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Red deer telemetry: Dependency of the position acquisition rate and accuracy of GPS collars on the structure of a temperate forest dominated by European beech and Norway spruce

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Abstract

Deer monitoring is crucial for wildlife management. A current method for monitoring is GPS telemetry, but the performance of GPS collars at each specific site needs to be tested. Here we determined the position acquisition rate (PAR) and accuracy of static GPS-GSM collars on ten different plots in the temperate forests dominated by European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) in the Bavarian Forest National Park; the four deciduous plots were tested both with and without foliation. Forest type and structure were considered key impact factors on the collar performance. We also tested the collars' performance mounted on 20 free-ranging deers. The static GPS test revealed a high overall PAR (96.7%) and accuracy (10 m). With regard to forest type, we found the highest PAR (98.8%) and accuracy (5 m) within mixed forests and the lowest PAR (91%) and accuracy (13.8 m) in coniferous forests. With regard to forest structure, we found the highest PAR in mid-aged deciduous stands without foliation (99.1%) and the lowest PAR in young coniferous stands (77.5%), and the highest accuracy (4.1 m) in dead-tree stands and the lowest accuracy (16.3 m) in mid-aged coniferous stands. The PAR of the free-ranging deer was lower than the PARs of the static GPS test, and we observed seasonal differences (January: 48.4%; August: 93.8%), probably owing to animal behaviour and different habitat selection. We attempted to determine GPS quality thresholds that identify imprecise fixings, but only identified a threshold (dilution of precision 12.4) that improved the median accuracy of the data. The results and values of this study will provide variables for subsequent habitat selection analyses of red deer.

Key words: GPS telemetry, GPS accuracy, GPS efficiency, GPS position acquisition rate, red deer, *Cervus elaphus*

Introduction

Protected areas, such as national parks, must fulfil contrasting functions. They provide recreation, tourism and environmental education, yet must also be sanctuaries for wild animals. These divergent functions could lead to conflicts. Wildlife management therefore has the task of making both sets of functions possible. The management guidelines chosen are based on the results of monitoring and research.

In the Bavarian Forest National Park, red deer (*Cervus elaphus*) is of special interest because it is both an attractive flagship species for tourism but also the largest herbivore species that could cause considerable browsing damages in adjacent commercial forests. The living conditions of the red deer within the national park area changed dramatically after proliferation of the European spruce bark beetle (*Ips typographus*) in the 1990s, the suspension of hunting in wide areas, increased tourism, and the reintroduction of Eurasian lynx (*Lynx lynx*) as a predator of young and female red deer. To determine how red deer cope with the changed habitat conditions and to implement management strategies, a study of red deer spatio-temporal behaviour is therefore crucial. One method used to survey a wide-ranging and elusive species like the red deer is telemetry with the Global Positioning System (GPS), which has been applied in the Bavarian Forest National Park since 2002.

Since the early 1990s, GPS telemetry has become a common technique in wildlife research owing to its predominant advantages. GPS provides a higher resolution in time and space compared to very high frequency (VHF) telemetry. The accuracy of GPS lies between that of homing-in, i.e., stalking a collared animal with the aid of VHF telemetry until visual contact, and most VHF positions (Rempel et al. 1995, Hulbert & French 2001). Since GPS functions autonomously, it reduces labour costs markedly, does not cause observer disturbances, and allows continuous data collection that is not disrupted by legal constraints, e.g., trespassing private land or labour time for field work at night. Owing to battery improvements, it is possible to record the location of the subject for long periods and to reduce the fixing intervals for small-scale data analysis, e.g., the high-resolution trajectory analysis in 5-min intervals. UHF or VHF download devices allow the observer to gain the collected data contemporarily and not only when the studied subject is recaptured.

The Global System for Mobile Communication (GSM) device used with GPS telemetry allows the two-way communication between the GPS device and the observer. Receiving positional data directly from the collar offers real-time tracking of the animal, and by sending messages containing new GPS schedules, the observer is able to change the study design as needed, or to react on unexpected events of interest, e.g., drive hunts or storms.

