Revisiting reptile home ranges: moving beyond traditional estimators with dynamic Brownian Bridge Movement Models

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Abstract

Animal movement, expressed through home ranges, can offer insights into spatial and habitat requirements. However, home range estimation methods vary, directly impacting conclusions. Recent technological advances in animal tracking (GPS and satellite tags), have enabled new methods for home range estimation, but so far have primarily targeted mammal and avian movement patterns. Most reptile home range studies only make use of two older estimation methods: Minimum Convex Polygons (MCP) and Kernel Density Estimators (KDE), particularly with the Least Squares Cross Validation (LSCV) and reference (h_{ref}) bandwidth selection algorithms. The unique characteristics of reptile movement patterns (*e.g.* low movement frequency, long stop-over periods), prompt an investigation into whether newer movement-based methods –such as dynamic Brownian Bridge Movement Models (dBBMMs)– are applicable to Very High Frequency (VHF) radio-telemetry tracking data. To assess home range estimation methods for reptile telemetry data, we simulated animal movement data for three archetypical reptile species: a highly mobile active hunter, an ambush predator with long-distance moves and long-term sheltering periods, and an ambush predator with short-distance moves and short-term sheltering periods. We compared traditionally used home range estimators, MCP and KDE, with dBBMMs, across eight feasible VHF field sampling regimes for reptiles, varying from one data point every four daylight hours, to once per month. Although originally designed for GPS tracking studies, we found that dBBMMs outperformed MCPs and KDE h_{ref} across all tracking regimes, with only KDE LSCV performing comparably at some higher-frequency sampling regimes. The performance of the LSCV algorithm significantly declined with lower-tracking-frequency regimes, whereas dBBMMs error rates remained more stable. We recommend dBBMMs as a viable alternative to MCP and KDE methods for reptile VHF telemetry data: it works under contemporary tracking protocols and provides more stable estimates, improving comparisons across regimes, individuals and species.

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1. Introduction

Animal movement is an underlying process in many ecological systems, and there is a growing understanding of how individuals behave through space and time (Nathan *et al.,* 2008; Gurarie *et al.,* 2016). Movement is often conceptualized then presented as a home range, defined as the area animals move through during "normal" activities, including resource acquisition and reproduction (Burt, 1943; Powell 2012). While the utility of the home range concept has been questioned in recent years (Kie *et al.*, 2010; Powell & Mitchell, 2012), home range estimates continue to have a range of applications: identifying behavioural adaptations to predictable environmental features (Riotte-Lambert & Matthiopoulos, 2019) or inferring habitat use (Fisher, 2000; Dickson & Beier, 2002; Tikkanen *et al.,* 2018; Marshall *et al.,* 2019). Applying a home range approach to ecological research questions requires careful consideration (Péron, 2019), as any conclusions drawn can be profoundly impacted by the natural history of the target species.

Terrestrial reptiles —broadly lizards, snakes, and tortoises— have *distinct* natural histories from mammals (*e.g.* as ectotherms), resulting in *distinct* movement patterns. Many reptiles move less frequently than comparatively sized mammals (Hailey, 1989), but more importantly, many terrestrial reptiles spend prolonged periods stationary under shelter (one day to several weeks; Guarino, 2002; Bruton, McAlpine, Smith, & Franklin, 2014; Mata-Silva, DeSantis, Wagler, & Johnson, 2018). These inconsistent movement patterns severely impact inferences drawn from home range analyses.

To properly inform desperately needed conservation actions (Gibbons *et al.*, 2000; Roll *et al.*, 2017), we must tailor our methodologies to the peculiarities of reptile movement (Péron, 2019) –otherwise we risk designing suboptimal solutions. We must assess the utility of newer methods designed for mammals, before applying them to reptiles (Silva, Crane, Suwanwaree, Strine, Goode, 2018).

With the rise of Global Positioning System (GPS) animal tracking, researchers have developed new statistical approaches for calculating home ranges that take advantage of the high number of location fixes. However, GPS tracking currently has limited application in reptiles (see Schofield *et al.*, 2007; Campbell *et al.*, 2013; Rosenblatt *et al.*, 2013; Smith, Hart, Mazzotti, Basille, & Romagosa, 2018) as their natural history poses several problems (Hebblewhite & Haydon, 2010; Wolfe, Fleming, & Bateman, 2018); *e.g.* weakened signal due to the surgical implantation or attachment of the tag, limited number of species which can be ethically attached due to body size (Smith *et al.*, 2018), reduced fix rate and precision due to sheltering underground (Bruton *et al.*, 2014, Wolfe *et al.*, 2018).

Given that traditional home range estimators –Minimum Convex Polygons (MCP) and Kernel Density Estimators (KDE)– present major limitations for telemetry-based reptile studies (see Row & Blouin-Demers, 2006), it is important to investigate whether newer methods developed for GPS tracking data can be applied to reptile-targeted Very High Frequency (VHF) radio-telemetry studies. Dynamic Brownian Bridge Movement Models (dBBMMs) are a technique intended for GPS telemetry, allowing for efficient and repeatable analysis of high-resolution data –particularly useful for animals with behaviourally distinct

74　movement patterns. The method creates a one-dimensional fix-frequency independent behavioural measure

75　(Brownian motion variance; Kranstauber, Kays, LaPoint, Wikelski, & Safi, 2012) that have been employed

76　to elucidate avian and mammal home range and movement patterns (*e.g.* Palm *et al.*, 2015; Byrne, McCoy,

77　Hinton, Chamberlain, & Collier, 2014; Lai, Bêty, & Berteaux, 2015; Buechley, McGrady, Çoban, &

78　Şekercioğlu, 2018).

79　Leveraging dBBMMs may benefit VHF studies (Silva *et al.*, 2018; Walter, Onorato, & Fischer, 2015); and

80　while multiple simulations studies have investigated how different methods interact with animal movement

81　and home range delineation (*e.g.* Katajisto & Moilanen, 2006; Row & Blouin-Demers, 2006; Knight *et al.*,

82　2009; Cohen, Prebyl, Collier, & Chamberlain, 2018), none have targeted reptile-specific movement

83　patterns.

