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Combining GPS Activity Measurements and Real-Time Video Recordings to Quantify the Activity Budget of Wild Reindeer (*Rangifer tarandus*)

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Preface

This thesis marks the end of my Master in Natural Recourse Management at the University of Life Science (NMBU). The process have provided me with in-depth knowledge about the wild reindeer and knowledge about the process of scientific studies and writing.

Growing up in a valley completely surrounded by wild reindeer habitat I have always been fascinated by the wild mountain reindeer. I have on several occasions had the chance to observe wild reindeer at a distance, but rarely closer than a couple hundred meters. These encounters have occurred when walking or skiing in the mountains or by actively seeking them during the hunting season. Because of this project, I have now had the chance to observe over 20 hours of the daily activities of two female reindeer during the summer months of 2014. I am grateful for the possibility given to me by the Norwegian Institute for Nature Research (NINA) that have provided me with data from their GPS monitoring project of wild reindeer in the Dovre Mountains.

First, a special thanks goes to my supervisor Leif Egil Loe (NMBU) for all the good advice and the constructive criticism throughout this period. I would also like to thank Per Jordhøy (NINA) for helping me getting started with this thesis, Olav Strand (NINA) and Roy Andersen (NINA) for providing me with the data and helping me with the planning face of the thesis, and Bram Van Moorter (NINA) for valuable input on the statistical analysis. Finally, I also would like to thank my family and friend for all the support during this period.

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Abstract

A resent advancement in the field of movement ecology is the use of GPS activity sensors for the identification of detailed patterns of animal activity. This can potentially yield knowledge about the detailed activity budget of free-ranging elusive animals. The aim of this thesis was to separate behavior types to identify the activity budget of wild reindeer. Two free-ranging wild reindeer were fitted with GPS collars with integrated activity sensor and video camera. The video camera recorded video while the activity sensor simultaneously measured activity intensity. I classified the visual observations of reindeer behavior and assigned them into different behavior categories. I then paired the behavior classification with the corresponding activity measurement. By predicting the true overlap and testing the differences in activity measurements between the behavior categories, I managed to separate the main behaviors laying/standing, walking slow, walking, trotting and running. I also managed to separate the secondary behaviors occasional grazing and grazing from the other secondary behaviors. My finding demonstrates that activity budgets can be identified by the use of activity sensors. Unlike other studies to date, my results shows that the behavior classification of free-ranging wild reindeer can be conducted directly in the wild, while simultaneously measure activity. The activity budget can be coupled with known rates of energy expenditure to develop the energetic landscape. This can be used to evaluate the effect of infrastructure, and other human activities, on reindeer spatio-temporal behavior and energy balance.

Sammendrag

En nylig utvikling innenfor feltet bevegelsesøkologi er bruken av GPS-aktivitetssensorer for å identifisere detaljerte mønster ved dyrs aktivitet. Dette kan potensielt gi oss kunnskap om det detaljerte aktivitetsbudsjettet til frittlevende dyr som er vanskelige å komme innpå. Målet med denne oppgaven var å skille ulike atferdstyper for å identifisere aktivitetsbudsjettet til villrein. Det ble satt på GPS-halsbånd med integrert videokamera og aktivitetssensor på to frittlevende villrein. Videokameraet filmet samtidig som aktivitetssensoren målte aktivitetsintensiteten. Jeg klassifiserte de visuelle observasjonene av villreinatferd og plasserte de i ulike atferdskategorier. Jeg koblet så sammen atferds klassifiseringene med den korresponderende aktivitetsmålingen. Ved å predikere det reelle overlappet og teste for ulikheter i aktivitetsmålingene mellom atferdene klarte jeg å skille hovedatferdene står/ligger, går sakte, går, traver og løper. Jeg greide også å skille beitekategoriene tidvis beiting og beiting fra annen sekundæratferd. Mine funn demonstrerer at aktivitetsbudsjett kan bli identifisert ved bruk av aktivitetssensorer. I motsetning til andre studier på nåværende tidspunkt viser mine resultat at atferdsklassifiseringen av frittlevende villrein kan utføres direkte i det fri, samtidig som man måler aktivitet. Aktivitetsbudsjettet kan kobles opp mot kjente rater av energibruk for å lage det energetiske landskapet. Dette kan benyttes til å vurdere hvilke effekt infrastruktur og annen menneskelig aktivitet har på villreinens atferd og energibalanse i tid og rom.

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1 Introduction

The use of GPS collars have revolutionized the study of animal movement ecology. By yielding accurate location data it has resulted in much better estimates of home range, migration rates and individual dispersal (Ensing et al. 2014; Gurarie et al. 2016; Panzacchi et al. 2013a; Panzacchi et al. 2015; Pape & Loffler 2016). These findings are highly relevant for the conservation, management and policy making of vulnerable species (Allen & Singh 2016; Jordhoy et al. 2012; Strand et al. 2015a; Strand et al. 2015b). The last decades technological advancement in biotelemetry have made it possible to send accurate position data directly to the researchers (Brown et al. 2013; Cooke et al. 2004), making it more convenient to extract data regularly for analysis. Location data is a useful mean for behavior ecologists and are often the only information available for free-ranging animals. However, GPS positions alone are not capable of reveal the detailed behavioral context or quantify fine-scale patterns of animal activity.

Studies on remote monitoring that uses activity sensors have exploded the last decade (Brown et al. 2013; Wilson et al. 2015). These sensors uses activity measurements to quantify locomotion and activity intensity of animals. How and where the activity sensor is mounted on an animal's body will decide which kind of movement that will be measured. When incorporated in a neck collar, locomotion is commonly measured on two or three axis, measuring the movement directions up-down, sideways, back-forth. The activity measurements from one sample only gives the intensity of locomotion relative to another sample, so when solely looking at activity measurements it is possible to identify patterns of locomotion and activity intensities (e.g. daily, seasonally or yearly patterns) (Brown et al. 2013; Krop-Benesch et al. 2011). Krop-Benesch et al. (2013) used an activity sensor to identified daily and seasonal patterns of activity intensity for free-ranging roe deer (*Capreolus capreolus*). However, to interpret the activity measurements further it has to be linked to other variables such as behavioral observations and energy expenditure.

Activity sensors were originally designed for locomotion studies on humans, but they have later been validated for use on animals. Van Oort et al. (2004) found that such devices could predict the behavior categories "active" and "inactive" for free-ranging wild reindeer (*Rangifer tarandus*) with an accuracy of 99%. However, there is a considerable challenge to be able to use activity data for more detailed behavioral classification. A common methodology for transforming activity measurements to behavior types is by observing captive animals that are fitted with activity sensors and classify the different behavior types (e.g. standing, walking, running, grazing etc.).

When mounted on human hips, activity sensors identified different basic daily movement like sitting, standing, laying and transitions between movements (Mathie et al. 2004). This tells more about the specific behaviors and not just the relative intensity of the movement. Such detailed information about daily behaviors of animals could increase our understanding of individual responses to external stimuli (e.g. human disturbance) and the patterns of these responses.

A major challenge in use of activity sensors is to validate the activity (Brown et al. 2013; Gaylord & Sanchez 2014) . This has so far mainly been done for animals in captivity (Heurich et al. 2012; Lottker et al. 2009; Mosser et al. 2014), but some attempts have been done on free-ranging animals. Wang et al. (2015) developed a classification algorithm that they applied to free-ranging pumas (*Puma concolor)*. Mobile behavior events were converted to distance traveled and then validated by comparing the results with GPS positions for the same individual. They found a strong positively correlation of travel distance modelled from the captive training dataset, supporting the accuracy of the captive measurements. However, distance traveled was only used to validate mobile and non-mobile events. Visual observation could be a more accurate and more suitable validation tool for studies that tries to differentiate several behavior categories. Nathan et al. (2012) demonstrated this by conducting visual validation of seven behavior categories by observing griffon vultures (*Gyps fulvus*) with binoculars and telescope.

Real-time animal borne video recording could be a highly useful tool for quantifying behavior types. Thompson et al. (2012) mounted high-resolution video camera with GPS on woodland caribou to identify the plant species in the caribou's diet. The video recordings also provided evidence of pregnancy, calving, habitat selection, social activities, foraging behavior and insect avoidance. Similar anecdotal findings about behavior have been recorded when studying food choice of white-tailed deer (*Odocoileus virginianus*) (Beringer et al. 2004). Rutz and Troscianko (2013) attached miniature-video cameras onto 19 New Caledonian crows (*Corvus moneduliodes*) and found that it generated datasets that contained large amounts of behavior types associated with social interactions, habitat use and foraging. The disadvantages to date is the high price tag and the time investment needed to manually screen through video recordings. Activity sensors are cheaper and yields measurements on a format directly suitable for analysis, enabling analysis of a much larger number of individuals. It is therefore relevant to investigate if activity sensors are capable of accurately separating activity types using a limited number of animal-borne video cameras as a validation tool for the activity sensors. When incorporating video camera and activity sensors in the same collars, behavior studies that earlier required pre-studies of captive animals, now can be done directly in the field.

