

## **New Possibilities of Observing Animal Behaviour from a Distance Using Activity Sensors in Gps-Collars: An Attempt to Calibrate Remotely Collected Activity Data with Direct Behavioural Observations in Red Deer *Cervus elaphus***

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## New possibilities of observing animal behaviour from a distance using activity sensors in GPS-collars: an attempt to calibrate remotely collected activity data with direct behavioural observations in red deer *Cervus elaphus*

Petra Löttker, Anna Rummel, Miriam Traube, Anja Stache, Pavel Šustr, Jörg Müller & Marco Heurich

Knowing what an animal is doing where and when is crucial for understanding habitat use as well as for detecting deviations from the norm, e.g. the animal's responses to disturbances or predators. While an animal's position can quite easily be assigned using VHF- or GPS-telemetry, determining its behaviour from a distance is still limited. A new generation of GPS-collars, equipped with a dual-axis acceleration sensor allows insights into the animal activity by continuously (5-minute intervals) delivering x- and y-values on a scale from 0 to 255. However, until now it has not been possible to tell which activity values can be attributed to which kind of behaviour. Therefore, the overall aim of our study was to find a method to distinguish different behavioural categories from these activity values. We used four captive red deer *Cervus elaphus* (one male and three females) and equipped them with GPS-collars while simultaneously observing their behaviour. Values for different behavioural categories were compared statistically using ANOVA with 'individual' as random effect and Tukey's follow-up test. Threshold values between the categories were determined by recursive partitioning and were assured by 5,000 bootstraps. While the difference between feeding and slow locomotion was significant in the x- but not in the y-values, each of these two categories differed significantly from resting and fast locomotion. Specific thresholds were established between the three categories resting, feeding with slow locomotion and fast locomotion. Subsequent comparison of the behaviour determined by these threshold values with observed behaviour revealed a high percentage of correctly assigned behaviour (93%). Taken together, this preliminary study demonstrates the potential of dual-axis acceleration sensors in GPS-collars for estimating the activity of wild-living red deer. However, further observations of activity on more individuals of each age and sex class should be performed to take into account inter-individual variability and to improve the predictive power of the threshold values.

*Key words:* activity, behaviour, *Cervus elaphus*, GPS-telemetry, red deer, spatio-temporal behaviour

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Knowing what an animal is doing where and when is crucial for understanding habitat use as well as for detecting deviations from the norm, e.g. the

animal's responses to disturbances or predators. Because of increasing interference of humans in natural habitats, wild-living animals are put under

growing pressure by man with regard to their space and time requirements (Berger et al. 2002, Gervasi et al. 2006). Therefore, investigation of the spatio-temporal behaviour of wild animals is relevant for the management of potentially disturbing anthropogenic activities, and hence for the conservation of endangered species. Additionally, data on animal activity are necessary to improve our understanding of their foraging behaviour, and may contribute to generate predictive models which may help wildlife managers and land use planners to integrate plant-herbivore relationships into forest and wildlife management (Coulombe et al. 2006).

The conflict between wildlife management and conservation on the one hand and requirements of human recreation and tourism on the other hand is especially pronounced in national parks, which by definition have to fulfil both functions. In the Bavarian Forest National Park, management of red deer *Cervus elaphus* is of great importance since the species is the largest herbivore which can cause considerable browsing damage, but which is also an attractive flagship species. With formation of the National Park in 1970 red deer living conditions have changed dramatically due to the suspension of hunting in a wide area, increased tourism, creation of large forest clearings and subsequent forest regeneration after spruce bark beetle *Yps typographus* calamity, and reintroduction of lynx *Lynx lynx*, which is an important predator for young and female red deer, into the area that was free of large predators for around 150 years. Studying red deer spatio-temporal behaviour is therefore crucial to assess how they cope with the challenges of the new situation.