Most GPS receivers determine and store quality criteria for each particular calculated GPS position. Common criteria are the dilution of precision (DOP), i.e. a value evaluating the geometry of the used satellites in the sky, and whether the position was calculated with only three (2D) or more than three satellites (3D). The collars used in our study (VECTRONIC Aerospace, www.vectronic-aerospace.com) provide an additional piece of validation information. These three quality criteria are sent via GSM, which is important because not all deployed collars can always be retrieved from the animal subjects. If the collars are retrieved, additional quality information, such as the exact number of satellites used and which satellites were used for each particular GPS position, can be downloaded from the collars. All these quality criteria should serve as information about the precision of the GPS position. Therefore, previous studies have attempted to apply thresholds based on these criteria to identify imprecise GPS positions (e.g., Moen et al. 1997, Hulbert & French 2001, D'Eon et al. 2002, D'Eon & Delparte 2005, Graves & Waller 2006, Cargnelutti et al. 2007)

Although the reliability and accuracy of GPS receivers has greatly improved over the past years, the position acquisition rates (PAR) and accuracy of the employed GPS collars in each research area still need to be tested (Rempel et al. 1995, Moen et al. 1997, Hulbert & French 2001, Adrados et al. 2003, Johnson & Gillingham 2008). Factors that influence the PAR and accuracy are, e.g., fixing intervals, topography, available sky and canopy cover (Rempel et al. 1995, Moen et al. 1997, Cain III et al. 2005, Hansen & Riggs 2008, Sager-Fradkin et al. 2007).

Here we studied the PAR and accuracy of GPS-GSM collars on red deer in the Bavarian Forest National Park. We conducted a static GPS test to evaluate the influence of the forest structure on the PAR of the collars and the accuracy of the successful fixings, and we also analysed the PAR of 20 collared free-ranging red deer. We attempted to determine a threshold based on GPS quality criteria, which would exclude imprecise fixings from further analysis. The determined PAR and accuracy of the employed GPS-GSM collars are essential for further analyses of habitat selection or movement analysis of red deer.

Materials and methods

Study area

The Bavarian Forest National Park is situated in south-eastern Germany (49°3′19″N, 13°12′9″E) at the border to the Czech Republic. This oldest German national park (244 km²) and the adjacent Czech Šumava National Park (685 km²) together form the Greater Bohemian Forest Ecosystem and comprise the largest strictly protected forested area in Central Europe. The sub-mountainous area of the Bavarian Forest National Park gently rises without steep slopes from 650 m a.s.l. in the west to 1450 m a.s.l. in the east. The slopes are exposed predominately to the west. On a larger scale, the Bavarian Forest lies in the temperate zone and is characterized by Atlantic and continental influences. The long-term mean annual temperature varies between 5.1°C in the valley sites, 5.8°C on hillsides and 3.8°C in the upper montane zones; the mean annual precipitation varies between 1200 and 1800 mm, depending on the altitude (Bässler et al. 2008), and its pronounced amount occurs as snow. The snow cover lasts for 7–8 months at the higher elevations and for 5–6 months in the valleys.

Ninety-eight percent of the national park area is covered by forest, which is graduated into three major forest communities: (1) above 1100 m altitude, upper montane spruce forests with Norway spruce (*Picea abies* L.) and some mountain ash (*Sorbus aucuparia* L.) (*Calamagrostio villosae-Piceetum barbilophozietosum*: 16% of the area); (2) between 600 and 1100 m altitude, lower mixed montane forests with Norway spruce, white fir (*Abies alba* Mill.), European beech (*Fagus sylvatica* L.), and sycamore maple (*Acer pseudoplatanus* L.) (*Luzulo-Fagion*, *Asperulo Fagetum*: 68% of the area); and (3) in wet depressions, often associated with cold air pockets in the valley bottoms, mire spruce forests with Norway spruce, mountain ash, and birches (*Betula pendula* Roth., *Betula pubescens* Ehrh.) (*Calamagrostio villosae-Piceetum barbilophozietosum*: 16% of the area; Heurich & Neufanger 2005).

Since the late 1990s, a massive proliferation of spruce bark beetle (*Ips typographus*) dramatically changed the forest structure. Virtually all mature trees of the upper montane Norway spruce forest stands died (ca. 6500 ha at the end of 2009; Bavarian Forest National Park, unpubl. data). Following the national park philosophy, no bark beetle management was undertaken, and the dead wood was left within the area. The increased light from the opened canopy and the nutrients from the dead-wood decay allowed natural regeneration to begin. An area-wide regeneration of Norway spruce mixed with mountain ash, European beech and sycamore maple created a habitat mosaic with dead-wood areas and young forest stands.

The Bavarian Forest National Park was mapped in 2002. The data, which describe the forest types and development phases, form the Bavarian Forest Inventory. The forest is divided into three "forest types": deciduous (stands with ≥80% deciduous trees), coniferous (stands with ≥80% coniferous trees) and mixed forest (stands containing <80% deciduous and <80% coniferous trees). The age of the stand and its density are coded in the category "forest development phase". Within this category, the diameter at breast height of the first tree layer and the number of tree layers are recorded (Table 1).

Table 1. Definition of forest development phases in the Bavarian Forest National Park.