84　We assess home range estimates resulting from variable study designs common in the reptile spatial ecology

85　literature: namely temporally low-resolution tracking regimes. We simulate movement data of three

86　archetypal reptile species, thoroughly examining the most common home range estimators —Minimum

87　Convex Polygons (MCPs) and Kernel Density Estimators (KDEs). We next compare traditional estimators

88　to a newer method: dynamic Brownian Bridge Movement Models (dBBMMs). Finally, we discuss the

89　implications of home range estimator choice, and present guiding principles for reptile spatial ecology

90　sampling designs.

91　2. Materials and Methods

92　2.1. SIMULATED ANIMAL MOVEMENT AND TRACKING DATA

93　We used the *SimData* function in the *momentuHMM* package (McClintock & Michelot, 2018) to simulate

94　movement data from a Hidden Markov Model (HMM). HMMs are time-series models where the movement

95　pattern of an animal is assumed to depend on the underlying behavioural state of the animal (Langrock *et*

96　*al.*, 2014). We simulated data for 32 individuals from three archetype reptile species, to represent three

97　main groups within reptile movement ecology: **Species 1** corresponds to highly mobile (active hunters)

98　with long-term shelter sites (*e.g.* monitor lizards, some skinks, and elapids like mambas and king cobras);

99　**Species 2** represents less mobile reptiles, capable of moving long distances but are ambush foragers, and

100　will still shelter for long periods (*e.g.* pythons); finally, **Species 3** represents smaller ambush predators,

101　infrequently moving and sheltering for shorter periods (*e.g.* viperid snakes, some smaller lizard species).

102　Each archetype had a unique set of state-dependent parameters and transition probabilities with the same

103　three behaviour states: "sheltering" (state 1), "moving" (state 2), "resting" (state 3). The state-dependent

104　data streams included step length (l_t) and turning angle (θ_t), which we generated from Gamma and von

105　Mises distributions, respectively. The simulations included a spatially correlated covariate for state 2, to

106　reflect habitat preferences, while states 1 and 3 followed a *cosinor* function, to reflect cyclical patterns of

107　long-term sheltering (state 1) and circadian rhythms (state 3). To simulate individual variation and

108　movement in a heterogeneous landscape we generated a random neutral landscape with fractal Brownian

109   movement, using the *NLMR* package (Sciaini, Fritsch, Scherer, & Simpkins, 2018). For further details on

110   these simulated species, as well as their specific step lengths, turning angles and transitional probabilities,

111   see Appendix S1, Supporting Information.

112   After creating the full simulated data set (regime 1), we generated six subsets of the data to represent various

113   field sampling regimes (regime 2-7): four locations per day, two locations per day, one location per day,

114   two locations per week, one location per week, and one location per month (Figure 1). For each subset, we

115   assumed a consistent regularly scheduled sampling protocol limited to the species' activity periods.
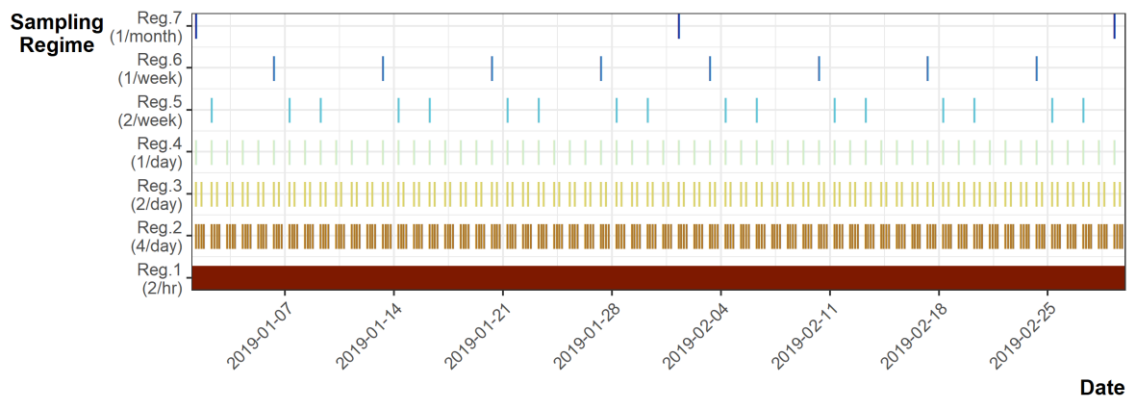
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117   **Figure 1.** Example two-month period showing how data is thinned to represent different tracking regimes.

118   The autocorrelated nature of tracking data poses difficulties for home range estimators that assume

119   independence between points, namely KDEs. Attempting to remove autocorrelation to fit these assumptions

120   can reduce the biological relevance of the home range (De Solla *et al*., 1999), but advocated in reptile home

121   range studies (Swihart & Slade, 1985; Worton, 1987).

122   We investigated the temporal autocorrelation present in our simulated dataset to determine whether our

123   coarser sampling regimes compiled with KDE independence assumptions. Other than less frequent

124   tracking, autocorrelation may be reduced by removing repeated locations. This method is particularly

125   relevant for reptiles that exhibit long term sheltering. We considered this special case –sampling regime 8–

126   where only animal relocations are included in the home range estimation. For regime 8 we used the four

127   location per day sampling regime, and then removed data points where the animal was stationary.

128   We described the autocorrelation in the simulated data using the *ctmm* package's variogram functionality

129   (Calabrese, Fleming, & Gurarie, 2016; Fleming *et al.*, 2017), and plotted the minimum number of days

130   until the autocorrelation became insignificant with raincloud plot code from Allen, Poggiali, Whitaker,

131   Marshall, & Kievit (2019).

132   2.2. HOME RANGE ESTIMATORS

133   2.2.1. *Minimum convex polygon*

134   We calculated the Minimum Convex Polygon (MCP) for each simulated individual that created the smallest

135   area convex polygon containing all animal locations. We used the 95% MCP, which removes outlying

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136   points on the assumption that these represent exploratory movements and thus not part of the home range,

137   as originally defined by Burt (1943). The MCP method has long been lauded as a way of maintaining

138   comparability and historical consistency with previous studies (Jennrich & Turner, 1969), yet has well

139   documented issues: extreme sensitivity to sampling size and tracking duration (Anderson, 1982), and

140   overestimated boundary delineation (Robertson, Aebischer, Kenwards, Hanski, & Williams, 1998), with

141   the inclusion of areas that the animals never use (Börger *et al*., 2006; Laver & Kelly, 2008). However, Row

142   & Blouin-Demers (2006) argued that MCPs are preferable to kernel density estimators specifically for

143   herpetofauna, and MCPs' use persists for "comparisons" in reptile telemetry studies (Petersen, Goetz,

144   Dreslik, Kleopfer, & Savitzky, 2019). An additional and considerable limitation of MCPs is that they do

145   not create a probabilistic utilization distribution.

