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Abstract

Reliable species population estimates are important for population conservation and management. Information about population sizes is needed to introduce certain preservation and regulation approaches. Several different methods, both performed in the field and analytical, can be used to estimate species densities. The aim of this thesis was to evaluate densities of moose (Alces alces), red deer (Cervus elaphus), roe deer (Capreolus capreolus), and fallow deer (Dama dama) in a confined area in Västerbotten, Sweden, via three different non-invasive wildlife census methods: camera trapping, traditional dung pellet group counts, and DNA-based ID-ing of dung samples. Due to analytical problems in the lab, the latter method was excluded from any further analysis. Species densities were estimated via the Random Encounter Model (REM) from recorded pictures of camera traps. Further investigations from camera trap data were made to compare sex-ratio, day- and night-capture events, the influence of snow depth and the use of habitat type among the ungulate species. Density estimates of dung counts considered the defecation rate of each species and the accumulation period of dung. For moose, camera traps yielded a population estimate similar to dung counts. However, estimated densities from the dung count approach were much lower for all other three ungulate species than densities from the camera trapping. Even though the use of camera traps is more time consuming and costly, this method is evaluated as a trustworthy estimator of population sizes. In addition, further information about habitat associations, activity patterns, behaviour, or community structure can be successfully accomplished.

1 Introduction

Monitoring and reliable assessing of animal populations is a challenging process in wildlife ecology (Caughley 1977; Williams, Nichols & Conroy 2001; Burton et al. 2015); especially for rare and elusive species that have a low probability of detection (Petit & Valiere 2006; Guschanski et al. 2009). However, species population estimates are important for population conservation and management to introduce certain preservation and regulation approaches (Eggert, Eggert & Woodruff 2003; Noon et al. 2012). Besides population size, data on habitat use, sex ratio, age structure, genetic variation, and intraspecific interactions are also required for effective species management, e.g. game species (Härkönen & Heikkilä 1999; Williams, Nichols & Conroy 2001; Eggert, Eggert & Woodruff 2003). Several different methods, both performed in the field and analytical, can be used to estimate species densities and determine population sizes. Census approaches can be performed directly or indirectly. Direct observations count the amount of detected animals via aerial, drive, waterhole or foot counts, whereas indirect counts are based on signs that are left behind by the animal such as dung, tracks or feeding signs (Cromsigt et al. 2009).

For ungulates and especially those species that are difficult to detect, indirect methods like dung pellet group counts are widely used (Hemami & Dolman 2005; e.g. red deer (*Cerphus elaphus*): Batcheler 1975; roe deer (*Capreolus capreolus*): Cederlund & Liberg 1995; fallow deer (*Dama dama*): Bailey & Putman 1981; forest elephants (*Loxodonta cyclotis*): Eggert, Eggert & Woodruff 2003; wild boar (*Sus scrofa*): Plhal et al. 2014). Already in 1940, Bennett et al. applied dung pellet group frequencies as index for deer population sizes to analyse trends in herd numbers and observe habitat use. This relationship between counted dung piles and species numbers has been well developed in the recent years for estimating population sizes (Eggert, Eggert & Woodruff 2003). According to Plhal et al. (2014) counts of dung pellet groups is one of the most common and most accurate methods for determining animal numbers. Furthermore, dung counts have been shown to give similar estimates compared to other methods for a wide range of vertebrate groups (Barnes 2001). Nevertheless, no information about sex ratio, age structure, activity patterns or the degree of relatedness between individuals can be obtained.

In recent years the use of camera traps has become increasingly popular for monitoring wildlife (O'Connell, Nichols & Karanth 2011; Rovero et al. 2013). Technological advances in infrared sensors and digital photography have led to non-invasive means of generating

reliable detection of elusive wildlife (Burton et al. 2015). Moreover, automated camera traps provide insight into wildlife habitat use (Kucera & Barrett 2011). In contrast to pellet counts, this non-invasive approach produces direct observations and provides not only information about species abundance but also about habitat associations, activity patterns, behaviour, and community structure such as sex-ratio and age-structure (Rovero et al. 2013; Flemming et al. 2014). Furthermore, mark-recapture protocols can be used to estimate population sizes for conspicuous species with unique natural markings, like coat and colour structures (Kays et al. 2011; e.g. tiger (Panthera tigris): Karanth & Nichols 1998; ocelot (Leopardus pardalis): Trolle & Kéry 2003; jaguar (Panthera onca): Silver et al. 2004). However, these protocols are not always easy to implement and are highly time consuming. In contrast, Rowcliffe et al. (2008) developed a method where individual recognition of animals is not needed. An estimator for animal density can be derived from rates of contact between animals and camera traps. This so called Random Encounter Model (REM) has since been applied in several studies (e.g. Harvey's duiker (Cephalophus harveyi): Rovero & Marshall 2009; European pine marten (*Martes martes*): Manzo et al. 2011; hares (Lepus): Caravaggi et al. 2015).

An even more recent development is the use of molecular techniques in conservation biology and wildlife management (Paxinos et al. 1997; Guschanski et al. 2009). Population estimates via the analysis of environmental DNA (eDNA) from non-invasively collected material like dung pellets involve the development of species-specific genetic markers. These markers can then be used to identify and survey elusive species or individuals without handling an animal (Paxinos et al. 1997; Petit & Valiere 2006). Individual identification using a molecular fingerprint allows a direct count of sampled individuals and provides a possible comparison with the numbers of individuals inferred from other approaches (Guschanski et al. 2009). Population estimates can be conducted via the general principle of capture-mark-recapture (CMR) experiments where individuals are marked in a first capture session. The proportion of marked individuals in subsequent recapture sessions can then be recorded and population size N is estimated from the ratio of marked to unmarked individuals in recapture sessions (Williams, Nichol & Conroy 2001; Petit & Valiere 2006). However, population sizes can also be estimated from single sampling sessions. So called accumulation curve methods (ACM) plot the number of unique molecular tags against the number of analysed samples where the asymptote gives the estimated population size (Eggert, Eggert & Woodruff 2003; Petit & Valiere 2006).

Furthermore, individual home ranges (Taberlet et al. 1997) or dispersal (Gerloff et al. 1999) can be studied.

