GPS approach to study fine-scale site use by wild red deer during active and inactive behaviors

Claire Adrados, Hélène Verheyden-Tixier, Bruno Cargnelutti, Dominique Pépin, Georges Janeau

GPS approach to study fine-scale site use by wild red deer during active and inactive behaviors

Christophe Adrados, Hélène Verheyden-Tixier, Bruno Cargnelutti, Dominique Pépin, and Georges Janeau

Abstract Studying fine-scale habitat selection of wild mammals relative to environmental parameters requires 1) correctly sampling the species' activity in time and space and 2) measuring the environmental variables at those locations. We propose a procedure using Differential Global Positioning System (DGPS) technology to achieve these goals. A data set from red deer (*Cervus elaphus*) was used to demonstrate the method. We validated an individual-based relative method using the count provided by a GPS collar activity sensor to separate active from inactive behaviors. This method allowed the correct classification of locations as active or inactive (82–97% of correct allocations depending on the fix interval used). We analyzed activity sampling using various fix intervals (5, 10, and 15 min) and the resulting spatial sampling when we retained only highly accurate locations (<10-m error radius). We demonstrated that long intervals between fixes could cause a loss of information for the shortest activity bouts, which make up 5 and 11.5% of the daily budget using 10- and 15-min fix intervals, respectively. The proposed spatial sampling allowed 65 to 73% of the total fixes to be kept. Active bouts were slightly undersampled, whereas inactive bouts were oversampled. We used a subsample of animal locations that were relocated using hand-held DGPS to measure several environmental variables *in situ* and examined the variations relative to animal and activity combinations.

Key words activity, activity sensor, *Cervus elaphus*, differential correction, GPS, Global Positioning System, habitat use, red deer

A wide range of environmental or behavioral factors can influence habitat selection in ungulates (e.g., Collins and Urness 1983, Merrill 1991, Bon et al. 1995, Conradt 1998, Carranza and Valencia 1999, Mysterud et al. 1999*a*). Spatio-temporal scale for studying ungulate distribution ranges from population units in the landscape to habitat use in individual home ranges and even further to plants and bites taken on individual feeding stations (Johnson 1980). In this paper we propose a methodology to study fine-scale site selection by wild ungulates using Differential Global Positioning System (DGPS) tools. Our objective was to test some predictions from the food-cover hypothesis (Staines 1977, Mysterud and Ostbye 1999, Stromeyer et al. 1999), focusing on third-order habitat selection (Johnson 1980). To demonstrate the methodology, we use a preliminary data set on red deer (*Cervus elaphus*).

We used Lotek GPS 1000 collars (Lotek Engineering Inc., Newmarket, Ont., Canada) in differential mode because the locations obtained were more accurate than in direct mode (Rodgers and Anson 1994, Moen et al. 1996*b*, Rempel and Rodgers 1997, Janeau et al. 1998, Dussault et al. 2001) even after Selective Availability (SA) error

Authors' address: Institut National de la Recherche Agronomique-Institut de Recherches sur les Grands Mammifères, CRA Toulouse, BP 27, 31326 Castanet Tolosan cedex, France; e-mail for Verheyden-Tixier: verheyde@toulouse.inra.fr.

was removed (Adrados et al. 2002). These GPS collars contain a sensor that can be used to assess animal activity (Moen et al. 1996*a*), but calibration for each animal and season is necessary because collar position and tightness along the neck may vary between and within animals (e.g., the neck circumference of male red deer increases during the rut). Because locations collected by DGPS are accurate to within a few meters, it is now conceivable to achieve the same level of accuracy to describe the habitat used in relation to activity. This level of precision cannot be obtained by traditional mapping methods using aerial or satellite imagery (e.g., Johnson et al. 2000, McClain and Porter 2000) because the map obtained does not describe precisely the conditions under the canopy (e.g., plant species, cover, visibility, ground litter).

To obtain data (activity and environment) on successive locations of an animal during a 24-hr cycle, it is necessary to:

1. Properly allocate each location to active or inactive behavior,
2. Obtain a sample of the activity and inactivity locations in time,
3. Measure the environmental characteristics on a sample of these locations.

To satisfy these prerequisites, we proposed the following:

1. An individual-based relative method that does not require further calibration to separate active from inactive behavior. We validated this procedure using experimental data.
2. A 2-order hierarchical sample of activity and inactivity locations, first in time and then in space. Using data from wild animals, we first assessed effects of various fix intervals on activity sampling to select the appropriate time interval. Secondly, we took the most spatially accurate locations and examined their distribution within activity and inactivity bouts.
3. A procedure to sample the environmental characteristics of the locations and to examine their variations relative to animal and to activity combinations.

Finally we discuss the advantages and disadvantages of this approach, needed improvements, and its potential to answer various questions about spatio-temporal behavior of wild ungulates.