146   *2.2.2. Fixed kernel home range*

147   Fixed KDE home ranges rely on a smoothing parameter (bandwidth) to generate a utilization distribution.

148   Bandwidth selection for KDE can dramatically influence home range estimation (Seaman *et al.*, 1999), and

149   thus we included two bandwidth selection algorithms, reference bandwidth (h_{ref}) and Least-Squares Cross-

150   Validation (LSCV), for our comparisons. Both bandwidth selection methods are frequently used in reptile

151   VHF studies, but potentially flawed for herpetofauna (Row & Blouin-Demer, 2006). The h_{ref} method tends

152   to overestimate home ranges while LSCV tends to underestimate (Hemson *et al.*, 2005). In general, fixed

153   KDE home ranges are not accurate when using autocorrelated data regardless of bandwidth selection

154   function (Noonan *et al*., 2018).

155   *2.2.3. Dynamic Brownian Bridge Movement Model*

156   Dynamic Brownian Bridge Movement Models (dBBMMs) provide utilization distributions based on animal

157   movement paths. The method accounts for temporal autocorrelation, so it requires all locations to be time

158   stamped. In addition, dBBMMs incorporate error associated with each triangulated location, which we kept

159   consistent across species and regimes (at 5 metres) for the following reasons: (1) neither MPCs nor KDEs

160   account for location error, so the evaluation of the impact of this metric would be solely on one method and

161   not effective for comparison purposes; (2) location error associated with VHF telemetry is extremely

162   variable, dependent on macro and micro-habitat characteristics as well as tracking protocols (which we are

163   not assessing); and (3) we wanted to account for cases where GPS error can be greater than step length (e.g.

164   viperids, small lizards). The dBBMM method also allows calculation of Brownian motion variance ($\sigma^2 m$),

165   which can help researchers determine how movement trajectories can occur due to a species' behaviour

166   and activity (Kranstauber *et al.*, 2012). Motion variance can help detect breeding and foraging behaviour

167   in reptiles, even with VHF telemetry data (Silva *et al.*, 2018).

168   2.3 METHOD COMPARISON

169   To compare the error generated from each home range estimator, we calculated the overlap with the

170   theoretical "true home range" for each individual. We generated an individual's "true home range" by

171   creating a buffer around all the simulated movement points with a width of two-times the step length

172   intersect from each simulated species' movement state (40-m for Species 1, 20-m for Species 2, 10-m for

173   Species 3). This provided a conservative home range estimate (excluding the impact of habitat), but more

174   generous and biologically sensible than only using simulated movement pathways. For each home range,

175   we calculated the omission (Type I, false positive) and commission (Type II error, false negative), using

176   the 95% contours for MCP, KDE and dBBMMs. We used the 95% contours, as this is the standard level

177   used in most home range estimates. We then calculated the F-measure $[2/(\text{recall}^{-1}+\text{precision}^{-1})]$, which

178   provides a balanced metric of Type I and Type II errors and is insensitive to true negative rates (Sofaer,

179   Hoeting, & Jarnevich, 2019).

180   We explored the relationship between methods, regimes, and F-measures using a Bayesian generalized

181   linear mixed model with the *brms* package (Bürkner, 2017). We specified a model set for each species, with

182   F-measure as our response variable following a beta distribution (as it is bound between 0 and 1), with

183   individual as a random effect to account for individual variation and a varying slope for the effect of method.

184   We excluded regime 8 (four locations a day, relocations only) as this sampling regime was not systematic.

185   We ran models with six Markov Chain Monte Carlo (MCMC) chains, each with 6,000 iterations (1,000

186   burn-in iterations, thin = 1), and we set Δ to 0.99. We fitted each model with half-Cauchy weakly

187   informative priors (Lemoine, 2019). We checked model convergence by inspecting trace plots and $\hat{R}$ values

188   (Bürkner, 2017), assessed model fit visually via posterior predictive diagnostic plots, and evaluated model

189   performance using leave-one-out cross-validation (Vehtari *et al.*, 2017) and Bayesian R^2. For further details

190   on model selection and validation, see Appendix S2, Supporting Information.

191   We compared the special case of regime 8 (similar to regime 2 but only relocation points) to the original

192   regime 2 in its own Bayesian model set; this allowed us to evaluate the impact of removing stationary

193   locations as a method of reducing data autocorrelation. Additionally, for this special case we only compared

194   the best performing KDE bandwidth (LSCV) and dBBMMs.

195   All datasets and R code to reproduce analyses is available at Zenodo repository platform

196   (DOI:10.5281/zenodo.3660796). We wrote code for R (v.3.5.2, R Core Team), using R studio (v.1.2.1335,

197   R Studio Team).

198   3. Results

199   3.1. SIMULATED ANIMAL MOVEMENT AND TRACKING DATA

200   The complete dataset for each simulated individual consisted of $n = 17{,}521$ data points for a full year, with

201   30-minute time steps (regime 1). Each regime progressively lowered the available data ($n^{\text{reg 2}} = 1{,}460$ data

202   points, $n^{\text{eg 3}} = 730$, $n^{\text{reg 4}} = 365$, $n^{\text{reg 5}} = 104$, $n^{\text{reg 6}} = 52$, $n^{\text{reg 7}} = 12$), while regime 8 varied for each species

203   and individual due to the variability in sheltering and resting behaviour ($n^{\text{species 1}} = 5{,}189 \pm 204$ data points

204   (mean $\pm$ SD); $n^{\text{species 2}} = 3{,}501 \pm 1{,}099$; $n^{\text{species 3}} = 3{,}873 \pm 573$). Visual validation of movement patterns