Wild reindeer is an ideal model organism to study detailed activity patterns. First, we have relatively good knowledge of reindeer behaviour characteristics, area use and movement patterns, (Panzacchi et al. 2013a; Panzacchi et al. 2015; Pape & Loffler 2016), energy content in their food (Iversen et al. 2014), and energetics associated with different behaviours (Boertje 1985). By combining the current knowledge and new knowledge about their activity budget, this can generate results with great management implications.

Secondly, Norway has an international responsibility for conserving wild reindeer. A main focus in conservation is area conflicts and disturbance. Much of the area utilized by wild reindeer in Norway are under protection with the purpose of conserving the whole ecosystem, but also to make these areas accessible for low-impact outdoors activities (Nature Diversity Act of 19 June 2009 No. 100, Chapter 5). Even though protection prevents further expansion of settlement, cabins and infrastructure in the remaining reindeer habitat, it still allows recreational activities (including hunting) that potentially have negative effect on the wild reindeer (e.g. Nellemann et al. 2010; Reimers et al. 2009; Vistnes & Nellemann 2008). When undisturbed, the reindeer would spend most of the day foraging in favorable habitat. It is therefore not possible to compensate for the loss of feeding time if the reindeer is being disturbed. Activity sensors can potentially quantify the loss of feeding time near infrastructure and during periods of human interference (including hunting). It can also quantify the different behaviours that are associated with different rates of energy expenditure as demonstrated by Mosser et al. (2014). Obtaining methodology to quantify the activity budget is therefore important for the conservation of wild reindeer.

Thirdly, behavior studies by direct observations in the field is especially time consuming and challenging to conduct on an elusive and wide ranging heard animal such as the wild reindeer (Reimers & Colman 2006). As long as observers are present when the behaviors are recorded it is always a possibility that they will affect the result. Thus, direct observations are time consuming, it is difficult to survey more individuals simultaneous and it is difficult to observe more than a fraction of the individual daily behavior. All these factors that are interfering with the possibility to study an individual continuously makes it difficult to accurately quantify behavior.

The aim of the current thesis is to assess if activity sensors can be used to accurately classify behaviour of wild reindeer. Classification of behavior types have been done based on video recordings from GPS collars mounted on two free-ranging wild reindeer. Three main questions have been addressed; (1) is it possible to differentiate high-intensity behaviors from low-intensity behaviors (e.g. standing from trotting)? (2) Is it possible to differentiate between behaviors with similar activity intensities (e.g. laying and standing)? (3) Is it possible to identify foraging behavior?

2 Materials and methods

2.1 Study area

The study was conducted in the Dovre mountain area in the central part of Norway (62°2'N, 9°3'E). Most of the study area is under protection as a part of the Dovrefjell-Sunndalsfjella National Park (1693 km^2) or its surrounding protected landscapes, nature reserves or habitat management areas. Parts of the area (165 km^2) were a military training area from 1923 to 2005. Completing of the restauration of this area is scheduled to 2020 (Forsvarsbygg 2016). The study was conducted during the summer months from July to September 2014. It is a large variation in topography and climate in the Dovrefjell-Sunndalsfjella National park. The area is dominated by alpine tundra vegetation and range from open plains with lush mountain vegetation to unproductive rocky hillsides. The reindeer habitat is situated above the tree line from approximately 1000 to 2000 meter above sea level, from low to high alpine zones. As much as 50% of this is classified as unproductive area (Hagen et al. 2006). The hunting season on wild reindeer started the 20^{th} of August and continued throughout the study period. In the growth season (May-September) of 2014, the average monthly temperature at Fokstugu weather station was 8.9°C (1.7°C higher than long-term average for the period 1968-2014) and the total amount of precipitation was 169mm (68% of the average for this period) (Meterologisk institutt 2014).

2.2 Study species

The wild reindeer (*Rangifer tarandus tarandus*) is a nomadic ungulate. Its physiological and behavioral features are the visible result of thousands of years of adaptation to a cold artic climate where the food resources are scarce and seasonal dependent. Limited food resources and their foraging behavior causes the wild reindeer's requirement for large habitats. Reindeer use different parts of their habitat range according to the seasonal shifts in environmental conditions (Falldorf 2012). Vegetation type and abundance are factors that influences where the reindeer forage, in both summer and winter (Heggberget et al. 2002; Iversen et al. 2014; Marell et al. 2002; Skarin et al. 2008; Skogland 1980) In Norway, they inhabits the alpine region of southern parts of the country. Earlier the wild reindeer could be found in most parts of the Norwegian mountain areas, migrating between optimal summer and winter habitat (Jordhoy 2008). Today they are only found in relatively small areas scattered around the southern parts of the country. This fragmentation is caused by human infrastructure and settlement that acts as barriers that limit the original habitat use (Panzacchi et al. 2013a).

2.3 Field work and collar specifications

The two adult female reindeers in this study were tranquilized from a helicopter and fitted with GPS-collars that had an incorporated activity sensor, video camera and thermometer. The video cameras were pre-programmed to start recording after the animal had recovered from the anesthetics. The activity sensors on the GPS Plus Collars (Vectronic Aerospace GmbH, Berlin, Germany) measure activity intensity on two axis. The X-axis measured forward and backward movements and the Y-axis measured rotary movements and sideways movements. The sensors measured movements as the acceleration force experienced by the collar. Activity was measured four times per second and the measurements were then averaged for a interval of 5 minutes. The measurement range was scaled to a value between 0 and 255 for both axis and was stored in the device with the date, time and temperature (Krop-Benesch et al. 2011). Due to the remotely operated release function of the collar, the animals were not tranquilized when the collars were removed. After the drop-off function was activated and the collar was recovered, the video recordings and the activity measurements were extracted from the devices and stored for further analysis.

2.4 Data collection

Female 1 (collar serial number 11408) recorded videos for a duration of 67 days from the 2nd of July 2014 to the 7th of September 2014. Each day the video camera recorded one sequence in the morning at approximately 09:00am and one sequence in the evening at approximately 06:00pm. Except for one video, the recording interval was 10 minutes (+5 seconds). The sequence that deviated from the rest had a length of 6 minutes and 19 seconds. Female 2 (collar serial number 12124) recorded videos for a duration of 62 days from the 20th of July 2014 to the 19th of September 2014. Recording interval was 10 minutes (+/-10 seconds). The video camera recorded approximately two sequences a day, but the timing varied throughout the day.

Activity sensors recorded activity for bouts of 5-minute intervals and were matched to the video data as closely as possible. Both activity measurements and video data were labeled with date and time of registration, thus making it possible to match the pair of X and Y values from the activity measurements with the corresponding video sequence. It was not a complete synchronicity between the two data types. While the activity measurements followed the 5-minute division of the clock (e.g. 00:00, 00:05, 00:10), the video sequences deviated from this pattern with +/- 3 minutes. When matching the 10-minute video sequence with the 5-minute activity measurement, the video had to be split up in two parts, so that each part corresponded with a 5-minute activity measurement. Because of the in-synchronicity, this produced one 5-minute interval with a complete overlap between video length and activity measure length, and one 5-minute interval where 0-3 minutes of video was missing. Samples were excluded from the study when >1 minute of video was missing, when the sample had missing values for activity measurements, or when bad light conditions or water vapor on the camera lense prevented identification of behavior type.

Female number 1 provided 169 samples (activity measurement and the corresponding video sequence) and female number 2 provided 79 samples. In total, this added up to 248 samples, which was included in the behavior classification and statistical analysis.

2.5 Behavior observations

Each of the 248 video sequences of approximately 5 minutes duration uncovered the second by second behavior of the reindeer carrying the video collar. It was only possible to visually identify movement of the head and lower jaw and the gate or the positioning of the body according to surrounding environment (figure 1). To be able to compare the observed behaviors with the measured activity from the activity sensors it was necessary to interpret these behaviors and classify them in terms of behavior types. There are no general method of explaining behavior, so behavior categories and their definition had to be developed for this particular study.

For every 5-minute interval of video data, an average observable behavior had to be identified. The behavior types had to include behaviors that stretched over a period of preferably a few minutes, or behaviors that were repeated so many times that they dominated the interval. Minor behaviors that had a duration of just a few seconds, or behaviors that were not repeated in one sample (e.g. drinking, scratching, sneezing), were behaviors that I did not expect to have an effect on the activity measurements for a 5-minute interval. However, when many of these minor behaviors occurred in one interval it could have an effect on the activity measurements. Therefore, it was convenient to gather these behaviors in the behavior category “head movement”.