Forest development phase	Diameter at breast height (cm)	Number of tree layers
Initial	≤7	1
Pole	≤35	1
Late pole	>35	1
Regeneration	>35	2 (with regeneration)
Optimal	>35	≥3
Mortality	Dead-wood areas	

Static GPS test

We choose ten plots for the static GPS test (see Results for a list of the different plots and forest types). The absolute positional accuracy of the chosen plots was achieved in three steps: (1) On each plot, a 10×10 m grid was measured with tacheometry. (2) At the outermost parts of each plot, at least two points were measured twice with differential GPS. If the plot was located in dense forest, two points were measured in the next clearing, and these points were connected to the plot via tacheometry. (3) With the help of a 2D+H-transformation, the positions were transformed to Gauß-Krüger-coordinates using a transformation parameter derived at the site. With subsequent error checking, a residual error with less than 5 cm was found (Heurich 2006). The four plots in the deciduous forest stands were tested twice, once with leaves during summer 2005 and once without leaves during spring 2006 and 2007.

For the static GPS test, we deployed a GPS-GSM deer collar (series 800; VECTRONIC Aerospace, Berlin, Germany) on a tripod at the average height of a red deer acromion, i.e., at 1.2 m, exactly above one of the poles that marked each plot. The collars were programmed to make fixings every 60 min (summer 2005) or every 20 min (spring 2006 and 2007). The collars were left on each plot for at least 24 h. The collars were deployed at three different positions on each plot. The collars functioned with 12-channel GPS receivers; for each fixing, the receivers were limited to 180 s of searching for available satellites and calculating a position. If a fixing was not obtained, the receiver was switched off to standby power until the next scheduled fix attempt. Fixings with impossible coordinates were identified. Such fixings had coordinates but were located far from the study area when projected in the Geographic Information System. These fixings arose from a malfunction and should occur randomly within the data set. We visually identified and eliminated these fixings from the raw data using ESRI®ArcGIS™ 9.2 (©1999–2006 ESRI Inc.).

We determined the position acquisition rate (PAR), i.e., the percentage of successful fixings. We calculated the Euclidean distance between the fixings and the actual collar position, and determined the deviation related to the different forest types, forest development phases and foliation. The data were normally distributed (Kolmogorov-Smirnov test; $D = 0.9995$, $p = 0.2707$) but skewed to the left. We decided to add the quartiles (25%, 50%, 75%) to the text. Analysis of variance (ANOVA) and Tukey's follow-up test (R Development Core Team 2007) were used to identify significant differences in the deviations between the positions of the known plots and the GPS positions in all four forest types.

GPS test of free-ranging red deer

We analysed the GPS position data gathered from 20 red deer (4 females, 16 males) wearing GPS-GSM collars between 2002 and 2006. Fixings were taken at 2-h intervals, and the monthly PAR of each collar was calculated. As the collars were developed over the years, the animals wore GPS-GSM collars of different series (300 to 2300). The collars of all series

Table 2. Definition of quality groups for GPS fixings taken by VECTRONIC Aerospace collars.

Quality group	Information sent via GSM	GPS quality	Fixes
1	Navigation	2D	Fixes taken with 3 satellites
2	Navigation	3D	Fixes taken with ≥4 satellites
3	Validation	Validated	Fixes taken with ≥5 satellites and DOP≤10
4	Validation	Not validated	Fixes taken with <5 satellites and/or DOP>10
5	Navigation and DOP	3D (4)	Fixes taken with ≥4 satellites and DOP≤4
6	Navigation and DOP	3D (8)	Fixes taken with ≥4 satellites and DOP≤8
7	Navigation and DOP	3D (12)	Fixes taken with ≥4 satellites and DOP≤12

worked basically with the same technical specifications (12-channel GPS, 180 s calculation time per fixing), but were equipped with different software versions and GPS components.

GPS quality information as a tool to identify imprecise fixings

We defined the different GPS qualities using information provided by the internal collar software and sent via GSM. The data contain the timestamp (UTM date; UTM time), the estimated UTM coordinates, the elevation a.s.l., and three quality criteria: navigation (2D or 3D), DOP, and validation (Val/not Val). Validation is defined by VECTRONIC Aerospace (see Table 2) and automatically calculated, and added by the internal software to each fixing. According to this available quality information, we sorted the fixings into seven quality groups (Table 2). For each group, we determined the PAR and median deviation.

To determine a threshold to improve the GPS accuracy, we calculated a conditional inference tree (Hothorn et al. 2006) for the deviation. The input variables were the GPS quality information DOP, navigation and validation. Tree size was restricted to one level. We applied the threshold to the data and analysed the two generated data sets with a Pearson's chi-squared test for count data (R Development Core Team 2007) for their rectangular distribution within the four forest types.

Data were statistically analysed using R 2.6.1 (R Development Core Team 2007).