205   matched with reported patterns in the literature (*e.g.* Parent & Weatherhead, 2000; Reed & Douglas, 2002;

206   Wasko & Sasa, 2009; Hart *et al.*, 2015; Smith *et al.*, 2018; Silva *et al.*, 2018; Marshall *et al.*, 2019), and the

207   predicted patterns of the three archetypes (Figure 2).
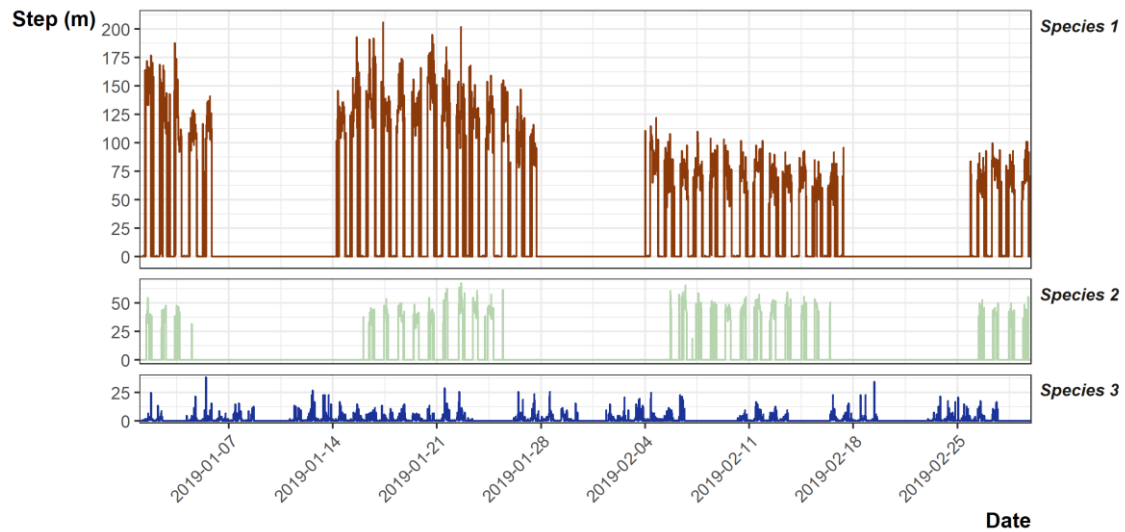
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209   **Figure 2.** Example two-month period illustrating how step distance (m) and its frequency differs between

210   our three species archetypes.

211   As expected, all simulated species and individual datasets showed strong autocorrelated structure. Time

212   until insignificant autocorrelation far exceeded even the coarsest tracking regime tested (regime 7, *i.e.*

213   1/month), indicating that all tracking regimes breach the assumption of independence required for KDE

214   methods (Figure 3).
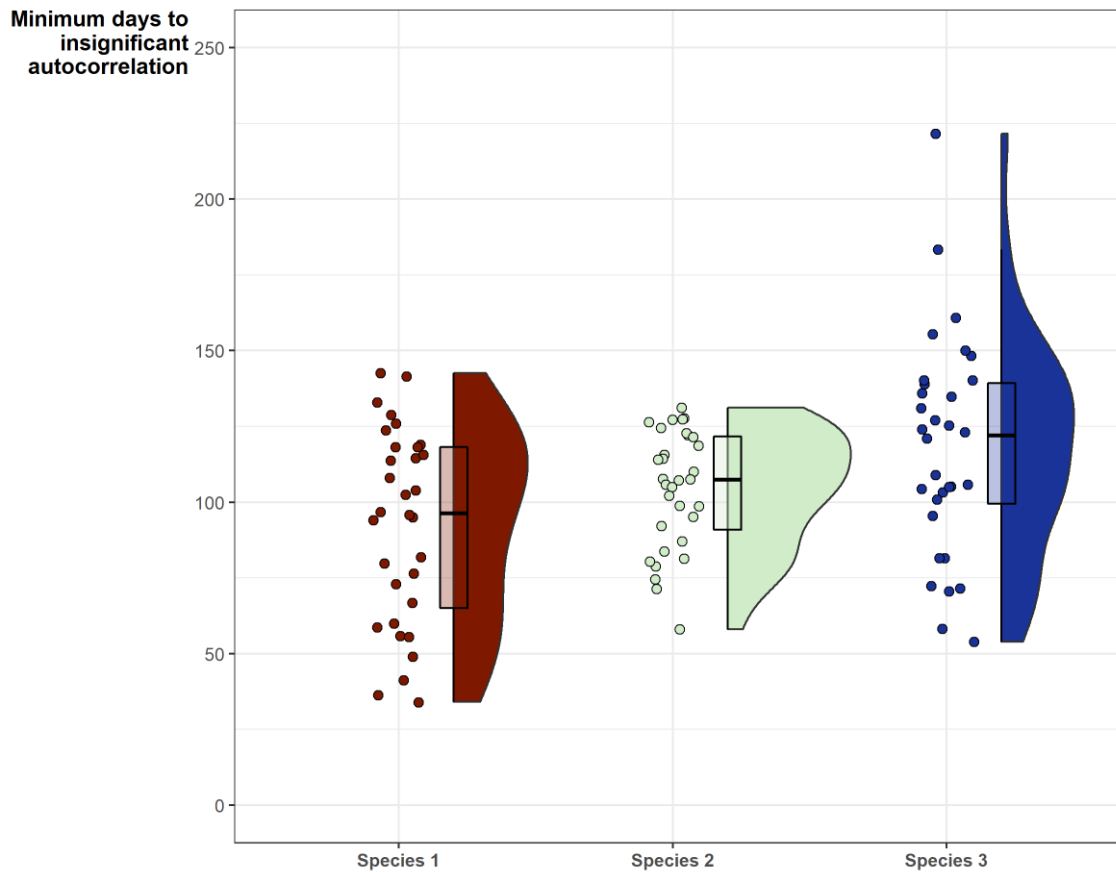
Figure 3. Minimum number of sampling days until the autocorrelation becomes insignificant and data points can be considered independent.

