



Using camera traps to identify the influence of seasonal climate variations on the passage rates of a multi-species ungulate community in Öster Malma, Sweden

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Abstract

Future climate change projections have consistently shown that globally we are heading for hotter summers, milder winters and less precipitation. Climate changes such as increasing temperatures will have an impact on the behaviour and distribution of both flora and fauna with shifts in their ranges in accordance with their climate boundaries. In Europe, ungulate species are expanding in both population size and distribution, leading to multi-species ungulate communities. It is important to understand what effect climate variations will have on the behaviour and movement of these communities. Sweden's climate could see temperatures rise by approximately 3°C by 2100, therefore, there is a need to understand the impact this and other climate variations could have on its ungulate community. I have investigated the relationship between the climate variables, temperature and snow depth and the patch use of four ungulate species, moose (*Alces alces*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) over a three year period in southern Sweden. I used images taken from camera traps at eight locations to calculate a monthly and seasonal passage rate for each species before carrying out statistical analysis in SPSS. The analysis showed a strong effect between temperature and roe deer monthly passage rates ($p = <.001$) while the other three species were not statistically significant. There was also a strong effect between snow depth and both monthly and seasonal fallow deer passage rates ($p = .001$; $p = .019$), the other three species were not statistically significant. While strong effects were found between some species and climate variations there is still a lot of uncertainty. It is more likely that other factors such as the site setup and forage availability had more of an influence over ungulate passage rates and therefore patch use. Further studies are needed to better understand the effect of climate variations on ungulate patch use.

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1. Introduction

Climate change projections have consistently shown that globally, surface temperatures are expected to continue to rise with most observed warming trends being seasonal, the largest increases occurring in winter and spring (Jones et al., 2005). Europe is heading towards a future with much milder winters, hotter summers with less precipitation and an increase in the frequency and intensity of extreme weather events (Kelemen et al., 2009; IPCC, 2014). Flood risk is also predicted to increase due to snowmelt floods shifting from spring to winter as a result of a reduced snow season and less accumulation during winter months (Behrens et al., 2010).

The climate changes outlined in the latest IPCC report (IPCC, 2018) are set to have serious effects on the behaviour and distribution of a range of both flora and fauna. Studies into the relationship between climate change and ecology have shown that plant and animal species are facing changes to their current range due to new climate conditions, with many expected to shift poleward and to higher altitudes, in keeping with expanding climate boundaries (Walther et al., 2002). Native plant and tree species may also be threatened by competition with the range expanding non-native species that may be better adapted to the novel climatic conditions (Katona et al., 2013). Such changes in plant community may affect food availability for animals as climate change is causing an advance in phenology, whether that be the flowering of a plant or breeding of an animal (Visser and Both, 2005). The shift in phenology of a plant species, for example, could cause the whole ecological system to become mistimed, posing a serious threat to the fitness of other species within the system which may depend on it for their own survival and reproduction (Visser and Both, 2005).

Ungulate species are expanding throughout Europe due to a combination of factors. These include a greater focus on conservation, displacement or removal of competitors and predators, and hunting establishments introducing native and non-native species that may be more desirable to hunt (Apollonio et al., 2010). Land-use change is another important factor that has influenced ungulate populations in Europe as changes to forestry practices has increased habitat size and quality, as well as more intense agriculture increasing high-quality crops (Kuiters et al., 1996; Cutini et al., 2015). Supplementary feeding of ungulates has also been used as a management tool to improve winter survival rates, reduce forest and crop damage and attempt to reduce human-animal conflict (Felton et al., 2017). With an increase in warmer winters in northern Europe, it is possible that ungulate species will expand further north as higher latitudes become more hospitable for more species (Büntgen et al., 2017).

