Towards the comparison of home range estimators obtained from
contrasting tracking regimes: the wild boar as a case study

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Abstract

Traditional VHF radio-tracking is gradually being replaced by GPS tracking devices in spatial ecology studies, although both technologies are currently in use. Differences between tracking regimes may report inconsistent home range estimates that make it difficult to establish direct comparisons between studies. Our primary aim was to test the reliability of comparisons in fixed kernel home ranges estimates of wild boar (*Sus scrofa*) using different approaches and also, provide an empirical basis for linking VHS and GPS tracking data. Moreover, to broadening the applicability of the results we have compared the kernel estimates with those of a third generation method, a dynamic brownian bridge model (dBBMM). Using GPS tracking data from wild boar, we simulated different tracking regimes (approaches) to compare the home range estimates. Data were obtained from 15 GPS-collared individuals from three areas in Mediterranean Spain. Results suggested that MCP produces the greatest differences in home ranges between approaches, while 95% kernel home range (Khr95) was the least biased parameter, both in size and utilization distribution overlap. From 50% kernel core range, similar estimates were also obtained across the less intensive approaches (typical of VHF tracking regimes). Using the most intensive sampling scheme, the Khr95 estimates did not differ significantly from those obtained with dBBMM. The home range estimates standardization is important due to the impact that spatial use knowledge has on management or conservation of species. In this sense, the proposed methodological approach allows comparison between studies that use different approaches to estimate home ranges.

Additional keywords: wild boar; fixed kernel; sampling intensity; GPS collars;
Sus scrofa.

1. Introduction

The concept 'home range' in ecology has evolved from simple definitions such as 'area crossed by individuals in their normal activities of feeding, reproduction and care of the offspring' (Burt 1943) to more elaborate definitions such as 'area with a defined probability of occurrence of an animal during a specified period of time' (Kernohan et al. 2001). Whatever definition is used, the size and patterns of home ranges are a consequence of resource availability, biology of a species as behaviour, physiology and population density and individual factors as body weight and sex (Rühmann et al., 2019). Human activities, hunting and tourism for example, would also affect the spatial patterns of a species (Keuling et al. 2008b). In addition, animals can react individually to these factors (Brown et al. 2012). Thus, study of spatial use through home ranges is a key factor in animal ecology to implement conservation and management strategies (Millsaugh and Marzluff 2001; Spencer 2012).

One of the older, simple and used home range estimators is the minimum convex polygon (MCP), which delimits the smallest polygon around locations with all interior angles less than 180 degrees (Millsaugh and Marzluff 2001). The main drawbacks of MCP estimates are that usually incorporates large areas in which the animal has not been or visits infrequently, are strongly

dependent to number of relocations and the lack of identification of multiple centers of activity/utilization (Borger et al., 2006).

To avoid such limitations, alternative methods are used, mainly methods based on quantification of utilization distributions (UDs), which allow the evaluation of size and intensity use of different areas within home range (Worton 1989; Kranstauber et al., 2012).

The first or second-generation home range methods as kernel density estimators (KDE), although not account the temporal or spatial correlation of the data, are frequently used in GPS telemetry (Walter et al., 2011). As generalization of MCP, nearest-neighbour-based polygon techniques has developed (e.g. Local Convex Hulls or cluster-based polygons), which have highlighted for investigating relationships between range size and other ecological factors (Kenward et al 2001, 2018). Third-generation methods were developed for incorporate in estimates, time, space, animal-specific parameters or habitat (Walter et al., 2015). As alternatives or extensions to KDE, appeared movement-based KDE methods, such as Brownian bridge (BBMM) and biased random walk models (Horne et al., 2007; Benhamou, S. 2011), autocorrelated KDE (AKDE) that account highly autocorrelated movement locations (Fleming et al., 2015) or time KDE for irregular sampling intervals (Katajisto and Moilanen 2006). As evolution of BBMM, appeared dynamic Brownian bridge movement (dBBMM) that incorporate temporal and behavioral characteristics of movement (Kranstauber et al. 2012).

Despite a large number of available methods to delimit home ranges (Walter et al., 2015), most studies still use MCP as a generic approximation of spatial

delimitation and, specially, KDE as a measure of the intensity of space use, also with GPS telemetry technology (Gula and Theuerkauf 2013; Schuler et al, 2014; Vieira et al., 2019).

The spread use of GPS telemetry in the last decade, which allows a number of animal relocations far superior to those obtained with traditional VHF tracking devices, has highlighted the constraints of traditional methods for home range estimation (Hemson et al. 2005; Kie et al. 2010).

The main differences between GPS and VHF monitoring are related to study design and sampling intensity. GPS devices are quite expensive in relation to VHF devices (approx. one GPS for every 10 VHF devices). This implies that the number of individuals that can be monitored for a research project is lower than that in traditional studies using VHF devices (Fieberg and Börger 2012). The higher fix rate also results in a limitation of the study period due to the lifespan of the batteries (Hebblewhite and Haydon 2010; Fieberg and Börger 2012). The number, sampling scheme or regime (i.e., the ability to perform daytime, night or continuous monitoring schemes) and precision of the locations **is** notably increased with GPS devices (Baubet et al. 2004; Barber-Meyer and Mech 2014; Schuler et al. 2014). Thus, today, GPS devices are gradually replacing VHF for wildlife monitoring (Cagnacci et al. 2010; Thomas et al. 2011; Barasona et al. 2014a). Nonetheless, VHF tracking is still in use (Keuling et al. 2008a; Saïd et al. 2012; Merli et al. 2017), mainly due to budget and battery weight limit the number of locations that can be acquired and therefore, lifespan (Thomas et al., 2011; Mitchell et al., 2019). Also, due VHF tags can be very light it nevertheless remains the only remote sensing tool available to track small species and cost-effective alternative to GPS (Ponchon et al. 2013).

Sampling intensity in general and all of these factors in particular can notably affect home range estimates (Seaman et al. 1999; Girard et al. 2002; Börger et al. 2006; Kie et al. 2010; Walter et al. 2011; Downs et al. 2012; Gula and Theuerkauf 2013; Mitchell et al., 2019). However, the number of studies comparing the results from VHF and GPS tracking devices –and therefore variations in sampling intensity– is low (see Pellerin, Saïd & Gaillard, 2008; Kochanny, Delgiudice & Fieberg, 2009). This is true even though inter-group networks for sharing data on wildlife (e.g., <http://euroboar.org/>) promote the use of different data sources and carry out meta-analyses to advance knowledge in species ecology.