The most unambiguous way to study animal behaviour is by direct observations of focal animals. However, direct observations bear several problems. Animals might be disturbed by the approaching observer and might flee. Moreover, direct observations depend much on the territory and are only possible during the day and in areas with little or no cover (Gervasi et al. 2006), and they are time and manpower consuming (Craighead et al. 1973). Elusive species, like red deer, which move great distances in a largely inaccessible area in the Bavarian Forest National Park require other, indirect methods. One such indirect method is VHF- or GPS-telemetry which was originally developed for position determination, but increasingly offers the possibility to study animal activity with little disturbance as well. Based on the assumption that animal movement can influence the transmission

of radio signals, early studies interpreted signal changes in tone or strength during a fixed time interval as active behaviour (see Gervasi et al. 2006 for a review). This method was, however, criticised to be rather subjective. Later radio-collars contained motion-sensitive devices. These devices are activated by animal movement, which leads to a change in the signal mode, usually in the pulse rate. Such changes in pulse rate allowed the discrimination between feeding and slow locomotion, and between rumination and sleeping in red deer (Georgii & Schröder 1978, Georgii 1981, Green & Bear 1990). In the 1990s specific collars for activity measurements were designed (ETHOSYS; Scheibe et al. 1998, Berger et al. 2002, Berger et al. 2003). These collars contain two sensors, one for acceleration and the other for position tracking of the animal's head (i.e. up or down). The two sensors permit the discrimination of feeding from general activity. In the past decade, GPS-collars have been equipped with dual-axis motion sensors sensitive to vertical and horizontal head and neck movements (GPS-collars from Lotek Engineering; e.g. Adrados et al. 2003, Ungar et al. 2005, Coulombe et al. 2006; GPS-collars from VECTRONIC Aerospace; e.g. Gremse 2004, Gervasi et al. 2006). These collars allow insights into animal activity by continuously delivering x- and y-values on a scale from 0 to 255. However, so far, studies using these collars reported that the sensor-measured values provided information on the degree of activity only at a broader scale (active vs passive), whereas discrimination of the different active behaviours failed (Adrados et al. 2003, Gremse 2004, Coulombe et al. 2006, Gervasi et al. 2006).

Considering this background, the overall aim of our study was to find a method to distinguish between different behavioural categories based on activity values generated by a dual-axis acceleration sensors in GPS-collars. More specifically, we wanted to 1) determine specific threshold values for the different behavioural categories in captive red deer, and 2) validate these thresholds through behavioural observations.

## Methods

### Technical details of the activity sensors

We used GPS-GSM collars from VECTRONIC Aerospace, Berlin, Germany. The collars are equipped with one dual-axis acceleration sensor, with the horizontal sensor being oriented perpendicular and

Table 1. Summary characteristics and observation period of the four (F1-F3 and M1) study animals.

Animal-ID	Sex	Age class	Date of collaring	Date of de-collaring	Remarks
F1	♀	Juvenile (0.5 years)	15/09/2006 <sup>1</sup>	16/10/2006 <sup>1</sup>	
F2	♀	Subadult (1.5 years)	14/09/2006 <sup>1</sup>	16/10/2006 <sup>2</sup>	
F3	♀	Adult (~10 years)	15/09/2006 <sup>1</sup>	16/10/2006 <sup>2</sup>	
M1	♂	Adult (~10 years)	16/08/2007 <sup>1</sup>	11/09/2007 <sup>3</sup>	With antler

<sup>1</sup> Immobilisation with 'Hellabrunner Mixture' (500 mg Xylazine dry substance dissolved in 4 ml 10% Ketamine solution; Wiesner 1998) in the following doses; F1: 1 ml; F2: 1.8 ml; F3: 2 ml; M1: 3 ml. Application IM with blowpipe.

<sup>2</sup> Shot to death.

<sup>3</sup> Drop-off device on GPS-GSM collar.

the vertical sensor being oriented parallel to the spine of the animal. Consequently, left-right and back-forth movements generate x- and y- values, respectively. Data are recorded continuously 6-8 times per second, and the resulting values are accumulated and averaged in the time interval between two successive activity fixes, here in 5-minute intervals. The mean activity values are arranged on a linear numerical scale and range from 0 to 255. All values are saved in the collar and can be downloaded after the de-collaring of the animal.

For our tests we used collars from the series 600, 2100 and 2300. These collars did not differ in the technical equipment concerning the activity sensors (VECTRONIC Aerospace, pers. comm.). However, the collars differed insofar as they were of different size/weight, ranging from ca 600 g to ca 900 g, with the lightest collar used for the juvenile female and the heaviest for the male. Additionally, in contrast to the female collars, the male collar was equipped with a drop-off device. The possible imbalance that this device might have caused was counterbalanced through another box of similar size at the opposite side of the collar.