Methods and study area

We fitted all animals with differential 6-channel GPS 1000 collars, software version 2.11. Location attempts were scheduled with GPSHost 1000 software, version 3.08 (Lotek Engineering Inc., Newmarket, Ont., Canada), and pseudo-ranges were downloaded via a radio modem command unit connected to a laptop computer. The pseudo-ranges were corrected using N3WIN software, version 2.40 (Lotek Engineering Inc.). The reference base station was a 12-channel GPS Pathfinder with Path Finder Community Base Station (PFCBS) software, version 2.67 (Trimble Navigation Ltd., Sunnyvale, Calif., USA). The distance between base station and animals with GPS collars was about 280 km for captive deer and 240 km for wild deer. We used a real-time differential hand-held GPS (GPS PRO XR, Trimble Navigation Ltd.) to find activity sites of red deer *in situ*. We collected the differential corrections from a geostationary satellite by a mobile receiver station (in open view of the sky) located in the study area and broadcast them to the hand-held GPS by a radio modem (up to 5 km). Fix accuracy obtained was submetric.

Tracking procedure

We used 4 captive, tame, adult, female red deer to validate the procedure of activity assessment based on the activity sensor in the GPS collars. We fitted the animals with the GPS collars and released them in a 1-ha park at the Institut National de la Recherche Agronomique (INRA) in Clermont-Ferrand, France (45°42′N, 03°30′E), where we observed them after a 7-day period of acclimation. Two of them (#1 and #2) belonged to a group of 15 hinds ranging in grassland and supplemented with pelleted food. Their GPS collars were scheduled for a 5-min fix interval during 24 hr and then for a 15-min fix interval during 24 hr. We continuously observed them from a watchtower during the morning and afternoon on 2 different days in April 1998. Animals #3 and #4 belonged to a group of 3 hinds ranging in an enclosure covered by woodland (oak [*Quercus robur*], chestnut [*Castanea sativa*], beech [*Fagus sylvatica*], fir [*Abies alba*], and pine [*Pinus sylvestris*]) and meadows. We tracked them with a 10-min fix interval, and 2 observers on foot followed 1 animal each at a distance <3 meters continually during daylight hours on 3 different days in October 2000.

We tracked adult wild red deer in the Parc National des Cévennes, France (44°19′N, 03°45′E), which is a mountainous area (800–1,700 m) with a wet climate (annual rainfall: 900–1,500 mm, mean annual temperature: 7–8°C). Vegetation consisted of a mosaic of mixed forest (pine, fir, beech, oak, chestnut), moorland (*Cytisus purgans*, *Vaccinium* sp., *Calluna vulgaris*, *Erica* sp.), and pasture used by cattle and sheep. We trapped red deer with the authorization of the Parc National des Cévennes and the French Ministry of Agriculture (permit n° 7382). We immobilized them using a combination of medetomidine (Orion Pharma, Espoo, Finland) and ketamine hydrochloride (Merial, Lyon, France). We administered atipamezole (Orion Pharma, Espoo, Finland) as an antagonist to medetomidine and released them at the capture site. First, we tracked 2 males and 1 female with a 5-min sampling interval to examine duration of activity periods, 1 male during 5 consecutive days in December 1997 and the 2 others during 24 hours in August 1998. We tracked 3 other adult deer, 2 males (A and B) and 1 female (C), with a 10-min sampling interval during a 24-hr cycle in April 2000 to assess the sampling of activity locations and the link with environmental variables.

Individual-based relative method to separate active from inactive behaviors

The dual-axis motion sensor of the GPS collars provided an activity value ranging from 0–255 for each fix attempt. This value was averaged over the 1-min time interval between 2 fixes (Lotek Engineering Inc. 1997). For each animal, we used a graphic method in which cumulative activity values were plotted against time to separate active from inactive points. The hypothetical straight line (L_0) of mean activity during the 24-hr period defined a referential slope (a_0). The observed slope between 2 successive points (a) was compared with a_0; the animal was considered active if $a > a_0$, and inactive if $a < a_0$. We classified the activity as "medium" when a could not be distinguished from a_0. This method provided a relative individual-based threshold value for each 24-hr cycle rather than an arbitrary absolute threshold that could fluctuate according to position of the collar along the neck (animal behavior) and tightening of the collar (season and animal) as pointed out by Moen et al. (1996*a*) and Obbard et al. (1998).

We compared data obtained from continuous observation of tame animals with data obtained by analysis of their GPS collar's activity sensor. The observation allowed us to separate 2 activity levels—"active," when females were feeding or moving, and "inactive," when they were standing immobile, grooming, ruminating, or sleeping. We obtained time and duration of each observed active or inactive bout. We fractionated the continuous observation periods into successive 10-min intervals corresponding to those obtained with the GPS collar. We considered a fix interval as "active" if the hind spent >60% of observed time active, "inactive" if the hind spent <40% of the time active, and "medium" for the remaining (40–60%). We predicted that $a > a_0$ for observed active behavior and $a < a_0$ for inactive behavior. We tested correspondence between the collar sensor activity classes defined above (excluding the uninformative "medium" class) and observed activity for each animal and fix interval using a χ^2 test or a Fisher's exact test when cell counts were <5.