The expansion of multiple species would create a situation where native and non-native species would occupy the same habitat areas forming novel species-rich ungulate communities. Where once there

may have only been one or two ungulate species within a habitat range, one can increasingly find four to six species, increasing pressure on the system supporting these species (Putman et al., 2011; Pfeffer et al., 2018). Such an increase in community size can have positive and negative impacts on the wider ecosystem. While in some cases it could lead to overexploitation of food sources, damage to the plant community and greater competition (Stewart et al., 2011; Bowyer et al., 2016; Lecomte et al., 2016) in others, ungulates can act as 'ecosystem engineers', altering their habitat through changes to plant, soil and water conditions as a result of grazing, trampling, urination and excretion (Baruzzi and Krofel., 2017).

The main threat to Sweden in terms of climate change might occur in the form of warmer summers, milder winters and an increase in extreme events. Scandinavia has seen the strongest warming in Europe, particularly in winter, since the 1980s and climate projections have shown temperatures could rise by up to 3 °C by 2100 (IPCC, 2014; Eklund et al., 2015). Currently, there is a gap in the knowledge of how changing climatic conditions such as variations in temperature and snow depth, affect the behaviour and movement of northern ungulates. Previous studies have focused to understand the relationship between a changing climate and topics such as supplementary feeding of ungulates, the influence of hunting on habitat selection, and moose-vehicle collisions (Seiler, 2004; Felton et al., 2017; Niemi et al., 2017). Understanding the impact climate has on ungulate behaviour is important for their survival as it allows identification of any ways in which ungulates might be affected by future climate change.

In this study, I have investigated the relationship between ungulate patch use and climate conditions over monthly and seasonal timescales in southern Sweden for a three year period from September 2015 to September 2018 using camera traps.

1.1. Background Information

The study focused on four of the main ungulate species found in Sweden, moose (*Alces alces*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). The survival of the four species depends on forage availability and quality, which are directly influenced by seasonal and climate variations.

1.1.1. Moose

Moose are one of the most common ungulates found in all parts of Sweden with an estimated population of 300,000-400,000 individuals (Apollonio et al., 2010). Their diet consists primarily of Scots pine (*Pinus sylvestris*), and willow (*Salix*), showing a preference for species with fewer, larger stems instead of those with many small stems (Shiple et al., 1998). Moose are susceptible to heat stress in both summer and winter when temperatures exceed 13.8°C & -5°C respectively (Rhines, 2014). In situations where moose are exposed to temperatures that will cause heat stress, they seek appropriate habitats to regulate their body temperature such as shaded patches and cool water (Rhines, 2014).

1.1.2. Red Deer

Red deer are mainly found in south-central Sweden. They are native to Sweden and their population is increasing in both size and geographical distribution (Stigum et al., 2019). Their diet consists mainly of herbaceous plants, leaves of deciduous trees and shrubs (Gebert and Verheyden-Tixier., 2008; Zweifel-Schielly et al., 2011).

1.1.3. Fallow Deer

Fallow deer have a diet consisting mainly of herbs, grasses, trees and shrubs, with their reliance on trees and shrubs decreasing between spring and autumn (Bruno and Apollonio., 1991). They are not native to Sweden but were introduced during the 16th Century, and are now present across much of southern Sweden (Menichetti et al., 2019). However, there is evidence to suggest that fallow deer were present in northern and central Europe during the last interglacial period (Apollonio et al., 2010). They have a large habitat range with populations found throughout Europe, the Mediterranean and the Middle East. Therefore fallow deer might be well suited to a large variety of climate conditions. While their distribution in Sweden is restricted to the regions surrounding the enclosures that they either escaped or were released from, it is possible that with more northerly latitudes becoming more hospitable, they will be able to expand their range (Apollonio et al., 2010).

1.1.4. Roe Deer

Roe deer diet consists primarily of the herbaceous and woody plants with some seasonal variance including seeds and fruits if available (Tixier et al., 1997). They are one of the most abundant deer species across the Eurasian continent. Recent studies have found that an increase in milder winters further north could lead to a northerly expansion of the range of roe deer and that increases in

environmental productivity as a result of climate change, is expected to increase the abundance of roe deer (Melis et al, 2009; Morellet et al., 2013).