It is currently unclear how novel wildlife census techniques such as camera traps and the analysis of eDNA compare to more traditional methods in their accuracy and efficiency of estimating population sizes, relative to the effort that each method involves. Within this Master thesis I applied the three above mentioned methods to estimate population sizes of moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*) on a peninsula in Västerbotten, northern Sweden (see Figure 1). The different approaches were compared in terms of their population estimates but also regarding their accuracy and effort. The following hypotheses were made:

- I expected the three methods to reveal similar population estimates for each of the four ungulate species.
- (II) I expected camera traps compared to dung counts and DNA-dung collections to require less effort in the field since data can be collected automatically over an arbitrary period of time. The following analysis of each recorded picture is expected to be rather time consuming. Time effort for the DNA analysis of collected dung pellets in the lab might be even higher, whereas data of dung pellet group counts can be analysed rather fast.
- (III) I hypothesized labour costs to be lowest for the conducted dung pellet group counts since no specialized equipment is needed. In contrast, costs for good cameras are rather high but can be worth to invest on a long time view. Expenses for DNA collections in the field via e.g. dung are expected to be similar to the dung counts. However, the following laboratory analysis requires a rather high budget.
- (IV) Last, validity of data (quality) is expected to be lower for the dung counts than for the other two tested methods due to the fact that a high empirical knowledge is required to classify species pellet groups correctly. Data quality, i.e. correct species assignment might be higher for the DNA results. Nevertheless, genotypic results cannot always be assigned to a unique individual with 100% confidence (Mills et al. 2000; Petit & Valiere 2006). I assumed the reliability of camera traps to be highest since species are in general clearly visible on the recorded pictures.

Additionally, I used further extracted information from the camera traps to investigate whether:

- (V) sex-ratio among species differed from equal proportions of females to males,
- (VI) the number of capture events was higher during the day than during the night due to low ungulate night activity,
- (VII) snow depth influences the number of capture events negatively by restricting movement, especially for a small ungulate species like roe deer. Moose was expected to be rather unaffected due to its large body size.
- (VIII) Last, I expected habitat types to be differently preferred by the four ungulate species.

2 Material and Methods

2.1 Study area

The study was conducted on Järnäshalvön which falls within the municipality of Nordmaling (province of Västerbotten, northern Sweden). The peninsula is expected to contain closed subpopulations of several species. A fenced highway and railway isolate the northern part of the peninsula from the mainland. The towns of Nordmaling and Hörnefors form further dispersal barriers at the top north-west and north-east side, respectively. Dispersal to the south is prevented by the Baltic Sea (see Figure 1). Animal movement from the peninsula to the mainland is only possible along rivers and a few gaps in the fence, suggesting a relatively isolated, enclosed population.

Four ungulate species are known to occur on Järnäshalvön: moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*). The status of moose has changed during the last 100 years. From being a relatively rare species it has become a widely distributed and dominant species in Fennoscandia (Lavsund, Nygén & Solberg 2003). Red deer and roe deer colonized Sweden via the land-bridge between Denmark and Sweden many thousand years ago. From the 18th century onwards, the latter one was excessively hunted. Only through a hunting-prohibition in the 1840s the population recovered and spread over the whole of Sweden (Svenska Jägareförbundet). In contrast to roe deer, red deer was introduced to Järnäshalvön in the 1970s by T. Gadelius from different enclosures in Skåne and brought onto his yard near Bredvik, Järnäshalvön. With 16-17 red deer T. Gadelius also brought 12-15 fallow deer. In the beginning of the 1980s deer escaped from the enclosures. These were the individuals from which wild populations in Västerbotten originated (Erik Augustsson, personal communication as cited in Fahlgren & Lodeståhl 2011).

2.2 Study design

The study design on Järnäshalvön included eleven 1x1 km tracts which were equally distributed across the peninsula (see Figure 1). Tracts were on average 1.8 km apart from each other, with the exception of the central part of the peninsula where several lakes prevented this equal spacing of tracts. Each tract included 16 predefined sampling locations along its boundary with four evenly spaced points along each side of the tract. Sampling locations within a tract were 200 m apart from each other (see Figure 2).



Figure 1: Study area Järnäshalvön (Västerbotten, northern Sweden). Eleven tracts (classified as no. 32, 33, 39, 40, 46, 47, 48, 49, 55, 56, and 62) with sampling locations of camera traps (black points), conducted dung pellet group counts (grey points), and predefined coordinate locations (white points) along the tract boundaries. At the latter mentioned locations no dung was counted due to freshwater or private ground. White line symbolizes the highway E4 with the adjacent railway track.



Figure 2: Tract-design. 16 coordinate locations represented the sampling points and were evenly distributed along the tract boundary with four points on each 1 km side and a distance of 200 m to each other.

2.3 Data collection

2.3.1 Camera trapping

Cameras were installed within a 100 m radius at 12 of the 16 sampling locations per tract to evaluate the visitation rate of ungulate species (see Figure 1). The pre-selection of the 12 camera locations was done semi-randomly, meaning that I excluded inappropriate locations before randomly determining the 12 sampling locations. Sampling spots needed to be at least 100 m away from human activity centres like houses and roads and should not have been located in lakes or on fields. Six out of 132 camera locations had to be offset by more than 100 m from their intended sampling location due to unforeseen houses or mires (46-2, 46-12, 46-13, 48-9, 56-12, and 55-13). Camera trapping started on the 7th March 2016. Two passive infra-red cameras were mounted at two sampling locations within each of the eleven tracts for a recording period of 12 days. Hereby, I used two different camera models: 20x Reconyx Hyperfire HC 500 and 15x HCO ScoutGuard SG 560C (for differences between the camera types see Appendix Table A). Each tract was equipped with one camera of each model during one recording period. To reduce time and effort in the field, I used a rotational system for camera deployment along the tract boundary, whereby the mounted cameras per tract were always placed at sampling locations that were next to each other. After a sampling period of 12 days, cameras were switched to the next predefined locations. During this camera switch, four new cameras of each model were brought into

the pool of cameras and all were placed randomly within the eleven tracts. This process was repeated until I had covered all 12 preselected sampling locations per tract on the 20th of May 2016. In total I accomplished 144 trapping days per tract (12 locations x 12 days). However, I had to replace two cameras of the model *HCO ScoutGuard SG 560C* with the model *Reconyx Hyperfire HC 500* due to sensitivity and time recording problems (see Appendix Table B for camera design).