Sampling of active and inactive locations of wild red deer

To determine the appropriate time interval between fixes for the kind of third-order analysis (Johnson 1980) we wished to conduct, we analyzed the distribution of activity-bout duration of wild red deer tracked with the minimal time interval of 5 min. We performed a graphic analysis to identify active and inactive periods, analyzed their distribution using descriptive statistics, and then estimated potential loss for 10-min and 15-min fix intervals as number of bouts lasting less than 10 min or 15 min and their cumulative duration. We separately analyzed data from December 1997 and August 1998 to take into account a seasonal effect on duration of activity periods.

We obtained the data set used from 3 wild animals located every 10 min in April 2000. In previous work with the same GPS devices, Adrados et al. (2002) showed that >90% of 3-dimensional fixes with a Dilution of Precision (DOP) of less than 10 were within a 10 m error radius. We used this rule, consistent with other works on differential location accuracy (Moen et al. 1996*b*, Rempel and Rodgers 1997), to discard less accurate locations (either 2D fixes or DOP >10). We considered that the coordinates of a 2D inactive fix could be replaced by those of the previous or following accurate 3D fix of the same inactive bout and called them extrapolated fixes. We assumed that during such inactive bouts, the animal did not move. We examined success of this spatial sampling in covering daily activity patterns of the animals.

Environmental characteristics for a subsample of activity locations

Within highly accurate locations, we selected points >20 m away from a previous location (e.g., twice the location error). We used this subsample of locations to characterize the environment encountered by the animals along their movements. After each 24-hr recording, we reached each localization of the subsample using a differential hand-held GPS. Several environmental variables were recorded in a 5-m radius and 2-m-high volume centered on the location. We used a point-intercepts method derived from the one used by Daget and Poissonnet (1971) to estimate vegetation abundance (see also Tixier et al. 1997). We held a thin stake vertically on the ground 5 m away from the center of the location, in 4 directions (N, E, S, W), and recorded number of species contacts with the stake. For analysis, we summed number of contacts by plant category: grass and forbs (GRASS), semi-ligneous (SHRUB), deciduous tree (DECIDU), and conifer (CONIF). We estimated visibility using a 40 × 40-cm grid frame placed 5 m away from the center of the location, in each of the 4 cardinal directions, and held vertically 20 cm high (corresponding to a bedded deer) or 140 cm high (standing deer). We summed the number of visible squares (>50% of the square area visible) to provide a measure of visibility for each height (V20 and V140, respectively). A high value indicated good visibility, and a low value indicated closed vegetation. We characterized each accurate activity location by its coordinates, period of the day (daytime vs. nighttime), activity value (active vs. inactive), and environmental characteristics. The same point of the subsample could represent several nearby activity locations (<20 m away). We measured environmental characteristics *in situ* on a subsample of 21, 25, and 32 locations for males A and B and female C, respectively. This subsample allowed us to characterize all 99, 106, and 95 high-precision fixes recorded for each animal, respectively.

As environmental variables were correlated and not normally distributed, we used Principal Component Analysis (PCA) to study differences between sites. We used between- and within-classes PCA (Dolédec and Chessel 1991) to separate total variability between and within animals or activity-period combinations. We then used permutations to test the significance of the partitioning observed (Manly 1991). These analyses were done with ADE.4 software (Thioulouse et al. 1995).

Results

Validation of the individual-based relative method to assess activity on tame deer

We found good correspondence between the activity derived from graphic analysis of the collar data and observed activity for the 5-, 10-, and 15-min fix intervals for each animal (Table 1). Fisher's exact tests (for cell counts <5) indicated we could not reject the hypothesis of greater probability for an active (or inactive) collar value to be an active (or inactive) observed value ($P<0.004$). We rejected the null hypothesis of equal proportions among

Table 1. Correspondence between sensor-measured activity and observed activity (number of records) of tame female red deer fitted with a GPS collar and free-ranging in a 1-ha park in Clermont-Ferrand, France during April 1998 and October 2000 (see footnotes). Sensor activity was determined using an individual-based relative method (see Methods).

Fix interval	Observed activity	Collar sensor activity classes: Active		Inactive		Medium	
5 min		ani 1[a]	ani 2[a]	ani 1[a]	ani 2[a]	ani 1[a]	ani 2[a]
	Active	16	17	2	2	1	1
	Inactive	7	8	80	86	10	10
	Medium	4	2	1	0	1	0
		61%[c]		97%[c]			
10 min		ani 3[b]	ani 4[b]	ani 3[b]	ani 4[b]	ani 3[b]	ani 4[b]
	Active	59	66	10	17	12	31
	Inactive	11	3	86	69	11	3
	Medium	1	5	4	3	3	3
		86%[c]		82%[c]			
15 min		ani 1[a]	ani 2[a]	ani 1[a]	ani 2[a]	ani 1[a]	ani 2[a]
	Active	6	11	3	0	1	3
	Inactive	4	2	26	16	0	4
	Medium	1	3	1	2	0	1
		62%[c]		88%[c]			

[a] Animal 1 and animal 2 were observed in the morning and afternoon of 2 days in April 1998.

