Are trapping data still suited for home range estimation? An analysis with various estimators, asymptotic models and data ordering procedures

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Abstract

Understanding the size of animals' home ranges is vital for studies in ecology and conservation. Trapping datasets are an important source of information when targeting the biodiversity of an area, inconspicuous species, or high numbers of individuals in contrast to more expensive telemetry-based methods such as radio- or GPS-collaring. Currently, studies relying on trapping lack an evaluation of the performance of existing home range estimation procedures comparable to those developed for telemetry. Using animal movement simulations, we evaluate three variables reflecting the trade-offs faced by ecologists when designing a trapping study, 1) the number of observations obtained per individual, 2) the trap density and 3) the proportion of the home range area falling inside of the trapping grid. We compare the performance of five estimators on these conditions, four commonly used (AKDE, KDE, MCP, LoCoH) and a possible alternative for situations with low trap density or high number of observations (bicubic interpolation). We further test suggested benefits of using asymptotic models (Michaelis-Menten and monomolecular) to assess the total home range area when information obtained per individual is scarce, as this situation might be common in trapping datasets. In addition, we propose sorting the observations based on the distance between locations to improve the performance of asymptotic models' estimates. Using the results of the different procedures we constructed a generalized additive model (GAM) that allows predicting the bias in home range size under the different scenarios investigated. Our results show that the proportion of the area covered by the trapping grid and the number of observations were the most important factors predicting the accuracy and reliability of the estimates. The use of asymptotic models helped obtaining an accurate estimation at lower sample sizes and this effect was further improved by distance-ordering. The autocorrelation informed KDE was the estimator performing best under most conditions evaluated. Nevertheless, bicubic interpolation can be an alternative under common trapping conditions with low density of traps and low area covered. We provide the current results to the constructed GAM as a prospective tool for ecologists planning a new study or with already collected

39   datasets that aim at assessing the potential biases in their estimates. Reliable and accurate home range

40   estimates using trapping data can optimize monetary costs of home range studies, potentially enlarging

41   the span of species, researchers and questions studied in ecology and conservation.

42

Introduction

44 Home ranges have been defined as "...the area traversed by the individual in its normal activities of food

45 gathering, mating, and caring for young" (Burt 1943). The intensity of resource use and competition, the

46 amount of gene flow, the mating system and social structure, and the spread of information and diseases

47 might all be inferred through animals' space use (Mueller and Fagan 2008, Schick et al. 2008, Dammhahn

48 and Kappeler 2008, Nathan et al. 2008). Knowledge on a species' use of space is therefore at the core of

49 understanding biodiversity and design effective conservation measures (Law and Dickman 1998, Allen

50 and Singh 2016, Oppel et al. 2018).

51 Although the ecological definition of the home range is not specific to any data type nor estimator, the

52 accurate estimation of home ranges is challenged by mismatches between the methods' assumptions and

53 the nature of the data collected (Hayne 1949, Andrzejewski 2002, Powell and Mitchell 2012, Noonan et

54 al. 2019, Wszola et al. 2019, Fleming et al. 2019). During the last century, an extensive body of literature

55 has been directed to describe and quantify biases arising from methods used (see e.g., Hayne 1949, 1950,

56 Worton 1989, Harris et al. 1990, Seaman et al. 1999, Andrzejewski 2002, Laver and Kelly 2008, Fleming et

57 al. 2018, 2019). Comparisons of different estimators for home ranges have suggested strengths of each

58 under different conditions (e.g., sample size, the time between measurements and autocorrelation)

59 (Hayne 1949, Van Winkle 1975, Rose 1982, Worton 1987, Plotz et al. 2016, Halbrook and Petach 2018,

60 Noonan et al. 2019, Vieira et al. 2019). Further spatial and temporal heterogeneities have also been

61 investigated (e.g., ecotypes, physical boundaries) and shown to have an effect (Ouellette and Cardille

62 2011, Halbrook and Petach 2018, Wszola et al. 2019). The (mis)match between weaknesses and strengths

63 of estimators and data collected is therefore a major potential source of error in home range estimates

64 that needs to be evaluated (Hayne 1949, Van Winkle 1975, Worton 1989, Seaman et al. 1999, Kie et al.

65 2010, Powell and Mitchell 2012, Fleming and Calabrese 2017, Halbrook and Petach 2018, Fleming et al.

66 2019).

67   Several authors have suggested that if animals exhibit site fidelity (e.g. Ebersole, 1980; Halbrook & Petach,

68   2018; Heupel, Simpfendorfer, & Hueter, 2004; Powell, Zimmerman, & Seaman, 1997; Reid &

69   Weatherhead, 1988; Spencer, Cameron, & Swihart, 1990), the information on space use obtained should

70   follow a saturation curve (Harris et al. 1990, Haines et al. 2009, Soanes et al. 2013, Leo et al. 2016,

71   Halbrook and Petach 2018, Wszola et al. 2019). Deviations from this saturation may thus indicate that i)

72   the animals being monitored are not range-resident (e.g., (Morato et al. 2016)), or ii) the individual has

73   been monitored for too short of a period for the range-resident behavior to be observable (Fleming et al.

74   2014). The latter problem represents a key challenge that can bias home range estimates and any

75   subsequent hypothesis testing, or decision making. Modelling the saturation curve can allow estimating

76   the true home range even if the information is still incomplete (e.g., (Soanes et al. 2013, Leo et al. 2016,

77   Halbrook and Petach 2018)), thus offering the possibility of reducing the amount of data needed for

78   accurate estimates. Nevertheless, most empirical studies do not make use of asymptotic models perhaps

79   because a thorough examination of the performance of this type of analyses is lacking.

80   The mentioned limitations and mismatches between the methods used for obtention of information and

81   description of space use in animals might be even more pronounced in trapping-based studies. While

82   trapping studies were once predominant in home range estimation (Mohr 1947, Hayne 1949,

83   Andrzejewski 2002), they have decayed in the last decades in favor of newer, more accurate and reliable

84   technologies based on radiotracking or GPS (Innes and Skipworth 1983, Ward 1984, Bergstrom 1988,

85   Ribble et al. 2002, Gil-Sánchez et al. 2011, Kays et al. 2015). Trapping studies suffer most importantly from

86   extreme uncertainty on the information obtained per individual which usually consists of few observations

87   (Dammhahn and Kappeler 2005, Lira and Fernandez 2009, Gil-Sánchez et al. 2011, Kane et al. 2015,

88   Kumbhojkar et al. 2020). Unlike for telemetry data, where temporal autocorrelation is the predominate

89   source of bias for home range estimation (Noonan et al. 2019, Silva et al. 2022), small sample sizes are a

90   key consideration. All home range estimators are sensitive to sample size (Schoener 1981, Fleming et al.

91   2019). Thus, the reliability of information on home ranges coming from trapping studies is often uncertain

92   and an evaluation of the necessary conditions for accuracy and reliability are needed.