I based the amount of trapping days per camera on previous studies. Shannon, Lewis & Gerber (2014) tested the combination of the number of sites (cameras) and occasions (survey days) across 13 different species. The optimal design varied widely between all tested species. However, a maximum of 120 survey days revealed stable detection rates for a wide range of species. Burton et al. (2015) suggested that trapping days per camera should range from 1 to 15 days.

The detection range of cameras depends on several factors including ambient temperature and size of the animal (Rovero et al. 2013). However, based on test trials I noticed that movement was recorded within a 10-15 m distance to the camera. Therefore, I tried to ensure a minimum field of view of 10 m at all camera locations. Furthermore, I marked points at a distance of 5 m, 10 m, and 15 m from the camera with red marking tape. This allowed me to estimate the distance of recorded animals from the camera as well as their position within the field of view.

I tried to maximize ungulate detection by selecting a location within a 100 m radius of my pre-selected sampling locations where signs indicated that ungulate visitation would be high. This included game trails, tracks in the snow, and forest gaps. Nevertheless, I conducted a passive sampling approach. There was no use of visual, acoustic or olfactory attractants to lure animals to the specific camera locations. Cameras were secured to the closest suitable tree at a height of 1 m. Due to differences in snow levels among locations and across time, height was measured as 1 m from my standpoint in the snow. I programmed cameras to take three photographs when triggered with no delay between trigger events, meaning as soon as wildlife was moving in front of the lens the infrared sensor was triggered and three pictures were taken in rapid-fire. Cameras recorded date and time and imprinted it on every picture taken. Additionally, the *Reconyx Hyperfire HC 500* recorded ambient temperature. When mounting the cameras, I measured snow depth in

front of the camera and noted the type of habitat. During every camera switch every 12th day I exchanged the SD-cards and if necessary batteries.

Additionally, two cameras of the model Reconyx Hyperfire HC 500 were mounted on both sides of the Öreälven River underneath the bridge of the highway E4 on the 22nd of February 2016 to record animal's migrations. This position was considered to be the main spot where individuals could enter and leave the peninsula. Cameras were left there until the 19th of May 2016.

2.3.2 Dung sampling for DNA analyses

Besides the camera trapping, I collected dung samples within each tract to be used for DNA-analyses to determine species, individuals, and sex using an ungulate SNP-chip. Each 1x1 km tract was sampled twice during the whole study period. I performed the first collection session myself between the 15th and 26th of February 2016 where I sampled one tract per day. The second collection took place approximately one month later. From the 19nd to 21st of March 2016 I collected again dung myself sampling one tract per day. On the 22nd of March 2016 six tracts were sampled in a joint effort of four people and on the 24th of March 2016 two people collected dung within two separated tracts each.

Dung was collected for all four deer species along an east-west-gradient on five transect lines that were equally spaced within each tract (see Figure 3). As far as possible, transects were walked along a straight line with a maximum deviation of 50 m. On average three pellets of each detected ungulate pellet group were placed in one vial and marked with tract number, transect line, sampled coordinate location, assumed deer species, and snow depth. For moose I only took two pellets due to their bigger size. At the end of each day I stored the vials in a -20°C freezer to conserve the DNA until its extraction.

Due to procedural problems with the ungulate SNP-chip, the analysis of the dung DNA could not be conducted during the time of my thesis. Therefore, this method was excluded from further investigations.



Figure 3: Transect sampling of dung for DNA-analyses within each 1x1 km tract along an east-west gradient. Transect lines indicated with black arrows are 250 m apart from each other.

2.3.3 Dung pellet group counts

As a last approach, dung pellet groups were counted during the spring 2016. With this method, all dung pellet groups of moose, red deer, roe deer, and fallow deer were counted within a 5.64 m radius (=100 m²) at each of the 16 sampling locations per tract between the 2nd and 22nd May 2016 (for exact date per tract see Appendix Table D). Seven locations needed to be excluded due to lakes, flooded areas or private gardens (39-10, 39-11, 48-7, 48-8, 56-6, 56-11, and 56-12, see Figure 1). The exact coordinate locations were found with a GPS device. As the GPS indicated a distance of 10 m to the preselected coordinate location, the position where the right heel of the person conducting the count hit the ground was selected as the middle of the survey circle. A string of 5.64 m length was attached to a stick and dung groups were counted within a circle of this radius. Dung of each species was identified by its size and shape. Due to difficulties in distinguishing between roe deer and fallow deer dung, the number of pellets per dung group for these species was classified as roe deer with <45 pellets per group and fallow deer with >45 pellets per group (Eckervall 2007). Furthermore, dung pellet groups were classified according to their degree of decomposition as either old or fresh. Only the latter, which referred to droppings from fall 2015 or fresher, were included in the subsequent analyses.

2.4 Data processing and analysis

All calculations and further statistical analyses were performed in RStudio (Version 0.99.903 – © 2009-2016 RStudio, Inc.).

2.4.1 Camera trapping



Figure 4: Photographs of red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) demonstrating clear interspecific differences enabling species ID from both diurnal (**a**) red deer, **b**) roe deer) and nocturnal (**c**) red deer, **d**) roe deer) camera trap footage.

For each taken picture I recorded tract, location, date, time, trigger sequence, temperature (if available), the species present, sex, age class, and group-size for each individual ungulate on each picture. Species classifications could be performed from both diurnal and nocturnal camera trap footage (see Figure 4). Age was determined based on the animal's size and separated into young and adult if possible. For males the presence of antlers was noted. Furthermore, detection events of species other than ungulates were recorded (see Appendix Table C). Any pictures that showed recordings of humans were immediately deleted.

2.4.1.1 Random Encounter Model

Animal visitation was recorded as individual capture events. When an animal left the camera's detection zone and walked back in front of the lens, it was considered as a new capture event (M. Rowcliffe, personal communication). Rovero et al. (2013) recommended an amount of approximately 50 captures per species to obtain reasonable results for population sizes with the used approach. Burton et al. (2015) mentioned that fewer than 1000 total trap-days are likely to be insufficient to detect rare species in a study area (see also Carbone et al. 2001). Unambiguous capture events of each species were therefore summed for all tracts, meaning that I could not focus my analysis on the tract level due to insufficient individual detections per tract. With the approach of 12 trapping days at 12 locations in 11 tracts I achieved 1584 total trapping days for the whole study area Järnäshalvön.