[b] Animal 3 and animal 4 were observed from dawn to dusk of 3 days in October 2000.

[c] Percentage of activity data derived from the graphic analysis of collar data that was correctly categorized.

Table 2. Distribution of activity bout durations of wild red deer in the Parc National des Cévennes, France during December 1997 and August 1998 (see footnotes).

	Mean number of bouts per 24 hr					
	December[a]			August[b]		
Mean number	Active	Inactive	Total bouts	Active	Inactive	Total bouts
of bouts per 24 hr	24.4	23.4	47.8	10	10	20
Duration (min)						
5	30%	35%	33%	15%	15%	15%
10	19%	18%	18%	15%	0%	7.5%
15–30	31%	10%	21%	15%	15%	15%
40–60	13%	15%	14%	40%	30%	35%
>60	7%	21%	14%	15%	40%	27.5%
Mean duration (min)	22.3	36.6	29.3	58.5	79.7	69.1
SD (min)	25.8	44.9	37	78.5	83.9	80.9
Median (min)	15	10	10	37.5	52.5	42.5

[a] Male tracked in December 1997; 1,440 records, 239 bouts.
[a] Female tracked in August 1998; 576 records, 40 bouts.

the collar activity classes between observed active or inactive values ($\chi^2 > 79$, df=1, $P < 0.0001$ when cell counts ≥ 5). Mean percentage correct classification for inactive collar values varied between 82 and 97%, depending on time interval, and between 61 and 86% for active bouts. Greatest correct classification for activity (86%) was obtained with the 10-min interval (vs. 61% and 62% for the 5- and 15-min intervals, respectively; Table 1). In contrast, we obtained the greatest correct classification for inactive bouts with the 5-min fix interval (97% vs. 82% for 10 min and 88% for 15 min; Table 1).

Sampling of activity locations of wild red deer

Time sampling. In December 70% of active periods lasted at least 10 min and 85% in August (Table 2). Duration of inactive bouts was at least 10 min for 65% of bouts in December and 85% in August. Median bout durations were 15 and 37.5 min for active, 10 and 52.5 min for inactive, in December and August, respectively. During a 24-hr cycle the animals presented a mean of 47.8 (SD=4.2) different activity bouts in December and only 20 (SD=5.7) in August (Table 2). Thus, duration of activity bouts varied between the 2 sampled months with more fragmented activity and shorter bout durations in late autumn and fewer but longer activity bouts in summer. Using a 10-min sampling interval could result in a maximum loss of information of 30% of active bouts and 35% of inactive ones (the shortest 5-min bouts in December), corresponding to a maximum of 78 minutes (15.6 short bouts) during a 24-hr cycle (e.g., 5.5% of total time; Table 2). A 15-min sampling interval could result in a maximum loss of information of 51% of the activity periods (5- and 10-min bouts), which totaled 166 minutes (e.g., 11.5% of 24 hours; Table 2).

Spatial sampling. On the 435 expected fixes from the free-ranging GPS collared deer, we recorded 13 failed, 179 2D and 243 highly accurate locations (3D, DOP < 10). We considered 57 more extrapolated inactive 2D locations as highly accurate. Percentage of accurate fixes varied from 65–73% of fix attempts, depending on the animal (Table 3). During a 24-hr cycle, animals spent 40–50% of their time active and 45–51% inactive (the remainder was the medium activity class). But distribution of activity among the set of highly accurate fixes was not the same with 28–37% active whereas 58–68% were inactive (Table 3). Almost all of the male's activity bouts contained at least one high-precision location (see Table 3 and Figure 1): 10/11 and 8/8 for active bouts, 9/11 and 7/8 for inactive bouts (males A and B, respectively). For the female (C), only 10 of 19 active bouts were

Table 3. Number, percent of fixes, and number of bouts collected on 3 wild red deer fitted with a GPS collar (a fix every 10 min) over 24 hr in April 2000 in the Parc National des Cévennes, France. Active and inactive fixes are shown (excluding the uninformative medium class).

	Male A			Male B			Female C		
	n[a]	%	*N*[b]	*n*[a]	%	*N*[b]	*n*[a]	%	*N*[b]
Total	145	(100%)	[22]	145	(100%)	[16]	145	(100%)	[38]
Active fix	65	(45%)	[11]	72	(50%)	[8]	58	(40%)	[19]
Inactive fix	73	(50%)	[11]	67	(45%)	[8]	74	(51%)	[19]
High-precision fixes[c]	99	(68%)	[19]	106	(73%)	[15]	95	(65%)	[23]
Active fix	28	(28%)	[10]	39	(37%)	[8]	27	(28%)	[10]
Inactive fix	43	(43%)	[9]	42	(40%)	[7]	48	(50%)	[13]
Extrapolated inactive[d]	25	(25%)		19	(18%)		13	(14%)	

[a] Number of locations.
[b] Number of bouts.
[c] 3D locations with Dilution of Precision <10.
[d] 2D locations included in inactive bouts comprising >1 highly accurate 3D location.