In this context, the main aim of the study was to assess variations in size and UD similarity in home range estimates in relation to: i) Sampling scheme, namely daytime vs. continuous monitoring, ii) fix frequency, from one relocation per day during three days in a week (VHF simulation) to daily monitoring of 24 relocations per day (GPS simulation) , and iii) traditional (KDE) vs. third-generation home range methods (dBBMM). The final goal of this study is to establish a scientific basis that allows direct comparison of home range estimates obtained from different tracking approaches and different methods.

2. Materials and methods

2.1. Study areas

Fifteen wild boars were monitored in three study areas in Mediterranean Spain, five individuals per area (Fig. 1). Sant Llorenç del Munt i l'Obac Natural Park (SNP), located in the northeast of the Iberian Peninsula (41°39' to 41°42' N,

1°53' to 2°09' W), is characterized by Mediterranean holm oak forest. Patches of mixed pinewood and a mixture of rocky cliffs with scarce vegetation are present (Pintó and Panareda 1995). Montes de Toledo (MT), in the region of Castilla-La Mancha, south-central Spain (39°25' to 39°16' N, 4°05' to 4°23' W), is characterized by evergreen oak (*Quercus ilex*), scrublands with scattered pastures and small crops, forming dehesas (savannah-like habitats). Finally, Doñana National Park (DNP) is a protected area on the Atlantic coast of southern Spain (37°0' N, 6°30' W). DNP presents a north–south humid ecotone between the elevated Mediterranean shrublands and the low marshlands, which highly affect the distribution and abundance of wild ungulates (Barasona et al. 2014b).

Figure1.

2.2. Capture and GPS-GSM monitoring

The field work was carried out between 2009 and 2015. Animals were captured with portable cage traps, approx. 3x1.5m (for further details see Barasona et al., 2013; Barasona et al., 2016; Casas-Díaz et al., 2013). Traps were baited with corn every 2-4 days both inside and outside the trap and monitored with camera traps (Model IR-3BU, Leaf River Outdoor, Taylorsville, Mississippi, USA) to determine the time of activation. Once activated, each trap was checked daily, early in the morning.

When a wild boar was captured, we proceeded to sedate it following Animal Experimentation legislation and procedures approved by the Animal Experiment Committee of Castilla-La Mancha University and Departament d'Agricultura, Ramaderia, Pesca, Alimentacio i Medi Natural - Generalitat de Catalunya, for

MT/DNP and SNP, respectively. The anaesthesia was injected intramuscularly in the femoral region with 5 ml anaesthetic darts (Telinject®, Römerberg, Germany) using a 14 mm diameter blowpipe (Telinject®, Römerberg, Germany) after visually estimating the weight of each animal in the trap (see protocol in Barasona et al., 2013; Casas-Díaz et al., 2011). After sedation, wild boar was removed from the traps and blindfolded.

We fitted GPS-GSM collars to adult wild boar monitored in MT and DNP (five adult wild boars from MT and five from DNP; Microsensory, Spain) and SNP (five adult wild boars; LOTEK GPS 3300S, Lotek Wireless, Ontario, Canada). Post-release monitoring was programmed to acquire 24 GPS locations per day in MT and DPN, while in SPN the collars were programmed to obtain twelve locations per day.

2.3. *Daily patterns of activity*

Taking into account the seasonal and daily activity patterns of wild boar provided by Keuling *et al.* (2008a), Tolon *et al.* (2009) and Carrasco-Garcia *et al.* (2016), the daily periods considered were (solar hour): daytime hours between 08:00 and 18:00 and night hours between 22:00 to 04:00. These time frames defined the ‘dawn’, ‘day’, ‘dusk’ and ‘night’ periods, which were first used to determine the daily patterns of wild boar activity. Mean hourly rate of movement i.e. the Euclidean distance between each consecutive fix divided by the time elapsed between them (i.e. speed; m/h) was estimated as a measure of the daily activity pattern of the animals, using data from GPS tracking (Cutrera et al. 2006). To estimate both the distance and the time elapsed

between consecutive fixes we used the *adehabitatLT* R package (Calenge et al., 2009).

2.4. Tracking approaches: sampling schemes and fix frequency

Individual relocations used in the analyses were obtained from GPS-GSM collars. A sub-sampling of the total relocations was randomly done to obtain five sets of data (hereafter approaches) for each animal, four of them simulating data usually obtained with VHF monitoring regimes for ungulates (Boitani et al. 1994; Keuling et al. 2008a; Pellerin et al. 2008), carnivores and meso-rodents (Stanley et al. 2007; Penteriani et al. 2013), birds (Dinkins et al. 2017) and amphibians and reptiles (Harless et al. 2010). In this section, to cover the wild boar greater activity periods at night hours, we include the exclusively nocturnal fixes (22:00 to 04:00 h) and also the dusk (04:00- 08:00) and dawn (18:00- 22:00) locations. : D1) day, low intensity: one relocation in the daytime three days per week; D2) day, medium intensity: seven relocations, once a day, during daytime; C1) continuous, low intensity: one relocation in the daytime and three at night, one day per week; C2) continuous, medium intensity: three fixes per night, three nights per week and one fix in the daytime three days per week; and C3) considering all available relocations. Finally, and in order to avoid the effects of the autocorrelation in home range estimations that could be derived from replication of points during the daytime (when the wild boar is mainly resting), we generated a new data set (C4) with all fixes of at night, dawn and dusk, and only 1 every day for the daytime.

2.5. Home ranges

MCP and kernel UD were used to estimate individual home ranges (Keuling et al. 2008a; Laver and Kelly 2008; Scillitani et al. 2010).