Results

Static GPS test

During the entire static GPS test, we obtained 4443 fixings, of which 4296 were successful, yielding a high overall PAR of 96.7%. We calculated an overall median deviation of 10 m, which indicates a high accuracy. The deviation ranged from 0.0 to 376.7 m. With regard to the forest types, the best PAR (98.8%) was obtained in deciduous forest stands without foliation and in mixed stands with foliation; the best accuracy (5.0 m) was found in the latter (Table 3). The accuracy of all forest types highly significantly differed ($p<0.001$; ANOVA with Tukey's follow-up), except for that of deciduous forest with foliation and coniferous forest, which only just significantly differed ($p<0.05$; ANOVA with Tukey's follow-up).

With regard to the forest development phases, the best PAR (99.1%) was found within late pole phase deciduous forest stands without foliation and the poorest PAR (77.5%) was found in pole phase coniferous forest stands (Table 4). The absolute deviation ranged between 0.0 m (deciduous pole phase with foliation) and 376.7 m (mortality phase). The median deviation was smallest (4.1 m) in the mortality stands and largest (16.3 m) in the late pole coniferous stands.

Table 3. Position acquisition rate (PAR) and deviation of deer GPS-GSM-collars (VECTRONIC Aerospace) analysed according to the different forest types (a = deciduous forest without foliation; b = deciduous forest with foliation; c = mixed forest with foliation; d = coniferous forest) in the Bavarian Forest National Park.

Forest type	N	PAR	Deviation (m)					
			Mean ±SD	Min.	25%	Median	75%	Max.
All positions	4443	96.7%	16.2±25.5	0.0	5.4	10.0	17.9	376.7
a	908	98.8%	14.6±20.5	0.4	6.3	10.2	17.5	364.6
b	1643	97.2%	17.5±19.6	0.0	7.5	12.5	19.7	222.2
c	1025	98.8%	12.1±33.3	0.1	2.9	5.0	8.9	376.7
d	867	91.0%	20.7±28.7	0.4	7.5	13.8	23.4	343.2

Table 4. Position acquisition rate (PAR) and deviation of deer GPS-GSM-collars (VECTRONIC Aerospace) analysed with regard to the different forest development phases in the Bavarian Forest National Park. Forest type: a = deciduous forest without foliation, b = deciduous forest with foliation, c = mixed forest with foliation, d = coniferous forest; N = number of possible fixings; Q = quartile.

Forest development phase	Forest type	N	PAR	Deviation (m)					
				Mean ±SD	Min.	25% Q	Median	75% Q	Max.
Initial	c	317	96.5%	11.6±19.1	0.4	4.7	7.5	11.8	239.2
Pole	b	416	98.8%	15.2±19.8	0.0	5.9	9.5	16.7	211.4
	a	289	99.0%	12.1±12.0	1.0	5.8	8.6	14.3	106.1
	d	191	77.5%	22.5±36.7	1.5	7.2	13.2	23.3	295.9
Late pole	b	530	96.6%	17.2±19.7	0.5	6.7	11.4	19.1	184.5
	a	218	99.1%	14.3±11.4	0.7	6.7	11.8	18.9	105.7
	d	343	95.0%	23.5±31.2	1.0	8.7	16.3	25.0	343.2
Regeneration	b	291	94.9%	20.3±21.7	1.6	9.4	14.6	23.1	222.2
	a	199	98.5%	15.3±12.3	0.4	7.3	12.5	19.4	74.9
	d	218	96.8%	17.1±16.1	0.5	7.6	12.7	21.0	151.4
Optimal	b	406	98.0%	18.3±17.2	0.9	9.9	14.8	20.0	186.5
	a	202	98.5%	17.8±37.2	0.8	6.3	9.8	17.2	364.6
	d	115	90.4%	17.1±26.2	0.4	6.5	9.1	19.7	236.8
Mortality	c	708	78.9%	12.3±37.8	0.1	2.3	4.1	7.0	376.7

GPS test of free-ranging red deer

During the 5 years of red deer GPS observation, 71611 GPS fixings would have been possible. Of these, 52116 were successful, which resulted in an overall PAR of 72.8%. The monthly medians of the PAR ranged from 48.4% in January to 93.8% in August (Fig. 1). In contrast to the results of the static GPS test, the PAR was higher during summer than during winter. Between November and April, the variance of the PAR was very large, whereas in July and August, i.e. in summer, the variance of the PAR was very small.

GPS quality information as a tool to identify imprecise fixings

In an analysis of the GPS quality groups, the median deviation ranged between 16.5 m (2D) and 7.4 m [3D (4)] and therefore decreased with increasing quality of the fixings (Table 5). But even the best quality group [3D (4)] contained the most imprecise fixing (376.7 m).