### Animals and housing conditions

For matching behavioural observations and activity data generated by GPS-collars, we used four red deer of different ages and sexes (one juvenile, one subadult, one adult female, and one adult male with ample antler) and equipped them with GPS-GSM collars for around one month each (Table 1). The females lived together with seven adult females, two adult males and several subadults and juveniles in an outdoor enclosure of 2 ha encompassing grassland and an open stable. The animals received daily supplemental feeding in form of hay or silage, and from time to time fruits or corn were fed as supplements. The male lived together with one adult and two subadult females in an outdoor enclosure of 7 ha encompassing half grassland and half mixed forest of Norway spruce *Picea abies* and European beech

*Fagus sylvatica*. The daily provisioning consisted of hay and grass pellets.

We intentionally chose females of different age classes and an adult male during the antler phase since the head movements and tightening of the collar can vary depending on the age and/or sex class of an individual (Gremse 2004, Coulombe et al. 2006, Gervasi et al. 2006). Since differences between age and/or sex classes may mask general differences in the values for different behavioural categories, this approach is conservative.

### Behavioural observations

We observed detailed behaviour using focal animal sampling and continuous recording (Martin & Bateson 1993) on the three female red deer, for a total of 83 observation hours during the time they wore the GPS-collars (see Table 1; the observers were Miriam Traube and Anna Rummel). The GPS-collared male was observed in the subsequent year in a similar manner by Sabine Schade for a total of 30 observation hours (see Table 1). We recorded the four behavioural categories resting, feeding, slow locomotion and fast locomotion (Table 2), as well as all shorter events (mainly head movements and change of body position) including the time information on a standardised data sheet. In order to be able to compare behavioural observations with activity values generated by the GPS-collars, a stopwatch was synchronised with the internal clock of the collars.

### Statistical comparison of activity values for different behavioural categories

For comparison of activity values for the different behavioural categories we used only 'pure' 5-minute intervals, i.e. intervals in which deer were observed performing only one of the four behaviours for the whole sampling period and which were virtually free of shorter events. Additionally, we used values in the middle of a longer time sequence for a certain behavioural category, and not values at the beginning

Table 2. Ethogramme of the recorded behavioural categories.

Behavioural category	Definition
Resting (R)	Persisting without leg movements, either standing or lying.
Feeding (F)	Pulling movement with mouth and subsequent mastication, head down, mostly with accompanying forward motion and incidental head up movements (vigilance).
Slow locomotion (sLoc)	Pace: forward motion in which all four legs are consecutively lifted from the ground and subsequently put on the ground further ahead; sequence: hind left, fore left, hind right, fore right.
Fast locomotion (fLoc)	Trot: forward motion in which two legs are lifted from the ground simultaneously and subsequently put on the ground further ahead; sequence: hind left with fore right, hind right with fore left or Gallop: forward motion in which initially one hind leg, then the other hind leg together with the diagonal fore leg, and finally the other fore leg are put further ahead; this is followed by a levitation phase in which all four legs are simultaneously released from the ground.

or at the end of resting- or feeding-periods (e.g. when a resting period lasted from 15:00 to 15:30 we chose values from 15:05 to 15:25). This was important since the clock that triggers the activity logger does not run synchronous with the internal clock of the collar, but is exposed to time lags (VECTRONIC Aerospace, pers. comm.). This means that although the internal clock is querying the activity values at definite points of time in 5-minute intervals (00:00, 00:05, 00:10, 00:15, ...), the measuring period at a query at 00:05 can range from 00:00:01 to 00:05:00 or in the other extreme from 00:05:01 to 00:10:00. When using values in the middle of a resting- or feeding-period, the time lags do not fall into account.

We calculated and plotted the median (25 and 75% quartiles) activity values for the different behavioural categories for the four individuals (M1, F1, F2, F3; see Table 1) separately as well as for the pooled data from all of them. We did this for x-values, y-values and for the sums of x- and y-values (xy-values) as a measure for the overall acceleration (total activity level) in the two orthogonal directions (Gervasi et al. 2006).