I then used the Random Encounter Model (REM) by Rowcliffe et al. (2008) to estimate species densities (see Figure 5). This method does not require the recognition of individuals. It estimates animal densities due to rates of contact between animals and camera traps.



Figure 5: **a**) Random Encounter Model (REM). **b**) Camera detection zone. *r* represents distance between camera and animal (red line), α the angle of first detection (red angle) referring to the middle field of view (black dashed line), $d_{1,2}$ the distance an individual is walking between two pictures (red dashed line), and *x* and *y* the horizontal and vertical distance of the detected animal to the camera (black arrows).

The REM calculates species densities according to several parameters that were extracted from the taken pictures for each capture event (see Figure 5b). For each individual capture event (*i*) I estimated the ungulates position within the field of view for the first taken picture to calculate the mean distance *r* of each species to the camera (see Equation (1)) and the species specific mean detection angle θ (see Equation (2) and Figure 5b).

$$r = \frac{\sqrt{x_1^2 + y_1^2} + \sqrt{x_2^2 + y_2^2} + \dots + \sqrt{x_i^2 + y_i^2})}{i}$$
(1)

$$\theta = \frac{2\alpha_1 + 2\alpha_2 + \dots + 2\alpha_i}{i} \tag{2}$$

To calculate the mean distance v that is travelled per day for each species, its mean speed s and its proportion of time p that is spent active needed to be calculated (see Equation (3)).

$$v = s \cdot p \tag{3}$$

I derived an individual's speed s_i as the distance d_i an animal was walking during its capture event divided by the events duration t_i (see Equation (4)).

$$s_i = \frac{d_i}{t_i} \tag{4}$$

In doing so, the time duration t_i considers the number of taken pictures per individual capture event pic_{i_max} , the number of pictures on which an animal was moving pic_i , and the total time duration of the capture event e_i (see Equation (5))

$$t_i = (pic_i - 1) \cdot \frac{e_i}{pic_{i_max} - 1}$$
(5)

To estimate the proportion p of time spent active, I created activity curves with the proportion of individuals being active against the captured hour during the day. The integration of this function revealed the amount of time A a species spent active per day. Dividing A by the total possible time B, I could estimate the daily proportion p of time spent active per species (see Figure 6).

Results for daily traveling distance of moose from these camera-based calculations were compared to moose telemetry data derived from 2004 (the same months as camera traps operated in 2016; Allen et al., (II), unpublished). To correct for the fact that walking distance was measured as straight-line connections between GPS locations every 30 min, a 3rd order polynomial regression was conducted where the intercept with the y-axis indicated the day range of moose (see Appendix Figure A).



Figure 6: Example of a daily activity curve. Proportion of time spent active per day results of time **A** spent active per total possible time **B**.

To extend densities to population size, I extracted vegetation and land cover within a 50 m radius around every camera location. Only these sampled habitats where taken into account when extrapolating species densities onto the scale of Järnäshalvön. Hereby I summed the total area of Järnäshalvön that was covered by the sampled habitats. To extract habitats around every camera location I used the Swedish land cover classes map from Lantmäteriet (smdb99: 2004 delivered to SLU) in ArcMap (ArcGIS Version 10.4.0.5524 – © 1999-2015 Esri Inc.). Relative proportions of each habitat were very similar between the 50 m buffers and the whole study area (see Appendix Figure Ca).

2.4.1.2 Sex ratio

To compare captures of females and males, I estimated the percentage of individual capture events per sex and species. When animals were hidden or picture quality was insufficient, sex remained unclassified. Differences between females and males were tested for each species with a χ^2 -test.

2.4.1.3 Day- and night-ratio

Besides sex-ratio, the relative amount of diurnal and nocturnal captures was tested with a χ^2 -test. Present or absent daylight on the picture was taken as reference for the classification to day- and night-capture events, respectively.

2.4.1.4 Snow depth

Snow height was measured on the first day of each 12 days trapping period in front of each camera. The influence of snow depth was analysed with a linear correlation between the number of capture events and mean snow depth per trapping period.

2.4.1.5 Habitat preference

To link species occurrence to habitat type, the habitat within the cameras field of view was recorded and classified into the categories *clear cut*, *coniferous forest*, *young coniferous forest*, *meadow*, *mire*, *mixed forest*, and *young mixed forest*. Hereby, a capture index *I* was calculated for each habitat and species that considered the amount of capture events *c* per species per habitat type and the amount of total trapping days *d* per habitat type (see Equation (6)).

$$I = \frac{c}{d} \tag{6}$$

2.4.2 Dung pellet group counts

To estimate population sizes on Järnäshalvön from the dung counts, Equation (7) was used to calculate species density D per km². This formula has been adopted by numerous authors (e.g. Cederlund & Liberg 1995; Härkönen & Heikkilä 1999; Daniels 2006). It considers the number of detected dung pellet groups n, the sampled area a, the accumulation period t of dung, and the daily defecation rate d of each species.

$$D = \frac{n/a}{t \cdot d} \tag{7}$$

Classical studies that use dung counts to estimate species densities use the decay rate of dung instead of the accumulation period in their analysis (e.g. Mayle, Putman & Wyllie 2000; Heinze et al. 2011). However, these approaches clear their plots from dung in a first field effort to count only newly accumulated dung pellet groups. Within this thesis plots were not cleared and the accumulation period overcomes the need to use the decay rate. To estimate the time period during which dung pellet groups accumulated, only the dung classified as fresh was taken into account. These fresh pellet groups had accumulated over the period from the first leave-fall in autumn 2015 (regarding to temperature data from SMHI: 07.10.2015) until the mean date when dung was counted (07.05.2016). Defecation

rate of moose, red deer, roe deer, and fallow deer was estimated on average with 14 (Härkönen & Heikkilä 1999; Persson, Danell & Bergström 2000; Rönnegård et al. 2008), 20 (Mitchell & McCowan 1984), 20 (Mitchell et al. 1985; The Deer Initiative 2008), and 25 pellet groups per day (Massei & Genov 1998; Heinze et al. 2011), respectively.

To extract densities to population size on Järnäshalvön, I used the same approach as for the camera tapping. Again I extracted vegetation and land cover within a 50 m radius around every sampled location and proceeded as described in section 2.4.1.1. Again, relative proportions of each habitat were very similar between the 50 m buffers and the whole study area (see Appendix Figure Cb).