We defined KDE UD contours (isopleths) at kernel 50% for the core range (Kcr50) and at kernel 95% as a home range estimate (Khr95), since they are the most frequent methods in old studies and also in current ones (Gula and Theuerkauf 2013; Schuler et al, 2014; Mitchell et al., 2019) and therefore, useful in the comparison between studies We also estimated UDs using a third-generation estimator, the dynamic Brownian Bridge Movement Model (Kranstauber et al. 2012, dBBMM) with C3 data, in order to assess the UDs estimates similarity across different generation methods, especially relevant in high fix rate (GPS) studies. dBBMM was selected since it quantifies the use distribution of an animal based on its movement path rather than individual points, accounts for temporal autocorrelation, high data volumes and heterogeneous movement behaviour across all data, and mainly, since it has been described as the most reliable estimator than KDE (Kranstauber et al. 2012; Walter et al., 2015; Cohen et al., 2018).

We estimated the Khr95 and Kcr50 using the *adehabitatHR* R package (Calenge 2006). To calculate the bandwidth or smoothing parameter 'h', we used a fixed value for each approach and study area, same value is used for Khr95 and Kcr50, since this provides a way to standardise home range estimates and allows for accurate comparisons between home ranges of different sizes and numbers of locations (Pellerin et al. 2008; Saïd et al. 2012). These fixed 'h' values were estimated as the median of individual h-values

obtained with the Likelihood Cross Validation (LCV) method, since this generally produces a better fit in the estimates and less variability (Horne and Garton 2006). The 'h' parameter was calculated with the *spatstat* R package (Baddeley and Turner 2005).

Home ranges estimated from different approaches were compared in size and UD overlap. We, also test the UD size estimates and overlap between methods (KDE and dBBMM) based on C3 data. For testing the overlap, methods based on the estimation of UD overlap in three dimensions (3D) were used because they are recommended over the comparison methods in 2D (Fieberg and Kochanny 2005). Specifically, the Bhattacharyya Affinity Index (BA; Bhattacharyya, 1943) was used since it is the most appropriate method to quantify the degree of similarity between two estimates of UD (Fieberg and Kochanny, 2005) . BA takes values between zero and one (where one suggests identical estimates) and considers the internal distribution or density of locations within the boundaries of the home range (Fieberg and Kochanny 2005). The BA index was estimated with the *adehabitatHR* R package (Calenge 2006) and comparisons of each approach in relation to C3 (reference approach; the most intensive tracking scheme) were performed, assuming that UD based on C3 approach was closest to the true value (Pellerin et al. 2008; Schuler et al, 2014). We therefore estimated KDE UD overlap for the following dyads: D1-C3, D2-C3, C1-C3, C2-C3 and C4-C3.

. For dBBMM UD estimation we used Move package (Kranstauber et al. 2018), incorporating the temporal characteristics of the movement paths. We selected same parameters for all animals; margin of 3 (12 h) to account for potential diurnal versus nocturnal movement pattern differences, location error of 11

meters and pixel size equal to kernel UD. To test the similarity between KDE and dBBMM UDs estimated by C3 samples we also use the BA index.

2.6. Data analysis

Differences among dawn, day, dusk and night in activity pattern were tested using a Linear Mixed Effect (LME) Model, including activity index as a response variable, sex, period and study area as fixed factors, and individual as a random factor. Activity index was transformed using a $\log(x+1)$ through the `log1p` R function. With this transformation, variation ranges are reduced and the zeros that represent inactivity of animals remains a null value (David 2017). Multiple comparisons were performed to test for differences among the different periods, using a Tukey post-hoc test with the `glht` (`multcomp`) function from R (Hothorn et al. 2008).

LME models were also used to assess possible differences in home range size among approaches. Thus, the response variables were MCP, Khr95 and Kcr50 (i.e. three models), with approach, sex, number of fixes and study area as fixed factors, and individual as a random factor. For test difference between methods estimates (KDE and dBBMM), another LME with the same variables was used. Response variables were log-transformed to meet assumptions of normality and homoscedasticity of residuals. For each response variable, we modelled all combinations of independent parameters. Due to a relatively small sample size, no interactions between them were included in our model set. Akaike information criterion (AIC), with a second-order correction for small sample size (AIC_c), was used to rank the models dependent on their fit (Burnham and

Anderson 2002). Models with the lowest AIC_c value were considered to be the best-fit models, and models with $\Delta AIC_c < 2$ were considered of similar quality to the most parsimonious model. Pairwise comparisons between approaches were also carried out using a Tukey post-hoc test to elucidate which approaches produce significant differences in KDE size estimates between them.

Similarly, and in order to explore the effect of tracking approach, and estimation methods on the BA overlay index (KDE UD similarity), a set of LME models was parameterized (Pinheiro et al. 2017) and ranked according to Akaike criterion: BA index as a response variable and the same fixed and random factors as in the previously described models was used, with the exception of the number of fixes which should not be included in the BA index model. Because the BA index was scored as a proportion, we used a logit transformation for these data (Warton and Hui 2011) with the *logit* function ($\log[p/(1 - p)]$) of the *car* R package (Fox and Weisberg 2011). As in Fieberg & Kochanny (2005), we infer a high degree of overlap in home range estimates among approaches with BA index values > 0.60 .

Because home range sizes were generally not normally distributed, most results are reported as medians and interquartile ranges (IQRs). All statistical tests were performed with the R program (R Core Team 2017), considering significant differences when $p < 0.05$.

3. Results

Details of the 15 monitored individuals (six females and nine males) are shown in Table 1.

Table1.

The median and interquartile range of the number of locations per animal and bandwidth h estimated with LCV used after sub-sampling at each tracking scheme is shown in Table 2.

Table2.

3.1. Activity

There was a significant effect of period and study area on the individual wild boar activity index (LME model: daily period: $F_{3,34703}=1221.5$, $p<0.0001$; area: $F_{2,11}=12.7$, $p=0.0014$; sex: $F_{1,11}=4.2$, $p<0.063$). Despite the differences between areas, the main activity occurred at night and dusk, while remaining at lower levels during the daytime hours (Fig. 2).

Figure2.

3.2. Comparison of home ranges

The best-fitting models explaining the variation in home ranges included all independent factors except number of fixes (Table 3). The largest MCP home ranges were obtained using the C3 approach (median= 2138.9 Ha, IQR= 952 - 3775.7), followed by those obtained with C1 and C2. In addition, the effect of approach on MCP estimates was significant (see Fig. 3 and Table 4). Among all comparisons between approaches only D1, D2 and C1 produced similar MCP size estimates. The MCP estimate based on C4 does not differ from those based on C3 or C2 (Fig. 3).

