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In this study, we compared kernel estimates of home-range size between VHF and GPS monitoring. We used three types of data to assess the monthly estimates of individual home-range size (VHF data based on 17 locations, subsampled GPS data based on 17 locations (with 1,000 replicates) and GPS data based on 720 locations) using three estimation methods for the smoothing parameter, h (reference, least-squares cross-validation (LSCV) and fix). For all the three smoothing parameters, individual home ranges estimated from VHF and GPS data using 17 locations had very similar size. On the other hand, the use of reference or LSCV h values led home-range sizes from VHF or GPS data using 17 locations to be larger than the estimate obtained from the whole set of GPS data (720 locations). Such results emphasise the influence of using too few locations per month. On the contrary, using h fixed at 60 led to a home-range size close to that obtained from the whole set of GPS locations. The centroid of locations for a given individual in a given month only changed a little according to the data set used (the difference being < 100 m), suggesting a high accuracy for our locations. VHF and GPS areas can therefore be pooled within the same analysis of habitat use, provided that the smoothing parameter and the number of locations are standardised.

Key words: Capreolus capreolus, Global Positioning System, home range, Kernel estimator, radio-tracking, roe deer, sample size

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Global Positioning System (GPS) collars are increasingly used in animal tracking and are gradually replacing Very High Frequency (VHF) collars because the use of GPS decreases the time required to monitor animals and provides a larger number of locations per animal than do VHF collars. The use of this new technology in the study of animal movement requires locations obtained from GPS collars to be tested for precision, accuracy and potential biases. Several authors have analysed location error (precision and accuracy) according to habitat type, vegetation structure, canopy cover, terrain slope, cloud cover, day period or animal position (i.e. lying/moving/standing; Rempel et al. 1995, Moen et al. 1996, Dussault et al. 1999, Bowman et al. 2000, Biggs et al. 2001, D'Eon et al. 2002). In other studies, it has been evaluated how location estimates could be influenced by collar characteristics. These include contrasting uncorrected and differentially-corrected GPS locations (Moen et al. 1997, Rempel & Rodgers 1997), choice of location time interval (Adrados et al. 2003), satellite number and HDOP (Horizontal Dilution of Precision; Dussault et al. 2001) and collar manufacturer (Di Orio et al. 2003).

Further, the relatively high initial costs of GPS collars often do not allow people to monitor as large a number of animals as can be done using VHF technology. Moreover, many studies based on GPS monitoring have been initiated with the use of VHF so that both types of data often occur in the same study. One of the most frequent outcomes for studies based on VHF locations is the home-range size, often estimated nowadays using the kernel method (Worton 1989). However, VHF radio-tracking is time-consuming, therefore, only a small number of locations can be obtained for a given individual. Estimates of home-range size based on VHF data could consequently be biased, either being overestimated (Seaman et al. 1999, Girard et al. 2002) or underestimated (Hansteen et al. 1997). To our knowledge, very few studies had so far reported a comparison of home-range size estimated from VHF and GPS data (but see Arthur & Schwartz 1999 for a notable exception). We tried to fill this gap by assessing whether home-range size estimated from VHF locations differs from that estimated from GPS locations during a monitoring of female roe deer *Capreolus capreolus*. We used three types of data to estimate monthly home-range sizes: VHF data based on 17 locations, subsampled GPS data based on 17 locations (with 1,000 replicates) and GPS data based on 720 locations. We furthermore quantified the differences between centroid coordinates of home ranges estimated from the three data types in order to check the overall accuracy of the home-range location in the study site.

Material and methods

Study area

Our study was carried out in the Chizé reserve, which covers 2,614 ha of game-proof fenced, mainly deciduous forest in western France (46°05'N, 0°25'W [WGS84]). The climate in the area is oceanic with mediterranean influences, and is characterised by mild winters and hot, dry summers. The elevation ranges within 47-101 m a.s.l. The Chizé forest includes three habitats contrasting in quality: an oak *Quercus* spp. forest with resource-rich coppices dominated by hornbeam *Carpinus betulus* in the northeastern part, an oak forest with coppices of medium quality dominated by Montpellier maple *Acer monspessulanum* in the northwestern part, and a poor beech *Fagus sylvatica* forest in the southern part (Fig. 1; Pettorelli et al. 2003). The roe deer population at Chizé was estimated using capture-mark-recapture methods to be approximately 400 individuals >1 year old in March 2003 (Gaillard et al. 2003; J-M. Gaillard, unpubl. data).