2.4.3 Time effort comparison

To compare the conducted methods regarding their effort, time spent in the field and time needed for data processing was estimated. Hereby, I calculated the time effort as man hours per method.

3 Results

3.1 Camera trapping

In total 173 capture events of the four investigated ungulate species were recorded in all tracts over a total period of 1584 trapping days (52 moose, 46 red deer, 69 roe deer, 6 fallow deer; see Appendix Table C). Additionally, there were four events of roe deer and one of fallow deer captured with the two cameras in the Öreälven valley. Due to the low numbers of detected fallow deer during the whole study, analyses were only performed for moose, red deer, and roe deer. Since capture events of red deer were only slightly below the recommended 50 captures by Rovero et al. (2013), the species was included into the REM analysis.

3.1.1 Random Encounter Model (REM)

Based on extracted parameters of camera traps (see Table 1), density estimates revealed 0.77 moose, 0.52 red deer, and 0.98 roe deer per km² (see Table 1). However, the estimated day range of moose from camera traps differed strongly from the day range determined with telemetry data (see Table 1). Inserting the telemetry day range of 2.93 km per day instead of the 6.21 km per day from the camera trap data into the REM, moose density was 1.64 per km² (see Table 1). When extrapolating densities to the scale of Järnäshalvön (185.07 km² excluding urban areas, freshwater, and coastal regions) the estimated population sizes on Järnäshalvön differed strongly between the camera and the telemetry approach with 143 and 303 individuals, respectively. Red deer and roe deer population size was estimated with 97 and 182 individuals, respectively (see Table 1).

Table 1: Parameters used for estimating density/numbers from camera traps. Number of individuals (n), mean detection distance to the camera (r), mean detection angle (θ), mean speed (s), proportion of time spent active (p), day range (v), density estimate (D), and population size (\hat{N}) on Järnäshalvön for the telemetry approach and the camera trapping.

Paramotor	Telemetry	Camera trappin	g	
rarameter	moose	moose	red deer	roe deer
n	22	52	46	69
r [km]	-	0.0085	0.0082	0.0056
θ [radiant]	-	0.55	0.47	0.48
s [km/d]	-	31.72	27.46	28.14
p -		0.196	0.273	0.318
v [km/d]	2.93	6.21	8.66	10.10
D [1/km ²]	1.64	0.77	0.52	0.98
Ñ	303	143	97	182

Regarding the estimated proportions of activity for the REM, all ungulate species were on average more often captured during the early morning and afternoon/evening during the whole study period (see Figure 7). This effect was especially pronounced for roe deer with high activity rates during the early morning and afternoon (see Figure 7c). Further, the proportion of moose captures corresponded with the distance moose walked on average each hour according to telemetry data from 2004 (see Figure 7a). This relationship could also be seen when focusing in detail on the certain investigated months March, April, and May. However, the effect was less pronounced in May (see Appendix Figure B).



Figure 7: Proportion of capture events per hour of **a**) moose (n=52), **b**) red deer (n=46), **c**) roe deer (n=69), and **d**) species in a stacked plot with moose (black), red deer (grey), and roe deer (white). **a**)-**c**) Black line represents activity fit through data points. **a**) Grey dashed line represents distance walked per hour [km] from telemetry data of moose.

3.1.2 Sex ratio

Moose and red deer showed significantly higher proportions of female capture events than of male events ($\chi^2(1) = 34.67$, p = 0.0005 and $\chi^2(1) = 33.14$, p = 0.001, respectively). In contrast, male roe deer were significantly more often captured than females ($\chi^2(1) = 11.27$, p = 0.0008; see Figure 8a).

3.1.3 Day- and night-ratio

Further, all three ungulate species were significantly more often captured during day light hours than during the night (moose: $\chi^2(1) = 8.65$, p = 0.003; red deer: $\chi^2(1) = 5.26$, p=0.022; roe deer: $\chi^2(1) = 53.04$, p < 0.0001; see Figure 8b).



Figure 8: Proportion of capture events per species regarding **a**) sex with females (grey), males (black), and undefined sex (white) and **b** day- (grey) and night- (black) captures.

3.1.4 Snow depth

Snow was clearly abundant during the first three trapping periods in March and beginning of April with up to 30 cm. After that snow rapidly melted. However, abundance of none of the three species significantly correlated with snow depth (see Table 2). Simply, roe deer was negatively affected by snow height but not significantly (p=0.055; see Figure 9b), whereas moose seemed to be totally unaffected (see Figure 9a).

Paramatar	Species							
	moose	red deer	roe deer					
S	0.005	0.299	-0.960					
R ²	0.046	0.098	0.644					
р	0.988	0.546	0.055					

Table 2: Regression between capture events and mean snow depth per trapping period giving values for slope s, R^2 - and p-value per species.



Figure 9: Linear regression of mean snow depth [cm] per trapping period and species capture events for **a**) moose and **b**) roe deer. Grey area indicates confidence interval.

3.1.5 Habitat preference

Moose was captured most when cameras pointed towards forest habitat, particularly young coniferous forest. Its capture index (probability of capture on one day in certain habitat) was at least twice as high in coniferous forest than in all other habitats (see Figure 10). Red deer and roe deer were captured more often in mixed forest. Especially roe deer reflected a high capture index in this habitat (see Figure 10). While moose, red deer, and roe deer were never recorded with the two cameras that faced towards a meadow, all six capture events of fallow deer occurred in this open habitat.



Habitat type

Figure 10: Capture events per trapping days of each habitat (=capture index) per habitat for moose (black), red deer (grey), and roe deer (white). Trapping days per habitat: 912 d coniferous forest, 180 d young coniferous forest, 84 d clear cut, 24 d meadow, 144 d mixed forest, 60 d young mixed forest, and 180 d mires.

Dung pellet group counts 3.2

In total 88 dung pellet groups were counted over all tracts with 45 for moose, 4 for red deer, 25 for roe deer (=under45), and 14 for fallow deer (=over45) (see Appendix Table D). When including species defecation rates and the period of dung accumulation, densities per km² resulted in 0.89 for moose, 0.06 for red deer, 0.35 for roe deer, and 0.16 for fallow deer (see Table 3). Extrapolating densities onto the scale of Järnäshalvön (185.07 km² excluding urban areas, freshwater, and coastal regions) the estimated population sizes differed strongly from population sizes suggested by the camera trapping approach. Only numbers of moose were similar with 165 individuals compared to 143 from the camera results (see Table 1 & Table 3).