The behavior categories and classification criteria are listed in table 1. For each 5-minute video sequence, I identified one main behavior and one secondary behavior: 1) Main behavior: behaviors involving leg movement and positioning of the torso, and 2) secondary behavior: grazing behavior or other behaviors, different from main behavior, which dominates the interval (e.g. scratching, shaking). See; figure 1. The behavior category “no secondary behavior” corresponded to the incidents when the animal did not have any secondary movement other than the inevitable movement cause by different gates or leg movement. The main behavior consisted of six behavior categories and the secondary behavior consisted of five behavior categories.

2.6 Statistical analysis

Statistical analyses were done in the program R version 3.2.4 (R Core Team 2016). All graphical output and models were generated from the n=248 samples from the two female reindeer. I first inspected associations amongst the main behavior categories and then the associations amongst the secondary behavior categories. The main behaviors and secondary behaviors were subsequently treated as explanatory variables in separate analyses. The following operations and analyses were done on both the main behavior data and the secondary behavior data.

Figure 1. Examples of behaviors that were classified as secondary behaviors. The photos on the top show behaviors classified as "head movement" and the photos on the bottom shows behavior classified as "occasional grazing" (left) and "grazing" (right). Screenshot from video sequences of female 1.

Table 1. Definition of the behavior categories and their classification criteria that were used on the behavior observations in this study.

Behavior categories		**Definition/criteria**
1) Main behavior	Laying	Laying down >75 % of the time
	Standing	Standing still >75 % of the time
	Walking slow	Slow movements >75 % of the time
	Walking	Walking
	Trotting	Trotting, >25% of the time, including short periods of running
	Running	Extensive running > 25%
2) Secondary behavior	Head movement	Shaking, scratching. Only included if the animal is not grazing and if the movement is intense or extensive
	Chewing	Only included if the animal is not grazing and if the movement is intense or extensive
	Occasional grazing	Grazing 10-50 % of the time
	Grazing	Grazing >50 % of the time
	No secondary behavior	No secondary behavior except from the movement caused by "main behavior"

2.6.1 Evaluating individual differences between the two females

Evaluation of individual differences in activity measurements was done by comparing the X-values of the activity samples for every behavior category, for each female. This was done to decide if individual differences should be accounted for in the analysis.

2.6.2 Principal component analysis (PCA)

The X and Y measurements from the GPS activity sensor (activity recordings from 5-minute periods) were plotted against each other to see if there were any correlation between the variables. Because the variables X and Y were strongly correlated, I did a Principal Component Analysis (PCA) on the data. A PCA converts a set of correlated variables (in this case the X and Y variables) to a set of linearly uncorrelated variables called principal components. This is done by rotating the data to optimally portion the variance along two axes. An algorithm does this operation in these two steps: 1) Finds the axis that have the maximum variance, 2) finds a new axis with the largest variance possible while rotating the data around axis 1 (axis 2 being orthogonal to axis 1). These two axis are termed the first and second principal component (PC1 and PC2).

2.6.3 Kernel densities and overlap between the behavior categories

Kernel densities were used to illustrate if any of the behavior categories could be differentiated based on the difference in activity measurements. This was done by converting the PC1 values to kernel densities. Most of the variation in the dataset was explained by PC1, so the PC1 values of each behavior category were converted to 1-dimensional Kernel densities. The one by one overlap between the PC1 for every behavior type were calculated using the overlap package in R (Meredith & Martin 2016). The methods are based on Ridout and Linkie's (2009) method of fitting kernel density functions to observations of animals and to estimate the overlap coefficient of two density functions (where 0 is no overlap and 1 is complete overlap). It uses trigonometric functions (sin, cos, tan) to fit density curves. The overlap coefficient is the area which lays under both density curves. The true overlap coefficients were calculated for every behavior type, (e.g laying and running, chewing and grazing).

2.6.4 Linear regression analysis

Linear regression for difference in PC1 values between behavior types were conducted to test if there were significant differences in activity measurements values for each behavior type of video data. The PC1 value was used as response variable and video behavior category as predictor variable. Residual errors were assumed to be normally distributed. A low p-value ($p<0.05$) in a "global" test (using the ANOVA function) demonstrate that the mean PC1 value differ significantly among video behavior categories. Differences between behaviors categories were assessed by plotting predicted model estimates (mean PC1 values with 95% confidence limits).

3 Results

There was a strong correlation between the X and Y activity measurements (r=0.96; figure 2 and 3). There was a clear clustering of behaviors, but no complete segregation for neither main behavior (figure 2) or secondary behavior (figure 3). Due to this strong correlation, the First Principal Component (PC1) captured most of the variation in activity measurements for both main behavior and secondary behavior (figure S1 and S2; appendix). Because nearly all the variation was explained by the PC1 axis, it was sufficient to use 1-dimentional Kernels. PC2 did not add much information and was therefore omitted from further analysis.

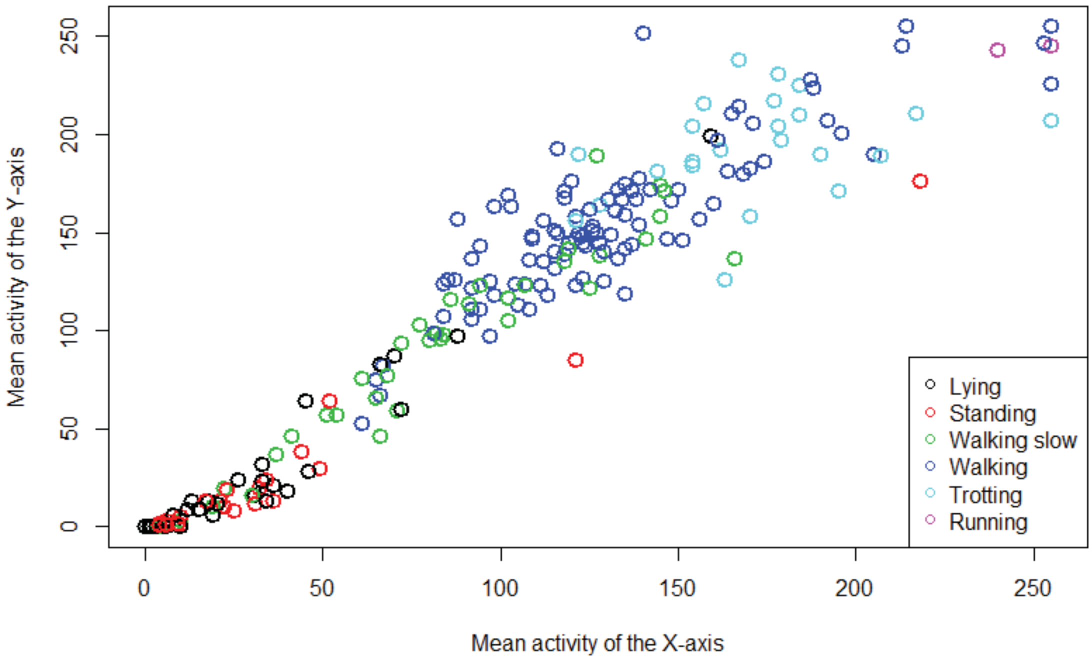

Figure 2. *Plot of activity measurements from dual-axis activity sensors in GPS-collars fitted on two wild reindeer. For each point, the X-axis shows measurements of forward-backward movements and the Y-axis shows the corresponding measurement of sideways and rotary movements. Main behaviors are differentiated by color. Some points lay on top of each other and concealed some of the clustering. This was particularly the case for the values of the minimum (x=0 and y=0) and maximum(x=255 and y=255).*

For the main behavior categories, there was a clear segregation in density distributions for most behaviors (figure 4). The linear regression analysis augmented these findings (table 2). “Running” was most clearly segregated from all other behaviors (maximum overlap 5%; table 2). “Trotting” was clearly segregated from “running” and the stationary behavior categories “laying” and “standing” (maximum overlap 5%), but had some overlap with “walking slow” (overlap 22%) and relatively large overlap with “walking” (overlap 44%). “Walking” were clearly segregated from the other behaviors (maximum overlap 13%), except for “trotting“ (overlap 44%) and “walking slow” (overlap 52%). “Walking slow” had a broad and flat density distribution compared to the other main activities. The overlap with the