GPS collars and VHF radio-tracking

Eight does were equipped with Lotek's GPS_3300 collars (Lotek Wireless, Fish & Wildlife Monitoring) in January-February 2003. These collars provided information on GPS positioning in differential mode (i.e. latitude, longitude, date and time) at pre-programmed intervals, fix quality (DOP = dilution of precision), ambient temperature and animal activity on two axes. Collars were programmed to record locations during six-hour long sessions per day (00:00-01:00, 04:00-05:00, 08:00-09:00, 12:00-13:00, 16:00-17:00, 20:00-21:00). Four locations were recorded at 20-minute intervals in each session giving a total of 24 positions per animal per day (720 locations per month).

The collars also transmitted a VHF signal for manual tracking of the animals. This was done using a TONNA five-element antenna (TONNA Electronique Company) connected to a Yaesu FT-817

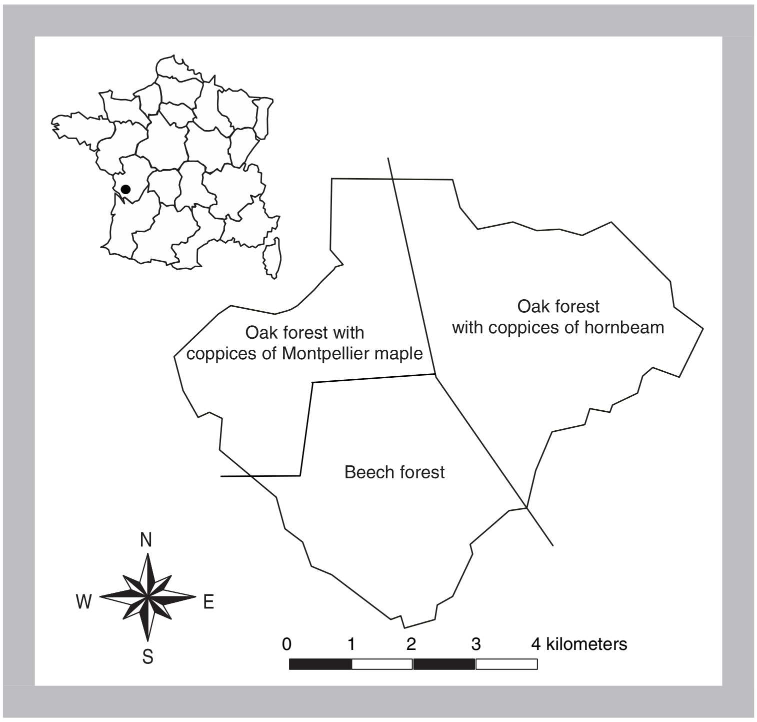

Figure 1. The Chizé reserve, which covers 2,614 ha of enclosed forest in western France with indication of the three habitat types. The inset shows the position of the reserve in France.

receiver (6 m, 2 m and 70 cm plus HF receiver, Yaesu; Amateur Radio Division of Vertex Standard). Collared animals were located at least 17 times per month during April - August 2003. The does were tracked every week to obtain one location in each of our four sampling periods (i.e. at dawn, midday, in the evening and at night) per week per animal, and equal numbers of observations were performed each month in each sampling period.

VHF and total GPS home-range

Radio-tracking and GPS data were analysed using the software R (version 1.9.1; R Development Core Team 2004) distributed under the GNU General Public License and the packages 'ade4' (Chessel et al. 2004), 'adehabitat' (Calenge 2006) and 'maps' (Becker et al. 2007). VHF fixes were assessed by triangulation (White & Garrott 1990). As the home-range size of roe deer females varies among months during spring-summer (Linnell 1994, Saïd et al. 2005), we analysed the data for each month separately. The minimum number of fixes per month was determined by plotting the estimates of home-range size against sample size (Stickel 1954, Seaman & Powell 1990) with radio-tracking locations, and corresponded to a home-range size (mean $\pm$ SD) between 90 and 110% of the home-range size estimated using all points. We used the fixed kernel method with reference smoothing ('ad hoc', href) and Least Square Cross Validation smoothing (LSCV, hLSCV; Silverman 1986, Worton 1989, Seaman & Powell 1996). We obtained a minimum of approximately 16 locations per animal per month (reference: mean = 16.1, SD = 5.7; LSCV: mean = 16.2, SD = 4.7, N = 25), and we therefore conservatively chose to keep a minimum of 17 locations per month to estimate home-range size. Kernel home ranges were then calculated using the fixed kernel method with three different forms of smoothing: href, hLSCV or hfix (h fixed at 60 corresponding to the mean of href values of all animals and months: mean = 62.8 and SD = 25.6). We conducted the analysis for the 95% kernel (Worton 1989), and also at the 50% level to obtain core areas. We plotted in the same way home-range sizes estimated from GPS locations against sample size and found a minimum of approximately 39 locations (href: mean = 39.4 $\pm$ 24.8; hLSCV: mean = 38.8 $\pm$ 14.4, N = 8 animals*4 months).