93   In addition to the low number of observations, the size of the trapping grid and its emplacement relative

94   to the center of an individual's home range can also impact the measurements in trapping studies (Rajska-

95   Jurgiel 2001, Lukacs et al. 2005, Bondrup-Nielsen 2011, Sun et al. 2014). Due to a lack of understanding

96   on the biases and limitations of carrying home range analyses with trapping data, researchers with

97   trapping datasets face extreme uncertainty on the error of their estimates and might even dismiss

98   conducting home range analyses altogether (Fig. 1). This situation can bias the knowledge on movement

99   ecology to only those species that can be monitored via telemetry. Trapping data harbor enormous

100   potential for home range analysis due to the range of species that can be studied and the reduced

101   budgetary constraints. For instance, camera- or live-trapping can be used to study animals that are too

102   small to carry a telemetry or GPS collar. Moreover, with the average all-in cost of tracking an animal being

103   ca. $10,000 USD (Thomas et al. 2011), collars are expensive, reducing the number of individuals and

104   species that can be monitored at a given location. In addition, the costs of telemetry-based methods might

105   set a boundary to the economic background of institutions or researchers in movement ecology. If

106   trapping based studies prove more reliable than previously thought they could enlarge the scope of

107   researchers, species and time of monitoring helping improve general knowledge on movement ecology

108   essential for fundamental and applied science.

109   To fill the current gap in knowledge on trapping datasets for home range analyses we conducted a

110   thorough evaluation of their accuracy under a vast array of conditions in a set of simulations. We

111   evaluated the performance of five estimators, two kernel based (autocorrelated kernel density estimation

112   AKDE, and traditional KDE), a polygon-based (minimum convex polygon MCP) and its generalization (local

113   convex hull LoCoH) and an interpolation-based method (bicubic interpolation BicubIt). Moreover, we

114   evaluated the performance of two asymptotic model predictions (Michaelis-Menten MicMen and

115   Monomolecular MonMol) as they have been suggested to help when information is incomplete, a

116   common situation for trapping datasets. In addition, we evaluated these asymptotic models on two

117   conditions for ordering the observations, time-ordered and distance-ordered as we suspected that the

118   latter could improve their predictions. The combinations of all mentioned variables were evaluated under

119   three key parameters for designing a trapping study: the trap density, the effective sample size, and the

120   proportion of the home range covered by the trapping grid. These measures correspond to the amount

121   of effort and money invested in a study based on animal captures and can impact the estimates of home

122   range size. Our analyses thus may point to optimal investments for describing animal home ranges in

123   studies relying on animal trapping, representing an important tool for ecologists that aim at study

124   movement using trap data.

Material and Methods

Simulating animal movements and trapping

127   We simulated home ranges with a circular area of 100 Hectares and a uniform distribution probability for

128   observing the animal across it. We simulated movement for 100 individuals moving within this type of

129   home range without any autocorrelation (i.e., using a I.I.D. movement model), as trap data are likely to

130   be free from meaningful autocorrelation. To capture the individuals, we generated a series of trapping

131   grids with varying densities measured as number of traps in each line of the grid per home range radius

132   (ranging from 2 to 42 over intervals of 10, see Fig. 2). Each trapping grid was placed with its center at

133   different distances from the center of the home range creating a coverage ranging from 20 to 100% (see

134   Fig. 2). We considered an animal captured if an observation fell within 200m of a trap (approx.

135   corresponds to 20m for small animals with home ranges of 1Ha). We chose this measure to simulate the

136   attraction of baiting in real-world scenarios with live trapping but can also be understood as a metric of

137   visibility for camera traps. Finally, for each individual in each condition of trap density and area covered

138   we simulated positions until it was captured 2000 times. The scripts necessary to reproduce these

139   simulations will be provided when published in a peer-review journal.

Fitting estimators and asymptotic models

Incremental analyses: home range area as a function of the number of observations

142   For each dataset we decided a set of ticks between 2 and 2000 observations on which to conduct the

143   estimates of home ranges. The interval between ticks increased progressively as we expected redundancy

144   in information because of the asymptotic behavior of spatial variance for range-resident animals. Based

145   on these observation number ticks we performed two orderings of the locations for each individual. The

146   first corresponds to standard use in home range analyses, with observations ordered by time (time-

147   ordered hereafter). The second one was achieved by taking each subset of observations from the time

148   ordered dataset and reordering based on distance using farthest point sampling (Fig. 3). Farthest point

149   sampling allows reordering the data, with each point being followed by its corresponding farthest point

150   in the dataset based on Euclidean distances, excluding computed points already used. By doing so, while

151   for each number of observations both the time ordered and the distance ordered dataset contained the

152   same exact records of space positions, the distance ordered included most information on space use

153   within the first observations (Fig. 3).

154   For each dataset we calculated the home range area incrementally. For the time-ordered dataset this

155   incremental analysis corresponded to calculate the home range area at each tick ($Area_i$), yielding a unique

156   incrementing curve of home range area per dataset from 2 to 2000 observations. For the distance-ordered

157   dataset a different curve ending at each tick was calculated (Fig. 3). Each tick had a different curve because

158   each subset had different farthest points being redistributed accordingly with more information clumping

159   in the first observations.

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160   *Home range estimators*

161   To calculate the home range areas, five estimators were used. A widely used method, the Kernel Density

162   Estimator (KDE) was chosen as it is the most statistically efficient non-parametric density estimator. We

163   further used a refined version of the KDE that takes autocorrelation into account (AKDE) and has further

164   refinements for small sample sizes, irregular sampling, and measurement error (Silva et al. 2022). For KDE,

165   an automatic bandwidth selection method was applied to each subset of the data based on bisection

166   algorithm that finds the smallest bandwidth generating n polygons (Kie 2013). We set n to 1 to have a

167   single continuous home range area. Two commonly used polygon-based methods, the minimum convex

168   polygon (MCP) and its generalization, the local convex hull (LoCoh) were also used (see Supporting

169   information, SI). Furthermore, we explored the properties of a home range estimation based on bicubic

170   interpolation (BicubIt). We expect this latter estimator to perform better under low trap densities as well

171   as with very large datasets when kernel-based estimators become ineffective due to the bandwidth

172   limiting to 0 when $n \rightarrow \infty$ (see SI).

173   *Asymptotic models*

174   A Michaelis-Menten model as described in (Leo et al. 2016) (eq 1) was fitted to the home range area as a

175   function of the number of observations with automatic initial values for the rest of parameters. The

176   Michaelis-Menten model is a saturating model that is well known in the biological sciences. A challenge

177   with this model, however, is that the asymptote can be difficult to estimate with data (Bolker 2008). We

178   therefore also explored the potential benefits of the monomolecular model (eq 2). The models were fitted

179   to each tick in the single curve for the time-ordered dataset using Levenberg-Marquardt nonlinear least-

180   squares algorithm. For the distance-ordered, the models were fitted to each curve created with the

181   observations until a given tick. The predicted asymptotes were retrieved and assigned as value for the

182   home range area to the number of observations it used.