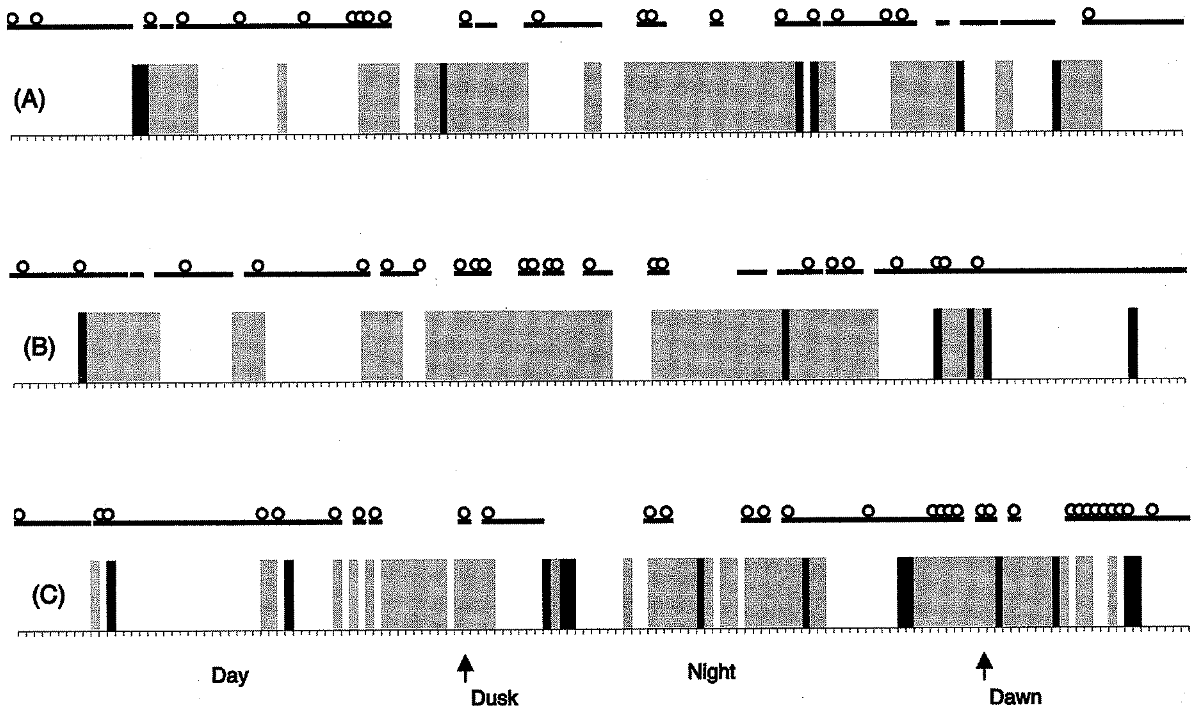


Figure 1. Temporal distribution of activity (histogram), high-precision fixes (line), and a subsample of fixes in which environmental parameters were recorded (circles) for three wild red deer fitted with GPS collars (one fix every 10 min) during a 24-hr cycle in April 2000 in the Parc National des Cévennes, France. Gray bars show active bouts, white are inactive, and black are medium-activity classes for 2 males (A and B) and 1 female (C). Arrows represent sunset and sunrise.

sampled with high precision fixes and only 13/19 for inactive ones. The female had a greater number of activity bouts (38) than the males (22 and 16, respectively) with a shorter mean duration (Figure 1). When pooling the 3 animals, 50% of 10-min bouts were sampled by at least one highly precise location, 70% for the 20-min bouts, 80% for those lasting between 30 and 60 min, and 100% of the longer bouts. The probability of obtaining a highly accurate location during a given bout increased with bout duration.

Environmental characteristics of the subsample of activity locations

The variability of the environmental parameters was resumed on the first 2 axes of a PCA analysis (explaining respectively 38.3% and 20.3% of total inertia). The first axis opposed V20, V140, and GRASS to CONIF and the second one SHRUB to DECIDU. Partitioning of inertia between animals was highly significant ($P=0.01$, permutation test) but explained only 5% of the total inertia, the remaining 95% being within-animal variation. Partitioning between activity-period combinations composed 8.31% of the total inertia and was highly significant ($P=0.002$), the remaining 91.7% being variation within activity-period combination. Partitioning based on activity-period combination was more pronounced than partitioning based on animal. Moreover, the 6 measured environmental variables allowed discriminating significant variation in locations used between animal and between activity periods. As an example, the between-classes PCA produced a first axis opposing coniferous to grasses and V140, which separated locations recorded during day (more coniferous) from those recorded at night (more grasses and visibility).