Kernel home ranges were also calculated with all the GPS locations (720 locations per animal per month) in order to get the best available estimate of home-range size of female roe deer (total GPS home ranges). We applied the same kernel method and smoothing parameters as used for the VHF data. Furthermore, we determined centroids of the kernel home ranges of VHF and total GPS data to assess possible differences in spatial location of home ranges within our study area.

Sampling and home-range simulations: subsampled GPS

To obtain home ranges of subsampled GPS data, we randomly drew 17 locations per animal per month among the 720 GPS locations available. We constrained the drawings to follow the same distribution as VHF monitoring in relation to the period of the day (i.e. four points, one dawn, one midday, one evening and one night, every week for the first four weeks, and one point among the different day periods in the fifth week). To reduce autocorrelation, all points were taken with a minimum time interval of 15 hours (Swihart & Slade 1985a, b, 1986, Hansteen et al. 1997). Home-range sizes were then estimated using the fixed kernel method, with the different forms of smoothing described above: href, hLSCV or hfix. We conducted the analysis for the 95% and 50% kernels. We also obtained centroids of the kernel home ranges. The entire procedure, described above, was repeated 1,000 times.

Sensitivity analyses from VHF and GPS data

In one sensitivity analysis, we estimated home-range sizes from the VHF and GPS data using different numbers of locations to detect the real minimum number of locations required to reliably estimate home-range sizes. We used $N = 10$, 12 and 15 randomly sampled VHF locations per month and $N = 10$, 12, 15, 18, 20, 30 and 40 randomly sampled GPS locations per month (repeated 100 times) to estimate home-range areas and calculated differences between these areas and total GPS home-range areas. We then compared these differences of areas with those obtained from the comparison between 17 locations (VHF or GPS) and total GPS data (see section Sampling and home-range simulations: subsampled GPS).

In another analysis, we estimated home-range sizes from GPS data for each hour session of the day (00:00-01:00, 04:00-05:00, 08:00-09:00, 12:00-13:00, 16:00-17:00 and 20:00-21:00). We performed two types of estimations: one including all the locations from each session (four locations per session per day corresponding to 120 locations per month) and one including 17 locations per session per month (repeated 100 times).

For both sensitivity analyses, we applied the fixed kernel method by considering the different forms of smoothing (href, hLSCV or hfix) and conducted the analysis for the 95% and 50% kernels. We also obtained centroids of the kernel home ranges.

Statistical analysis

We used Wilcoxon tests to determine whether home-range sizes differed among the three data types, and one-way ANOVAs to test the effect of factor h on differences of home-range sizes and on distances between centroids. The whole analysis was performed using the software R (version 1.9.1), and statistical significance was fixed at $P \leq 0.05$.

Results

Precision of the locations

The location error estimated from VHF and GPS data was 95 m (mean = 95.3, SD = 43.0) and 25 m (mean = 25.6, SD = 34.0), respectively.

Comparing VHF (17 locations) and GPS (17 and 720 locations) home-range size

We did not find any effect of the factor h when we compared differences of home-range sizes between VHF and subsampled GPS data according to the smoothing parameter h (One-way ANOVA: $F = 0.75$, $df = 2$, $P = 0.48$ and $F = 0.45$, $df = 2$, $P = 0.64$ for home-range size at 95 and 50%, respectively). For all the three smoothing parameters, the home-range sizes estimated from VHF and subsampled GPS data did not differ at the 95% (Wilcoxon tests: href: $V = 22$, $P = 0.64$; hLSCV: $V = 12$, $P = 0.46$; hfix: $V = 20$, $P = 0.84$) and 50% levels (Wilcoxon tests: href: $V = 17$, $P = 0.94$; hLSCV: $V = 11$, $P = 0.383$; hfix: $V = 17$, $P = 0.945$; Fig. 2).

