# New possibilities of observing animal behaviour from distance using activity sensors in GPS-collars – An attempt to calibrate remotely collected activity data with direct behavioural observations in red deer

Short Title: Calibration of Remotely Collected Activity Data in Red Deer

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

***Abstract:*** 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. responses to disturbances or predators. While an animal's position can quite easily be assigned by VHF- or GPS-telemetry, determining its behaviour from distance is still limited. A new generation of GPS-collars, equipped with a dual-axis acceleration sensor allows insights into animal activity by continuously (5-min intervals) delivering x- and y-values on a scale from 0 to 255. However, until now it was not possible to tell which activity values can be attributed to which kind of behaviour. Therefore, the overall aim of this study was to find a method to distinguish different behavioural categories out of these activity values. We used four captive red deer (*Cervus elaphus*; 1 male, 3 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 them were determined by recursive partitioning and assured by 5000 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 improve the predictive power of the threshold values.

## Introduction

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. responses to disturbances or predators. Because of the increasing interferences of humans in the 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 spatial-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 foraging behaviour, and can contribute to generate predictive models that will 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 a National Park, which by definition has to fulfil both functions. In the Bavarian Forest National Park the management of red deer (*Cervus elaphus*) is of great importance since it is the largest herbivore which can cause considerable browsing damage but which is also an attractive flagship species. With the National Park formation in 1970 their living conditions changed dramatically due to the suspension of hunting in a broad area, increased tourism, the creation of large forest clearings and subsequent forest regeneration after spruce bark beetle (*Yps typographus*) calamity, and the reintroduction of lynx (*Lynx lynx*) as 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 spatial-temporal behaviour is therefore crucial to assess how they deal 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 that move great distances in a largely inaccessible area like red deer 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 which 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 review). This method was, however, criticized to be rather subjective. Later radiocollars 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 measurement 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 (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; Unger 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 found that the sensor-measured values provided information on the degree of activity only at a broader scale (active vs. passive) while the discrimination of different active behaviours failed (Adrados et al. 2003; Gremse 2004; Coulombe et al. 2006; Gervasi et al. 2006).

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

# Methods

## Technical details of the activity sensors

We used GPS-GSM collars from VECTRONIC Aerospace, Berlin (Germany). The collars are equipped with a dual-axis acceleration sensor with the horizontal sensor being oriented perpendicular and 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-min intervals. The mean activity values are arranged on a linear numerical scale and range from 0-255. All values are saved on the collar and can be downloaded after de-collaring 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.* 600g to *ca.* 900g, 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 this device might be able to cause was counterbalanced through another box of similar size at the opposite side.

**Animals and housing conditions**

For matching behavioural observations and activity data generated by GPS-collars, we used four red deer individuals (*Cervus elaphus*) of different ages and sexes and equipped them with GPS-GSM collars for around one month each: 1 juvenile, 1 subadult, and 1 adult female, as well as 1 adult male with ample antler (Table 1). The females lived together with seven adult females, two adult males and several subadult and juvenile individuals in an outdoor enclosure of 2ha size encompassing grassland and one 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 7ha size encompassing half grassland and half mixed forest (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-sex class of an individual (Gremse 2004; Coulombe et al. 2006; Gervasi et al. 2006). Since differences between age-sex classes may mask general differences in the values for different behavioural categories, this approach is conservative.

**Behavioural observations**

We did detailed behavioural observations 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 (Table 1; observers: 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 (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 standardized data sheet. In order to be able to compare behavioural observations with activity values generated by the GPS-collars, the stop-watch was synchronized on 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-min intervals, i.e. intervals in which deer were observed performing only one of the four behaviours for the whole sampling period and that were virtually free of events. Additionally, we used values in the middle of a longer time period for a certain behavioural category, not values at the beginning or at the end of a resting- or feeding-period (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 collars but the clocks are 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-min intervals (00:00, 00:05, 00:10, 00:15, ...), the measuring period at a query at 00:05h 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 (and 25- / 75% quartiles) activity values for the different behavioural categories for the four individuals (M1, F1, F2, F3; compare Table 1) separately as well as for the pooled data from all of them. We did this for x-values, y-values as well as 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 with 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 effect. According to Westfall & Young (1993), for each response variable a post-hoc test (Tukey 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 5000 bootstraps.

In a second step, we divided the data-set into two parts of equal size, and used only half of the 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 with 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-min intervals only (see above). In the first step, we counted the observed number of intervals per behavioural category and determined the percentage 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 are underestimated (assigned values lower than observed ones) and which are overestimated (assigned values higher than observed ones).

Significances between the observed and telemetry-based distributions of behaviours were tested with a G-Test with William's Correction (compare Green & Bear 1990) using SsS1.0b (Rubisoft Software GmbH). Due to multiple pair wise testing, significance levels 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 a significant difference. Both steps were performed with the pooled data of all individuals as well as with all four individuals (M1, F1, F2, F3; compare Table 1) separately.

## Results

### Statistical comparison of values for different behavioural categories

For both, x- and y-values, as well as for the sum of them (xy-values), 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: Table 3). In all values the median (and 25-75% 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 as well as in xy-values. The male, however, differed from the females and had considerably lower medians in 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.