All statistical analyses were performed using R2.5.1 (R Development Core Team 2004). To test our global hypothesis of independence of the x-values (in same way y- and xy-values) among the four behavioural categories, we fitted a linear mixed-effect model using the function `glht` in the package

'lme4'. We used the pooled data and considered our four individuals as random effects. According to Westfall & Young (1993), for each response variable a post-hoc test (Tukey's all-pair comparison) was applied additionally in order to assess the differences between each pair of the four behavioural categories using the function `mcp` in the package 'multcomp'.

#### Determination of threshold values

Based on the previous analyses, we determined threshold values from pooled data using recursive partitioning with single branching (Hothorn & Zeileis 2008, Zeileis et al. 2008). This statistic procedure incorporates parametric models into trees and, in this special case, finds the value (split point) that separates best between two behavioural categories. Since in red deer locomotion is mostly linked with feeding (Georgii & Schröder 1978), meaning that the animals feed where they walk or walk where they feed, and the difference between feeding and slow locomotion was not significant in y-values (Table 3), we united these two categories into one category. Consequently, thresholds were built between resting and feeding/slow locomotion and between feeding/slow locomotion and fast locomotion. Afterwards, 95% confidence intervals for the threshold values were determined by 5,000 bootstraps.

In a second step, we divided the data set into two parts of equal size, and used only half of the

Table 3. Results of ANOVA with random effect and Tukey's follow-up test for the comparison between the four behavioural categories resting (R), feeding (F), slow locomotion (sLoc), and fast locomotion (fLoc; see Fig. 1). Analyses were performed with pooled data from all individuals (see Fig. 1 columns 'all')

Test variables	X-value		Y-value		XY-value	
	Z-value	P-value	Z-value	P-value	Z-value	P-value
R vs F	-26.5	<0.0001	-31.05	<0.0001	-30.34	<0.001
R vs sLoc	-14.53	<0.0001	-12.35	<0.0001	-13.97	<0.001
R vs fLoc	-41.72	<0.0001	-29.11	<0.0001	-36.5	<0.001
F vs sLoc	-4.77	<0.0001	-0.82	n.s.	-2.74	<0.05
F vs fLoc	-32.53	<0.0001	-18.16	<0.0001	-25.87	<0.001
sLoc vs fLoc	-20.83	<0.0001	-12.94	<0.0001	-17.31	<0.001

data/every second value from each individual for determination of threshold values. The other half was used for validation of the threshold values (see below).

The analyses were performed using R2.5.1 (see above) and the add-on packages 'party' and 'coin'. Again, thresholds and confidence intervals were determined for x-values, y-values and the sums of x- and y-values.

### Validation of threshold values

The validation of threshold values was done in two steps with the second half of the data set consisting of 'pure' 5-minute intervals only (see above). In the first step, we counted the observed number of intervals per behavioural category and determined the per-

centage of correctly assigned intervals when using the threshold values based on the x-, y- and xy-values. In the second step we compared the number of intervals per behavioural category as observed with the number of intervals per behavioural category as determined from x-, y- and xy-values. This second step was performed in order to reveal which behaviours were underestimated (assigned values lower than those observed) and which were overestimated (assigned values higher than those observed).

Significance between the observed and telemetry-based distributions of behaviours were tested using a G-Test with William's Correction (see Green & Bear 1990) using SsS1.0b (Rubisoft Software GmbH). Due to multiple pair-wise testing, significance levels