Discussion

Activity classification

The individual-based relative method provided a valid classification of the collar sensor activity value distinguishing most active and inactive locations during a 24-hr cycle. Total percentage of correct classification ranged from 79% (15 min) to 88% (5 min) and was high for inactive behaviors (82–97%). Percentage of correct classification appeared to depend slightly on the time interval between fixes, especially for active values. However, the lower percentage of correct active classification obtained from the 5- and 15-min time intervals (vs. 10 min) also could have been due to the different periods of the 24-hr cycle where the animals were observed. For the 5- and 15-min time intervals, animals were observed only during morning and midafternoon, when they were mainly inactive, whereas for the 10-min intervals animals were continuously observed from dusk to dawn and presented a greater number of active locations. The lower percentage of correct active classifications obtained from the 5- and 15-min time intervals (vs. 10 min) also could be related to different periods of the year (April vs. October) and to individual animals involved. The correspondence between observed and collar-sensor-derived activity values could be improved with a more balanced data set between active and inactive behaviors and between seasons. This individual-based method avoided observational calibration for each tracked animal and was not affected by the potential variation in collar tightening among seasons (neck size) and animals (Moen et al. 1996*a*).

Sampling of wild animal activity locations

Assuming that a 5-min sampling interval gave an exact picture of successive activity bouts, we demonstrated that a 10-min interval could induce a decrease in the accuracy of identifying "active" periods (more medium classes) and therefore could induce a bias in the sampling of activity if the shortest bouts were unequally distributed among active and inactive behaviors (e.g., if most of the active bouts were short).

Spatial sampling could induce an additional loss of information if it was unbalanced between active and inactive behavior and between short versus longer activity bouts (if habitats used were not similar for short and longer bouts). In this red deer data set, the highly precise fixes corresponding to active bouts were slightly undersampled (41%) and the inactive ones oversampled (58%) compared to the entire activity data set (47% active, 53% inactive excluding the medium cases). This trend increased if we decided to add the extrapolated inactive fixes (e.g., the animals did not move): 63% inactive versus 37% active. Moreover, the probability of sampling bouts with a precise location increased with bout duration; thus, short bouts were likely to be spatially undersampled. Therefore, the results must be discussed knowing these quantifiable spatial sampling biases. The above information could help the researcher to choose the best location interval (trade-off between collar lifetime and level of spatio-temporal sampling) relative to the biological questions investigated.

Our results apply to red deer behavior, but a similar approach could be applied to other animals in accordance with their daily activity patterns. For animals with more distinctive and longer activity bouts, the bias due to the loss of shortest bouts should decrease and the time interval between fixes could be longer. For smaller animals, activity time increases with decreasing body size (Mysterud 1998, Perez-Barberia and Gordon 1999), leading to more fragmented activity patterns with an increased number of shorter bouts per day (e.g., for ruminants, Cederlund 1989, Hoffman 1989, and Jeppesen 1989). Therefore, it would be appropriate to choose a shorter sampling interval if recording of all bouts was required, especially during summer when activity bouts are shorter. However, this choice would result in quicker attainment of the collar memory capacity. General characteristics of the animals' range also must be considered because the percentage of highly accurate locations is influenced by obstruction caused by tall trees or by topography (Moen et al. 1996*b*, Edenius 1997, Rempel and Rodgers 1997, Janeau et al. 1998, Dussault et al. 1999). If studied animals inhabit an open landscape, researchers should obtain more 3D locations and would be able to choose a longer fix interval if large animals were studied.

Environmental characteristics

The recorded environmental parameters allowed us to detect variations between activity sites as well as between individuals. Because each animal used several habitat types, the variation for environmental parameters was greater within than between animals, and it was the same for variation within activity-period combinations. These results demonstrate the possibility of relating environmental parameters on the site used by wild red deer to behavior (active or inactive) and period of the day.

Relocation in the field and description of the environment at each location is time consuming (from 5 to 30 min to relocate and describe one location). However, the main inconvenience is the financial investment required to acquire GPS technology. This approach can be used to obtain small-scale information on the environment used by an individual animal, and a wide range of environmental parameters can be recorded, depending on the researcher's aim.

Management implications

Depending on the research questions, our approach could be useful to test scale-dependent processes in habitat selection (see, for example, Mysterud et al. 1999a, *b*) because a very small spatio-temporal scale can be achieved. For this purpose, unused habitat must be described in the same way to assess selection (use relative to available). This approach also could give a consequent amount of useful data in other fields of theoretical ecology of wild animals. For example, precise knowledge of the animal's movements and physical environment encountered, like slope and climatic conditions, allow estimations to be made about energy costs according to season and food-resource availability. It also would improve the understanding of the limiting factors for wild animals year round (e.g., Parker et al. 1999 for black-tailed deer [*Odocoileus hemionus*]). The applications to wildlife management also are considerable to provide a habitat database to understand population dynamics. In a context of increased deer damage to forests in Europe, another application could be to construct spatially explicit predictive models of damage based on characteristics of sites used for each activity by animals.