The conditional inference tree of the parameters navigation, validation and DOP revealed that the DOP value of 12.4 was a breaking point that divided the data at a significance level of $p<0.001$ (Fig. 2). Applied to our static GPS test data, the overall median deviation would decrease from 10.0 m for all data to 9.8 m if only fixings with a DOP<12.4 were considered, and would cause a data loss of ca. 3% (127 fixings). An analysis of these groups with a Pearson's chi-squared test for count data (R Development Core Team 2007) with regard to forest types revealed that the data were not distributed rectangularly (χ^2 = 41.5304, df = 3,

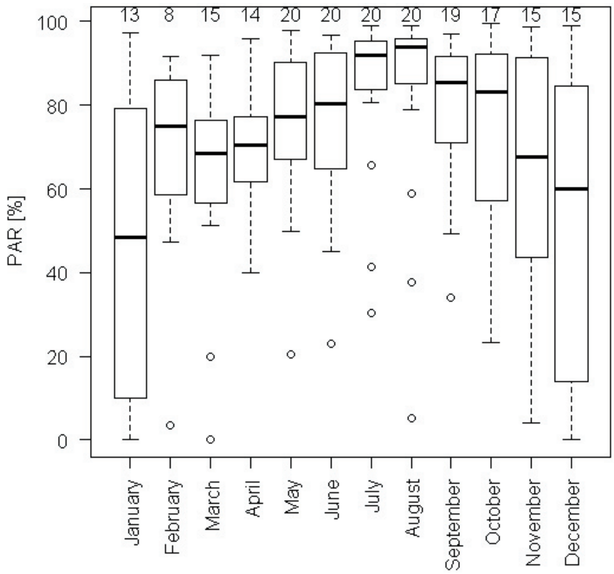

Fig. 1. Position acquisition rate (PAR in %) of deer GPS-GSM collars (series 300, 400, 600, 800 and 2300; VECTRONIC Aerospace) worn by 20 red deer in the Bavarian Forest National Park between 2002 and 2006. The number of observed animals each month is given above each bar.

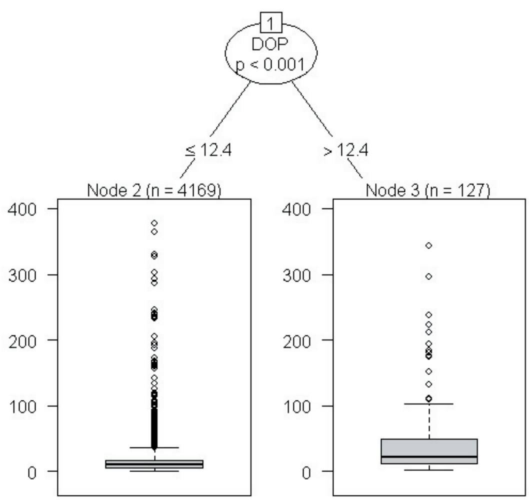

Fig. 2. Conditional inference tree of the deviation of GPS fixings. The tree size was restricted to one level. The parameters given were dilution of precision (DOP), validation and navigation. The cut-point and p-value are given at the node, and the number of GPS fixings are given at each branch.

Table 5. Deviation of deer GPS-GSM collars (VECTRONIC Aerospace) with regard to the different GPS qualities tested in the Bavarian Forest National Park (all = all data; 2D = fixes taken with 3 satellites; 3D = fixes taken with ≥4 satellites; not Val = fixes taken with <5 satellites and/or a DOP>10; Val = fixes taken with ≥5 satellites and a DOP≤10; 3D(4) = fixes taken with ≥4 satellites and a DOP≤4; 3D(8) = fixes taken with ≥4 satellites and a DOP≤8; 3D(12) = fixes taken with ≥4 satellites and a DOP≤12; n = number of fixings).

GPS quality	n	% of n (all)	Deviation (m)					
			Mean±SD	Minimum	25%	Median	75%	Maximum
All	4296		16.2±25.5	0.0	5.4	10.0	17.9	376.7
2D	791	18.4	26.5±33.9	0.0	8.6	16.5	30.2	343.2
3D	3505	81.6	13.9±22.6	0.0	5.0	9.1	16.0	376.7
not Val	1368	31.8	23.7±31.1	0.0	8.3	15.1	26.0	343.2
Val	2928	68.2	12.7±21.6	0.0	4.4	8.4	14.7	376.7
3D(4)	1772	41.2	12.2±23.4	0.1	4.0	7.4	13.6	376.7
3D(8)	3167	73.7	13.5±22.9	0.0	4.7	8. 9	15.3	376.7
3D(12)	3412	79.4	13.6±22.4	0.0	4.9	9.0	15.7	376.7

$p<0.0001$). Within the data set, we found more fixings with DOP>12.4 in coniferous stands and fewer in the mixed stands than could have been expected by a rectangular distribution (Fig. 3).