3.2. METHOD COMPARISON: OMISSION VS. COMMISSION

Overall, coarser tracking regimes lead to greater % error when compared to true home ranges. However, the balance between omission and commission is inconsistent and varies between home range estimation methods (Figure 4). There is also a general trend towards commission error when estimating home ranges because omission error is bounded between 0 and 100%.
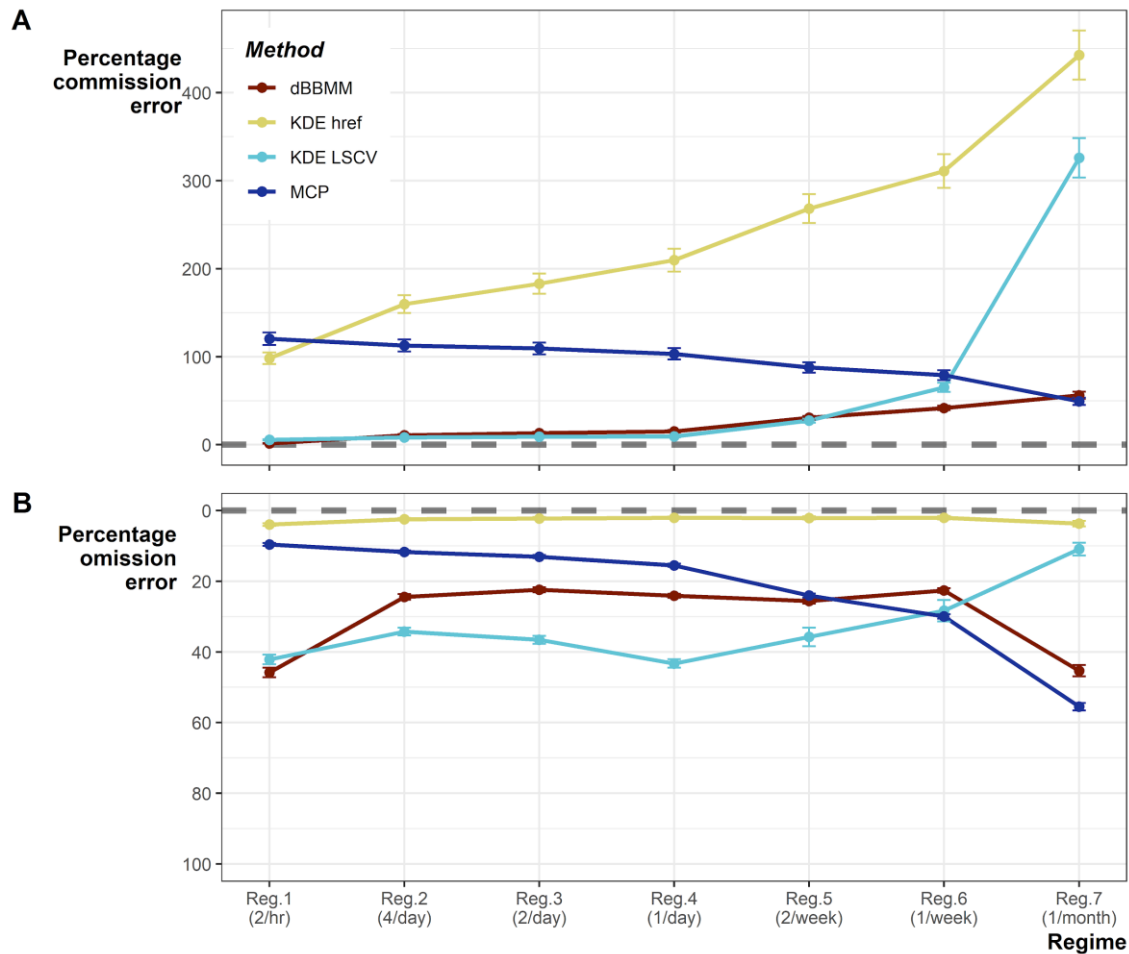
Figure 4. Percentage error from the true home range using 95% contours. **A)** Commission error represented by positive values **B)** omission error represented by negative values. Error bars represent standard error of means across species (3) and individuals (96). Note the different scales for error, as omission error cannot exceed 100% of the true home range area.

3.2.1. *Minimum convex polygon*

Minimum convex polygons were the only method that showed a constant offset between omission and commission, as one increases the other decreases nearly 1:1. In addition, MCPs were the only method that decreased their commission error as tracking regime became temporally coarser. At frequent tracking regimes, MCPs only introduced minimal omission error, but their starkest failure is in their simple shape leading to the greatest commission error at highest resolution tracking regime (Figure 4, 5).

3.2.2. *Fixed kernel home range*

The fixed kernel home range using h_{ref} smoothing factor was by far the worst estimator for commission error. At low resolution tracking regimes, the >400% overestimation leads to near complete loss of home range edge fidelity (Figure 4). Due to this heavy emphasis on generous home range estimation KDE h_{ref} produced negligible omission error (Figure 5).

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239   By comparison KDE LSCV produced consistently lower commission error at higher resolution tracking

240   regimes, but once the regime was once a week or coarser LSCV commission error spikes (up to 300%

241   overestimation). LSCV consistently performed worse in terms of omission error when applied to tracking

242   regimes with multiple tracks per day. Additionally, the LSCV algorithm frequently failed to converge

243   (68.5% of all LSCV home ranges failed). Only regime 7 converged consistently; the inclusion of more data

244   exacerbated convergence failure (regime 1-4, 100%; regime 5, 43.8%; regime 6, 33.3%). Using only

245   relocations reduced convergence failures (regime 8, 2.08%) compared to its closest parallel regime (regime

246   2,100%).

247   For both KDE methods, omission and commission error variability (displayed as SE on Figure 4) increased

248   as tracking regime became coarser.