Table3.

Figure3.

Significant effects of approach were also found by comparing the sampling approaches with Khr95 home range estimates. (Fig. 3, Table 4). In Tukey post-hoc comparisons, only the C1-D2 and C2-D2 dyads showed significant differences and interestingly no differences in relation to C3 were found. Finally, we found a significant effect of approach when Kcr50 estimates were compared (Fig. 3, Table 4). The pairs of core areas C1-D2, C1-C3, C2-C3, D1-C3 and D2-C3 showed significant differences in their estimates. In Kcr50, differences between approaches were observed in comparison with C3, however, there are no differences between diurnal D1 and continuous medium sampling intensity C2 (Fig. 3).

Table4.

We did not observe significant differences between the estimated Khr95 with samples C3 and C4, neither between them and the dBBMM with 85 isopleths (LME model: approach (Khr95_{C3}, Khr95_{C4} and DBMM85): $F_{2,28} = 0.37$, $p = 0.68$; area: $F_{2,11} = 12.7$, $p = 0.0047$; sex: $F_{1,11} = 19.15$, $p = 0.0011$).

3.3. *Overlap index*

The best-fitting models included the approach and sex predictors to explain differences between the BA index in Khr95. The study area is also included in the second best model. For the BA index of Kcr50, the best model included all the independent variables considered (Table 5).

Table5.

In the comparisons of the different BA similarity indexes of the Khr95 for the different approaches with C3, differences were found between approaches (Fig. 4, Table 6). BA values for the monitored individuals ranged from a median of 0.81 (IQR: 0.78- 0.83) in the D1-C3 approach comparison to 0.93 (IQR: 0.91- 0.95) in the C2-C3 comparison. In the same comparisons for the Kcr50, significant differences between approaches were found (Fig. 4, Table 6). BA values for the monitored individuals ranged from a median value of 0.65 (IQR: 0.52- 0.74) in the D1-C3 comparison to 0.81 (IQR: 0.76- 0.84) in the C2-C3 dyad.

Figure4.

Table6.

The median overlap BA index between Kernel UDs estimated with C3 and C4 samples was high 0.96 (IQR: 0.63- 0.97). Similarly, median BA index between Kernel UD and dBBMM UD home range wild boars was also high 0.9 (IQR: 0.88- 0.95).

4. Discussion

Methodological procedures evaluated in this paper have identified the conditions under which direct comparisons of home range estimates obtained from different tracking schemes may be addressed. Despite of the importance for a correct selection of h , the use of Khr95 allows similar estimates of home range (size and UD similarity) and therefore, facilitates the comparison between studies carried out with different tracking schemes. We should be more cautious with Kcr50 comparisons since there are differences due to tracking schemes,

mainly between estimates based on higher sampling intensities and those of smaller ones.

One of main problems argued in the application of kernel estimates with GPS data (large volume of fixes) is the autocorrelation, or independence in locations (Kernohan *et al.* 2001, but see Fieberg and Börger 2012). The similarity, both in size and in the utilization distributions, between two methods, KDE and dBBMM home range estimates with all fixes allow different generation methods comparison. .

The activity pattern of the wild boar is mainly nocturnal, also presenting activity at dusk and dawn, and is low during the day (Massei *et al.* 1997; Russo *et al.* 1997; Keuling *et al.* 2008b). These differences in activity would lead us to expect differences in UD estimates using different approaches (Tolon *et al.* 2009), especially between diurnal and continuous sampling schemes (Ds and Cs approaches), and therefore support the selection of wild boar as a relevant case study. We found differences among approaches in home range size estimates, but these were not consistent in relation to the parameter studied. Specifically, if we take into account the MCP calculation, maximum differences between tested approaches were observed. This result agrees Börger *et al.* (2006) study, which showed that the MCP method should be used with caution in the comparison of estimates of home ranges. Also at KDE, a small number of locations for each animal or different sampling intensity may imply home range size underestimation, the non-consideration of zones that may be of great importance in terms of biological aspects, the selection or use space and/or species management. However, no approach shows differences regarding continuous high-intensity sampling approach (C3) when considering Khr95. As

for the Kcr50, the Ds approaches do not differ from continuous medium-intensity C2 (VHF sampling approach).

In relation to home range UD, differences between approaches in relation to overlap with C3 were found. In general, the UD similarity increased as the sampling intensity increased. However, the levels of overlap are high (above 0.75) in all cases considering Khr95, confirming that this is an appropriate parameter to compare approaches in terms of UD. When we take into account the same comparisons using the Kcr50, the overlaps are somewhat smaller, only surpassing the value of 0.75 in the C2-C3 comparison. These values of degree of overlap are high and similar to those obtained by Kochanny et al. (2009) although It should be noted that the values of the BA index are sensitive to the number of locations, as in the estimation of the kernel (Fieberg and Kochanny 2005). The high degree of similarity of the home ranges with Khr95 between the diurnal and continuous approaches indicates that the diurnal monitoring allows the total Khr95 area to be estimated with precision. Frequent variation in resting places, at small and large scales, the location of resting places near the centre of their areas of activity and some daytime activity of wild boar, are likely the reasons why diurnal resting sites produce good approximations of the total home ranges.

It is worth noting that while for most authors the sampling effort is crucial to consider when comparing estimates of home range from different studies (Girard et al. 2002; Börger et al. 2006), other authors focus on the choice of h factor if the main focus is the study of habitat use (Huck et al. 2008; Schuler et al., 2014). In addition, there is no consensus regarding the best method to obtain home range estimates (Fieberg and Börger 2012). Setting smoothing

factor h by LCV for each approach and study area has produced similar Khr95 estimates among approaches.

The choice of methods and their parameterization influence massively home range results and therefore, spatial ecology analysis. The results reveal the feasibility of KDE estimates comparisons between technologies (VHS and GPS) and between different generation methods (KDE and dBBMM), what makes this potentially relevant in comparison between studies.

5. Conclusions

The results obtained here suggest that not all estimates (MCP, Khr95 and Kcr50) are equally affected by tracking schemes. Khr95, paying special attention to h selection, is the most consistent between approaches, with VHF simulated approaches producing equivalent estimations of home range size and UD to GPS high fix frequency.. Accordingly, we suggest the standardization of the KDE estimates by setting a smoothing factor value by population and approach, since the UD estimates (especially the Khr95) did not differ significantly between tracking approaches. Moreover the similarity between the KDE and dBBMM estimates reinforces usefulness of that proposal.