183    $Area_i = \frac{\alpha * i}{B + i}$ eq (1)

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184 $$Area_i = \alpha * (1 - e^{-e^{k}*i}) \qquad eq\ (2)$$

Evaluating the different methods for home range estimation on trapping data

186 We transformed the areas obtained in the previous analyses to a proportion of the true 95% home-range

187 area. Using the variables describing the estimator used, the time-ordering procedure, the asymptotic

188 model used and the three variables for study design (number of observations, trap density and area

189 covered) we modelled the accuracy of area estimates using a generalized additive model (GAM) in the

190 mgcv package (Wood 2017) in R version 4.0.5 (R Core Team 2019). GAM was chosen to capture the

191 possible complex non-linear relationships between our variables of interest and the home range area

192 predicted. The proportion of the true area was made dependent on the number of observations, the trap

193 density and the area covered by the trapping grid using a gaussian link function (eq. 3). Since asymptotic

194 models can overestimate the area dramatically under low number of observations, we filtered out

195 extreme outliers before fitting the GAM. We defined extreme outliers as those that overestimated or

196 underestimated the true area by a factor of 10. This type of aberrant predictions can be easily detected

197 by researchers in their datasets once some knowledge on the species is available.

198 $Area = Intsem + f_1(\log_{10} NbObs) \cdot Intsem + f_2(TrapD) \cdot Intsem + f_3(AreaC) \cdot Intsem +$

199 $f_4(\log_{10} NbObs \cdot TrapD) \cdot Intsem + f_5(\log_{10} NbObs \cdot AreaC) \cdot Intsem + f_6(TrapD \cdot AreaC) \cdot$

200 $Intsem + f_7(\log_{10} NbObs \cdot TrapD \cdot AreaC) \cdot Intsem + \varepsilon \qquad eq\ (3)$

201 *where f_{1-3} are smooth and f_{4-7} partial tensor product interaction smooth functions estimated by*

202 *restricted maximum likelihood*

203 The number of observations was transformed using its base ten logarithm and the knots for the basis

204 functions were placed according to a logarithm function in the range of observed values. Placing the knots

205 in this way allowed to model the variation at low observation numbers when small changes are likely to

206 induce much stronger effects than at the higher end. We included a three-way interaction as a tensor

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207   product interaction between the number of observations, the trap density and the area covered as their

208   effects are all conditional on each other (eq. 3). All lower-level interactions combinations and main effects

209   of the three variables were also included as tensor product interactions and smooth terms respectively.

210   Furthermore, a factor variable gathering the home range estimator, the asymptotic model and the

211   sampling ordering procedure (intsem) was generated. "intsem" was included as a main effect and as a "by

212   variable" on each smooth and tensor product interaction term. Including this smooth-by-factor

213   interactions allowed fitting a smooth term separately for each level of "intsem". Such flexibility was

214   needed to capture the likely different shapes that the functions for each level and combinations of the

215   variables of interest might have. The use of a common variable, "intsem", reduced the computational

216   burden of modelling the home range estimator, the asymptotic model and the sampling order procedure

217   as separate terms. The sufficiency of the basis dimensions for each smooth term were evaluated by using

218   the standard procedures for GAM evaluation in the mgcv package including the tests of gam.check

219   function and the diagnostics of linear modelling assumptions. For further details on other parameters see

220   SM.

221   We then evaluated the accuracy and reliability of home range estimates in trapping settings using our

222   simulations. To visually identify the parameter spaces of interest for trapping studies, predictions were

223   considered accurate if fell within $\pm10\%$ of the true area and reliable if the confidence interval had a

224   breadth not exceeding $\pm20\%$ of the estimate. For each graphic representation we described with

225   emphasis only the values that were accurate and reliable according to the above definitions. When

226   possible, we also described the conditions that allowed reaching accuracy instead of under- or over-

227   estimation and reliability.

228   To produce the graphic representations summarizing the results, we predicted the home range area as a

229   function of the two-way interactions between the number of observations and the trapping density (while

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230   setting the area covered to 100%), between the number of observations and the area covered (setting

231   the trap density to 2), and between the area covered and the trap density (setting the number of

232   observations to 7) using the constructed GAM. The fixed values of low trap density and low number of

233   observations were chosen to describe possible common situations in field studies using trapping

234   procedures. Further graphic representations including fixed values at low, mean, and high values can be

235   found in the SI.

Results

237   The 43 individuals simulated yielded a total number of 415,612 observations based on the combination

238   of 5 estimators, 2 ordering procedures, 3 model types (including no model), 6 trap densities, 6 area

239   covered proportions and 28 different number of observations. Overall, the GAM model performed

240   satisfactorily with most residuals being close to 0 (see SI). There existed some level of heteroskedasticity

241   with high variance characterizing the areas at low number of observations. Moreover, residuals were non-

242   normally distributed due to a positive skew resulting from i) the distribution of the response (bounded at

243   0 but unbounded at positive infinity) and ii) high overestimated asymptotic models' predictions at low

244   number of observations (see SI).

Interacting effects of number of observations and trap density

246   When the trapping grid covered the home range entirely, the number of observations was the primary

247   factor driving the accuracy of the estimates (Fig. 4 see vertical color bands and accuracy niches). The

248   reliability of estimates also depended more strongly on the number of observations than on the trap

249   density with an estimator-specific minimum above which estimates were consistently (Fig. 4). The

250   estimators that conformed more strongly to the described general patterns were the two Kernel-based.

251   The two polygon-based estimators followed in conformity, deviating from the described pattern when

252   used with time-ordered asymptotic models where accuracy niches reacted more strongly to trap density.

253   BicubIt stand out from the rest by having the accuracy and reliability dependent equally on the number

254   of observations and the trap density (Fig. 4 see diagonal color bands and lines).

255   The two Kernel density estimators outperformed the rest with accurate estimates at 9 and 20

256   observations (AKDE and KDE respectively). The rest underestimated the true area before ~1000 (MCP and

257   LoCoH) and ~600 (BicubIt, only at low trap density) observations where gathered. The reliability of

258   estimates was obtained at very low number of observations except for BicubIt where the higher the trap

259   density the more observations were needed for a reliable estimate.

260   Interestingly, using the asymptotic models generated accuracy and reliability patterns that had estimator-

261   specific optima generally lacking asymptotic consistency (i.e., adding more observations after the accuracy

262   and reliability niche was attained induced its loss). The two Kernel-based methods suffered by needing

263   more observations for an accurate estimate than when using the raw data alone, particularly at low trap

264   densities. At higher trap densities, though, KDE benefited from using MonMol through improved accuracy

265   of estimates at low sample sizes. MCP became unreliable when used with MicMen and never reached

266   accuracy while MonMol allowed accurate and reliable estimates at lower number of observations. LoCoH

267   benefitted from using MicMen by reaching reliability and accuracy at ~10 observations while using

268   MonMol led to very limited accuracy niches. Similarly, BicubIt benefited only from MicMen and not from

269   MonMol. MicMen allowed to have accurate and reliable predictions between 3 and 80 observations for

270   the smallest trap densities.

271   Distance-ordering helped through stabilization of the accuracy and reliability niches after their advent and

272   through a higher set of conditions yielding reliable estimates. Nevertheless, this procedure only benefited

273   accuracy with KDE by reducing the minimum number of observations and with BicubIt by expanding the

274   range of trap densities yielding an accurate estimate.