Discussion

Static GPS test

Due to the gentle relief and a very homogenous western elevation in our research area, slope and exposition were regarded as secondary in their influence on GPS collar function. Canopy cover was identified as the crucial factor influencing the functioning of GPS collars as dense foliage shielded the GPS receiver from satellite signals, and accordingly all obstacles, such as leaves and trees, caused refraction of GPS signals and resulted in failed or inaccurate fixings. Attributes influencing the canopy cover are composition of deciduous and coniferous trees, age of the forest stands and vertical structure.

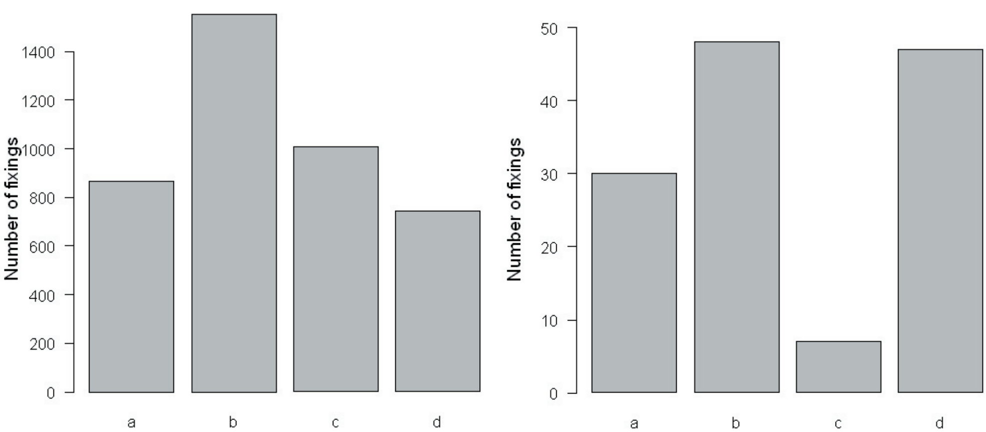

Fig. 3. Distribution of data with fixings taken with a DOP≤12.4 (left) or a DOP>2.4 (right). The results are plotted according to the forest types: a = deciduous forest without foliation; b = deciduous forest with foliation; c = mixed forest with foliation; d = coniferous forest.

In the static GPS test, the GPS fixings had a high PAR and accuracy. The median deviation of the static GPS test data (10 m) was lower than the mapping units of the geographical data available for the Bavarian Forest National Park, i.e., ca. 15 m for forest inventory data, a size recommended by Rempel & Rodgers (1997) and Hulbert & French (2001). The PAR differed little between "leave on" and "leave off" conditions. The fixings done without foliation were slightly more accurate than those done with foliation, which suggested that the canopy cover decreases accuracy, as confirmed by the significantly higher accuracy in deciduous stands without foliation than in deciduous stands with foliation. This is in line with findings from other studies, which have shown the influence of canopy cover on PAR (Rempel et al. 1995) and the accuracy of fixings (Moen et al. 1997, Cargnelutti et al. 2007, Sager Fradkin et al. 2007, Hansen & Riggs 2008). Canopy cover creates manifold obstacles between the satellites and the receiver, possibly shields some satellites, and probably causes multi-path effects that affect both the PAR and the accuracy of a GPS collar.

The static GPS test also revealed a relationship between forest characteristics and the PAR and accuracy of GPS fixings. The values found in the various forest development phases were more or less than expected: PAR and accuracy were better in more-open stands and poorer in young dense stands, especially in coniferous stands and stands with more than one tree layer. However, when the data were examined more closely, poor efficiency did not always correlate with poor accuracy. For example, within the mortality phase, the most accurate fixings but also the lowest PAR values were found. By contrast, the deciduous late pole phase (mature stands with one tree layer) without foliation had the best PAR but only a medium accuracy.

Our results from the static GPS test indicate that in future studies of red deer habitat use in the Bavarian Forest National Park, the influence of forest type and structure on GPS PAR and accuracy should be taken into account.

GPS test of free-ranging red deer

The PAR values obtained in the static GPS test were better than those obtained with free ranging collared animals. We did not verify the accuracy of the animals' GPS positions, but we assume that the accuracy of these data is also lower than that of the static GPS test data.