VHF and subsampled GPS home ranges were either overestimated or underestimated compared with total GPS home ranges, depending on which smoothing parameter h was used (see Fig. 2). We found a significant effect of h on the difference between total GPS and VHF estimates (One-way ANOVA: $F = 5.01$, $df = 2$, $P = 0.012$ and $F = 4.54$, $df = 2$, $P = 0.017$ for home-range size at 95 and 50%, respectively) and between total GPS and subsampled GPS estimates (One-way ANOVA: $F = 13.70$, $df = 2$, $P < 0.001$ and $F = 10.34$, $df = 2$, $P < 0.001$ for home-range size at 95 and 50%, respectively). We then compared home-range sizes for each smoothing parameter. At both 95 and 50% kernels, the use of href or hLSCV led to overestimated home-range sizes from VHF data (Wilcoxon tests: href: $V = 36$ at 95% and 35 at 50%, $P = 0.008$ at 95% and 0.016 at 50%; hLSCV: $V = 32$ at 95 and 50%, $P = 0.055$ at 95 and 50%) and subsampled GPS data (Wilcoxon tests: href and hLSCV: $V = 0$ at 95 and 50%, $P = 0.008$ at 95 and 50%) compared with the total GPS data. On the other hand, when we used hfix, the VHF home ranges did not differ significantly from total GPS home ranges (Wilcoxon tests: $V = 5$ at 95% and 7 at 50%, $P = 0.078$ at 95% and 0.148 at 50%), but subsampled GPS home ranges were slightly underestimated compared with the total GPS home ranges (Difference of area