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Interacting effects of number of observations and area covered

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276   When the trap density was four traps per grid line per home range radius, increasing both observations

277   and area covered led to higher accuracy. Reliability depended on an estimator-specific minimum number

278   of observations above which increasing the area covered led to more reliable estimates. The accuracy of

279   Kernel-based estimators was affected more strongly by the area covered than by the number of

280   observations (Fig. 5, see "v" shaped accuracy niches along the x axis). The polygon-based estimators were,

281   on the contrary, more affected by the number of observations, once a minimum area covered was

282   attained. BicubIt offered a bimodal accuracy were the extremes of area covered tended to yield more

283   accurate estimates. AKDE performed best, followed by KDE, BicubIt, MCP and LoCoH. AKDE was able to

284   offer accurate and reliable estimates with 5 observations and an area covered as low as 50%, while KDE

285   needed at least 40 observations. MCP and LoCoH were unable to offer accurate estimates while BicubIt

286   needed the highest area covered and number of observations.

287   Using asymptotic models offered some benefits albeit the accuracy niches were not consistent when

288   increasing sample sizes. Accuracy niches had a "v" shape (except for BicubIt, indicating optimal values

289   changing with the upper space in the "v" risking overestimation. AKDE and KDE benefited by lowering the

290   minimum area covered (~30%) in order to retrieve an accurate estimation. MCP benefited from MonMol

291   reducing the minimum number of observations to~15, while MicMen yielded unreliable estimates. Both

292   asymptotic models helped LoCoH achieve accurate estimates, despite only MicMen with reliability at ~15

293   observations. BicubIt benefited from asymptotic models from increased reliability and accuracy, but more

294   so from MicMen. Using MicMen allowed to retrieve accurate estimations at as low as 4-5 observations

295   with both high and low area covered.

296   Use of distance-ordering generated more consistent accuracy and reliability niches only for the polygon-

297   based methods while the others were affected idiosyncratically. AKDE was disturbed because the ctmm

298   package algorithm did not perform consistently with reordered data generating low sample sizes used to

299   fit GAM (see SI). KDE with distance-ordering did not improve but rather shifted the optimal value of area

300   covered with increasing observations. For MCP distance-ordering only improved the reliability of

301   estimates. The use of distance-ordering allowed better estimates than the raw LoCoh without reaching

302   our criteria. With BicubIt, using distance-ordering did not improve or hampered but changed the shape of

303   the accuracy niche.

Interacting effects of trap density and area covered

305   When the number of observations was fixed to 7, depending on the estimator used, only the area covered,

306   or a combination of area covered and trap density values determined the accuracy and reliability. Kernel-

307   based estimators offered reliable estimates the accuracy of which was determined solely by variation in

308   the area covered (Fig. 6, see elongated accuracy niches along the x axis). The patterns for the remaining

309   three estimators were more complex. Only AKDE was able to recover an accurate estimate at

310   intermediate-high values of area covered when estimators were used alone.

311   Using asymptotic models yielded improvements in accuracy for all estimators. AKDE improved by reducing

312   the area covered needed for an accurate estimate (MonMol 20% to 40%; MicMen 40% to 60%; for lowest

313   and highest trap densities respectively). KDE greatly benefitted from an increase in accuracy that achieved

314   our criteria when the area covered was between 20 and 60% for all except the lowest and highest trap

315   density values. The use of MonMol allowed accurate estimates at all trap densities but for a narrower

316   range at intermediate area covered values at the lowest trap densities and to 20% at the highest trap

317   densities. Using MicMen allowed MCP to yield reliable and accurate estimates for all area covered values

318   at intermediate trap densities while MonMol only for two values of area covered, 50 and 70%. Asymptotic

319   models helped increasing accuracy of LoCoH but these weren't reliable according to our criteria. BicubIt

320   was empowered by MicMen yielding accuracy at the smallest trap densities for 20% and 100% area

321   covered while MonMol yielded accurate estimates only at 20% area covered.

322   Using distance-ordering impacted negatively AKDE impairing its reliability. KDE on the contrary benefited

323   substantially by having more accuracy overall despite needing an increase in area covered (MicMen 40%

324   to 80% and MonMol 60% to 100% for low and medium/large values of trap density respectively). For MCP

325   MonMol with distance-ordering helped retrieving reliable estimates from 40% area covered and accurate

326   at 100% area covered from medium to high values of trap density. LoCoh benefited from distance ordering

327   by increasing reliability, but accuracy was not reached. Distance-ordering did not improve or hamper

328   BicubIt estimates.

Discussion and conclusion

330   Our results indicate that estimators used with telemetry and GPS data can yield reliable estimates of home

331   range size when used with trapping data. Depending on the methodology, estimators examined were able

332   to retrieve accurate and reliable estimates even in the challenging scenarios including very low spatial

333   resolution and reduced information per individual. Such performance indicates that, despite having gone

334   underused in favor of more modern methodology, trapping data can continue to prove a valuable source

335   for home range studies.

336   Under most scenarios investigated, AKDE was able to recover an accurate estimate at lower sample sizes

337   than the other estimators. KDE usually followed behind while MCP, LoCoH and BicubIt needed a much

338   higher number of observations. This behavior is consistent with the accuracy of these estimators on

339   telemetry data (Noonan et al. 2019). The use of asymptotic models helped all estimators except AKDE in

340   reaching an accurate estimation with fewer observations. Nevertheless, counterintuitively, under most

341   scenarios the use of asymptotic models' predictions reduced the consistency of the reached accuracy. For

342   example, as hypothesized by (Gautestad and Mysterud 1995), MCP (and LoCoH) needed more than 1500

343   observations to reach the asymptote with the true home range. While using asymptotic models'

344   predictions helped MCP, LoCoH and BicubIt reduce by one or two orders of magnitude the number

345   observations needed for an accurate estimation, increasing the number of observations further led to

346   changes in the predicted area. The use of distance ordering prior to calculating the home range areas and

347   fitting the asymptotic models allowed both reducing the number of observations albeit more moderately,

348   between 5 to 10 times, while maintaining consistency and attaining reliability at lower sample sizes (see

349   SI). Thus, we suggest the use of asymptotic models in home range analyses cautiously, possibly with

350   distance ordering and additional checks on the reliability of asymptotic estimates as developed in (Haines

351   et al. 2009).

352   Promisingly, accurate estimates of the home range area were obtained with as few as 3 observations per

353   individual, a finding that could encourage movement ecologists to plan trapping studies and other

354   researchers to exploit their existing trapping datasets for home range estimates. Our findings of accuracy

355   and reliability of estimators for home range analyses with trapping data might offer an additional push to

356   enlarge the range of species and researchers in home range studies. A higher diversity of species and

357   researchers can result in new questions being addressed by a more inclusive research milieu not limited

358   by the large budgets needed for telemetry-based monitoring. A standard metallic foldable trap for small

359   animals might cost on the order of tens of dollars while the average, all-in cost of tracking an animal is on

360   the order of tens of thousands of dollars (Thomas et al. 2011). Since traps can be used for several years if

361   well maintained and are not used for a unique individual, they might turn a smaller budget into a

362   competitive alternative.