One factor influencing the PAR is the fixing interval, with shorter intervals leading to better PAR (Cain III et al. 2005). Our static GPS test data were collected with an interval of 20 or 60 min, and the collars worn by red deer collected data at an interval of 120 min. Sager-Fradkin et al. (2007) observed a similar discrepancy in PAR between their GPS test data and field data; however, they assumed that the discrepancy could not be explained only by different fixing intervals. Also other studies reported poorer PAR in the field data (Cargnelutti et al. 2007, Zweifel-Schielly & Suter 2007), and reasons for this have been identified to be, e.g., the animal body size (Graves & Waller 2006), activity (D'Eon & Delparte 2005, Moen et al. 2001, Schwartz et al. 2009, Mattisson et al. 2010), and behaviour (Zweifel-Schielly & Suter 2007, Bourgoin et al. 2009, Mattisson et al. 2010). Zweifel-Schielly & Suter (2007) also tested GPS collars, and collected data first from a static test and then from collars worn by free-ranging red deer. Their analysis considered habitat variables and animal activity level. The observed higher PAR during the night was caused by red deer using open areas for feeding during the night and resting in the forests during the day. However, the authors found no significant influence of habitat type on the PAR of the collars in static tests and therefore concluded that the different behaviour of the animals within the different habitat types (i.e., resting in the forests and feeding in open areas) and not the habitat itself downgraded the PAR from open to closed structures. Graves & Waller (2006) found that the height above ground of the receiver and the animal body size (neck circumference, girth and weight) influenced PAR: the PAR was lower closer to the ground, e.g., bedded animals, and the PAR decreased with increasing body size (but see SCHWARTZ et al. 2009). ADRADOS et al. (2003) have shown that fixings of moving red deer are more precise than fixings of resting red deer (see also BOWMAN et al. 2000, D'EON & DELPARTE 2005). However, animal movement can probably also negatively influence GPS collar performance. Walking or browsing animals pass obstacles, which could prevent or constrain the contact to satellites, thereby leading to no fixings or a reduced accuracy lower than that of a static GPS receiver. Static GPS tests are done under ideal circumstances – the collar is not moved and it is placed 1.2 m above the ground. Such circumstances are probably rare with collared animals. When red deer rest, the collar is close to the ground, and during their active phase, the deer are usually browsing or walking.

The results of our static GPS test revealed that owing to the absence of foliation, the PAR was slightly better than without. In contrast, the PAR of collared animals was worse during winter than in summer. This discrepancy could be caused by physical aspects of the receivers, e.g., snow cover or collar contortion, or by a combination of factors directly connected to the animals, e.g., behaviour or seasonal differences in habitat use. In the study area, the snow cover lasts normally from November until April, which matches the lower PAR during these months. During the static GPS test, there was no snow cover. Although we found no study on the influence of snow cover on GPS performance, it is well known that large water surfaces can increase multi-path effects, which are difficult to classify or even identify. The freshly fallen snow on branches, especially of coniferous trees, probably influences the permeability of satellite signals. The signals might not be shielded completely, but might be refracted and cushioned, which could constrain the GPS calculation. A negative influence of collar contortion, on the other hand, has been shown by D'EON & DELPARTE (2005) and GRAVES & WALLER (2006). The deployed deer collars are oval, with the most weight (battery) opposite to the GPS receiver. Contortion should therefore be a minor problem. But once distorted, possible especially during winter with the dense and long winter fur, the collar may remain long in the disadvantageous position.

FRAIR et al. (2004), ZWEIFEL-SCHIELLY & SUTER (2007), and BOURGOIN et al. (2009) also found seasonal differences within the PAR of GPS data gathered on animals, and SAGER-FRADKIN et al. (2007) found a prominent influence of animal activity, behaviour and microhabitat use on data losses. In studies of mouflon, BOURGOIN et al. (2009) identified a relationship between temperature and PAR: as the temperature increased, the PAR decreased. They explained this decrease in PAR by the changed habitat use of mouflons during hot summer days, on which the animals used shady areas with reduced available sky. In our study area and with red deer, the crucial season is winter, with six months of snow cover and snow heights up to 3 m at the higher elevations. In contrast, the summers are mild but not hot. Telemetry data indicate that red deer in the Bavarian Forest National Park seasonally migrate (unpublished data). The animals live at the higher elevations during summer (mortality and initial phase, both mixed forest stands) and descend to the lower elevations after the rut in October and latest with the first snow. There in the valleys, mire spruce forests are the dominating stands. Owing to the low temperatures in these areas, these stands are only little affected by the spruce bark beetle and are therefore still very dense. Red deers in the Bavarian Forest National Park are also less active during winter (unpublished data) and reduced activity probably results in longer resting periods. Therefore, it is possible that red deers in the Bavarian Forest National Park change their habitat use during winter and search for young dense spruce stands for long resting periods because such stands shield against cooling. And there, close to the tree trunk and shielded by the branches, the chances of calculating a GPS position are probably smaller.

The large variance in the PAR of the 20 collared animals during winter contrasts with the small variance during July and August and provides evidence for the large influence of the individual animal behaviour and habitat selection on GPS performance. These results confirm the conclusion of ADRADOS et al. (2003), and points toward the importance of the analysis of the habitat selection and movements of individual animals.