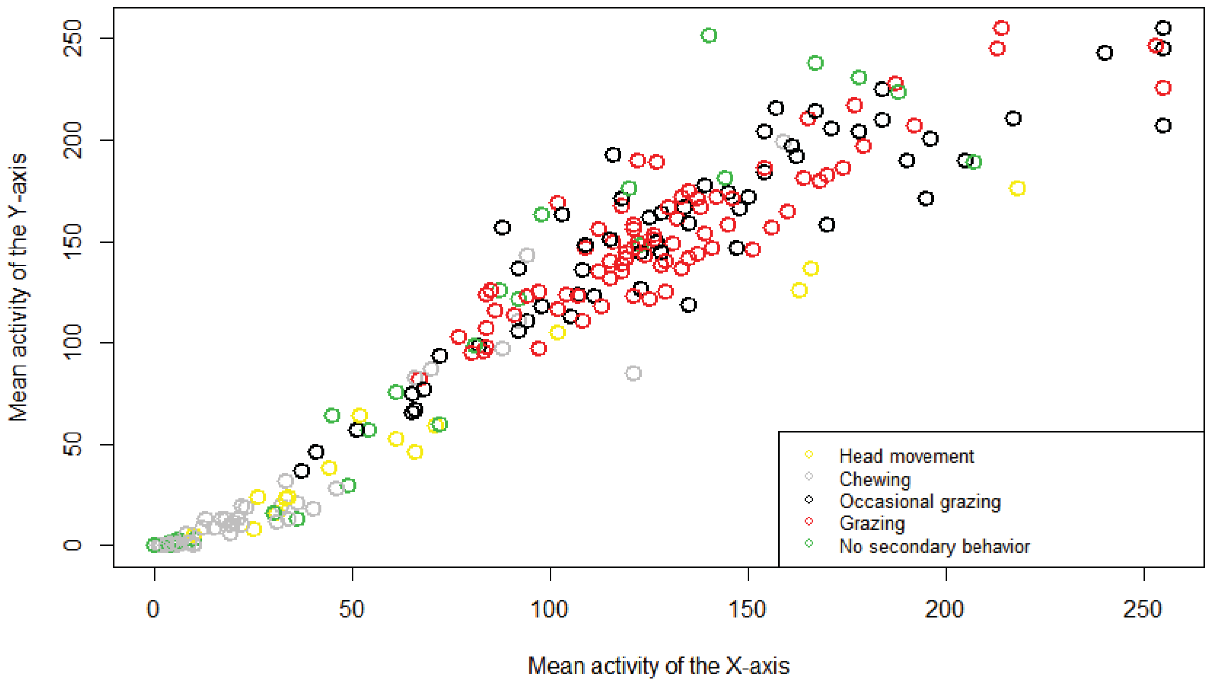

Figure 3. *Plot of activity measurements from dual-axis activity sensors in GPS-collars fitted on two wild reindeer. For each point, the X-axis shows measurements of forward-backward movements and the Y-axis shows the corresponding measurement of sideways and rotary movements. Secondary behaviors are differentiated by color. Some points lay on top of each other and concealed some of the clustering. This was particularly the case for the values of the minimum (x=0 and y=0) and maximum(x=255 and y=255).*

other behaviors except for "running" were relatively large (minimum overlap 22%). "Laying" and "standing" did not show a statistical significant difference in PC1 values from the regression analysis and had a similar density distribution. The overlap between the behaviors was large (overlap 73%). Both "laying" and "standing" had some overlap with "walking slow" (maximum overlap 31%), but were clearly segregated from the other behaviors (maximum overlap 10%). With exception of "laying" and "standing", the predicted mean values from a linear model were clearly segregated with non-overlapping confidence limits (figure 6). Predicted mean values followed the expected order with the highest predicted values for "running" and the lowest for "laying" and "standing".

For the secondary behavior categories, there was some segregation between the density distributions for the grazing behaviors ("occasional grazing" and "grazing") and the other secondary behaviors (figure 5). The linear regression analysis augmented these findings (table 3). It was no significant difference in PC1 values for the regression analysis of "occasional grazing" and "grazing" and the overlap was large (overlap 73%). Compared with the other behaviors, it was some overlap between grazing behavior and "chewing" (maximum overlap 17%), and "head movement" (maximum overlap 42%). "No secondary behavior" had a larger overlap with "occasional grazing" (overlap 73%) than "grazing" (overlap 37%). Between the categories "head movement", "chewing" and "no secondary behavior" the overlap were relative large (minimum overlap 42%). However, except for "head movement" and "no secondary behavior" all these had significant difference in PC1 values for

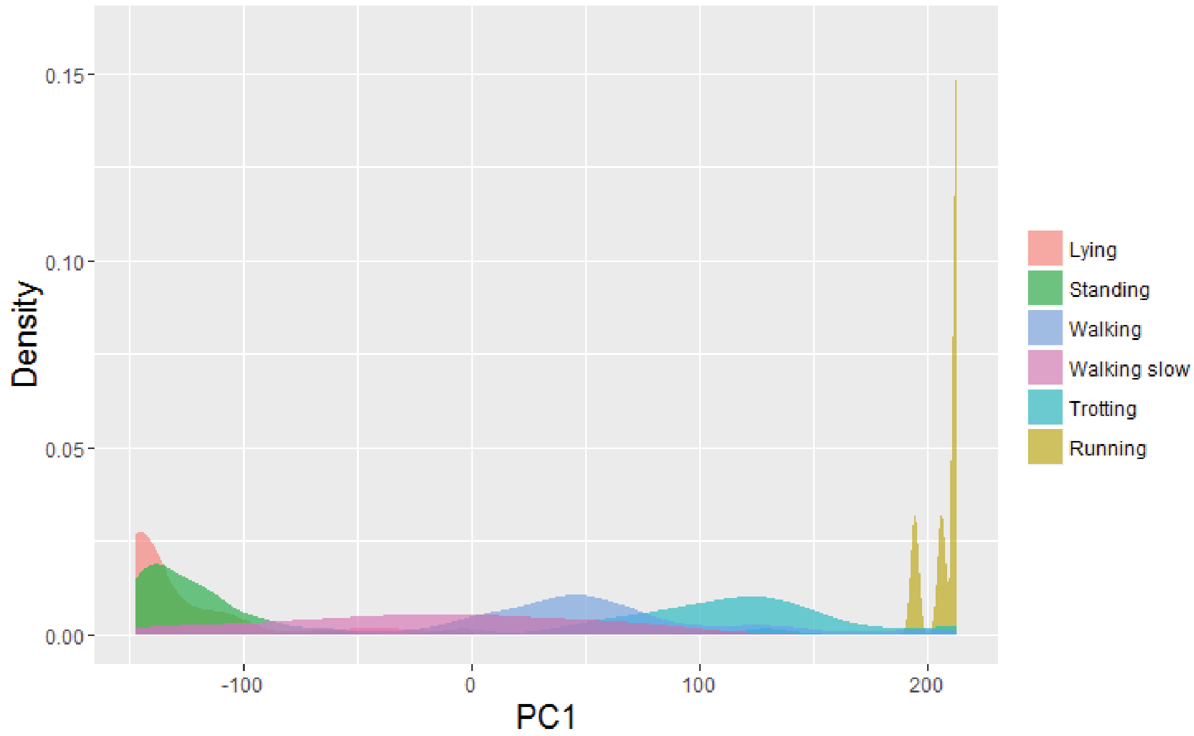

Figure 4. *Density distribution of the activity measurements (converted to First Principal Component values (PC1)) for each main behavior for two wild reindeer fitted with video camera and activity sensor.*