### 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 the sums of x- and y-values (Fig. 2; Recursive Partitioning: all combinations $P < 0.001$). Values below or equal to 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 above 15 (21), 27 (30), and 30 (50) and below or equal to 189 (189), 183 (168), and 338 (317) for x-, y- and xy- values, respectively, indicated feeding / slow locomotion. Values above 189 (189), 183 (236), and 338 (369) for x-, y- and xy- values, respectively, indicated fast locomotion.

When using only half of the data, threshold values differed slightly from the values above: Values below or equal to 18 (9), 27 (19), and 31 (28) for x-, y- and xy-values, respectively, indicated resting. Values above 18 (23), 27 (27), and 31 (64) and below or equal to 189 (143), 178 (157), and 369 (299) for x-, y- and xy- values, respectively, indicated feeding / slow locomotion. Values above 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 when using 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 well (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 prodedure: 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%), while 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%), while 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%), while the fit in fast locomotion was 100%.

## Discussion

We present a method to distinguish different behavioural categories out of 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 further increased when applying the threshold values to intervals of mixed behaviour or intervals in which behavioural events of short duration occurred. Here it turned out that all in all, resting was underestimated while 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 shake', 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-min 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 since they behave relatively constant and usually remain within one behavioural category for longer time-intervals (e.g. feeding periods last from 30min to 2.5h: Bützler 2001). Therefore, in red deer the problem of wrong classification can be further reduced by considering longer time-intervals (e.g. 30 min, see above) instead of one 5-min 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-min interval but this interval is surrounded by 5-min 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-min interval would not fall into account. Concerning the transferability to other study species, it should, however, be noted that the problem of misclassifications could be elevated in species that behave less constant and that are more excited or vigilant.

Second, the processes of generating and validating the threshold values were based on behavioural observations of four red deer individuals of different age-sex classes. Other studies found that the head movements and tightening of the collar can vary depending on the age-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-sex classes. Indeed, in our study, too, the activity values of the male differed from the females insofar as they were considerably lower, while 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. Here, in the male only the x- but not the y-value was elevated (x: 255: y: *ca*. 100). This difference between x- and y-value 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 or if it reflects the general movement pattern of stags in the antler-phase (compare Gremse 2004) or if 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 fitted quite well to 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 got significant results. Finally, for a long-term study on the spatial-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 are available in respect to the differences between x- and y-values in red deer stags in fast locomotion, we recommend the use of the x-values for determination of behaviour in red deer – especially when individuals of both sexes and different ages are involved.

Third, the behavioural observations were carried out in outdoor enclosures. It might well be that the behaviour of captive red deer differs from 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, since 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 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-fixings 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 done here, 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 together, this 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 out of 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 improve the predictive power of the threshold values.

**Acknowledgements**

This study is part of a project on the predator-prey-relationship of lynx, red deer, and roe deer carried out by the Bavarian Forest National Park Administration, Department of Research and Documentation. Immobilizing, GPS-collaring and behavioural observations complied with German laws. Financial support was provided by T-mobile, the EU-program Interreg IIIa, the "Jagdabgabe Bayern" and the Bavarian Forest National Park Administration. We are grateful to Günter Sellmayer and Ingo Brauer for providing access to their captive red deer and for permitting GPS-collaring and behavioural observations. We kindly thank Rüdiger Fischer for immobilizing the animals, Sabine Schade for carrying out the behavioural observations on the male red deer, Martin Gahbauer and Horst Burghart for technical support, and Maren Huck and two anonymous referees for helpful comments on an earlier draft of the manuscript.

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Table 1. Summary characteristics and observation period of the study animals.

| Animal-ID | Sex | Age class | Date of collaring | Date of de-collaring | Remarks |
|---|---|---|---|---|---|
| F1 | female | juvenile (0.5 years) | 15/09/2006[1] | 16/10/2006[1] | |
| F2 | female | subadult (1.5 years) | 14/09/2006[1] | 16/10/2006[2] | |
| F3 | female | adult (~ 10 years) | 15/09/2006[1] | 16/10/2006[2] | |
| M1 | male | adult (~ 10 years) | 16/08/2007[1] | 11/09/2007[3] | with antler |

[1] Immobilization with "Hellabrunner Mixture" (500mg Xylazine dry substance dissolved in 4ml 10% Ketamine solution: Wiesner 1998); F1: 1ml, F2: 1.8ml, F3: 2ml, M1: 3ml; application IM with blowpipe

[2] Shot to death

[3] Drop-off device on GPS-GSM collar

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<br>or<br>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 |

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

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[1] | | 324 | 97.3 | 87.9 | 93.1 |

[1] 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. (Percentage of assigned to observed No 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[1] | | | n.s. | n.s. | n.s. |

[1] 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)

**Figure legends**

Figure 1. Activity 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 Table 1). a) x-values, b) y-values, c) sums of x- and y-values. Thick horizontal lines = medians; box = 25- and 75%- quartiles; dashed lines include 100% of data, except dots = 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 Fig. 2). For significant differences between the behavioural categories see Table 3.

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 5000 bootstraps. White bars denote 95% confidence intervals after 5000 bootstraps. Thresholds are built from pooled data of four individuals (compare Table 1).