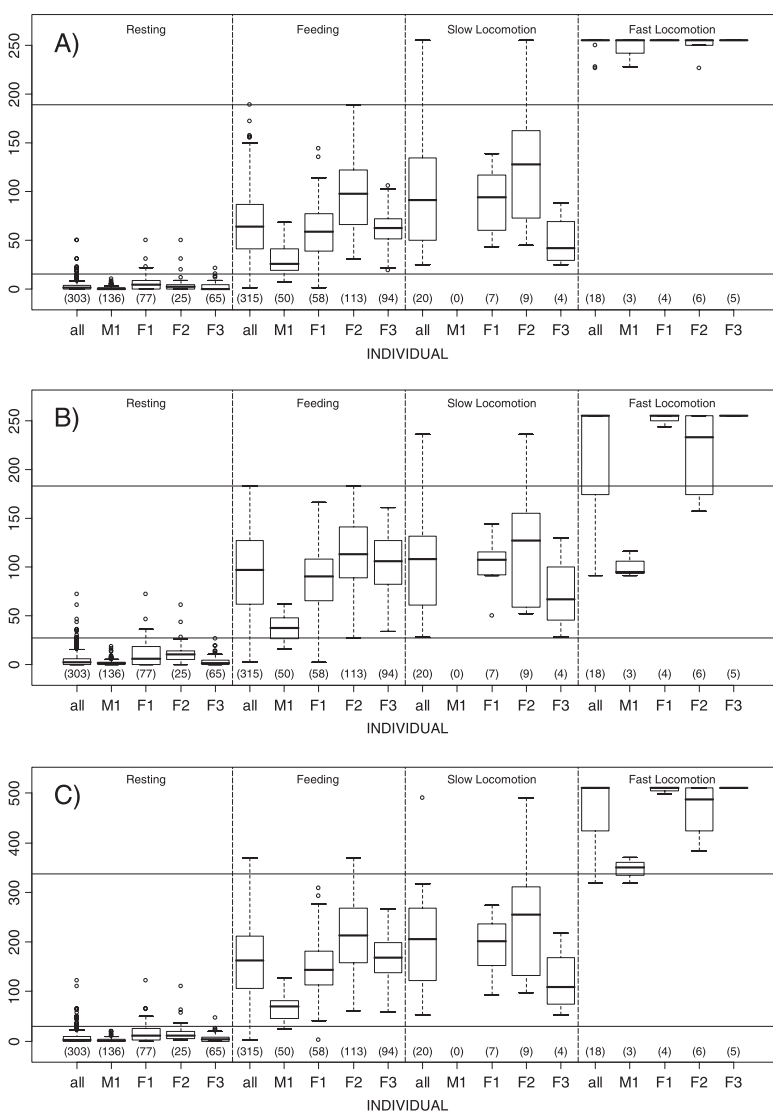


Figure 1. Activity values (A): x-values, B): y-values and C): sums of x- and y-values) for the behavioural categories resting, feeding, slow locomotion and fast locomotion for the pooled data 'all' as well as the four individuals M1, F1, F2 and F3 (compare with Table 1). Thick horizontal lines indicate medians, box = 25- and 75%-quartiles and dashed lines include 100% of data; except dots indicate outliers. Sample size is given in parentheses. Horizontal lines are threshold values between resting and feeding/slow locomotion (lower line), and between feeding/slow locomotion and fast locomotion (upper line) after recursive partitioning (compare with Fig. 2). For significant differences between the behavioural categories see Table 3.

had to be adapted by Holm's sequential Bonferroni procedure (Holm 1979); in this case  $P \leq 0.0167$ , 0.025 and 0.05 for the three ranked P-values (from small to large) denoted significant difference. Both steps were performed using the pooled data of all individuals and with all four individuals (M1, F1, F2, F3; see Table 1) separately.

## Results

### Statistical comparison of values for different behavioural categories

For both x- and y-values, and for the sum of these values (xy), the differences between all four behavioural categories were very highly significant, except the difference between feeding and slow locomotion which was significant in xy-values but not significant in y-values (Fig. 1 columns 'all'; ANOVA with random effect and Tukey's follow-up test see Table 3). In all values, the median (and the 25 and 75% quartiles) was lowest in resting and highest in fast locomotion. Feeding and slow locomotion were intermediate.

Concerning the different individuals, the medians for the different behavioural categories in the three females were very much alike in both x- and y-values, and in xy-values. The male, however, differed from the females and had considerably lower medians for resting and fast locomotion (for slow locomotion there were no values available for the male). This difference was especially pronounced in y-values for fast locomotion which lay below the threshold for fast locomotion.