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References

- Baddeley A, Turner R (2005) spatstat : An R Package for Analyzing Spatial Point Patterns. J Stat Softw 12:1–42. doi: 10.18637/jss.v012.i06
- Barasona JA, Latham MC, Acevedo P, et al (2014a) Spatiotemporal interactions between wild boar and cattle: Implications for cross-species disease transmission. Vet Res 45:122. doi: 10.1186/s13567-014-0122-7
- Barasona JA, Mulero-Pázmány M, Acevedo P, et al (2014b) Unmanned aircraft systems for studying spatial abundance of ungulates: Relevance to spatial epidemiology. PLoS One 9:e115608. doi: 10.1371/journal.pone.0115608
- Barasona JA, Ramón López-Olvera J, Beltrán-Beck B, et al (2013) Trap-effectiveness and response to tiletamine- zolazepam and medetomidine anaesthesia in Eurasian wild boar captured with cage and corral traps. BMC Vet Res 9:107. doi: 10.1186/1746-6148-9-107
- Barber-Meyer SM, Mech LD (2014) Accuracy of estimating white-tailed deer diel May-June home ranges using only daytime locations. Wildl Biol Pract 10:62–68. doi: 10.2461/wbp.2014.10.8

471 Baubet E, Brandt S, Vassant J, et al (2004) Can wild boar be surveyed using
 472 GPS? Mem Natl Inst Polar Res 188–195

473 Bhattacharyya A (1943) On A Measure of Divergence Between Two Statistical
 474 Populations Defined by their Probability Distributions. Bull Calcutta Math
 475 Soc 35:99–109

476 Boitani L, Mattei L, Nonis D, Corsi F (1994) Spatial and activity patterns of wild
 477 boars in Tuscany, Italy. J Mammal 75:600–612. doi: 10.2307/1382507

478 Börger L, Franconi N, De Michele G, et al (2006) Effects of sampling regime on
 479 the mean and variance of home range size estimates. J Anim Ecol
 480 75:1393–1405. doi: 10.1111/j.1365-2656.2006.01164.x

481 Burnham KP, Anderson DR (2002) Model selection and multimodel inference : a
 482 practical information-theoretic approach, Second edi. Springer Verlag New
 483 York, New York, USA

484 Burt WH (1943) Territoriality and home range concepts as applied to mammals.
 485 J Mammal 24:346. doi: 10.2307/1374834

486 Cagnacci F, Boitani L, Powell RA, Boyce MS (2010) Animal ecology meets
 487 GPS-based radiotelemetry: a perfect storm of opportunities and challenges.
 488 Philos Trans R Soc B Biol Sci 365:2157–2162. doi: 10.1098/rstb.2010.0107

489 Calenge C (2006) The package “adehabitat” for the R software: A tool for the
 490 analysis of space and habitat use by animals. Ecol Modell 197:516–519.
 491 doi: 10.1016/j.ecolmodel.2006.03.017

492 Carrasco-Garcia R, Barasona JA, Gortazar C, et al (2016) Wildlife and livestock

493 use of extensive farm resources in South Central Spain: implications for
 494 disease transmission. Eur J Wildl Res 62:65–78. doi: 10.1007/s10344-015-
 495 0974-9

496 Casas-Díaz E, Closa-Sebastià F, Peris A, et al (2013) Recorded dispersal of
 497 wild boar (*Sus scrofa*) in Northeast Spain: implications for disease-
 498 monitoring programs. Wildl Biol Pract 9:19–26. doi: 10.2461-
 499 wbp.2013.ibeun.3

500 Cutrera AP, Antinuchi CD, Mora MS, Vassallo AI (2006) Home-Range and
 501 Activity Patterns of the South American Subterranean Rodent *Ctenomys*
 502 *Talarum*. J Mammal 87:1183–1191. doi: 10.1644/05-MAMM-A-386R1.1

503 David V (2017) Data treatment in environmental sciences, 1st editio. ISTE
 504 Press - Elsevier

505 Downs JA, Heller JH, Loraamm R, et al (2012) Accuracy of home range
 506 estimators for homogeneous and inhomogeneous point patterns. Ecol
 507 Modell 225:66–73. doi: 10.1016/j.ecolmodel.2011.11.010

508 Fieberg J, Börger L (2012) Could you please phrase “home range” as a
 509 question? J Mammal 93:890–902. doi: 10.1644/11-MAMM-S-172.1

510 Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the
 511 importance of the utilization distribution. J Wildl Manage 69:1346–1359.
 512 doi: 10.2193/0022-541X(2005)69

513 Fox J, Weisberg S (2011) An R Companion to Applied Regression. In: Second
 514 edi. SAGE Publishing, Thousand Oaks, California, USA, p 472

515 Girard I, Ouellet J-P, Courtois R, et al (2002) Effects of Sampling Effort Based
 516 on GPS Telemetry on Home-Range Size Estimations. *J Wildl Manage*
 517 66:1290–1300. doi: 10.2307/3802962

518 Gula R, Theuerkauf J (2013) The need for standardization in wildlife science:
 519 Home range estimators as an example. *Eur J Wildl Res* 59:713–718. doi:
 520 10.1007/s10344-013-0726-7

521 Hebblewhite M, Haydon DT (2010) Distinguishing technology from biology: a
 522 critical review of the use of GPS telemetry data in ecology. *Philos Trans R*
 523 *Soc B Biol Sci* 365:2303–2312. doi: 10.1098/rstb.2010.0087

524 Hemson G, Johnson P, South A, et al (2005) Are kernels the mustard? Data
 525 from global positioning system (GPS) collars suggests problems for kernel
 526 home-range analyses with least-squares cross-validation. *J Anim Ecol*
 527 74:455–463. doi: 10.1111/j.1365-2656.2005.00944.x

528 Horne JS, Garton EO (2006) Likelihood cross-validation versus least squares
 529 cross-validation for choosing the smoothing parameter in kernel home-
 530 range analysis. *J Wildl Manage* 70:641–648. doi: 10.2193/0022-
 531 541x(2006)70[641:lcvlsc]2.0.co;2