249   *3.2.3. Dynamic Brownian bridge movement model*

250   Overall dBBMMs performed best. The method produced low commission error levels, matching KDE

251   LSCV performance (Figure 4). Unlike LSCV, dBBMMs commission error remained more stable and lower

252   when applied to coarser tracking regimes. Only MCPs produced a comparative level of commission error

253   at the coarsest tracking regimes, but dBBMMs kept some semblance of shape fidelity and connectivity

254   (Figure 5). Unlike other methods, dBBMM error remained low and balanced between omission and

255   commission, never exceeding 75%.
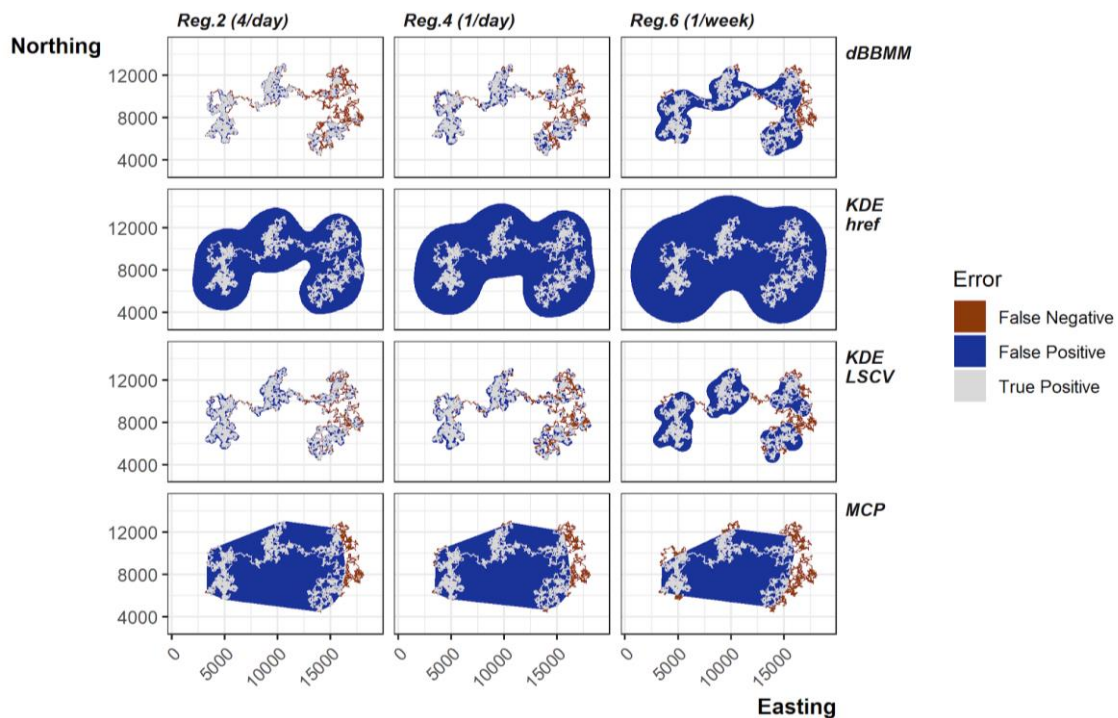
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257   **Figure 5.** An example of how method and regime can interact to produce different levels of false negative,

258   false positive against the true home range. All contours shown are produced from the 95% utilization

259   distribution.

260   3.2.4. *Special case of regime 8*

261   Tracking regime 8 (four locations per day, relocations only) cannot be directly compared to the other

262   regimes as the structure of the tracking is different. A fairer comparison is between regime 8 and 2 (four

263   locations per day). Similar to all other regimes, regime 8 fails to remove autocorrelation to insignificance

264   (Figure 3); however, it did improve the performance of KDE LSCV estimation despite still breaching the

265   fundamental independence assumption (Figure 5, 6). The removal of repeated stationary points prevented

266   the LSCV smoothing from grouping too tightly to point concentrations (i.e. long-term shelter sites),

267   ultimately countering the tendency towards omission error for LSCV. However, on average, dBBMMs

268   performed very similarly and balanced the omission and commission well (Figure 4). The dBBMMs had

269   the added advantage of assuming serial dependence of points and, unlike LSCV, perform well when

270   provided high quantities of data.
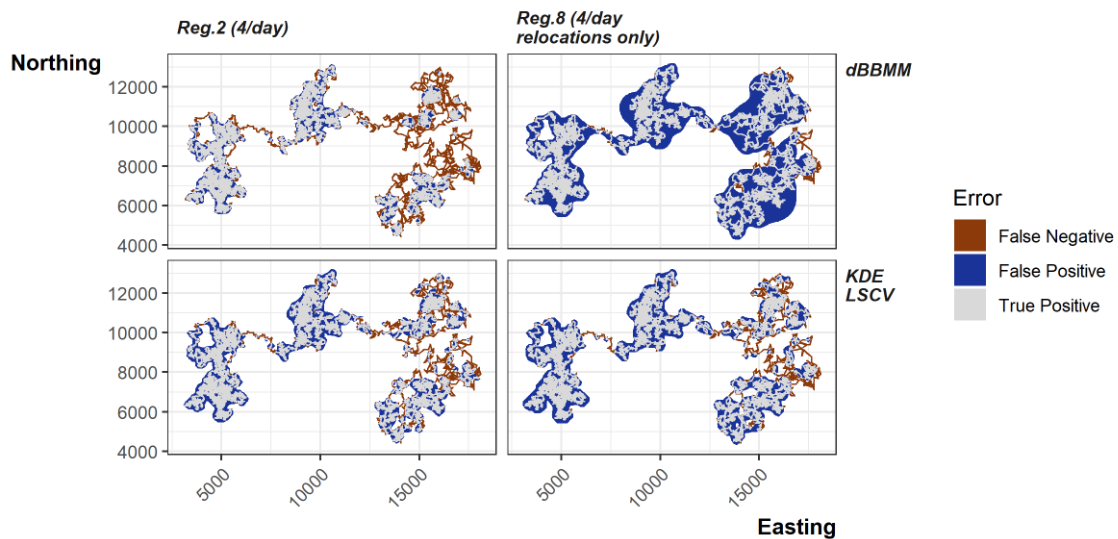
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272   **Figure 6.** Comparison between the error rates produced by the KDE LSCV and dBBMM 95% contour

273   ranges when using data from sampling regime 2 (four locations per day) and regime 8 (four locations per

274   day, relocations only).