363   Telemetry devices are also best deployed on animals large enough to carry them or else become

364   extremely limited by their small battery life. Although tag sizes have been rapidly decreasing, most species

365   are still too small to be monitored by telemetry (Kays et al. 2015). Our results show how the home range

366   area of small animals unsuited to collaring can be accurately monitored using traps. Nevertheless,

367   trapping in wild animals is not free of costs. Traps might be disease vectors and harmful if not maintained

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368   properly. Moreover, the psychophysiological welfare of animals should not be neglected, and the time

369   spent in the trap minimized. Reducing the time in the trap might also improve survival because captured

370   animals are vulnerable to predation. An alternative to live trapping could be the use of camera traps or

371   sound recorders (Chavel et al. 2017). The considerations of trap density, number of observations and area

372   covered all should hold if autocorrelation between detections is taken into account.

373   Over the range of conditions examined, the proportion of the home range area covered by the trapping

374   grid and the number of observations had a much stronger impact than the trap density. Thus,

375   theoretically, the effort of trapping studies could be redirected to expanding the grid to encompass a

376   greater study area instead of densifying it. However, for animals that have overlapping home ranges,

377   reducing the trap density might lead to reduce the chances of relocating a focal individual several times.

378   Under scarcity of traps other residents may be trapped impeding gathering enough observations per

379   individual. To increase the number of observations per individual and the number of individuals, one could

380   increase the number of traps on each knot of the grid, thereby slightly reducing the working time by

381   clumping traps in space. In addition, in our simulations, traps were highly effective having a range of

382   attraction of 200m for a home range of 1 Ha as we tried to mimic high visibility or bated traps. If traps

383   have a lower range of action, sparsening the grid might significantly reduce the sample size per individual.

384   Reducing the number of grid knots may also alter other properties in real-world studies. For example,

385   having a sparser grid could lead to more individual home ranges being only partially covered, impacting

386   the information obtained. Depending on the severity of the loss of area covered by the grid, AKDE, KDE

387   or BicubIt should be preferred, the latter two being most performant if used with asymptotic models

388   under the smallest area covered and sparser grids here examined. In combination with monomolecular

389   asymptotic models, BicubIt can retrieve an accurate and reliable estimate at as low as 2-3 observations.

390   Thus, a possibility for reducing the costs of trapping studies would be to drastically sparse the grid and

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391   use BicubIt. This could serve for example with trapping studies using sophisticated camera traps. Further

392   investigations on wild populations simultaneously monitored with telemetry or GPS and trapping should

393   be conducted to confirm our findings in such challenging scenarios. We suggest studies reduce the trap

394   density in favor of long term or more intense monitoring but ideally researchers should have a sense of

395   the mean home range radius of the species of interest, the degree of territoriality as well as the range of

396   attraction of the traps. By doing so, they might be able to assess the "sweet spot" between reducing the

397   number of traps and the reliability and accuracy of the information obtained.

398   In this study we have used the simplest type of home range, one that is circular, and the animal movement

399   independent within it to have a first sense of how common and uncommon methods performed with

400   trapping data. Due to the complexity and computational burden of the range of methods here used we

401   opted for the simplest case of uncorrelated movement detections. Given that the most reliable and

402   accurate estimator was the only one that doesn't assume uncorrelated observations (AKDE), we suspect

403   that adding autocorrelation to the data shouldn't change the main conclusions of the study (i.e., that trap

404   data contain sufficient information for home-range estimation). On scenarios with autocorrelated data,

405   the difference between AKDE and the other estimators should broaden as the rest of estimators become

406   impacted by the autocorrelation in the observations. Besides this, animal locations obtained with trapping

407   methods should generally be less autocorrelated, at least for live trapping. The elapsed time between one

408   observation and the next for the same individual should generally exceed the range crossing time. It would

409   be important though in trapping studies to control for the time of the day since animals may repeatedly

410   use the same locations for resting or sleeping. Thus, if traps are always set before the onset of activity, a

411   given individual might be trapped always near the resting place generating autocorrelation. In addition,

412   non-circular shapes of home ranges, which might be common in nature, could trigger biases in estimates

413   (Seaman et al. 1999, Halbrook and Petach 2018). A possibility to improve the presented methodology in

414   this context could be to tune the reference bandwidth allowing non-continuous polygons or use habitat-

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415   informed versions of KDE (Halbrook and Petach 2018). Nevertheless, these considerations might be

416   irrelevant for conservation studies were the target might be the area that encompasses all resources used

417   by an animal *sensu* (Burt 1943), even if they use linear corridors to travel between food patches or

418   shelters. Overall, the results of the current study might offer a valuable reference to assess bias in home

419   range analyses with trapping data.

420   The evidence here presented can act as a useful building block for future research. Although further

421   research might nuance the results here presented, the main finding that trapping data is a useful

422   alternative to more expensive technology for home range size estimates is unlikely to change. The use of

423   trapping data might enlarge the range of ideas that can be explored by broadening the scope of

424   researchers pursuing, and species used in, home range analyses.

Acknowledgments

Authors contributions

429   L S-M and L P developed the ideas that served as first step of this project. MJ N suggested simulations as

430   a tool for testing, the use of bicubic interpolation and further research goals. L S-M led the coding and

431   wrote the first draft while all authors contributed to coding and writing the final version of the manuscript.

Data availability

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Figures and tables

558 Figures were generated using R packages base v 4.0.5 (R Core Team 2019), ggplot2 v 3.3.5 (Wickham
559 2016), ggpubr 0.4.0 (Kassambara 2020), lemon v 0.4.5 (Edwards 2020) and directlabels v 2021.1.13
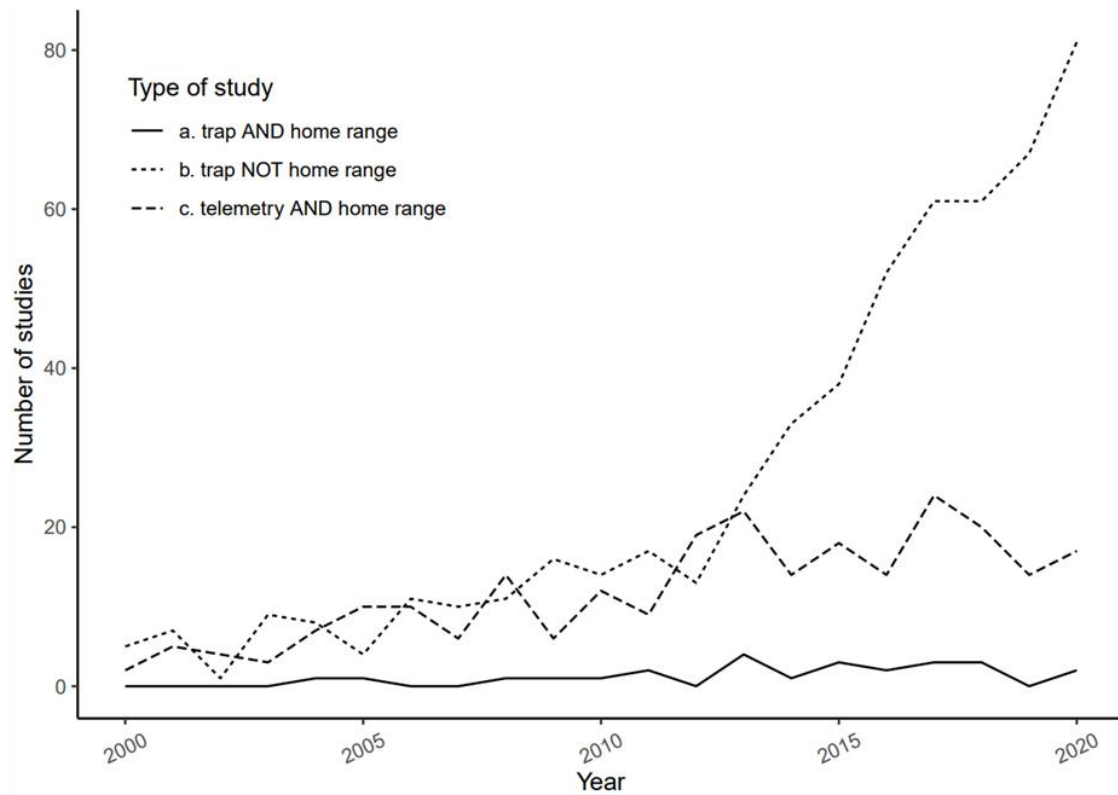560 (Hocking 2021).