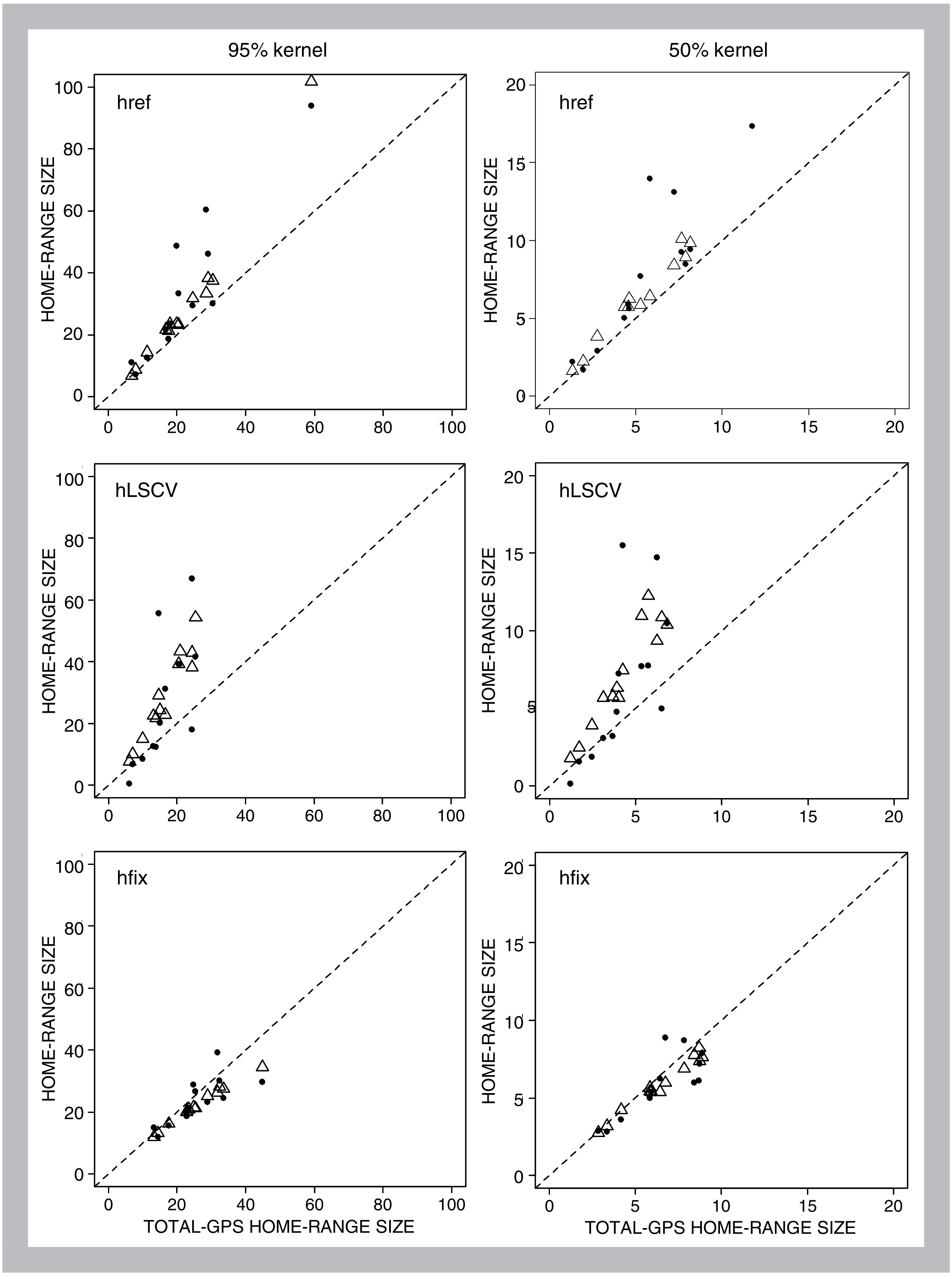

Figure 2. Size of monthly home ranges (in ha) estimated from 17 locations for VHF (•) and subsampled GPS (△) versus size of monthly home ranges estimated from 720 locations (i.e. total GPS), using the smoothing parameters href, hLSCV, and hfix for 95 and 50% kernels, respectively.

= -3.9 ± 2.52; Wilcoxon tests: V = 36 at 95 and 50%, P = 0.008 at 95 and 50%).

Effect of sample size on home-range estimates

For both all the sample sizes and the three smoothing parameters, the home-range sizes estimated from VHF and subsampled GPS data did not differ at the 95% (Wilcoxon tests for 10, 12 and 15 locations: href: V = 16 to 19, P ≥ 0.47; hLSCV: V = 16 to 20, P ≥ 0.375; hfix: V = 17 to 20, P ≥ 0.38) and 50% levels (Wilcoxon tests for 10, 12 and 15 locations: href: V = 15 to 18, P ≥ 0.58; hLSCV: V = 16 to 18, P ≥ 0.58; hfix: V = 17 to 21, P ≥ 0.297).

We then compared home-range sizes from subsampled GPS and total GPS data. For both all the sample sizes and the three smoothing parameters, the home-range sizes estimated from subsampled and total GPS data significantly differed at the 95 and 50% levels (Wilcoxon tests for 10, 12, 15, 18, 20, 30 and 40 locations: href, hLSCV and hfix: V = 0 at 95 and 50%, P = 0.016 at 95 and 50%; Fig. 3). However, our results showed that differences between subsampled and total GPS home-range sizes were small with a minimum of 17 locations (differences of area at the 95% level: 17 locations: hfix = -3.9 ± 2.52 ha). Moreover, home-range sizes estimated from 40 locations when using href or hLSCV were similar to total GPS home-range sizes, and the differences of area were similar to those found with 17 locations using hfix (differences of area at the 95% level: 40 locations: href = 3.4 ± 3.55 ha; hLSCV = 3.8 ± 3.11).

For the comparison of VHF and total GPS home-range sizes, the use of hLSCV led to overestimated VHF home-range size at the 95 and 50% levels (Wilcoxon tests for 10, 12 and 15 locations: V = 27 to 28, P ≤ 0.031 at 95%, V = 25 to 28, P ≤ 0.039 at 50%), whereas the use of href or hfix led to similar areas of VHF and total GPS data at the 95% (Wilcoxon tests for 10, 12 and 15 locations: href: V = 24 to 28, P = 0.016 to 0.109; hfix: V = 0 to 5, P = 0.016 to 0.156) and 50% levels (Wilcoxon tests for 10, 12 and 15 locations: href: V = 23 to 24, P = 0.109 to 0.156; hfix: V = 1 to 8, P = 0.031 to 0.375; see Fig. 3).