Table 3: Parameters used for estimating density/numbers from dung pellet group counts. Area sampled (a), time period of dung accumulation (t), number of dung pellet groups (n), defecation rate (d), density estimate (D), and Population size (\hat{N}) on Järnäshalvön for dung pellet group counts of each species.

Paramatar		Spe	cies	
	moose	red deer	under45	over45
a		0.016	9 km²	
t		21	3 d	
n	45	4	25	14
d	14	20	20	25
D	0.89 per km ²	0.06 per km ²	0.35 per km ²	0.16 per km ²
Ñ	165	10	64	29

3.3 Time effort comparison

Camera trapping

It took two and a half days to perform one camera switch in all of the eleven tracts alone. On average I spent 1.5 to 2 h in each tract to switch two cameras – including walking to the positions and driving to the next tract – which results in ~25 man hours per camera switch. The analysis of pictures to extract the needed values could be performed in 4 days (4 x 8 h) for 22 cameras in one trapping period. Over the whole study period this results in ~217 man hours for field work and analysis.

Dung sampling for DNA analysis

To sample dung pellets along the transect lines I needed ~4.5 h for one tract. Depending on snow conditions and vegetation cover I could walk 1.25 km in 45 min to 1 h. Therefore, dung collections for the genetic approach resulted in ~99 man hours. Time effort for further data analysis in the lab is missing. The required time effort for lab work and analysis could not be assessed due to analytical problems. Therefore, no DNA analyses had been carried out at the time of writing.

Dung pellet group counts

Counting dung pellet groups at the 16 locations in one tract could be performed in ~4 h and the following analysis could be conducted in ~2 days. This resulted in ~60 man hours.

4 Discussion

In this thesis, I compared two different non-invasive approaches for calculating ungulate population sizes in an area in Västerbotten, Northern Sweden. For both conducted methods one key assumption was the presence of closed animal populations (see for camera traps: Rowcliffe et al. 2008; for dung pellet group counts: Hedges & Lawson 2006). This assumption was strongly supported by data from the mounted cameras in the Öreälven valley. Over a period of 87 days merely five ungulates were captured traversing in or out of the study area. These minimal immigration and emigration rates are expected to lead to reliable population estimates for the Järnäshalvön peninsula through both, the camera trapping and the dung pellet group count approach.

Researchers have claimed dung pellet group counts to be a common and accurate method for determining animal densities (Barnes 2001; Plhal et al. 2014). Several ungulate studies have found correlations between dung counts to direct population counts (e.g. red deer (Cerphus elaphus): Batcheler 1975; fallow deer (Dama dama): Bailey & Putman 1981). In this study, moose population estimates from dung counts were similar to numbers extracted from camera traps, with 165 and 143 individuals of moose, respectively (see Table 1 & Table 3). However, the two methods did not provide similar population estimates of red deer, roe deer, and fallow deer. Due to their conspicuousness, dung pellet groups of moose were more frequently detected than those of any other ungulate species (see Table 3). Due to the smaller pellet size of red deer, roe deer, and fallow deer dung, the detected number of dung pellet groups could be an underestimation compared to moose. Vegetation cover is often a challenging factor when counting dung pellets in the field and especially small pellets are easily missed (The Deer Initiative 2008). Therefore, the detection probability for deer dung might have been less than 100%, leading to an underestimation of actual population sizes. Further, in the case of dung pellet detections, it is not always easy to link them to the right species. To avoid misinterpretations of species classifications via dung pellets, a high level of empirical knowledge and experience are required, especially in instances when dung shapes and sizes are very similar (Smith 2012). The classification rule of less than 45 dung pellets for roe deer and more than 45 for fallow deer, which was used in this study, might not represent correct species assignment in all cases.

Effective wildlife management and conservation require reliable monitoring data (Newey et al. 2015). However, cameras can also have an imperfect detection rate due to technical

problems or the undetected processes of animal movement within the field of view (Burton et al. 2015). The efficiency of producing reliable density estimates relies on a particularly appropriate and detailed survey design due to cameras limited field of detection (Shannon, Lewis & Gerber 2014). Additionally, spatial variability such as differences in visibility and vegetation cover can create sampling errors (Burton et al. 2015). However, Rovero and Marshall (2009) assumed population overestimates via the REM of Rowcliffe et al. (2008). Tests of estimated Harvey's duiker (*Cephalophus harveyi*) abundances from the REM against estimates of a transect survey in the same area revealed higher estimates from the former mentioned REM approach. However, the degree of overestimated through the transect approach (Manzo et al. 2011). Accurately estimating the model parameters from field data can be challenging. For example, differential movement rates can severely bias the REM density estimates as shown in this study via day range calculations of the camera and telemetry approach.

In this thesis, extracted data from camera traps seemed to have revealed consistent species estimates with similar results for moose as from the dung count approach. The density estimates of both methods were within the range of densities predicted by Allen et al. ((I), unpublished) with 7.81 to 9.51 moose per 10 km² for the study area. To test the accuracy of each method, the variation, both within and between methods, could be measured by repeating the experiments (Daniels 2006). To improve the technique of camera trapping, more distance markings in the vertical but also horizontal plane should be set up within the cameras field of view to improve the extraction of distance values for each picture. Caravaggi et al. (2015) used a more modern approach. In this study detailed field marks were arranged to calculate an overlaid grid which was superimposed on each detection image to extract the exact position of each detected animal. Furthermore, a larger sequence of pictures taken per trigger event could minimize the time gap between triggers and, therefore, the loss of information for walked distances (see Rowcliffe et al. 2016 with 10 pictures per trigger). Due to time gaps of a few seconds between trigger events, walking distances could be overestimated for each individual capture event. This might explain the huge difference between calculated day ranges from camera traps and telemetry data (see Table 1). In contrast, the extracted day range from telemetry data could more likely be an underestimate. First, positions of moose were recorded only every 30 min. The polynomial regression indicated that the decline in movement rate was most pronounced with recording