275   3.3. METHOD COMPARISON: F-MEASURES

276   The Bayesian models converged and performed well for all three species, with $\hat{R}$ values $\simeq 1.00$ (Appendix

277   S2, Supporting Information), and R^2 values indicating considerable predictive power (Species 1: Bayesian

278    $R^2 = 0.960$, 95% CrI: 0.958–0.962; Species 2: Bayesian $R^2 = 0.946$, CrI: 0.755–0.786; Species 3: Bayesian

279    $R^2 = 0.905$, CrI: 0.897–0.911). Overall, our best models showed an interaction effect of methods and

280   regimes on F-measures; all species had a non-zero positive relationship between F-measures and regimes,

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281   with higher estimates for dBBMM and KDE LSCV, while both MCP and KDE h_{ref} showed considerably

282   worse F-measures. However, Species 1 home range estimations were associated with lower F-measures,

283   suggesting that the home ranges of species with high movement and long periods of sheltering are harder

284   to model than those with more stable movement patterns.
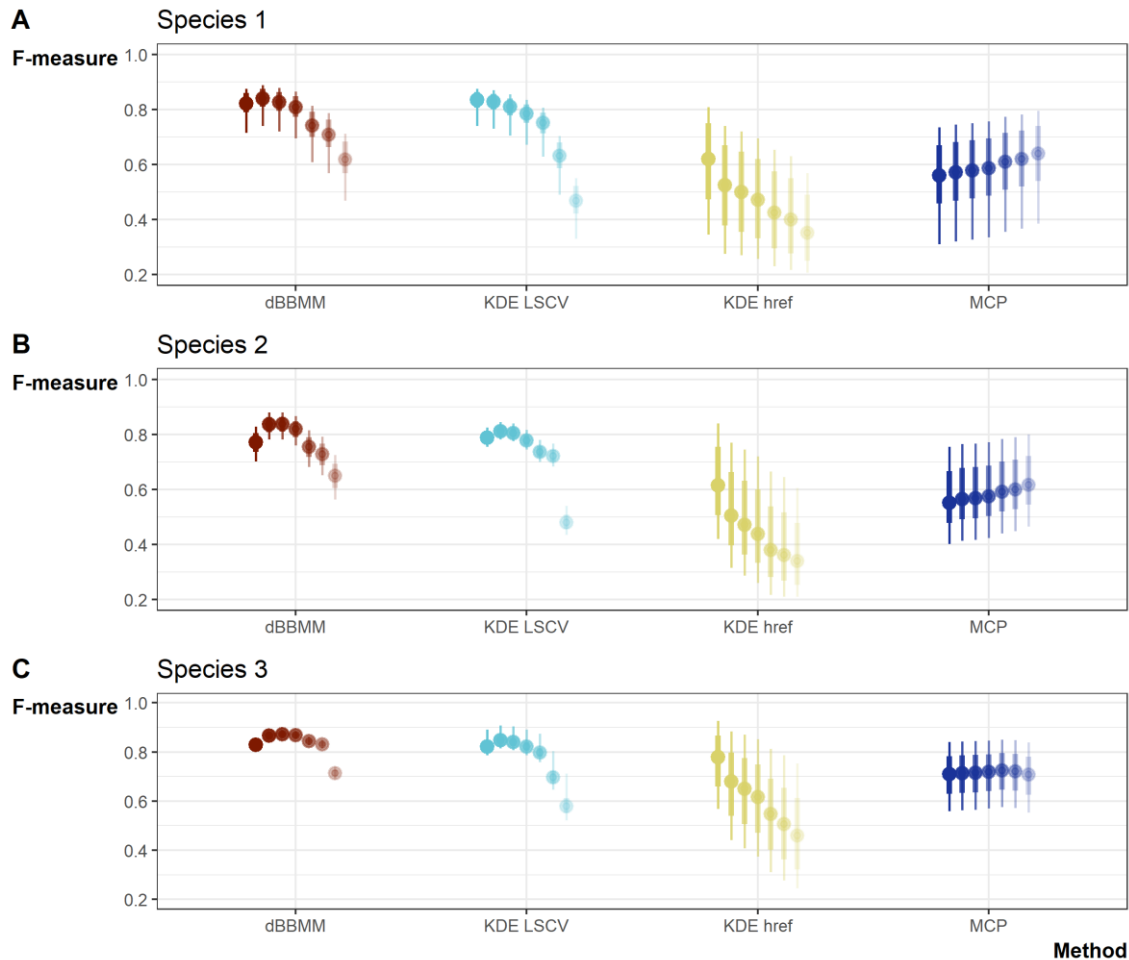
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286   **Figure 7.** Model results that aimed to predict F-measures using method, regime, and individual ID by

287   species. Tracking regime 1-7 are shown left to right with lowering levels of opacity. Fitted draws were

288   taken only from the first 5000 samples.

4. Discussion

290   Many published terrestrial reptile spatial ecology papers reuse the same two methods: Minimum Convex

291   Polygon (MCP), and Kernel Density Estimation (KDE), or variants. Both MCPs and KDEs produced high

292   error rates and failed to properly reflect simulated reptile home ranges. While originally intended for GPS

293   telemetry, we found that dBBMMs perform well across a range of lower fix rates sampling regimes, and

294   for our three archetypical reptile species.

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295   4.1. CHOICE OF FIX FREQUENCY AND ESTIMATOR IMPACTS ESTIMATIONS

296   The data resampling throughout different tracking regimes led to a 91.7–99.9% data loss from our starting

297   point at 30-minute time steps: removing non-relocations (regime 8) still reduced data points by 70.4–80.0%.

298   Seamen *et al.*, (1999) suggested a minimum of 30-50 locations and both regimes 6 ($n = 52$) and 7 ($n = 12$)

299   failed to meet this criteria. A more stringent criteria (Girard *et al.,* 2002) recommending 300 locations also

300   excludes regime 5 ($n = 104$). Based on this fact alone, many reptile studies likely fail to meet KDE

301   requirements.

302   The use of MCP and KDE h_{ref} produced large false positive errors, which if carried forward are liable to

303   impact habitat and space-use inferences (Fieberg, 2007; Nilsen *et al.,* 2008). By comparison, both KDE

304   LSCV and dBBMM estimations fared better, although LSCV failed to produce F-measures comparable to

305   dBBMMs under low-resolution tracking regimes. Thus, dBBMMs can improve upon both traditional MCP

306   and fixed KDE methods. As a fix-frequency independent method (Kranstauber *et al.*, 2012), dBBMMs

307   performed most consistently across sampling regimes with the lowest error rates, even in low-resolution

308   datasets. To match dBBMM performance at the sparsest regimes ($n = 12$) KDEs required four times the

309   data. Maximizing performance under low-resolution regimes is critical for VHF studies because the data

310   are time, effort, and cost intensive (Recio *et al.,* 2011).