Effect of day period on home-range estimates

We first compared home-range sizes from subsampled GPS data, with all locations of each hour session, and total GPS data (Fig. 4). Areas did not differ using href at the 95% (Wilcoxon tests: V = 4 to 30, P = 0.055 to 0.945) and 50% levels (Wilcoxon tests: V = 6 to 30, P = 0.109 to 0.844), whereas the use of LSCV or hfix led to differences between subsampled GPS and total GPS home-range sizes (Wilcoxon tests: hLSCV: V = 35 to 36, P ≤ 0.016 at 95% and 50%; hfix: V = 36, P = 0.008 at 95% and V = 33 to 36, P ≤ 0.039 at 50%), except at 16:00 for hLSCV (Wilcoxon tests: V = 27, P = 0.250 at 95% and V = 28, P = 0.195 at 50%) and at 20:00 for hfix (Wilcoxon tests: V = 31, P = 0.078 at 95% and V = 26, P = 0.312 at 50%).

We then compared home-range sizes from subsampled GPS data, with 17 locations sampled in each hour session, and total GPS data. For both href and hLSCV, areas did not differ significantly (Wilcoxon tests: href: V = 1 to 10, P ≥ 0.109 at 95% and V = 6 to 15, P ≥ 0.109 at 50%; hLSCV:

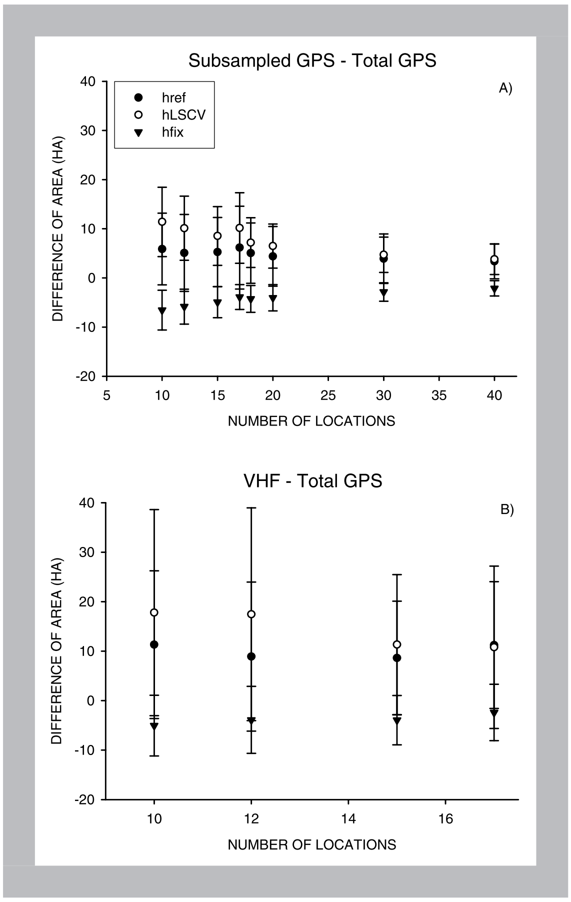

Figure 3. Difference of area between subsampled GPS home ranges estimated from 10, 12, 15, 18, 20, 30 and 40 locations per month and total GPS home ranges (720 locations per month (A) and between VHF home ranges estimated from 10, 12 and 15 locations per month and total GPS home ranges (720 locations per month (B), using the smoothing parameters href (•), hLSCV (○) and hfix (▼).