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Figure 1: Published studies using telemetry and trapping data: Results from a search in ScienceDirect for article sections title-abstract-keywords using the search words: a. ' ("camera trap" OR "live trap") AND "home range" ' for studies using trapping datasets evaluating home ranges, b. ' ("camera trap" OR "live trap") NOT "home range" ' for studies collecting trapping datasets but not using them for home ranges and c. '(GPS OR radio) AND "home range" ' for studies on home range using telemetry methods. Only articles in the fields "Agricultural and Biological Sciences", "Environmental Science" and "Biochemistry, Genetics and Molecular Biology" were included.

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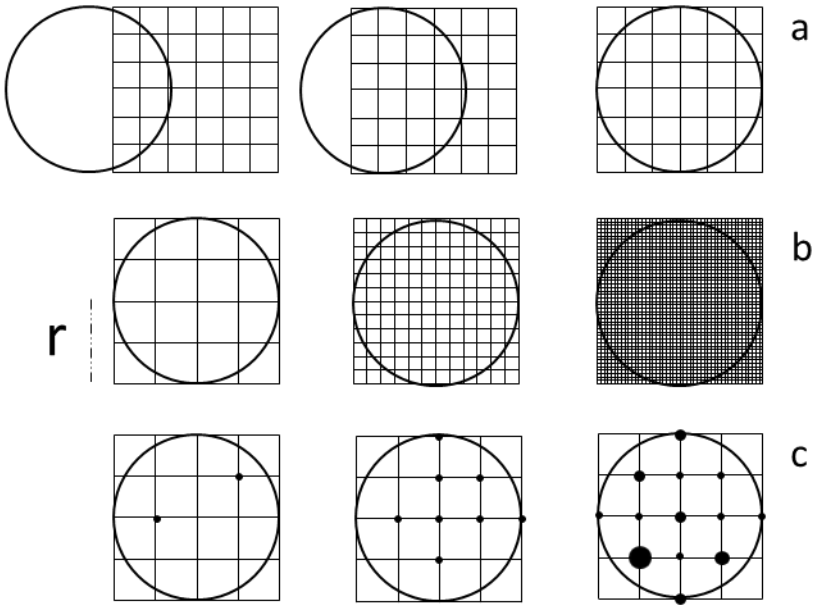
Figure 2: The three variables of interest for study design: a. The area covered by the trapping grid, with low, medium and total coverage from left to right, **b.** the trap density, with again low, medium and high values of traps per home range radius (illustrated with the dashed bar and the "r" symbol), and **c.** the number of observations, with dots indicating their location and the size of dots their number in a given location.
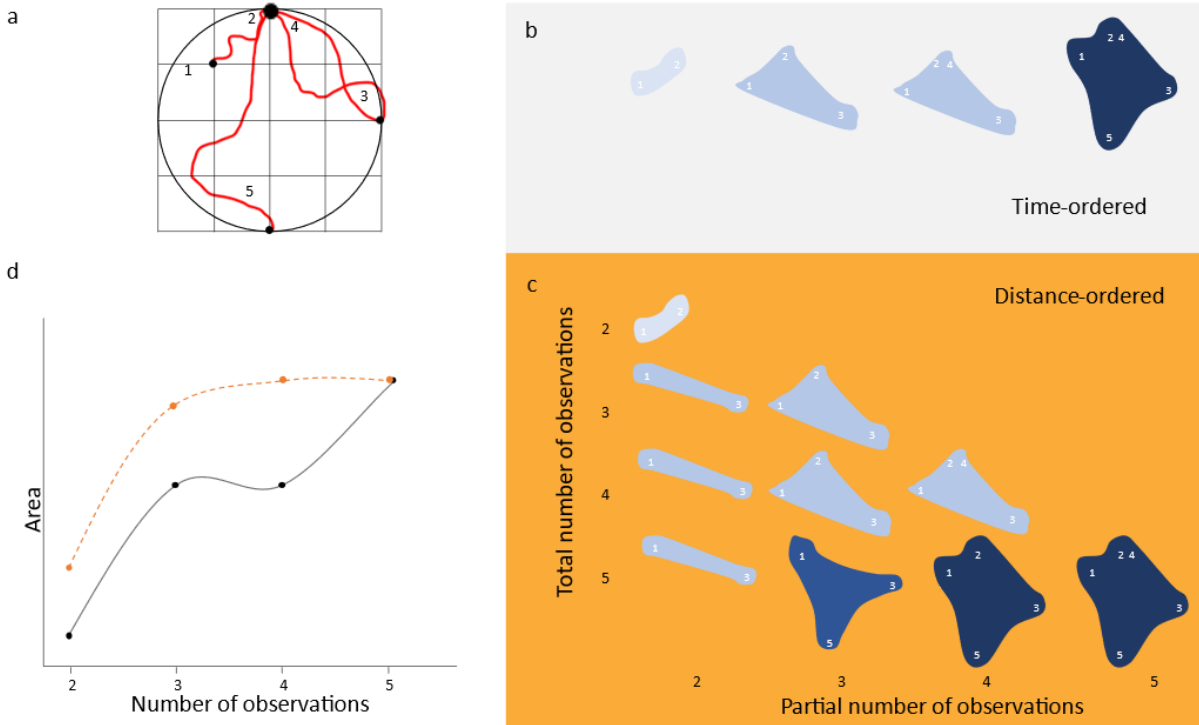
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Figure 3: Time-ordered and distance-ordered sampling curves: a. A hypothetical trapping of an individual with 5 observations, **b.** the succession of home range areas calculated from a. with standard time-ordered incremental analyses, **c.** the different areas estimated from a. by ordering the data based on farthest-point sampling with partial datasets from two to five observations and **d.** representation of the different curves obtained with five observations using either time-ordered (grey continuous) or distance-ordered (orange dashed) incremental analyses.