Acknowledgments. We thank the INRA and Office National des Forêts for financial support. We acknowledge the Parc National des Cévennes and the INRA of Clermont-Ferrand for technical support. We thank J. M. Angibault, N. Cebe, D. Picot, N. Hewison-Cransac, M. Verdier, F. Anglard, C. Mallet, and P. C. Renaud for assistance in the field. We thank N. Morellet, M. Hewison, S. Aulagnier, and F. Spitz for their help on the statistical analysis and for their comments on the manuscript. We acknowledge P. Winterton for checking the English language. We thank J. M. Gaillard, M. Chamberlain, C. Dussault, and an anonymous referee for their comments. Capture methods were approved by the French Ministry of Environment, and 2 authors of this paper (G. J. and D. P.) were entitled by the French Ministry of Agriculture to experiment on free-living mammals (certificates no. 7382 and 7060).

Literature cited

Adrados, C., I. Girard, J.-P. Gendner, and G. Janeau. 2002. GPS location accuracy improvement due to selective availability removal. C. R. Biologies 325:1-6.

Bon, R., J. Joachim, and M. L. Maublanc. 1995. Do lambs affect feeding habitat use by lactating female mouflons in spring in areas free of predators? Journal of Zoology (London) 235: 43-51.

Carranza, J., and J. Valencia. 1999. Red deer females collect on male clumps at mating areas. Behavioural Ecology 10: 525-532.

Cederlund, G. 1989. Activity patterns in moose and roe deer in a north boreal forest. Holarctic Ecology 12:39-45.

Collins, W., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. Journal of Wildlife Management 47:646-663.

Conradt, L. 1998. Could asynchrony in activity between the sexes cause intersexual segregation in ruminants? Proceeding of the Royal Society of London Series B 265: 1359-1363.

Daget, P., and J. Poissonnet. 1971. Une méthode d'analyse phytologique des prairies. Critères d'application. Annales d'Agronomie 22:5-41.

Dolédec, S., and D. Chessel. 1991. Recent developments in linear ordination methods for environmental sciences. Advances in Ecology 1:133-155.

Dussault, C., R. Courtois, J.-P. Ouellet, and J. Huot. 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. Wildlife Society Bulletin 27: 965-972.

Dussault, C., R. Courtois, J.-P. Ouellet, and J. Huot. 2001. Influence of satellite geometry and differential correction on GPS location accuracy. Wildlife Society Bulletin 29:171-179.

Edenius, L. 1997. Field test of a GPS location system for moose *Alces alces* under Scandinavian boreal conditions. Wildlife Biology 3:39-43.

Hoffman, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443-457.

Janeau, G., J. M. Angibault, B. Cargnelutti, J. Joachim, D. Pépin, and F. Spitz. 1998. Le Global Positioning System (GPS) et son utilisation (en mode différentiel) chez les grands mammifères: principes, précision, limites, contraintes et perspectives. Arvicola Actes Amiens 97:19-24.

Jeppesen, J. L. 1989. Activity patterns of free-ranging roe deer (*Capreolus capreolus*) at Kalo. Danish Review of Game Biology 13:32.

Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management 64: 685-697.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Lotek Engineering Inc. 1997. GPS collar user's manual. Newmarket, Canada.

Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London, United Kingdom.

McClain, B. J., and W. F. Porter. 2000. Using satellite imagery to assess large-scale habitat characteristics of Adirondack Park, New York, USA. Environmental Management 26:553-561.

Merrill, E. 1991. Thermal constraints on use of cover types and activity time of elk. Applied Animal Behaviour Science 29: 251-267.

Moen, R. A., J. Pastor, and Y. Cohen. 1996*a*. Interpreting behavior from activity counters in GPS collars on moose. Alces 32: 101-108.

MOEN, R. A., J. PASTOR, Y. COHEN, AND C. C. SCHWARTZ. 1996*b*. The effects of moose movement and habitat use on GPS collar performance. Wildlife Monograph 122:1–57.

MYSTERUD, A. 1998. The relative roles of body size and feeding type on activity time of temperate ruminants. Oecologia 113:442–446.

MYSTERUD, A. K. L, R. A. IMS, AND E. OSTBYE. 1999*a*. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Canadian Journal of Zoology 77: 776–783.

MYSTERUD, A., L. B. LIAN, AND D. O. HJERMANN. 1999*b*. Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. Canadian Journal of Zoology 77: 1486–1493.

MYSTERUD, A., AND E. OSTBYE. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin 27:385–394.

OBBARD, M. E., B. A. POND, AND A. PERERA. 1998. Preliminary evaluation of GPS collars for analysis of habitat use and activity patterns of black bears. Ursus 10:209–217.