532 Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general
 533 parametric models. *Biometrical J* 50:346–363. doi:
 534 10.1002/bimj.200810425

535 Huck M, Davison J, Roper TJ (2008) Comparison of two sampling protocols and
 536 four home-range estimators using radio-tracking data from urban badgers
 537 *Meles meles*. *Wildlife Biol* 14:467–477. doi: 10.2981/0909-6396-14.4.467

538 Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use
 539 and movements. In: Millspaugh JJ, Marzluff JM (eds) Radio tracking and
 540 animal populations. Academic Press, San Diego, California, USA, pp 125–
 541 166

542 Keuling O, Stier N, Mechthild R (2008a) Annual and seasonal space use of
 543 different age classes of female wild boar *Sus scrofa* L. *Eur J Wildl Res*
 544 54:403–412. doi: 10.1007/s10344-007-0157-4

545 Keuling O, Stier N, Roth M (2008b) How does hunting influence activity and
 546 spatial usage in wild boar *Sus scrofa* L.? *Eur J Wildl Res* 54:729–737. doi:
 547 10.1007/s10344-008-0204-9

548 Kie JG, Matthiopoulos J, Fieberg J, et al (2010) The home-range concept: are
 549 traditional estimators still relevant with modern telemetry technology?
 550 *Philos Trans R Soc Lond B Biol Sci* 365:2221–2231. doi:
 551 10.1098/rstb.2010.0093

552 Kochanny CO, Delgiudice GD, Fieberg J (2009) Comparing Global Positioning
 553 System and Very High Frequency Telemetry Home Ranges of White-Tailed
 554 Deer. *J Wildl Manage* 73:779–787. doi: 10.2193/2008-394

555 Kranstauber B, Kays R, Lapoint SD, et al (2012) A dynamic Brownian bridge
 556 movement model to estimate utilization distributions for heterogeneous
 557 animal movement. *J Anim Ecol* 81:738–746. doi: 10.1111/j.1365-
 558 2656.2012.01955.x

559 Kranstauber B, Smolla M, Scharf A (2018) move: Visualizing and analyzing
 560 animal track data

561 Laver PN, Kelly MJ (2008) A critical review of home range studies. *J Wildl*
562 *Manage* 72:290–298. doi: 10.2193/2005-589

563 Massei G, Genov P V, Staines BW, Gorman ML (1997) Factors influencing
564 home range and activity of wild boar (*Sus scrofa*) in a Mediterranean
565 coastal area. *J Zool London* 242:411–423

566 Merli E, Grignolio S, Marcon A, Apollonio M (2017) Wild boar under fire: the
567 effect of spatial behaviour, habitat use and social class on hunting
568 mortality. *J Zool* 303:155–164. doi: 10.1111/jzo.12471

569 Millspaugh JJ, Brundige GC, Gitzen RA, Raedeke KJ (2000) Elk and hunter
570 space-use sharing in South Dakota. *J Wildl Manage* 64:994–1003. doi:
571 10.2307/3803209

572 Millspaugh JJ, Marzluff JM (2001) Radio tracking and animal populations, 1st
573 editio. Academic Press, San Diego, California, USA

574 Pellerin M, Saïd S, Gaillard J-M (2008) Roe deer *Capreolus capreolus* home-
575 range sizes estimated from VHF and GPS data Roe deer *Capreolus*
576 *capreolus* home-range sizes estimated from VHF and GPS data. *Wildlife*
577 *Biol* 14:101–110. doi: 10.2981/0909-6396(2008)14

578 Pinheiro J, Bates D, DebRoy S, Sarkar D (2017) nlme: Linear and Nonlinear
579 Mixed Effects Models

580 Pintó J, Panareda JM (1995) Memòria del mapa de la vegetació de Sant
581 Llorenç del Munt. Aster, Terrassa, Spain

582 R Core Team (2017) R: a language and environment for statistical computing

583 Rowcliffe JM, Carbone C, Kays R, et al (2012) Bias in estimating animal travel
 584 distance: The effect of sampling frequency. *Methods Ecol Evol* 3:653–662.
 585 doi: 10.1111/j.2041-210X.2012.00197.x

586 Russo L, Massei G, Genov P V (1997) Daily home range and activity of wild
 587 boar in a Mediterranean area free from hunting. *Ethol Ecol Evol* 9:287–294.
 588 doi: 10.1080/08927014.1997.9522888

589 Saïd S, Tolon V, Brandt S, Baubet E (2012) Sex effect on habitat selection in
 590 response to hunting disturbance: the study of wild boar. *Eur J Wildl Res*
 591 58:107–115. doi: 10.1007/s10344-011-0548-4

592 Schuler KL, Schroeder GM, Jenks JA, Kie JG (2014) Ad hoc smoothing
 593 parameter performance in kernel estimates of GPS-derived home ranges.
 594 *Wildlife Biol* 20:259–266. doi: 10.2981/wlb.12117

595 Scillitani L, Monaco A, Toso S (2010) Do intensive drive hunts affect wild boar
 596 (*Sus scrofa*) spatial behaviour in Italy? Some evidences and management
 597 implications. *Eur J Wildl Res* 56:307–318. doi: 10.1007/s10344-009-0314-z

598 Seaman DE, Millspaugh JJ, Kernohan BJ, et al (1999) Effects of sample size on
 599 Kernel home range estimates. *J Wildl Manage* 63:739–747. doi:
 600 10.2307/3802664

601 Silverman BW (1986) Density estimation for statistics and data analysis.
 602 Chapman and Hall/CRC

603 Spencer WD (2012) Home ranges and the value of spatial information. *J*
 604 *Mammal* 93:929–947. doi: 10.1644/12-MAMM-S-061.1

605 Thomas B, Holland JD, Minot EO (2011) Wildlife tracking technology options
606 and cost considerations. *Wildl Res* 38:653–663. doi: 10.1071/WR10211

607 Tolon V, Dray S, Loison A, et al (2009) Responding to spatial and temporal
608 variations in predation risk: space use of a game species in a changing
609 landscape of fear. *Can J Zool* 87:1129–1137. doi: 10.1139/Z09-101