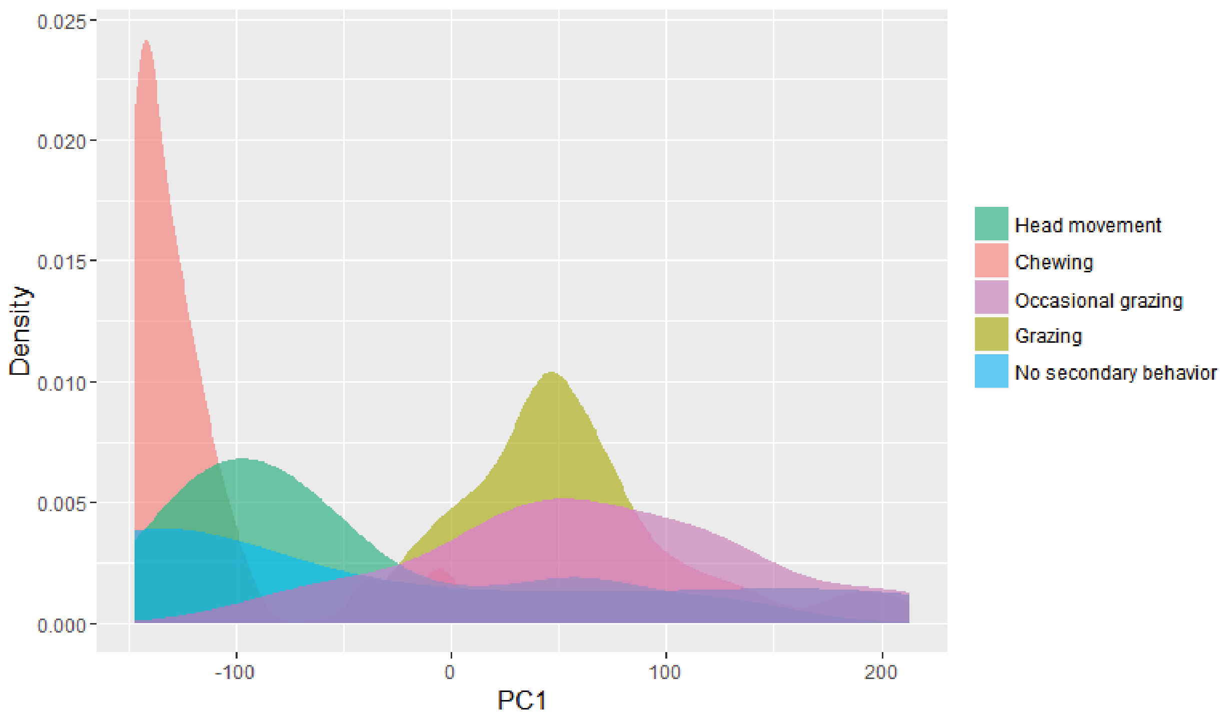

Figure 5. *Density distribution of the activity measurements (converted to First Principal Component values (PC1)) for each secondary behavior for two wild reindeer fitted with video camera and activity sensor.*

the regression analysis. The predicted mean values for the grazing behaviour categories “occasional grazing” and ”grazing”, had overlapping confidence limits and could therefore not be segregated (figure 7). However, the grazing categories had the highest predicted activity values and were clearly segregated from the rest of the secondary categories. Predicted mean values “chewing” and “no secondary behaviour” had non-overlapping confidence intervals and could also be segregated. “Head movement” had overlapping confidence interval with both “no secondary behaviour” and “chewing”.

For every main behavior, it was also a corresponding secondary behavior that could have influenced the outcome. Number of samples for each behavior category is displayed in table 4. Some combinations were more common: “Walking” and “trotting” (55 samples), “walking” and “occasional grazing” (34 samples) and “laying” and “chewing” (34 samples). The ruminating behavior “chewing“ was mostly associated with main behaviors of low intensity and grazing behavior mostly associated with intermediate intensity behaviors. The behavior category “walking slow” was associated with foraging behavior (“occasional grazing” and “grazing”) in 70 % of the samples and “walking” was associated with foraging behavior in 90% of the samples. “Running” and “trotting” were associated with “occasional grazing” in about half of the samples. In contrast, none of the stationary behaviors

Table 2. *Overlap and linear regression output for main behaviors with corresponding activity measurements from GPS-collars of two wild reindeer. Activity measurements are converted to First Principal Component values (PC1 values). Overlap is the true overlap of PC1 values between each pair of main behaviors. The linear regression tests if there are any significant differences in PC1 values between each pair of main behaviors.*

	Overlap	Linear regression			
	Proportion	Mean difference	SE	t-value	p-value
Laying vs. Standing	0.731	13.897	12.847	1.082	**0.280**
Laying vs. Walking slow	0.287	102.127	11.427	8.937	<0.001
Laying vs. Walking	0.083	179.791	8.953	20.081	<0.001
Laying vs. Trotting	0.019	242.978	12.847	18.913	<0.001
Laying vs. Running	0.000	332.652	21.335	15.592	<0.001
Standing vs. Walking slow	0.308	88.23	13.83	6.381	<0.001
Standing vs. Walking	0.104	165.89	11.86	13.983	<0.001
Standing vs. Trotting	0.043	229.08	15.02	15.250	<0.001
Standing vs. Running	0.000	318.75	22.71	14.036	<0.001
Walking slow vs. Walking	0.516	77.664	10.309	7.534	<0.001
Walking slow vs. Trotting	0.221	140.851	13.826	10.187	<0.001
Walking slow vs. Running	0.000	230.525	21.938	10.508	<0.001
Walking vs. Trotting	0.435	63.186	11.864	5.326	<0.001
Walking vs. Running	0.030	152.861	20.757	7.364	<0.001
Trotting vs. Running	0.052	89.67	22.71	3.949	<0.001

Table 3. *Overlap and linear regression output for secondary behaviors with corresponding activity measurements from GPS-collars of two wild reindeer. Activity measurements are converted to First Principal Component values (PC1 values). Overlap is the true overlap of PC1 values between each pair of secondary behaviors. The linear regression tests if there are any significant differences in PC1 values between each pair of main behaviors.*

	Overlap	Linear regression			
	Proportion	Mean difference	SE	t-value	p-value
Head movement vs. Chewing	0.459	-61.26	23.34	-2.625	0.009
Head movement vs. Occasional grazing	0.424	117.11	22.99	5.094	<0.001
Head movement vs. Grazing	0.321	109.75	22.47	4.883	<0.001
Head movement vs. No secondary behavior	0.727	19.47	23.81	0.818	**0.414**
Chewing vs. Occasional grazing	0.169	178.37	15.09	11.822	<0.001
Chewing vs. Grazing	0.125	171.02	14.29	11.965	<0.000
Chewing vs. No secondary behavior	0.423	80.73	16.31	4.949	<0.001
Occasional grazing vs. Grazing	0.729	-7.35	13.713	0.536	**0.592**
Occasional grazing vs. No secondary behavior	0.731	-97.644	15.805	-6.178	<0.001
Grazing vs. No secondary behavior	0.366	-90.289	15.049	-6.000	<0.001

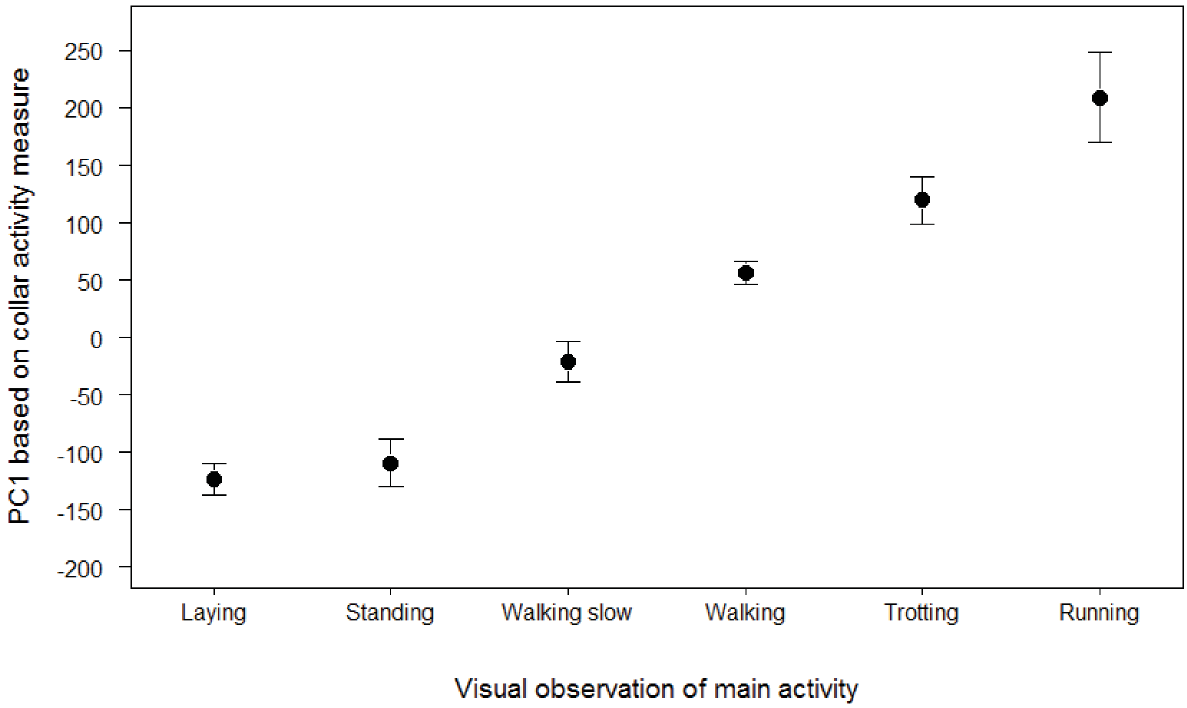

Figure 6. *Predicted mean values with confidence intervals from a linear model of the activity measurements (converted to First Principal Component values (PC1)) for each main behavior. Based on real-time video recordings and activity measurements from GPS-collars fitted on two wild reindeer.*

were associated with grazing behavior. Except for two incidents of antler chewing, shaking and scratching were the only behaviors in the "head movement" category. These behaviors occurred together with the low intensity main behavior categories ("laying", "standing" and "walking slow").