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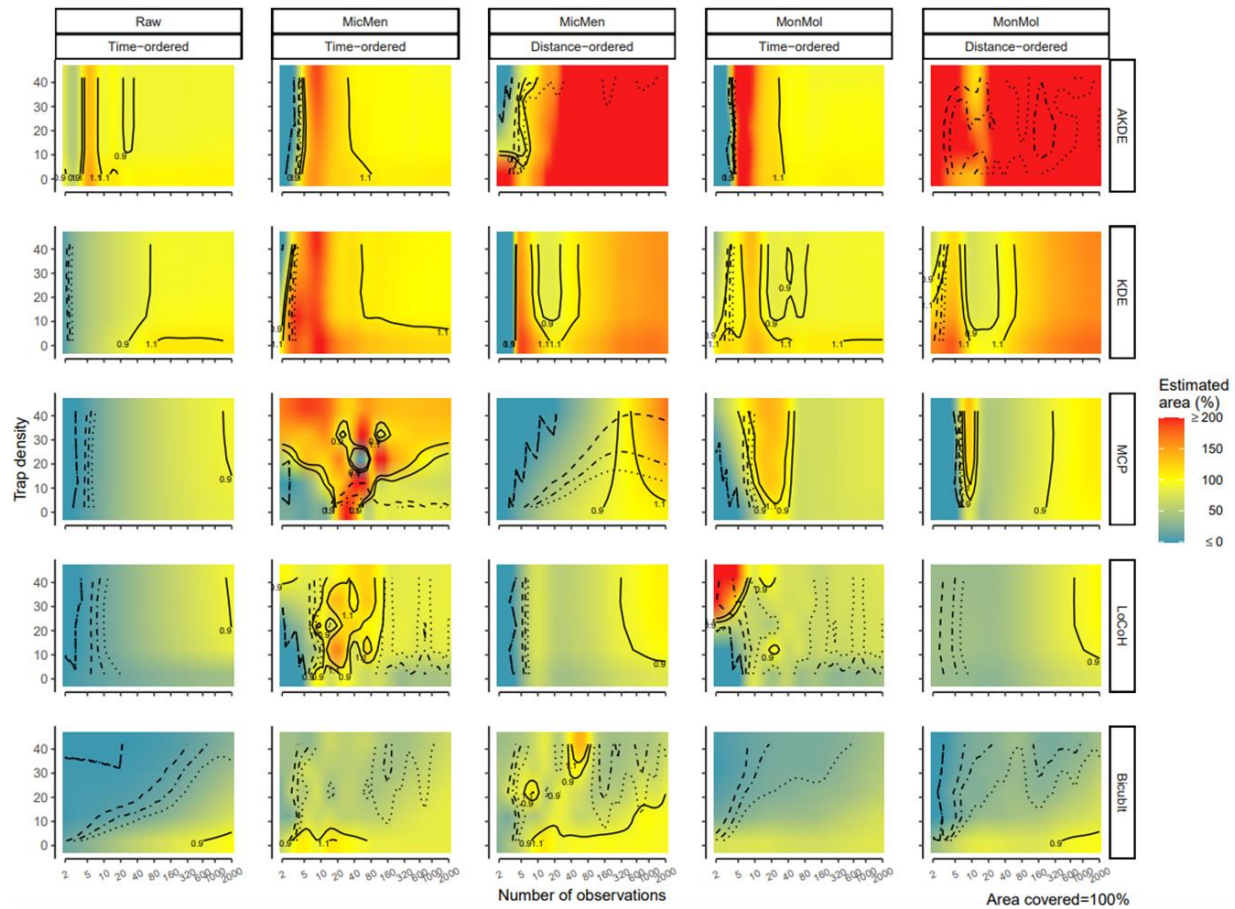
Figure 4: Interacting effects of number of observations and trap density on home range area estimations: Rows gather different estimators, from top: autocorrelated Kernel density estimator (AKDE), the traditional version (KDE), minimum convex polygon (MCP), local convex hull (LoCoH) and bicubic interpolation (BicubIt). Columns gather the combination of two factors, the ordering procedure (time or distance) and the asymptotic model used ("Raw" indicating no model, "MicMen" Michaelis-Menten and "MonMol" Monomolecular). The x axis displays the number of observations and the y axis the trap density, the area covered was fixed at 100%. The colors in the plots indicate the estimated area as a percentage of the true area predicted by the GAM model, yellow values approximate the true area, and red indicate over-estimation while blue underestimation. Values above 200% where trimmed and given a 200 while values below 0% where also trimmed as 0 to concentrate color variation on a meaningful range. The solid lines indicate the contour of accurate estimations, defined as ±10% of the true area. Pointed lines indicate the reliable estimations measured as those where the confidence interval was ±20% of the estimated area, point-dashed ±40% and dashed ±60%. Finally, on the lower-right corner the fixed variable value is indicated.
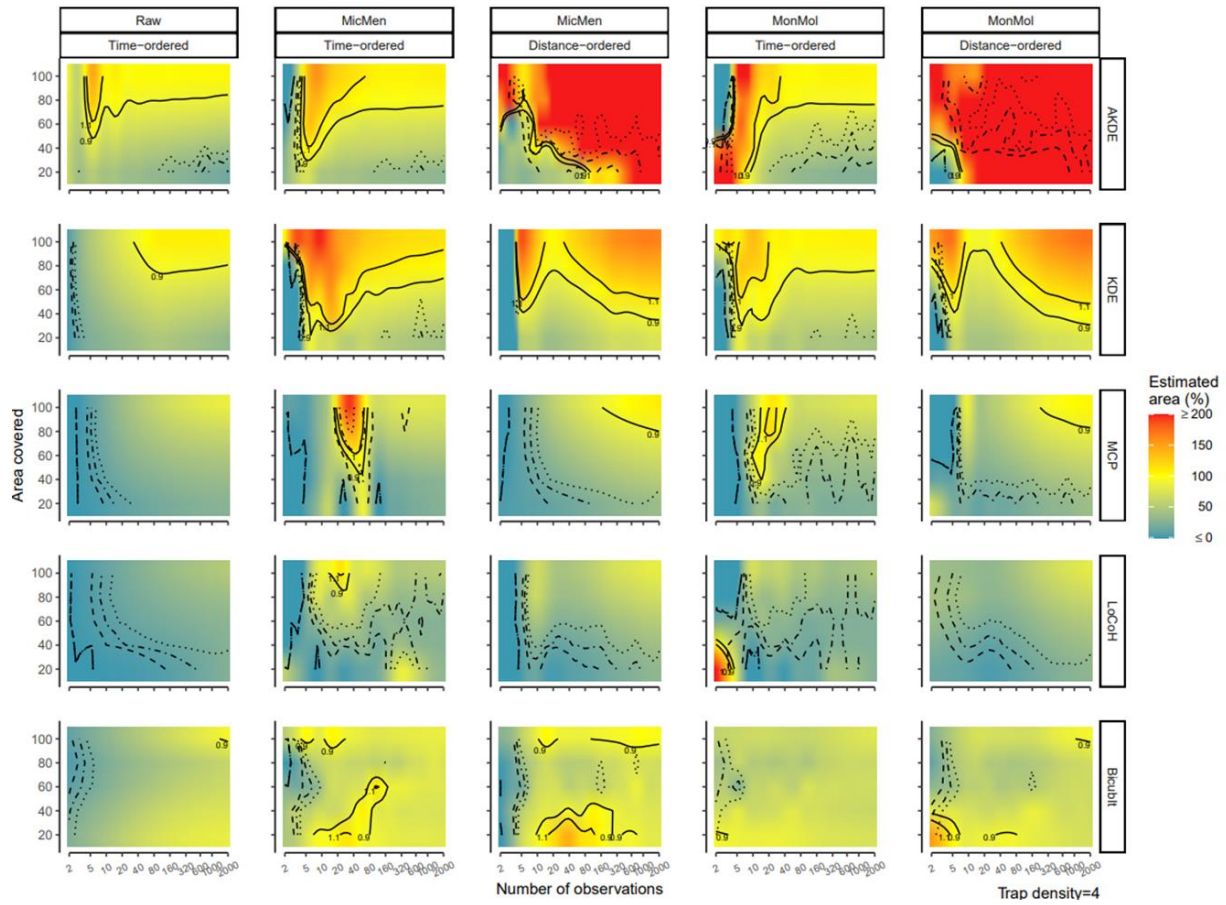
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Figure 5: Interacting effects of number of observations and area covered by the grid on home range area estimations: Rows gather different estimators, from top: autocorrelated Kernel density estimator (AKDE), the traditional version (KDE), minimum convex polygon (MCP), local convex hull (LoCoH) and bicubic interpolation (BicubIt). Columns gather the combination of two factors, the ordering procedure (time or distance) and the asymptotic model used ("Raw" indicating no model, "MicMen" Michaelis-Menten and "MonMol" Monomolecular). The x axis displays the number of observations and the y axis the proportion of the area covered by the trapping grid, the trap density was fixed at 4 traps per HR