610 Walter WD, Fischer JW, Baruch-Mordo S, VerCauteren KC (2011) What is the
611 proper method to delineate home range of an animal using today's
612 advanced GPS telemetry systems: the initial step. In: Krejcar O (ed)
613 *Modern Telemetry*. InTech, pp 249–268

614 Warton DI, Hui FKC (2011) The arcsine is asinine: the analysis of proportions in
615 ecology. *Ecology* 92:3–10. doi: 10.1890/10-0340.1

616 White GC, Garrott RA (1990) *Analysis of wildlife radio-tracking data*. Academic
617 Press Inc., San Diego, California

618 Josse Rühmann, Manuel Soler, Tomás Pérez-Contreras & Juan Diego Ibáñez-
619 Álamo (2019): Territoriality and variation in home range size through the
620 entire annual range of migratory great spotted cuckoos (*Clamator*
621 *glandarius*), *Nature Scientific reports*, 9:6238,
622 <https://doi.org/10.1038/s41598-019-41943-2>

623 Walter, W.; Onorato, D.; Fischer, J. Is there a single best estimator? Selection
624 of home range estimators using area-under-the-curve. *Mov. Ecol.* 2015, 3,
625 10.

626 Horne JS, Garton EO, Krone SM, Lewis JS. Analyzing animal movements using
627 Brownian bridges. *Ecology*. 2007;88: 2354–2363. [PubMed] [Google

628 Scholar]

629 Benhamou S. Dynamic approach to space and habitat use based on biased
630 random bridges. PLoS One. 2011;6 10.1371/journal.pone.0014592 [PMC
631 free article] [PubMed] [CrossRef] [Google Scholar]

632 Fleming CH, Fagan WF, Mueller T, Olson KA, Leimbruber P, Calabrese JM.
633 Rigorous home range estimation with movement data: a new
634 autocorrelated kernel density estimator. Ecology. 2015;96: 1182–1188

635 Katajisto J, Moilanen A. Kernel-based home range method for data with
636 irregular sampling intervals. Ecol Modell. 2006;194: 405–413.

637 Schuler, K, Schroeder G, Jenks J, Kie J. (2014). Ad hoc smoothing parameter
638 performance in kernel estimates of GPS-derived home ranges. Wildlife
639 Biology. 20. 259-266. 10.2981/wlb.12117.

640 Thomas B, Holland JD, Minot EO. Wildlife tracking technology options and cost
641 considerations. Wildlife Research. 2011;38(8):653–63. 10.1071/WR10211

642 Mitchell LJ, White PCL, Arnold KE (2019) The trade-off between fix rate and
643 tracking duration on estimates of home range size and habitat selection for
644 small vertebrates. PLoS ONE 14(7): e0219357.
645 <https://doi.org/10.1371/journal.pone.0219357> Calenge, C., Dray, S. and
646 Royer-Carenzi, M. 2009. The concept of animals' trajectories from a data
647 analysis perspective. Ecological Informatics, 4, 34–41.

648 Cohen, B. S., T. J. Prebyl, B. A. Collier, and M. J. Chamberlain. 2018. Home
649 range estimator method and GPS sampling schedule affect habitat
650 selection inferences of wild turkeys. Wildlife Society Bulletin 42:150–159.

- Borger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T (2006) Effects of sampling regime on the mean and variance of home range size estimates. *J Anim Ecol* 75:1493–1405
- Vieira, W.F., Kerry, C. & Hockings, K.J. *Primates* (2019) 60: 355.
<https://doi.org/10.1007/s10329-019-00724-1>
- Ponchon, A., D. Gremillet, B. Doligez, T. Chambert, T. Tveraa, J. González-Solís and T. Boulinier. 2013. Tracking prospecting movements involved in breeding habitat selection: insights, pitfalls and perspectives. *Methods in Ecology and Evolution* 4: 143-150.
- Harless, Meagan & Walde, Andrew & Delaney, David & Pater, Larry & Hayes, William. (2010). Sampling considerations for improving home range estimates of Desert Tortoises: effects of estimator, sampling regime, and sex. *Herpetological Conservation and Biology*. 5. 374-387.
- Penteriani, V., et al. 2013. Responses of a top and a meso predator and their prey to moon phases. *Oecologia* 173:753–766.
- Stanley D. Gehrt, Suzanne Prange, Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis, *Behavioral Ecology*, Volume 18, Issue 1, January 2007, Pages 204–214, <https://doi.org/10.1093/beheco/arl075>
- Dinkins, J. B., K. J. Lawson, K. T. Smith, J. L. Beck, C. P. Kirol, A. C. Pratt, M. R. Conover, and F. C. Blomquist. 2017. Quantifying overlap and fitness consequences of migration strategy with seasonal habitat use and a conservation policy. *Ecosphere* 8:e01991.

Kenward, R.E., Clarke, R.T., Hodder, K.H. & Walls, S.S. 2001. Density and linkage estimators of home range: nearest-neighbor clustering defines multi-nuclear cores. *Ecology* 82:1905-1920.

Kenward, R.E., Arraut, E.M., Robertson, P.A., Walls, S.S., Aebischer, N.J. 2018. Resource-Area-Dependence Analysis: Inferring animal resource needs from homerange and mapping data. *PLoS ONE* 13(10): e0206354.

Brown, C., A. Hardy, J. Barber, K. Fristrup, K. Crooks, and L. Angeloni. 2012. The effect of human activities and their associated noise on ungulate behavior. *PLoS One* 7 (7): e40505.

Figure 1. Location of the study areas in Spain: Sant Llorenç Natural Park (SNP),
Montes de Toledo (MT) and Doñana National Park (DNP).

Figure 2. Activity index marginal means, measured as mean speed (in
meters/hour) at each daily period. Classes sharing a lowercase letter do not
differ significantly ($P > 0.05$) in the post-hoc statistical tests. Error bars indicate
95% confidence intervals.

Figure 3. Marginal means of log-transformed home range estimates (a: MCP; b:
Khr95 and c: Kcr50) for each approach. Classes sharing a lowercase letter do
not differ significantly ($P > 0.05$) in the post-hoc Tukey with p-adjusted values. E
rror bars indicate 95% confidence intervals.