The “no secondary behavior” category were set as a default when no other secondary behavior were recorded. This category was the secondary behavior that most frequently was associated with the main behavior category “laying”. It also was associated with “running” in 4 out of 7 samples (43%). “Occasional grazing” was most often associated with the main behavior categories “walking” and “trotting”, which are of intermediate to high intensity.

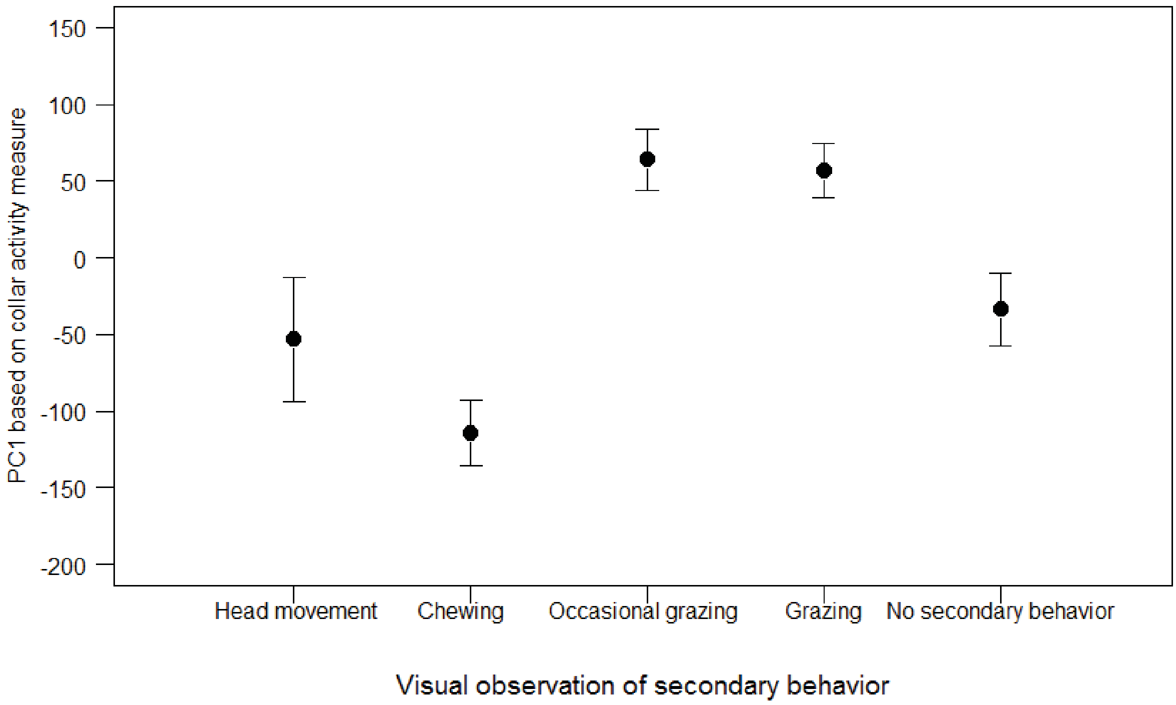

Figure 7. *Predicted mean values with confidence intervals from a linear model of the activity measurements (converted to First Principal Component values (PC1)) for each secondary behavior. Based on real-time video recordings and activity measurements from GPS-collars fitted on two wild reindeer.*

Table 4. Both main behavior and secondary behavior were classified for each sample. Number of every possible combination of these two are shown in the table. Percentage relative to main activity is shown in brackets.

	Secondary behavior				
Main behavior	Head movement (n=15)	Chewing (=52)	Occasional grazing (=60)	Grazing (=77)	No secondary behavior (n=44)
Laying (n=54)	3 (6%)	34 (63%)	0 (0%)	0 (0%)	17 (31%)
Standing (n=25)	6 (24%)	14 (56%)	0 (0%)	0 (0%)	5 (20%)
Walking slow (n=36)	4 (11%)	2 (6%)	8 (22%)	17 (47%)	5 (14%)
Walking (=101)	1 (1%)	2 (2%)	35 (35%)	55 (54%)	8 (8%)
Trotting (n=25)	1 (4%)	0 (0%)	14 (56%)	5 (20%)	5 (20%)
Running (n=7)	0 (0%)	0 (0%)	3 (43%)	0 (0%)	4 (57%)

Except from the secondary behavior category “no secondary behavior”, female 2 yielded on average slightly higher activity measurements than female 1 (figure S3 and S4; appendix). For the “no secondary behaviors” category the difference in activity values were large. However, individual differences were on average relatively small and was not accounted for in the analysis.

4 Discussion

The use of activity sensors has become widespread in the last decade. However, this is to my knowledge the first study that evaluates the possibility of differentiate between behaviors of free-ranging wild animals with the use of GPS video collars with incorporated activity sensors. I found that it is possible to differentiate if the reindeer is stationary, walking slow, walking, trotting or running based on the activity measurements. My results also suggest that grazing behaviors could be separated from other secondary behaviors. The implications of my findings are that after calibration from video, activity sensors presents a relatively inexpensive method of remote monitoring the behavior of the wild reindeer, that can yield useful knowledge on detailed activity patterns and energy expenditure. This can further be used to study the effect of anthropogenic infrastructure and other human activities on reindeer behavior and energy balance.

4.1 The capacity of the method – which categories can be separated

The majority of ungulates display the gaits walk, trot and gallop. In contrast to predatory mammals, they also have similar foraging movements and patterns. I managed to separate the high intensity behavior category "running" from the intermediate intensity behavior "trotting". These gaits cost most in term of energy expenditure, being similar with energy expenditure of climbing up almost vertical terrain (Boertje 1985). My findings were similar to what Heurich et al. (2012) found for captive red deer (*Cervus epaphus)* and what (Lottker et al. 2009) found for captive roe deer. They used the same type of activity sensor with the same 5-minute sample interval. Out of their four behavior categories they managed to separate resting, slow movement/foraging and fast movement. They also validated the threshold values for these three behavior categories. Because of the small sample sizes of some of my behavior categories, I could not test the performance of my result in the same manner. For free-ranging ungulates, the activity measurements have rarely been assigned to several different activity types as I have done. Most of them have only related the measurements to relative activity intensities (Krop-Benesch et al. 2013) or high or low behavior intensity (Gottardi et al. 2010; Van Oort et al. 2004). Mosser et al. (2014) fitted activity sensors on captive reindeer and recorded their behaviors for 53 hours. They then assigned energetic expenditure to each of the eight behavior categories. Models were developed based on the results from the captive study and were used to estimate activity pattern and energy expenditure on 131 free-ranging woodland caribou (*Rangifer tarandus caribou*) for a period of 13 months. Being able to differentiate activity into the same types, this demonstrate that my method is able to quantify an accurate activity budget, which is the first step toward an energy expenditure model. The use of activity sensors to quantify energy expenditure is a recent development (Mosser et al. 2014; Nathan et al. 2012; Wilson et al. 2012). It uses activity measurements (in terms of activity intensity or behaviour types) as a proxy for energy expenditure. The next step for my data would be to quantify the energy expenditure during each activity (Boertje 1985; Nilssen et al. 1984). Then the activity measurements could be combined with location data, to model where and when the environment drain energy and where and when it provides energy. These energetic landscapes can accurately identify effects of different stimuli in different temporal and spatial scales. However, the laboratory to field approach has its limitations since the behaviors can yield different activity measurements when the animal is moving in a heterogeneous environment (Mosser et al. 2014). Unlike other studies to date, my study shows that the behavior classification of wild reindeer can be conducted directly in the wild, while simultaneously measure activity.