intervals < 90 minutes (see Appendix Figure A). It is possible that the intercept did not fully correct for missed walking distances, leading to an underestimation of the daily movement rate. Second, it has to be considered that the telemetry data for moose was recorded more than 10 years ago in a study that covered a far bigger range than Järnäshalvön with possible different age groups of moose in 2004. Further, snow conditions inland (here north of the highway E4) differ in general from the coast with less snow in coastal areas like Järnäshalvön (Singh et al. 2012). Even though moose movements seemed to be less restricted by snow depth according to data from the camera traps (see Figure 9a), this may change as snow depth increases. Coady (1974) suggested that movement is slightly restricted when snow reaches up to two-thirds of moose chest height, whereas moose is definitely impeded when snow depths are greater than 70 cm. However, differences between sex and age classes must be considered. The effect of migratory and activity limitations might be observable earlier in smaller deer species like roe deer. This is supported by my data as I found a negative correlation between capture events and snow depth for roe deer but not moose (see Figure 9, hypothesis (VII)). Nevertheless, the big difference of day range calculated from camera traps compared to telemetry data remains unclear. Thus, the telemetry-based day range should be used with caution in the REM as it might result in an overestimate of moose densities. However, this approach was deployed by Caravaggi et al. 2015 with consistent estimates for hares (Lepus).

Within an additional analysis I found – in accordance with hypothesis (V) – that sex-ratio among species differed from equal proportions with significantly higher proportions of females than males for moose and red deer. Sex ratio of roe deer indicated the opposite (see Figure 8a). Higher frequencies of male roe deer cannot be explained by snow cover since males are only marginally bigger than females. Furthermore, there is no evidence that males are more active during winter/spring which would result in a higher capture probability. Wahlström & Liberg (1995) investigated the patterns of dispersal and seasonal migration in roe deer and did not reveal a sex-bias in median walking distance or dispersal. Further, the phenomenon of 'antlered females' and 'antlerless males' might have led to misidentifications of the species sex (Mysterud & Østbye 1999). However, frequencies of females with true antlers (1.3%) were too low to explain differences in the existing data. Therefore, drivers of differences in the sex-ratio between the three ungulate species remain unclear.

Significantly more animals were captured during the day than during the night for all species (see Figure 8b). This leads to the assumption of higher activity rates during the day and agrees with my previous assumption (hypothesis (VI)). However, the analysed data could be differentiated further regarding the intensity level of day light. It is well known that ungulate species show higher activity rates during sunrise and sunset (Cederlund 1989; Olsson, Widén & Larkin 2007). This effect is also visible in Figure 7. All species were more often captured during the early morning or evening. Therefore, a basic day-night-differentiation might miss important activity rates during dawn and dusk.

As a last approach, the type of habitat where species were detected was analysed by which hypothesis (VIII) could be approved. It could be clearly shown that the probability of moose capture events was highest in young coniferous forest (see Figure 10) dominated by scots pine (*Pinus sylvestris*). Moose might have such a clear preference for this forest type due to the increased availability of fresh and nutritious food. Cederlund & Okarma (1988) showed that female moose preferred clear-cuts and young to medium-aged forests, whereas mature stands and bogs were avoided. In contrast, roe deer and red deer seemed to prefer (young) mixed forest. Future camera trap studies could focus on theses preferred habitat types for certain species. Thus, capture rates might be maximized. However, this study design seemed to be not suitable for the detection of fallow deer. According to Ciuti et al. (2006) particularly non-calving fallow deer females prefer open meadows as a function of their high productivity. This agrees with my results. The six individual capture events of fallow deer were recorded only with the two cameras facing meadows. This suggests that fields and open meadows should be included into the study design to maximize the detection rate of fallow deer.

Looking at all results one needs to consider different kinds of disturbances within this study. In general, my human activity appeared every 12th day in certain tracts when switching cameras. Dung pellet group counts took place at the end of the camera trapping. This might have had an influence on the presence of animals. Further, trap shyness might have occurred since animals need to get used to an unnatural disturbance such as camera traps in their ecosystem (Rowcliffe et al. 2008). Moose showed a high curiosity to the cameras itself. Several individuals sniffed at the camera case. Further, some moose responded to the red marking tape that indicated 5 m, 10 m, and 15 m distances in the pictures. Technically, the colour red was chosen since it is not seen by ungulates (von

Besser 2010). However, it seemed as if the smell of its synthetic material might have attracted the attention of moose. This might have created a bias since individuals walked less in front of the cameras and stayed for a longer time period. However, for the calculation of walked distances per individual trigger event, only pictures in which animals were walking were considered.

In conclusion, camera traps and dung pellet group counts provided only similar density estimates for moose, whereby, hypothesis (I) could be only partly approved. Reasons for different estimates might be related to insufficient parameter calculations such as distance and speed parameters of the camera traps and estimated defecation rate of dung counts. Further, future investigations should correct for the deviation of estimated activity proportion and travel speed as suggested in Rowcliffe et al. (2014) and Rowcliffe et al. (2016). However, worldwide camera traps are seen as a reliable source for environmental monitoring and data collection without environmental disturbance in all kind of habitats due to their ease of deployment and their high rate of flexibility regarding their possibilities of usage (Silveira et al. 2003; Rowcliffe et al. 2008; Kays et al. 2011). Furthermore, continuous data can be simultaneously collected on multiple species and in difficult terrain (Shannon, Lewis & Gerber 2014). However, time effort during the data collection in the field depends in general highly on the surveyed area, terrain, study design, available resource at hand etc. for all methods (Singh & Milner-Gulland 2011). However, effort in the field was higher than expected for camera traps than for dung counts due to a rather short trapping period of 12 days. Longer recording periods per camera could strongly minimize effort relative to an increasing total trapping period and maximize simultaneously species capture rates. Nevertheless, the following analyses were more time consuming for camera traps than dung counts (hypothesis (II)). Further, hypothesis (III) could be approved. The purchase of infra-red triggered cameras requires a rather high budget compared to traditional dung counts. But on a long time view, the deployment of camera traps is an attractive tool in wildlife ecology. It is a non-invasive survey method which reduces disturbance and does not require the capture and handling of study animals (Newey et al. 2015). Despite of cameras advantages, their efficiency of producing data relies on a particularly appropriate and detailed survey design due to their limited field of detection (Shannon, Lewis & Gerber 2014). Depending on the target species, sampling period (time during the year), sampling length (amount of trapping days) and number of cameras must be well considered (MacKenzie at al. 2006). In general, it is hard to predict which method

produces more accurate data. Therefore, hypothesis (IV) is hard to prove. Only repeated measurements can test the accuracy of each method (Daniels 2006). However, one needs to deploy an appropriate census approach regarding his/her needed information, available time and budget. Besides population indices camera traps can reveal further information about habitat associations, activity patterns, behaviour, or community structure. Still, it is unclear how camera traps and dung pellet group counts compare to DNA analyses of sampled dung. This is a goal for future studies.