radius. The colors in the plots indicate the estimated area as a percentage of the true area predicted by the GAM model, yellow values approximate the true area, and red indicate over-estimation while blue underestimation. Values above 200% where trimmed and given a 200 while values below 0% where also trimmed as 0 to concentrate color variation on a meaningful range. The solid lines indicate the contour of accurate estimations, defined as ±10% of the true area. Pointed lines indicate the reliable estimations measured as those where the confidence interval was ±20% of the estimated area, point-dashed ±40% and dashed ±60%. Finally, on the lower-right corner the fixed variable value is indicated.
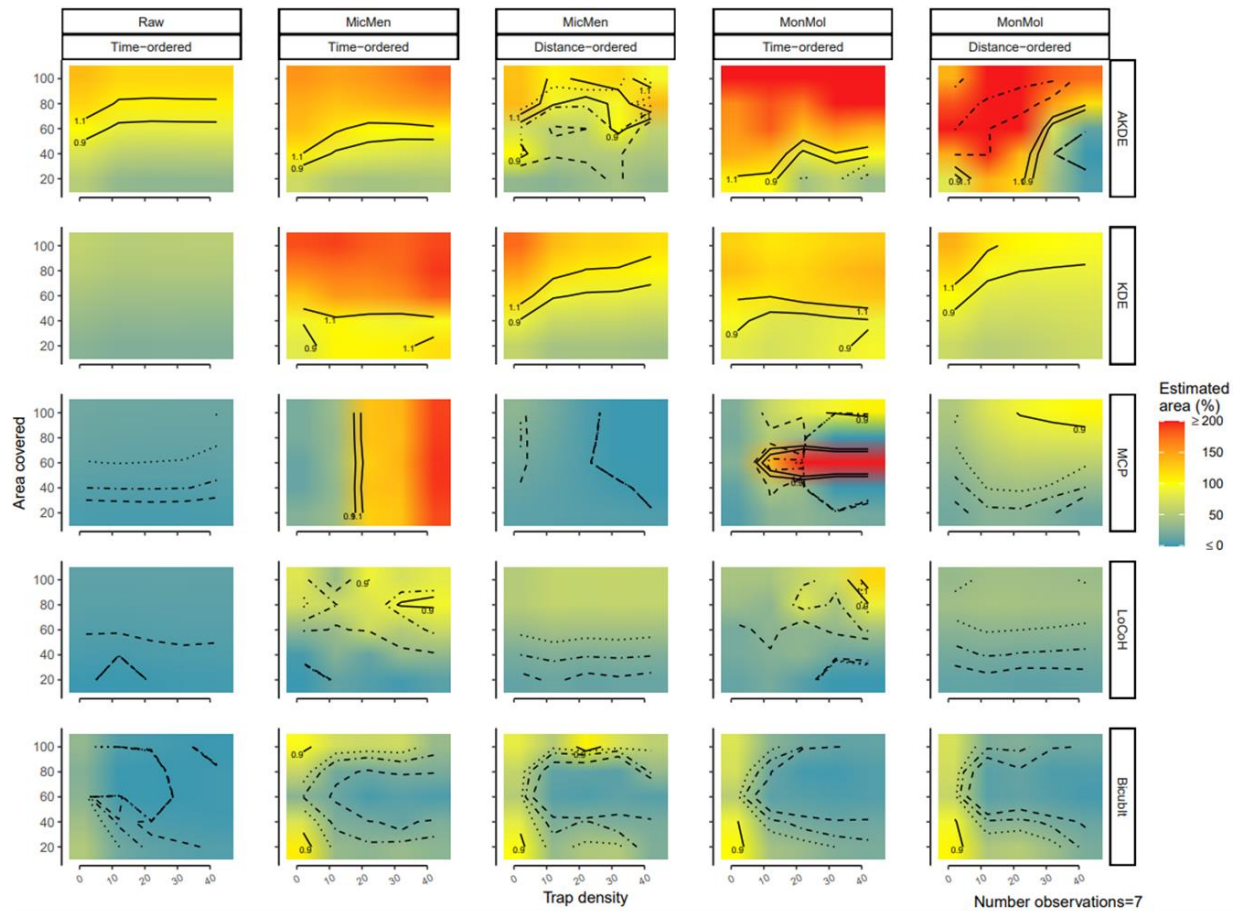
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Figure 6: Interacting effects of trap density and area covered by the grid on home range area estimations: Rows gather different estimators, from top: autocorrelated Kernel density estimator (AKDE), the traditional version (KDE), minimum convex polygon (MCP), local convex hull (LoCoH) and bicubic interpolation (BicubIt). Columns gather the combination of two factors, the ordering procedure (time or distance) and the asymptotic model used ("Raw" indicating no model, "MicMen" Michaelis-Menten and "MonMol" Monomolecular). The x axis displays the trap density and the y axis the proportion of the area covered by the trapping grid, the number of observations was fixed at 7. The colors in the plots indicate the estimated area as a percentage of the true area predicted by the GAM model, yellow values approximate the true area, and red indicate over-estimation while blue underestimation. Values above 200% where trimmed and given a 200 while values below 0% where also trimmed as 0 to concentrate color variation on a meaningful range. The solid lines indicate the contour of accurate estimations, defined as ±10% of the true area. Pointed lines indicate the reliable estimations measured as those where the confidence interval was ±20% of the estimated area, point-dashed ±40% and dashed ±60%. Finally, on the lower-right corner the fixed variable value is indicated.

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