311   Furthermore, dBBMMs require no *a priori* knowledge of an animal's movements (necessary to identify the

312   correct smoothing bandwidth for KDEs), and can be put to use with current telemetry practices or to re-

313   analyse previously collected VHF data. The dBBMM method is easily compatible with low-resolution data

314   from herpetofauna spatial ecology studies still reliant on VHF. As gains from long-term high-resolution

315   tracking methods (GPS) still remain elusive for herpetofauna (Price-Rees, Brown, & Shine, 2013; Wolfe *et*

316   *al.*, 2018), improving analytic methods represents a cheap, immediate alternative.

317   At high resolutions the KDE LSCV came closest to performing comparably with dBBMMs despite critical

318   flaws beyond failing the initial point independence assumption. Under higher resolution tracking regimes,

319   the LSCV algorithm fails to converge making the smoothing parameter estimate unusable (supporting

320   findings from Hemson *et al.*, 2015). High site fidelity in reptiles leads to unstable KDE LSCV because

321   non-convergence issues are compounded by large numbers of identical locations or very tight clusters (*i.e.*

322   site fidelity). We did not simulate any site fidelity which could inflate LSCV performance. Hemson *et al.,*

323   (2015) suggest ignoring site fidelity in simulation studies leads to inappropriate conclusions advocating

324   KDE LSCV (*e.g.* Worton, 1995; Seaman & Powell, 1996; Seaman *et al.*, 1999). Even with optimal

325   conditions for LSCV, dBBMMs performed similarly or better.

326   Removing non-relocations (regime 8) improved KDE LSCV while hindering dBBMMs. However, this fix

327   compromises the biological relevance of home range estimates (see De Solla, Bonduriansky, & Brooks,

328   1999) as the autocorrelated nature of animal movement is inherently biologically relevant (Cushman, Chase

329   & Griffin, 2005). The loss of stationary data points harms inferences drawn upon species that shelter for

330   long periods. Explorations using real GPS data show consistent problems with KDE LSCV omission error,

331   leading to severe undersmoothing, and frequent convergence failures (Hemson *et al.*, 2005). Jones, Marron,

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332   & Sheather (1996) found that LSCV smoothed utilization distributions had unacceptable variability, that

333   can undermine comparisons between individuals, populations or studies.

334   Archetypal species movement characteristics influenced our range estimates (MCP, KDE and dBBMM).

335   The active hunter (Species 1), with its sporadic long-distance moves, had lower F-measures and higher

336   error rates than the ambush predators (Species 2 and 3). When comparisons between species are required,

337   researchers should explore how regime and estimation method effect comparisons. Ideally, researchers

338   should be able to access original data from previous studies. We encourage greater use of open data

339   repositories in reptile studies (*e.g.* Movebank). To date, reptile data on Movebank is lacking (11 species,

340   10 testudines and 1 serpentes). Without readily available data, researchers cannot confidently compare

341   between species.

4.2. CAVEATS

343   Herpetofauna and VHF tracking studies can be plagued with uncertainty due to inhospitable terrain and

344   associated costs. Failures to detect animals during tracking are inevitable, and we did not assess how the

345   frequency of missed or inconsistent tracks affects each method. Our results indicate that non-symmetrical

346   tracking regimes (*e.g.* tracks performed on Tuesdays and Thursdays) still appear to work well with

347   dBBMMs. Ultimately, accuracy of home range estimation will be dependent on resources, tracking

348   frequency and study duration (Mitchell, White, & Arnold, 2019). All directly impact the viability of

349   answering research questions. A clearly defined research question (Fieberg & Börger, 2012) enables

350   researchers to identify potential trade-offs in context.

351   While dBBMMs provide a more direct modelling approach for movements –a critical component of

352   assessing habitat use (Van Moorter, Rolandsen, Basille, & Gaillard, 2016)– there is scope for more

353   advanced methods when more is known about a species' movement patterns. dBBMMs provide an instant

354   option for estimating movement pathways of herpetofauna because they require no *a priori* knowledge. In

355   cases where more data are available, researchers can look at methods that integrate more about the

356   landscape, such as dBBMM with covariates (Kranstauber, 2019), or behaviour (Michelot & Blackwell,

357   2019). The more advanced methods may require data at higher resolution than is feasibly collectable by

358   VHF.

4.3. RECOMMENDATIONS AND CONCLUSIONS

360   Researchers must consider tracking regime during study design. There are practical considerations of cost,

361   time and ethics, but they must be paired with how the tracking regime will directly impact estimations and,

362   ultimately, the ability to answer research questions. There will always be spatial uncertainty. Tracking

363   regime should minimize spatial uncertainty with reference to the research question and targeted behaviours

364   (Fleming *et al.,* 2014; Schlägel & Lewis, 2016; Bastille-Rousseau *et al.*, 2017). Direct consideration of how

365   biology and movement impact home range will improve inferences drawn from telemetry studies.

366 The insights into reptile ecology can be invaluable despite data collection costs, and data utility should be
367 maximized. Better home range estimators are an inexpensive way of optimizing returns from tracking data
368 compared to technological advances or increasing field work. Reptile movement is peculiar: we revealed
369 the impact of long-term sheltering (essentially a zero-inflated movement dataset) on home range
370 estimations, which introduced error by under- and over-smoothing with traditional estimators. Inferences
371 based on traditional estimators have likely led to biases in reptile studies. Carrying these biases forward can
372 lead to misallocation of resources.

373 Our study concurs with previous studies *e.g.* Signer *et al.* (2015) stating problems with both MCP and
374 KDEs. Despite known problems researchers continue to justify use of MCPs and KDEs to maintain
375 comparability with previous studies. We find this deeply flawed in cases where tracking regime or estimator
376 differ which produce dramatically different error rates. However, we also demonstrate the stability of
377 dBBMMs and their suitability for comparisons. The information provided here can help optimise reptile
378 spatial ecology by yielding more accurate and reproducible home range estimations.

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