The high degree of overlap between the grazing categories in my study indicates that it is difficult to differentiate between high and low grazing frequency. Grazing behaviors were most often associated with the main behavior categories "walking" and "trotting", which are of intermediate intensity. This means that even though a reindeer was grazing only a short period of the interval, it was still moving at an intensity that possibly could yield similar activity measurements as a reindeer that was grazing intensively. Even though Lottker et al. (2009) and Heurich et al. (2012) only used pure samples of foraging and slow locomotion they did not manage to separate the activity measurements for these two categories. Other studies on wild ungulates have to my knowledge not tried to differentiate activity measurements for walking and grazing. Activity sensors mounted on a neck collar have its limitations, since it only can detect the movements experienced by the animal's neck. To further improve the quantification of foraging behavior, it is possible to use a collar with three axis or incorporating a gyroscope (Wilson et al. 2013). A gyroscope could possibly be more suitable for identification of foraging behavior because it uses the Earth's gravity to determine orientation. The results for the secondary activities suggest that it is possible to differentiate grazing from non-grazing events. However, these effects could arise merely because a reindeer that was moving at an intermediate speed also, more often than not, was foraging at the same time. The stationary main behavior categories "laying" and "standing" did not show a statistical significant difference in PC1 values for the activity measurements. This is not surprising since the activity sensor cannot differentiate between body positions, if the intensity of the activity of the movement do not differ. Some studies have however managed to identify such small differences (Nathan et al. 2012).

Failing to separate "laying" and "standing" should not be of great concern, since the expected energy expenditure between two stationary behaviors should be similar (Boertje 1985). I propose that the broad and flat kernel density distribution of the "walking slow" behavior category compared to the other main behaviors is due to the classification criteria. It allowed for the interval to included up to 25% movement that have higher intensity than a reindeer that was only walking slow (e.g. walking or short periods of trotting). It could also be affected by the secondary behaviors, which could be both high and low in intensity, such as “grazing” or “no secondary behavior”.

It is important to find an optimal sampling interval for the activity measurements. In my study, the activity measurements were measured four times per seconds, but since it was averaged for a 5-minute interval the sampling length were much larger than the duration of the minor behaviors. I found that it was difficult to identify minor behaviors such as rumination with the use of an activity sensor mounted on a neck collar. As the activity measurements were averaged, high intensity behaviors could then conceal these minor behaviors when they occurred in the same interval. To identify rare and short-lasting behavioral events, the sampling length should be shorter than the event that we want to identify (Ropert-Coudert & Wilson 2004). Consistently with other studies on reindeer and caribou (Mosser et al. 2014; Thompson et al. 2012), my study also demonstrates that a video camera could be used to identify these behaviors. When shortening the sample interval, the chance of overlooking the low activity periods will be lower. However, for the common activity types the resolution is sufficient and could even be longer. Lottker et al. (2009) and (Heurich et al. 2012) also used the method of averaging the activity measurements for every 5-minute interval for red deer and roe deer. They suggested that the activity measurement could be averaged for up to 30-minute intervals to prevent that minor movements (e.g. the transition from laying to standing position) would affect the measurements. For the wild reindeer, I recorded frequent shifts in behavior types (e.g. standing to running) within the 5-minute interval. I therefore expect that larger intervals could miss some important features of the activity pattern.

Both the calibration of the device, fitting of the collar, different physiological features and different environmental features like terrain and vegetation could affect activity measurements, even though the animals’ activity intensity were the same. In my study the in-synchronicity between the activity measurements and the video recordings yielded intervals where up to one minute of behavior were unknown. This could possibly have affected the accuracy of the behavior classification of these intervals, and demonstrates the importance of calibration between different devices. If the fitting of the neck collar deviates between individuals, the movement experienced by a loosely fitted collar will be greater than by a tightly fitted one. This type of bias can be prevented by standardizing the fitting procedure of the collars (Gervasi et al. 2006). Individual differences like age or sex could affect the activity measurements (Lottker et al. 2009). I have combined activity measurements and video recordings from two adult females. Female 2 yielded on average only slightly higher activity measurements. It should however be kept in mind that such differences could be larger between other individuals. Augustine and Derner (2013) suggested that different vegetation types should be accounted for by calibration. Despite the large variety of terrain the reindeer encountered, I still managing to segregate different behaviors. When GPS collars with activity sensors are adequately calibrated, my classification criteria could likely be applied to activity measurements from other reindeer. Some studies have also found that the same methodology could be applied on a different species (Heurich et al. 2012, Lottker et al. 2009). This new approach to behavior studies will make studies more comparable, it removes the observer bias and it is cost and time efficient. In conclusion, my findings demonstrates that activity sensors can be used to quantify key behavioral types such as running and grazing in free-ranging wild reindeer.

4.2 Relevance to management of wild reindeer

Fragmentation, habitat loss and disturbance are key elements in conservation of wild reindeer in Norway. Fragmentation is caused by human infrastructure and settlement that acts as barriers that limit the original habitat use (Panzacchi et al. 2013a). In some areas it is still ongoing plans for anthropogenic developed that will have negative effects on migration patterns (Panzacchi et al. 2013b). Human activity, such as different types of outdoor activities are known to influences reindeer habitat use and avoidance (review: Reimers & Colman 2006; Vistnes & Nellemann 2008). A road or a tourist trail that act as an impermeable barrier, or an area that is completely avoided, will easily be identified by monitoring location data. However, the detailed activity pattern (including loss of feeding time) close to these areas is more challenging to quantify. In some cases, it is also reasonable to presume that the reindeer cross or utilize areas that have a more subtle negative effect. By enabling identification of the activity budget in these areas, the spatio-temporal management can be adapted to minimize the negative effect on the reindeer.

Much of the reindeer habitats in Norway are protected. This imposes restrictions on its use, even though recreational outdoor activities are allowed. In my study area, a former military training field is undergoing a nature restauration with the purpose of incorporate the area into the surrounding protected areas (Forsvarsbygg 2016). This has caused a conflict with the local farmers that would like to keep the roads to gain access to their livestock. This illustrates the conflicts that could arise between the local community's interests and the interests of nature conservation. To justify these kinds of restrictions and not make the regulation more restraining than necessary, more knowledge about reindeer's response to potential disturbances is crucial. This will ensure an optimal management strategy for both the mountain ecosystem and the local community.

In the future, global warming can potential change the migratory pattern and result in increased pressure on the last remaining areas with intact alpine ecosystems. My study demonstrates that activity sensors could be useful devices for monitoring activity budgets in relation to anthropogenic disturbances and habitat changes. This will provide information that can be used for rapid adaptation of reindeer management strategies to enhance sustainable use.

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6 Appendix

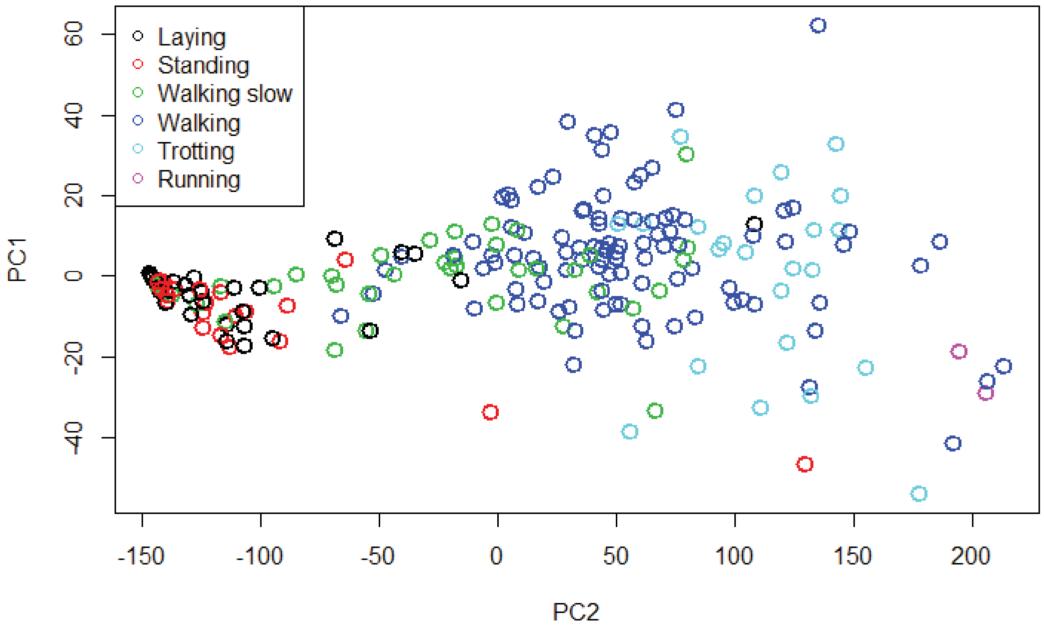

Figure S1. *Values of the First Principal Component (PC1) and Second Principal Component (PC2) for the main behavior categories.*