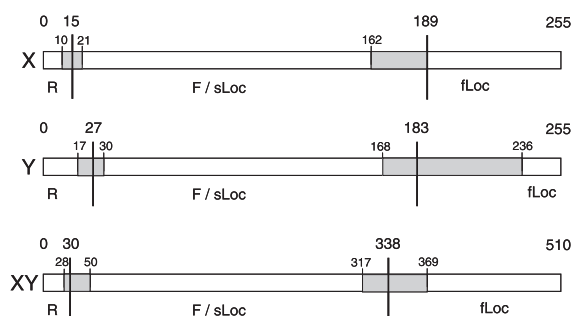


Figure 2. Threshold values (thick vertical lines) to separate resting (R) from feeding/slow locomotion (F/sLoc) and the latter from fast locomotion (fLoc) for x-values, y-values and the sums of x- and y-values as determined by recursive partitioning, and overlapping zones (grey bars) after 5,000 bootstraps. White bars denote 95% confidence intervals after 5,000 bootstraps. Thresholds are built from pooled data of four individuals (compare with Table 1).

### Determination of threshold values

With high levels of significance, threshold values were built and approved to separate resting from feeding/slow locomotion and the latter from fast locomotion in x-values, y-values and in the sums of x- and y-values (Fig. 2; Recursive Partitioning: all combinations  $P < 0.001$ ). Values  $\leq 15$  (10), 27 (17) and 30 (28) for x-, y- and xy-values, respectively, indicated resting (values in parentheses represent values beyond which the 95% confidence interval was reached). Values  $> 15$  (21), 27 (30) and 30 (50) and  $\leq 189$  (162), 183 (168) and 338 (317) for x-, y- and xy-values, respectively, indicated feeding/slow locomotion. Values  $> 189$  (189), 183 (236) and 338 (369) for x-, y- and xy-values, respectively, indicated fast locomotion.

Table 4. Validation of threshold values - 1. Percentage of correctly assigned intervals for x-, y- and the sums of x- and y-values.

Behaviour	Individual	Observed no. of intervals	% of correctly assigned intervals for		
			X-value	Y-value	XY-value
Resting	All	150	98	96.7	94.7
	M1	68	100	100	100
	F1	38	97.4	92.1	86.8
	F2	12	83.3	83.3	75
	F3	32	100	100	100
Feeding/slow locomotion	All	166	94	92.2	97
	M1	25	72	68	88
	F1	32	93.8	93.8	96.9
	F2	60	98.3	95	98.3
	F3	49	100	100	100
Fast locomotion	All	8	100	75	87.5
	M1	1	100	0	0
	F1	2	100	100	100
	F2	3	100	66.7	100
	F3	2	100	100	100
Total <sup>1</sup>		324	97.3	87.9	93.1

<sup>1</sup>Percentage = Mean percentage calculated from the pooled data ('all').

Table 5. Validation of threshold values - 2. Number of intervals per behavioural category as observed and as determined from x-, y- and the sums of x- and y-values, and significance levels for the assigned vs the observed distributions. The percentage of assigned to observed number of intervals is given in parentheses.

Behaviour	Individual	Observed no. of intervals	Assigned no. of intervals		
			X-value	Y-value	XY-value
Resting	All	150	156 (104)	156 (104)	146 (97.3)
	M1	68	75 (110.3)	76 (111.8)	71 (104.4)
	F1	38	39 (102.6)	37 (97.4)	34 (89.5)
	F2	12	10 (83.3)	11 (91.7)	9 (75)
	F3	32	32 (100)	32 (100)	32 (100)
Feeding /Slow locomotion	All	166	159 (95.8)	160 (96.4)	170 (102.4)
	M1	25	18 (72)	18 (72)	23 (92)
	F1	32	31 (96.9)	33 (103.1)	36 (112.5)
	F2	60	61 (101.7)	60 (100)	62 (103.3)
	F3	49	49 (100)	49 (100)	49 (100)
Fast locomotion	All	8	9 (112.5)	8 (100)	8 (100)
	M1	1	1 (100)	0 (0)	0 (0)
	F1	2	2 (100)	2 (100)	2 (100)
	F2	3	4 (133.3)	4 (133.3)	4 (133.3)
	F3	2	2 (100)	2 (100)	2 (100)
Significance level <sup>1</sup>			n.s.	n.s.	n.s.

<sup>1</sup>Significance levels after G-Test with William's Correction and Holm's sequential Bonferroni procedure as calculated for the pooled data ('all'): n.s. = non significant difference (for P-values see text).