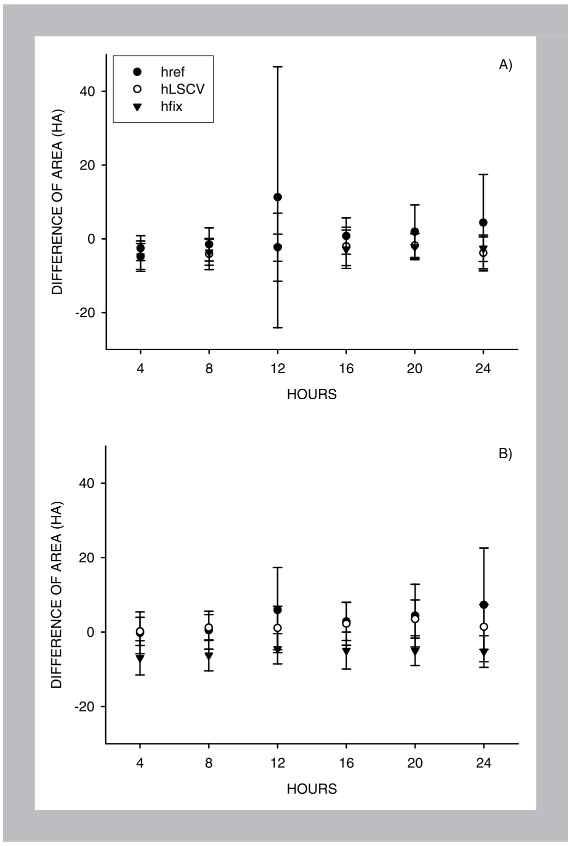

Figure 4. Difference of area between subsampled GPS home ranges estimated from all locations of each hour session (120 locations per month) and total GPS home ranges (720 locations per month (A) and between subsampled GPS home ranges estimated from 17 locations per hour session per month and total GPS home ranges (720 locations per month (B), using the smoothing parameters href (•), hLSCV (○) and hfix (▼).

$V = 4$ to 18, $P \geq 0.057$ at 95% and $V = 8$ to 26, $P \geq 0.195$ at 50%), except at 12:00 and 20:00 for href (Wilcoxon tests: $V = 1$, $P = 0.016$ at 95% and $V = 2$, $P = 0.023$ at 50%). The use of hfix led to underestimated subsampled GPS home-range sizes for each hour session (Wilcoxon tests: $V = 36$, $P = 0.008$ at 95 and 50%).

Precision of home-range centroid location in space

We compared the distances between centroids of VHF, subsampled GPS and total GPS home ranges obtained with the three smoothing parameters for different sample sizes. For all the sample sizes, distances between centroids of VHF and subsampled or total GPS home ranges were not significantly different (and close to 80 m) for the three parameters (One-way ANOVA: $F \leq 0.44$, df = 2 and $P \geq 0.65$ for subsampled GPS; $F \leq 0.57$, df = 2 and $P \geq 0.57$ for total GPS). When we compared subsampled GPS versus total GPS home ranges, distances between centroids did not differ significantly among the three smoothing parameters when using 17 locations per month (One-way ANOVA: $F = 2.2$, df = 2 and $P = 0.125$), but means and standard deviations of distances were smaller than in the two other comparisons (close to 35 m) because we used the same method of location (GPS), and therefore data were not independent. In contrast, distances between centroids of subsampled GPS and total GPS home ranges differed significantly between the three smoothing parameters for the other sample sizes (One-way ANOVA: $F \geq 6.43$, df = 2 and $P \leq 0.003$) with distances estimated using hLSCV being greater than those obtained using href and hfix. All distances were significantly different from 0, however, they were low (i.e. < 1/3 of the average radius of a roe deer home range at Chizé).

We then compared the distances between centroids of subsampled and total GPS home ranges obtained from different hour sessions using all the locations or only 17 locations per month. For both home ranges estimated with all the locations and with 17 locations, distances differed significantly among the three smoothing parameters for all the hour sessions (One-way ANOVA: $F \geq 4.1$, df = 2 and $P \leq 0.021$), but at 12:00 for all the locations because of a very large standard deviation (distance = 81.2 ± 88.7 m).