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7 Appendix

Table A: Differences between the two used camera models.

	Reconyx Hyperfire HC 500	HCO ScoutGuard SG 560C
Motion detector		
(depending on ambient	up to 30.5 m	un to 22 m
temperature, sensitivity	up to 50.5 m	up to 22 m
settings, etc.)		
Field of view	40°	52°
Image resolution	3.1 MP	5 MP
Time lapse	24 h	8 h
Working temperature	-29°C to 49°C	-20°C to 60°C
Imaga data	date, time, temperature, moon	data tima trigger picture
mage uata	phase, trigger picture	uate, time, trigger picture
Batteries	12 NiMH AA	8 NiMH AA

Table B: Time schedule and setup of cameras.

Date	Tract	Location 1	HCO Camera	Location 2	Reconyx Camera
	48	2	15	3	7
07.02.2016	47	2	8	1	11
07.03.2010	55	2	1	1	5
	46	1	2	2	2
	33	1	12	2	10
08 03 2016	32	2	4	3	1
08.03.2010	40	3	10	2	8
	39	1	5	2	4
	62	2	13	3	9
09.03.2016	49	6	9	3	3
	56	3	3	1	6
19.03.2016	48	5	7	4	12
	47	5	15	3	7
	55	3	8	4	20
	46	5	1	4	11
	33	4	2	3	14
20.02.201c	32	6	14	5	10
20.03.2010	40	5	4	6	1
	39	3	11	5	8
	62	5	5	4	18
21.03.2016	49	7	6	8	4
	56	8	9	7	5
	48	9	13	10	9
31 03 2016	47	6	7	7	12
51.05.2010	55	8	15	6	7
	46	9	Reconyx 19	7	20

Date	Tract	Location 1	HCO Camera	HCO Camera Location 2 Recony				
	33	8	1	7	11			
01 04 2016	32	8	10	7	6			
01.04.2016	40	7	14	8	10			
	39	8	12	7	1			
	62	6	11	7	17			
02.04.2016	49	10	5	9	14			
	56	9	3	10	13			
	48	12	9	11	4			
12 04 2016	47	10	13	8	18			
12.04.2010	55	11	7	10	12			
	46	10	15	11	2			
	33	10	4	9	20			
12 04 2016	32	9	1	10	8			
13.04.2010	40	9	Reconyx 11	10	7			
	39	11	14	9	10			
	62	11	12	9	1			
14.04.2016	49	12	11	11	9			
	56	11	6	12	14			
	48	13	Reconyx 5	14	3			
24.04.2016	47	11	9	14	16			
	55	12	13	13	17			
	46	13	7	12	12			
	33	13	15	11	2			
25.04.2016	32	11	5	12	20			
23.04.2010	40	12	1	14	8			
	39	12	Reconyx 11	14	7			
	62	14	10	13	6			
26.04.2016	49	14	12	13	18			
	56	13	3	14	9			
	48	15	6	16	14			
06.05.2016	47	16	Reconyx 3	15	1			
00.03.2010	55	14	14	15	19			
	46	14	9	16	17			
	33	16	7	14	12			
07.05.2016	32	15	15	13	2			
07.03.2010	40	15	13	16	20			
	39	16	4	15	8			
	62	16	Reconyx 11	15	16			
08.05.2016	49	15	5	16	10			
	56	16	11	15	6			



Figure A: 3rd order polynomial regression to correct for the fact that walking distance was measured as straight-line connections between GPS locations every 30 min. The intercept indicates the day range of moose.

Tract							Spee	cies						GUID
Tract	badger	bear	beaver	bird	crane	fallow deer	fox	hare	human	moose	red deer	roe deer	unknown	Sum
32							2	1		11	2	1		17
33									1		1	6	2	9
39								5		11	2	13	4	35
40								1	1	1	5			7
46	1			1		6	2	1	15	1	4		1	17
47											10	3		13
48							1	1		5	1			8
49	2						1	12	1	4		1	2	22
55				1	2			5		5	4	3	2	22
56	1			1				2		9	16	26	3	58
62		1					6	2		5	1	16	1	36
Öreälven			1			1	4	1	9			4		11
sum	4	1	1	3	2	7	16	31	27	52	46	73	15	255

Table C: Number of individual trigger sessions per species during a period of 1584 trapping days (12 days * 12 positions per tract * 11 tracts). Species section bird represents singing birds (*Passeri*).





Figure B: Proportion of capture events for moose per hour in **a**) March. **b**) April. **c**) May. Black line represents activity fit. Grey dashed line represents distance walked per hour [km] from telemetry data.



Figure C: Proportion of area per habitat type **a**) within a 50 m radius buffer around all camera locations, **b**) within a 50 m radius buffer around dung pellet group count locations against the proportion of area per habitat type of Järnäshalvön. Dotted line indicates $y \sim x$.

Treat	Data		Sp	ecies		anna
Tract	Date	moose	red	under45	over45	sum
32	03.05.2016	9	1	1	2	13
33	04.05.2016	16	0	1	0	17
39	03.05.2016	1	2	1	2	6
40	03.05.2016	4	0	1	0	5
46	07.05.2016	0	0	1	4	5
47	02.05.2016	2	0	2	0	4
48	02.05.2016	3	0	0	5	8
49	22.05.2016	0	0	0	0	0
55	07.05.2016	2	1	0	1	4
56	13.05.2016	2	0	0	0	2
62	11.05.2016	6	0	18	0	24
sum		45	4	25	14	88

Table D: Counted dung pellet groups (fresh) per species and tract.

8 Affidavit

I hereby certify that I wrote this thesis independently, using no other than the stated sources and aids and that the work had previously not been submitted to any other examination authority to take a degree.

Umeå, 15th August 2016

Sobine Pfeffer

SENASTE UTGIVNA NUMMER

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