When using only half of the data, threshold values differed slightly from the values above: Values  $\leq 18$  (9), 27 (19) and 31 (28) for x-, y- and xy-values, respectively, indicated resting. Values  $> 18$  (23), 27 (27) and 31 (64) and  $\leq 189$  (143), 178 (157) and 369 (299) for x-, y- and xy-values, respectively, indicated feeding/slow locomotion. Values  $> 189$  (189), 178 (180) and 369 (369) for x-, y- and xy-values, respectively, indicated fast locomotion. The significance level was high as described above (Recursive Partitioning: all combinations  $P < 0.001$ ).

### Validation of threshold values

Overall, the percentage of correctly assigned intervals was high (93%; Table 4). With 94.7-98% it was slightly higher in resting than in feeding/slow locomotion (92.2-97%) and in fast locomotion (75-100%). Concerning the different activity sensors, the percentage of correctly assigned intervals was highest in the horizontal sensor (x-values: 97.3%), and slightly lower in the vertical sensor (y-values: 87.9%) and the combination of both sensors (sum of x- and y-values: 93.1%). Concerning the different individuals, the percentage of correctly assigned intervals was highest in F3 (always 100%), slightly lower in F1 and F2 (ranges: 86.8-100 and 66.7-100%, respectively), and lowest in M1 (range: 0-100%).

When comparing the number of intervals per behavioural category as observed with the assigned

number when using x-, y- or xy-values as reference (Table 5), it turned out that the fit for all three behavioural categories was quite good (assigned values almost equal to observed values). Accordingly, the differences between the observed and the assigned distribution of behavioural categories were not significant in either case (G-Test with William's correction and Holm's sequential Bonferroni procedure: x:  $G=0.32$ ,  $df=2$ ,  $P=0.851$ ; y:  $G=0.22$ ,  $df=2$ ,  $P=0.893$ ; xy:  $G=0.1$ ,  $df=2$ ,  $P=0.951$ ). Concerning the different individuals, the fit was best for F3 (always 100%). In M1, resting was slightly overestimated (104.4-111.8%), whereas feeding/slow locomotion was underestimated (72-92%; for fast locomotion there was only one data point so that no clear picture emerged). In F2, resting was underestimated (72-92%) and fast locomotion was overestimated (133.3%), whereas the fit for feeding/slow locomotion was quite good (96.9-103.3). In F1, resting was slightly underestimated (85.5-97.4%, except in the x-value: 102.6%) and feeding/slow locomotion was overestimated (103.1-112.5%, except in the x-value: 96.9%), whereas the fit in fast locomotion was 100%.

### Discussion

We present a method to distinguish different behavioural categories from activity values generated by



a dual-axis acceleration sensor in GPS-collars. By means of threshold values built after behavioural observations, we differentiated resting from feeding/slow locomotion and the latter from fast locomotion in red deer. The validation of these threshold values revealed a high percentage of correctly assigned behaviour.

However, despite the successful generation and validation of threshold values, some methodological problems emerged. First, although the overall percentage of correctly assigned behaviour was high, some classification errors occurred even though we exclusively used 'pure' intervals of one behavioural category for validation. The number of misclassifications increased further when applying the threshold values to intervals of mixed behaviour or intervals in which behavioural events of short duration occurred. It turned out that all in all, resting was underestimated, whereas both feeding/slow locomotion and fast locomotion were overestimated (data not shown). Being placed around the animal's neck, the acceleration sensor is especially affected by head movements (Gervasi et al. 2006). Therefore, head movements but also events like 'getting up', 'body shaking' and 'jumping' during a resting (feeding/slow locomotion) period caused higher activity values than usual for this period and thus lead to a shift from resting to feeding/slow locomotion (or from the latter to fast locomotion). This is a technical problem resulting from the fact that activity data are mean values for a 5-minute interval, and can only be solved by the collar-producing companies by either shortening the interval or by completely avoiding the averaging process and displaying the raw data instead. However, red deer are not so problematic in this respect as they behave relatively constant and usually remain within one behavioural category for longer time intervals (e.g. feeding periods last from 30 minutes to 2.5 hours; Bützler 2001). Therefore, in red deer the problem of wrong classification can be further reduced by considering longer time intervals (e.g. 30 minutes, see above) instead of one 5-minute interval only, and by subsequent determination of the prevailing behaviour in this extended period (i.e., when an animal's assigned activity is feeding in a 5-minute interval but this interval is surrounded by 5-minute intervals of resting, it is assumed that the animal was resting during all this time). By doing so, misclassifications due to short events during one 5-minute interval would not fall into account. Concerning the transferability to other study species, it should, however, be noted that the problem of mis-

classification could be elevated in species which behave less constant and are more excited or vigilant than red deer.