Discussion

Kernel estimates of home-range size using href and hLSCV showed that sizes estimated from VHF and subsampled GPS data were almost the same for all the sample sizes but they were larger than sizes obtained for total GPS home ranges. These results are consistent with Arthur & Schwartz's (1999) findings from simulations on VHF and GPS data. Contrasting this, home-range estimates using hfix were very similar for VHF and subsampled GPS data for all the sample sizes, but also similar for the three data types when using 17 locations for VHF and subsampled GPS home ranges. Thus, when a constant number of points was used, the three smoothing parameters provided almost identical home-range sizes. On the other hand, href and particularly hLSCV seemed highly sensitive to the number of locations because they led to smaller areas from total GPS data (i.e. about 720 fixes per animal and per month), whereas hfix led to total GPS areas similar to VHF and subsampled GPS areas. To get reliable estimates, a minimum of 17 locations per animal per month seemed to be required when using VHF locations. However, when plotting home-range sizes estimated from GPS locations against sample size, we found a minimum of approximately 39 locations. Moreover, our results showed that home-range sizes estimated from 40 locations when using href or hLSCV were similar to total GPS home-range sizes. This indicates that 17 locations is not enough, and accounts for the overestimation we reported when using either href and hLSCV from VHF and subsampled GPS data. This overestimation of home-range size when using kernel with too small sample size thus corroborates results of Arthur & Schwartz (1999), Belant & Follmann (2002) and Girard et al. (2002). Our results also support Seaman et al.'s (1999) findings that using the hLSCV value leads to overestimated home-range size, but they are not consistent with the underestimation induced by href values when a small number of locations is used as reported by Hansteen et al. (1997). According to Seaman et al. (1999), the discrepancy between Hansteen et al.'s (1997) results and ours would result from the behaviour of hLSCV versus href values, and from the small number of home ranges involved in the comparison. Furthermore, Hemson et al. (2005) recently showed that the use of hLSCV is not optimal when animals exhibit intensive use of core areas and site fidelity as it is the case for roe deer, and produce variable results at small sample size and failures at large sample size. Our results on roe deer, a highly sedentary species (Strandgaard 1972), support the overestimation and high variability of home-range size using hLSCV values. Finally, our results show that fixing h at the same value for all home ranges (i.e. $h = 60$) stabilises the estimate of home-range size and thereby provides a better way to compare home ranges of different size and number of locations. On the contrary, the use of href or hLSCV values requires a similar or larger number of locations for reliable comparisons.

The home-range sizes estimated from 17 locations all sampled during a specific day period were underestimated compared to total GPS home ranges when using hfix, whereas the use of href or hLSCV led to similar areas. However, we previously showed that home-range sizes were similar between subsampled GPS (with 17 locations sampled over all the day periods (i.e. at dawn, midday, in the evening and at night)) and total GPS data using hfix, and were overestimated using href or hLSCV. Consequently, the estimation of only one part of the home range by hour session led to underestimation using hfix and to similar areas using href and hLSCV. Moreover, distances between centroids of subsampled GPS and total GPS home ranges were significantly different and also indicated poor assessment of home ranges. These results corroborate Belant & Follmann's (2002) findings showing that acquiring locations during only a portion of the 24-hour period could involve potential biases when estimating home-range size.

Distances between home-range centroids were often significantly different from 0 but consistently $< 1/3$ of the average radius of a roe deer home range at Chizé. This rather good precision of home-range position indicates on the one hand a high accuracy of radio-tracking and GPS positions, and on the other hand, an appropriate sampling of VHF and subsampled GPS data. In fact, equal numbers of observations were made each month at dawn, midday, in the evening and at night, covering in that way all periods of activity and inactivity of the animals. However, we observed a slight difference according to the h values used because the mean distances with the href values were smaller than with the hLSCV or the hfix values ($h = 60$) in the three comparisons. Thus, the href values seem to provide the most precise home-range centroid.

In this study, we evaluated differences between home-range areas for eight female roe deer monitored for four months. Such analyses allowed us to compare the behaviour of kernel estimators when using different h values from field data, and thereby complement the simulations performed by Seaman et al. (1999). However, the scope of our data is too limited to allow us to generalise about the performance of the estimators.

The use of field data leads to autocorrelation among observations. The analyses based on 720 GPS locations per month included higher autocorrelation than the analyses based on 17 locations (VHF or subsampled GPS) per month. However, several authors (Reynolds & Laundre 1990, McNay et al. 1994, Swihart & Slade 1997, Otis & White 1999) have concluded that a large set of autocorrelated data provide a better estimate of the true home-range size than a small set of independent data.

Conclusion

Our results indicate that home-range sizes estimated from VHF and GPS data are similar, provided that the smoothing parameter and the number of locations are standardised. Both GPS and VHF collars can therefore be used to estimate home ranges from a given field study, at least when the species under study share the same spatial patterns as roe deer (i.e. relatively small home range and high site fidelity; Strandgaard 1972). Our work could thus help managers to feel more comfortable with mixing data from GPS and VHF collars when analysing home ranges. Moreover, our data indicate that, while more locations obviously lead to better home-range estimates, a minimum sample size of 17, which is much smaller than the threshold of 40 assessed from simulation studies (Seaman et al. 1999), can provide reliable estimates of home-range size of highly sedentary animals such as roe deer (Saïd et al. 2005). With a careful sampling design, reliable estimates of home-range size can even be obtained by kernel methods when using <10 locations (Börger et al. 2006).

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