Figure 4. Marginal means and 95% CI of the BA (Bhattacharyya Affinity) index
between each approach compared with C3. Horizontal dashed line delimits the
0.6 value, above which it can be considered a high overlap between home
ranges. Classes sharing a lowercase letter do not differ significantly ($P > 0.05$)
in the glht pairwise comparisons with fdr p-adjusted values. a) BA at Khr95 and
b) BA at Kcr50.

711 Table 1. Tracked animals.

712 Age, sex and tracking period of the monitored wild boar in the three study
 713 areas: Sant Llorenç Natural Park (SNP), Montes de Toledo (MT) and Doñana
 714 National Park (DNP).

ID	Sex	Area	date_in	date_end	days
F1	Females	SPN	21/08/2011	22/10/2011	62
F2			04/12/2013	22/02/2014	80
F3			05/12/2014	02/06/2015	179
F4		DPN	02/12/2012	30/07/2013	240
F5		MT	06/07/2009	01/01/2010	179
F6			08/11/2009	15/04/2010	158
M1	Males	SPN	03/05/2012	02/06/2012	30
M2			04/05/2015	04/08/2015	92
M3		DPN	15/12/2011	12/02/2013	425
M4			27/07/2011	03/03/2012	220
M5			07/08/2011	31/12/2012	512
M6		MT	11/10/2012	10/08/2013	303
M7			02/11/2009	14/07/2010	253
M8			28/05/2010	08/05/2011	345
M9			07/08/2010	08/04/2011	244

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Table 2. Sampling characteristics of different approaches.

Values of median and interquartile range of number of fixes and h value (LCV estimated) for each approach at each study area: Sant Llorenç Natural Park (SNP), Montes de Toledo (MT) and Doñana National Park (DNP). D1) day, low intensity: one relocation in the daytime three days per week; D2) day, medium intensity: seven relocations, once a day, during daytime; C1) continuous, low intensity: one relocation in the daytime and three at night, one day per week; C2) continuous, medium intensity: three fixes per night, three nights per week and one fix in the daytime three days per week; and C3) considering all available relocations.

Approach	N. fixes	h-value	N. fixes	h-value	N. fixes	h-value
	DNP	DNP	SNP	SNP	MT	MT
D1	104 (94-156)	137.1 (119.3-242.3)	34 (31-40)	202.8 (168.1-919.7)	94 (78-96)	216.7 (169.9-355.4)
D2	231 (193-343)	114 (88.6-149)	59 (50-81)	147.7 (89.4-463.6)	182 (171-201)	216.7 (134.6-238.8)
C1	163 (127-176)	152.7 (128.1-215.1)	56 (52-76)	168.3 (136.4-770.3)	125 (103-133)	202.7 (122.2-382.1)
C2	371 (254-461)	97.4 (95.9-110.1)	125 (99-163)	120.5 (110.4-337.5)	308 (300-351)	137 (133.2-171.8)
C3	2727 (2161-3035)	66.4 (63.6-70.1)	781 (729-1160)	71.2 (48.5-106.4)	2998 (2249-4145)	115.1 (63.1-120.4)

Table 3. Home range estimation best models selected.

Set of LMEs with $\Delta AIC_c < 2$ for variables explaining home range estimates (MCP, Khr95 and Khr50) in Mediterranean Spain. Number of model parameters (K), corrected Akaike information criterion (AIC_c) values, the best fitting model (ΔAIC_c) and Akaike's weights (ω_i) are shown. The models were ranked dependent on the AIC_c value and in descending order (the most parsimonious models are on the top of each list).

Home range	Model	K	AIC_c	ΔAIC_c	ω_i
MCP	appr+zone+sex	10	88.53	0.00	0.57
	appr+sex+zone+fix	11	90.12	1.59	0.26
Khr95	appr+sex+zone+fix	11	49.1	0.00	0.71
Khr50	appr +sex+zone+fix	11	87.3	0.00	0.92

Table 4. Variables statistics of home ranges models estimation.

Results of the best-fitting LME models explaining home range estimates (MCP, Khr95 and Khr50) in Mediterranean Spain.

	Num. df	Den. df	F-value	p-value
MCP				
(Intercept)	1	56	1702.5	<0.0001
Approach	4	56	27.4	<0.0001
Sex	1	11	15.3	0.0024
Zone	2	11	5.0	0.0277
Khr95				
(Intercept)	1	55	2759.6	<0.0001

Approach	4	55	4.1	0.0049
Sex	1	11	3.9	0.0726
Zone	2	11	8.6	0.0055
Fixes	1	55	4.6	0.0354
Khr50				
(Intercept)	1	55	1098.14	<.0001
Approach	4	55	9.55	<.0001
Sex	1	11	0.4	0.5425
Zone	2	11	10.9	0.0025
Fixes	1	55	8.6	0.0049

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740 Table 5. Home range overlays best models.

741 Set of LMEs with $\Delta AIC_c < 2$ for variables explaining the BA (Bhattacharyya
742 Affinity) index (of Khr95 and Khr50) with relation to the C3 approach in
743 Mediterranean Spain. Number of model parameters (K), corrected Akaike
744 information criterion (AIC_c) values, the best fitting model (ΔAIC_c) and Akaike's
745 weights (ω_i) are shown. The models were ranked dependent on the AIC_c value
746 and in descending order (the most parsimonious models are on the top of each
747 list).

BA index	Model	K	logLik	AIC_c	ΔAIC_c	ω_i
Khr95	appr +sex	7	-25.56	67.3	0.00	0.57
	appr+sex+zone	9	-23.42	68.5	1.18	0.32
Kcr50	appr+sex+zone	9	-18.98	59.6	0.00	0.75

748

749 Table 6. Variables statistics of home ranges overlay models.

750 Results of the best fitting LME models explaining the BA (Bhattacharyya
 751 Affinity) index (Khr95 and Khr50) in Mediterranean Spain.

BA index	Num. df	Den. df	F-value	p-value
Khr95				
(Intercept)	1	42	333.52	<.0001
Approach	3	42	48.58	<.0001
Sex	1	13	6.86	0.02
Kcr50				
(Intercept)	1	42	155.75	<.0001
Approach	3	42	26.02	<.0001
Sex	1	11	5.35	0.0411
Zone	2	11	12.12	0.0017

752

Figure 1

Figure 2

a)

b)

c)

Figure 3

a)

b)

Figure 4