Second, the processes of generating and validating the threshold values were based on behavioural observations of four red deer of different age and sex classes. Other studies found that the head movements and tightening of the collar can vary depending on the age and/or sex class of an individual (Gremse 2004, Coulombe et al. 2006, Gervasi et al. 2006), and would suggest to build different threshold values for different age and sex classes. Indeed, also in our study, the activity values for the male differed from the females insofar as they were considerably lower, whereas the distribution of values within the females (despite their different age classes) was much more homogeneous. The difference between the male and the females was especially pronounced in the behavioural category fast locomotion; in the male, only the x-, but not the y-value, was elevated (x: 255; y: ca 100). This difference between x- and y-values was confirmed in data of wild-living red deer stags during the antler phase (data not shown). Whether this is a general phenomenon in male red deer, if it reflects the general movement pattern of stags in the antler phase (see Gremse 2004), or whether it is caused by other factors (e.g. increase of neck circumference and thus collar tightness during the rutting season) should be investigated in further studies. However, despite the difference between the male and the female red deer, the universal threshold values built from the pooled data of all individuals fit quite well with all of them (high percentage of correctly assigned intervals in all four individuals). Additionally, our statistically conservative approach is supported by the fact that despite the pooling of data we obtained significant results. Finally, for a long-term study on the spatio-temporal behaviour of red deer like our study, in which animals are GPS-collared for several months up to several years, comprising different seasons and possibly different age classes, universal thresholds that can be used year round and for all individuals seem to be much more feasible and reasonable. Until new insights become available in respect to the differences between x- and y-values in red deer stags in fast locomotion, we recommend the use of x-values for determination of behaviour in red deer, especially when individuals of both sexes and different ages are involved.

Third, our behavioural observations were carried out in outdoor enclosures. It might well be that the

behaviour of captive red deer differs from the behaviour of wild living individuals, and that some behavioural patterns do not occur in captivity. For example, we only recorded few intervals of fast locomotion in our captive individuals and they did not show extended periods of slow locomotion without feeding. Maybe, a higher number of intervals for both fast and slow locomotion would have allowed a better fine-tuning of the threshold values, and would have allowed distinguishing feeding from slow locomotion as well. However, fast locomotion over extended periods seems to be generally rare in red deer, and differentiating between feeding and slow locomotion might not be essential, as in this species locomotion is mostly linked with feeding and 90-95% of red deer active time can be attributed to feeding (Bützler 1974, Georgii & Schröder 1978, but also see Berger et al. 2002). Alternatively, a future approach could be to include GPS-data into the analysis and to use the distance walked between two GPS-fixes as an additional criterion to discriminate between these two behavioural categories (Frair et al. 2005, Ungar et al. 2005, Šustr 2007). Concerning the transferability of our approach to other study species, it should be noted that a careful generation and validation of threshold values, as we have done, requires the availability of tame or captive individuals of the respective species, at least when working in a forested area in which direct observations are not feasible, and can thus be a limiting factor.

Taken altogether, our preliminary study demonstrates the potential of dual-axis acceleration sensors in GPS-collars for estimating the activity of wild-living red deer. While other systems might be more suitable for remotely collecting behavioural data (ETHOSYS: Scheibe et al. 1998, Berger et al. 2002, Berger et al. 2003), the dual-axis acceleration sensors in GPS-collars clearly bear the advantage of simultaneously collecting behavioural and position data. In combination, these data will offer new and exciting insights into red deer behaviour in the natural ecological context in terms of habitat use and the temporal distribution of behavioural categories. For the current developmental status of the GPS-collars, our method to distinguish different behavioural categories from activity values seems to be vital and transferable to other species as well. However, further observations of activity on more individuals of each age and sex class should be performed to take into account inter-individual variability and to improve the predictive power of the threshold values.

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