018 all female cohort. Circles indicate times of significantly cohesive (blue) or incoherent (red) movements between individuals. Triangles at the lower area of each plot show breeding activity observations (Nb. breeding observations positions are compiled from all study years). Nb. DI-index ranges from -1 to 1.

Table S1. Results from non-interactive step-selection models. "tar" = the individual's whose subset dBBMM occurrence distribution was used in the model. "opp" = the individual's whose movement data was used in the model. "res" = whether the model completed. "coef" = the point estimate for attraction/avoidance. "se" = the standard error associated with the point estimate. "n" = the total number of points in each model (observed and random). "nevent" = the number of time steps examined by the model. "warn" = warning connected to model convergence. "opp.sex" = the sex of the opponent of the model. "tar.sex" = the sex of the target of the model. "avoid" = whether the point estimate suggested avoidance or attraction. "overlap0" = whether the standard error overlaps with zero.

Table S1 see: <https://osf.io/6vfp9/>