GPS quality information as a tool to identify imprecise fixings

GPS determines the position of a receiver by calculating the differences between the time when radio signals are sent by various satellites and the time when the signals are received by the receivers. The orbit of each satellite is also taken into account (ephemeris data). The accuracy of GPS fixings are determined primarily by the synchronization of the receiver and the satellite clock (RODGERS 2001), but to date no atomic clock, e.g., satellite clock, provides the "real" time. Furthermore, the signal has to pass the ionosphere and troposphere, which absorbs and distorts the signal. If the signal impacts physical obstacles (e.g., houses, trees), two things happen. First, the signal diffracts in another direction, causing so-called multi-path effects, and second, it passes the obstacles but becomes absorbed by water, i.e., becomes slower, regardless whether the water occurs as a surface or within a stem or foliage. When the GPS receiver receives the signals, it calculates its position under the assumption that nothing is absorbing or diffracting the signal. But the receivers "judge" this ideal situation by calculating the geometrical constellation of the satellites used, i.e. the DOP.

Although we found that an increasing quality of the fixings leads to a decreasing median deviation, it was not possible to exclude imprecise fixings. The analysis of the GPS qualities revealed that the criteria sent via GSM that provide information about the number of satellites used and their geometry in the sky are not useful to identify and exclude imprecise fixings from the positioning data. For example, the fixing with the highest deviation (376.7 m) in the entire test was obtained with more than three satellites and had a DOP of 3.8, i.e., the best quality by our definition. This phenomenon, i.e., fixings with a small DOP having high deviations and high DOP fixings being very accurate, has been observed in other studies (MOEN et al. 1997, HULBERT & FRENCH 2001, D'EON et al. 2002, D'EON & DELPARTE 2005, GRAVES & WALLER 2006, CARGNELUTTI et al. 2007). A possible explanation could be that the receiver calculates the constellation of the satellites (leading to the DOPs) without being able to judge the quality of the received signal. The DOP calculation is based on the assumption of ideal conditions, i.e., obtaining a pure, unaffected and non-absorbed signal from the satellites, but multi-path effects could have heavily influence the signals.

However, the search for a threshold using a conditional inference tree revealed, as in previous studies (ADRADOS et al. 2003, D'EON & DELPARTE 2005), that the DOP apparently serves as a measure to increase accuracy. The determined threshold was DOP 12.4. Applied to the static GPS test data, the overall accuracy slightly improved by 0.2 m. But most of the filtered data (deletion of fixings with DOP>12.4) would have been in coniferous forests, in which the efficiency of the collars was poorer. Therefore, pre-selecting data based on quality information does not seem to be a proper method to filter inaccurate fixes. Instead, it would discriminate data collected in habitat types in which fewer fixings would be expected. D'EON & DELPARTE (2005) suggested positional dilution of precision (PDOP) value as a possible method of reducing location error, but also warned about the risk of data loss, which can lead to new biases. This in turn could lead to other problems, as pointed out by NIELSON et al. (2009), who showed that even small data loss could bias results within a habitat analysis. Taken together, we can conclude that applying the determined threshold would only slightly increase the accuracy of the fixings, would cause data loss and would be unsuitable for excluding imprecise fixings. We therefore rejected the application of the threshold value. Other approaches seemed more promising, such as making use of the actual number of satellites used for each particular fixing (e.g., Moen et al. 1997, Hulbert & French 2001) or this variable combined with the DOP (Cargnelutti et al. 2007). We analysed only parameters sent via GSM and the actual number of satellites used was not included in these data sets. This information could be downloaded from the collars after their retrieval from the animals, but this requires retrieving all collars, which is difficult to accomplish.

Conclusion

GPS positions are measurements based on complex mathematical calculations that imply a very high accuracy and reliability. However, the determination of a position is influenced by factors that cannot be quantified, minimized or even determined, e.g., multi-path effects or asynchrony between satellite and receiver clocks. Therefore, GPS positions will always include some outliers, which cannot be identified by objective technical thresholds, such as DOP or the number of satellites (2D or 3D) in our study. This quality information could not serve as reliable criteria for the accuracy of the determined positions.

Approaches that cope with reduced PAR and accuracy must be fitted by the needs of a clear research hypothesis, where the topic must be defined. Such topics include movement (Swain et al. 2008), habitat selection (Frair et al. 2004, Johnson & Gillingham 2008, Nielson et al. 2009), and scale, e.g., individual vs. population or landscape scale vs. microhabitat analysis. Within these approaches, the site-specific PAR and the accuracy of the deployed GPS collars would be variables for the models. Our study provided these basic parameters for temperate European beech and Norway spruce forests.

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