PARKER, K. L., M. P. GILLINGHAM, T. A. HANLEY, AND C. T. ROBBINS. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural environment. Wildlife Monograph 143:1–48.

PEREZ-BARBERIA, F. J., AND I. J. GORDON. 1999. The relative roles of phylogeny, body size and feeding style on the activity time of temperate ruminants: a reanalysis. Oecologia 120:193–197.

REMPEL, R. S., AND A. R. RODGERS. 1997. Effects of differential correction on accuracy of a GPS animal location system. Journal of Wildlife Management 61:543–551.

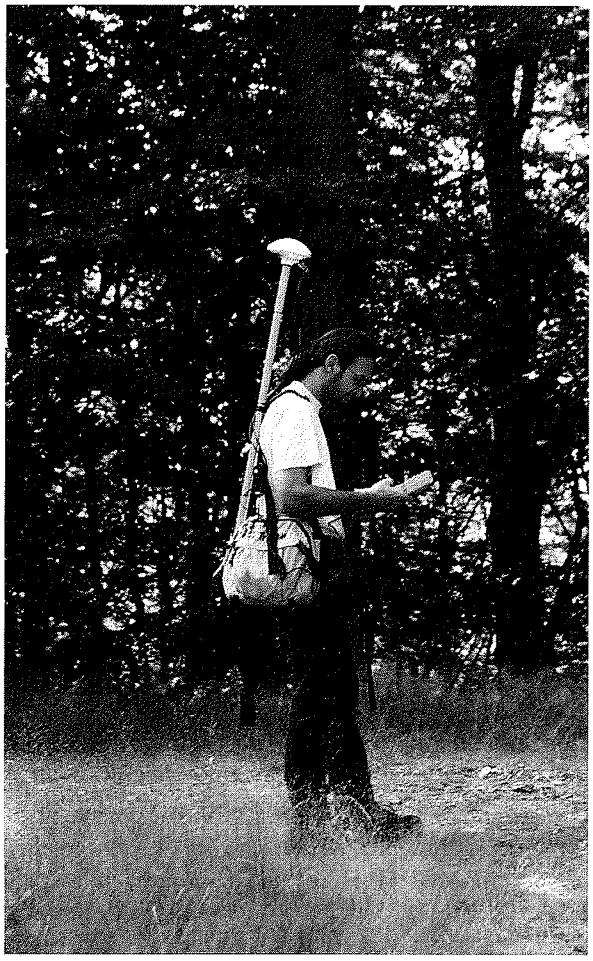
RODGERS, A. R., AND P. ANSON. 1994. Animal-borne GPS: tracking the habitat. GPS World 5:20–32.

STAINES, B. W. 1977. Factors affecting the seasonal distribution of red deer (*Cervus elaphus*) in Glen Dye, north-east Scotland. Annals of Applied Biology 87:495–512.

STROMEYER, D., J. M. PEEK, AND T. BOWLIN. 1999. Wapiti bed sites in Idaho sagebrush steppe. Wildlife Society Bulletin 27: 547–551.

THIOULOUSE J., S. DOLÉDEC, D. CHESSEL, AND J. M. OLIVIER. 1995. ADE software: multivariate analysis and graphical display of environmental data. Pages 57–62 *in* G. Guariso and A. Rizzoli, editors. Software per l'ambiente, Bologna, Italy.

TIXIER, H., P. DUNCAN, J. SCEHOVIC, A. YANI, M. GLEIZES, AND M. LILA. 1997. Food selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional value of their diets. Journal of Zoology (London) 242:229–245.



Christophe Adrados (photo) received his B.S. in biology and his M.S. in population biology and ecosystems from Université François Rabelais in Tours, France in 1996 and 1998, respectively. He obtained his Ph.D. in eco-ethology from the Université P. Sabatier in Toulouse in 2002. His areas of interest are wildlife ecology and tracking, GPS, and GIS. ***Hélène Verheyden-Tixier*** is a research scientist at the Institut de Recherche sur les Grands Mammifères (IRGM), Institut National de la Recherche Agronomique (INRA) in Toulouse, France. She obtained her Ph.D. in biology, focused on roe deer feeding behavior, from Université de Paris XIII in 1996. Her research interests are diet choice, feeding-site selection, and habitat use in ungulates. ***Bruno Cargnelutti*** is an engineer-assistant at IRGM-INRA in Toulouse. He obtained his B.S. in management-applied computing from the Université P. Sabatier in Toulouse in 1992. His work includes database management and wildlife tracking. ***Dominique Pépin*** is a research director at IRGM-INRA in Toulouse. A wildlife biologist since 1970, he has worked on small and large mammals. ***Georges Janeau*** is a research engineer at IRGM-INRA in Toulouse. He obtained his Ph.D. in eco-ethology from the Université P. Sabatier in Toulouse. He has been a specialist in wildlife spatio-temporal behavior and biotelemetry for more than 30 years and has applied GPS technology to wildlife research since 1997.

Associate editor: *Chamberlain*