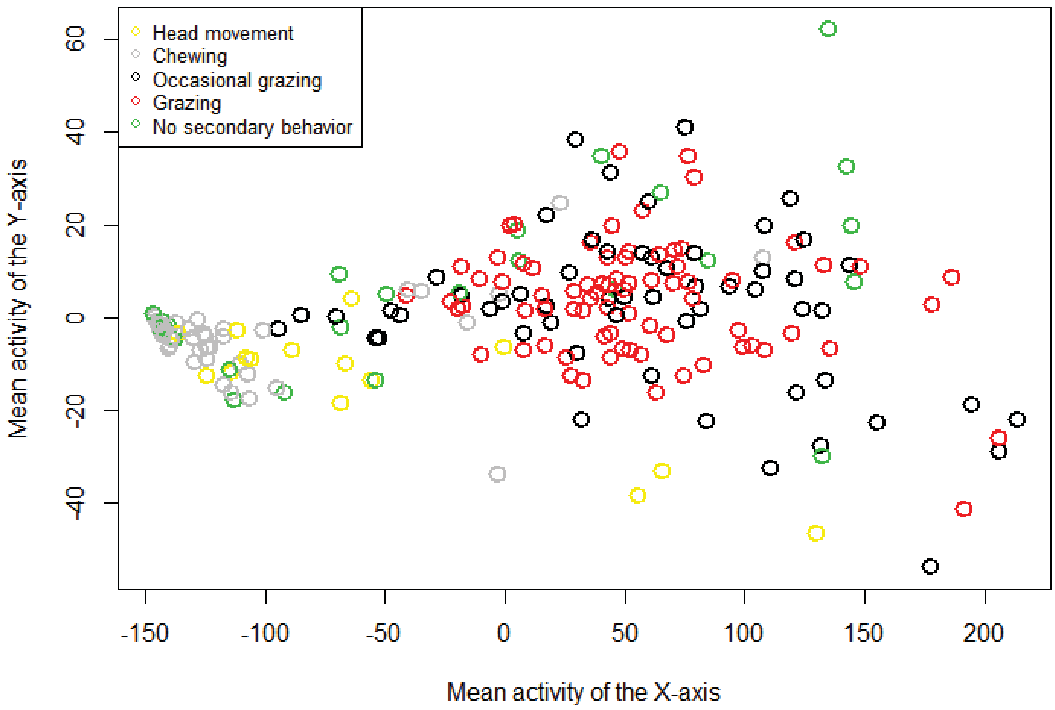

Figure S2. *Values of the First Principal Component (PC1) and Second Principal Component (PC2) for the secondary behavior categories.*

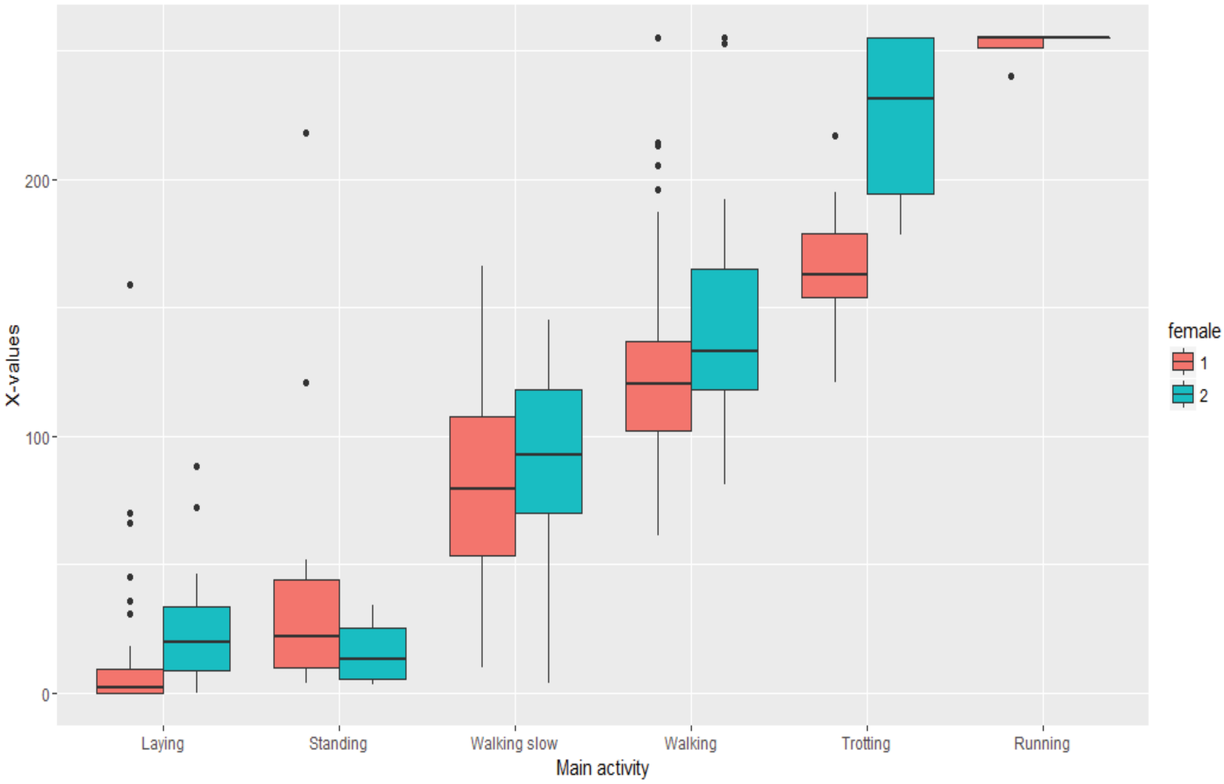

Figure S3. *Box plot of the X-values (back and forth movements) of activity data for each of the main behavior categories. Values for female 1 are shown in red and values for female 2 are shown in blue.*

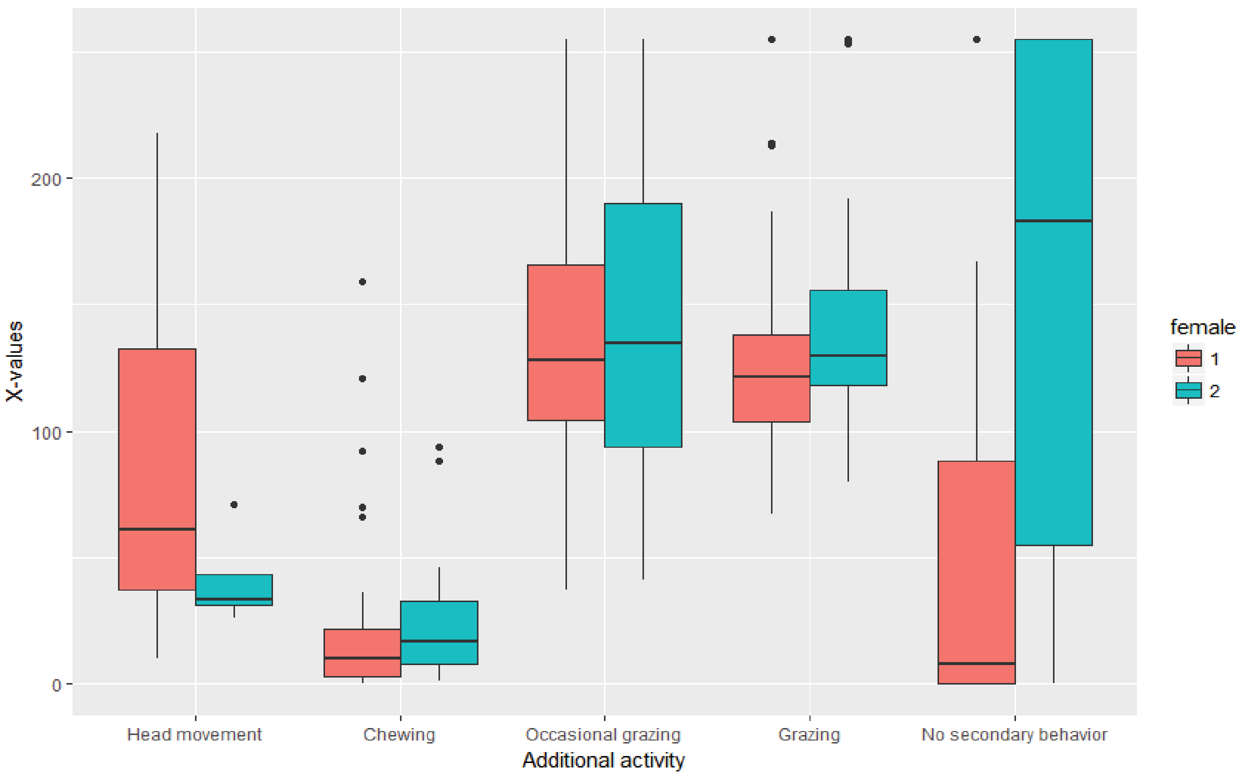

Figure S4. *Box plot of the X-values (back and forth movements) of acceleration data for each of the secondary behavior categories. Values for female 1 are shown in red and values for female 2 are shown in blue.*

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