1.2. Key Concepts

1.2.1. Climate Influences

Climate changes has been found to have an effect on the distribution of many animal species and the plant community, such as fauna range expansions due to factors like deglaciation, an advance in phenology or a shift in plant species distribution (Comes and Kadereit., 1998; Walther et al., 2002; Wu et al., 2017). Temperature effects on spatial behaviour is well documented in previous studies. Van Beest et al (2012) found that moose foraging behaviour in Norway was influenced by increasing temperature. Their study shows that once summer temperatures exceeded critical thresholds, moose chose to select forest areas with increased thermal cover and therefore less forage availability. By selecting closed-canopy forested areas for increased thermal cover the moose is showing a preference for regulating body temperature over forage quality (Van Beest et al., 2012). Deep snow is also detrimental to moose home range size (Van Beest et al., 2011).

In a hot winter or summer, plant growth will be affected by the climate deviating from the norm. For example, where spring temperatures are higher than average, plant species may flower earlier than normal, or extreme heatwaves can cause drought conditions which will prevent plant species from flowering or reaching their full growth potential, again reducing the amount and quality of forage available for ungulates (Hanley et al., 1989; Siegmund et al., 2016). Forested areas with significant canopy cover will be less affected by snowfall and as such, ungulates may show a preference for foraging in these areas as there is greater food availability (Van Beest et al., 2012). Due to climate change, broadleaf trees might expand northwards, therefore, increasing ungulate food availability (Feurdean et al., 2017).

1.2.2. Body Size

Body size can also have an effect on ungulate behaviour in relation to regulating body temperature as a response to different weather conditions, with the thermal niche of an endotherm being determined by their body size and shape (Porter and Kearney, 2009). In African ungulates heat stress is a threat to survival and fitness regardless of body size, particularly in summer months, but for larger ungulates with reduced ability to dissipate heat, hot spring conditions can also have a negative effect on their activity levels compared to smaller bodied ungulates (Shrestha et al., 2014).

1.2.3. Foraging Limitations

Forage intake rates of ungulates is determined by two main factors, the rate at which they encounter a source of food and the rate at which food is consumed. Foraging limitations are therefore separated into encounter-limited and handling-limited (Robinson and Merrill, 2012). In locations with a temperate climate, where there is significant snow cover in winter months, an ungulate may become encounter limited due to the food source being covered by snow and requiring more time to uncover it as well as their movement being snow limited (Richard et al., 2014). The same ungulates may also be handling limited in summer months as there is an abundance of food, with the limiting factor being the amount of time taken for them to consume it (Robinson and Merrill, 2012).

1.3. Research Question & Hypotheses

Main question:

How is the patch use of a multi-species ungulate community in Öster Malma, Sweden, influenced by temperature and snowfall?

1.3.1. Hypotheses

I hypothesised that (I) passage rates will be highest during spring and summer as forage availability and quality increases and (II) winter passage rates will be considerably lower than summer passage rates as ungulates show a preference towards energy conservation, therefore reducing their activity. I also predict that (III) as average monthly snow depth increases, monthly ungulate passage rates will decrease as snow limits movement of ungulates and covers ground forage. Finally, I expect that (IV) passage rates will decrease during hot months as ungulates choose to stay in shaded areas to maintain a lower body temperature than if they were moving through patches.

2. Methodology

2.1. Study Area

The study area 'Öster Malma' is located in the province of Södermanland, South-East Sweden, within the surrounding area of the city of Nyköping (Figure 1). The area has a temperate climate with average summer temperatures between 15.4 °C and 17.2 °C and mean winter temperatures between -0.6 °C and -2.6 °C (Climate-data.org, 2015). Precipitation varies (including rain and snow) with a minimum of 27 mm of precipitation in March and a maximum of 66 mm in August (Climate-data.org, 2015). There are five ungulate species present in the study area, which include moose, fallow deer, roe deer, red deer and wild boar (*Sus scrofa*).

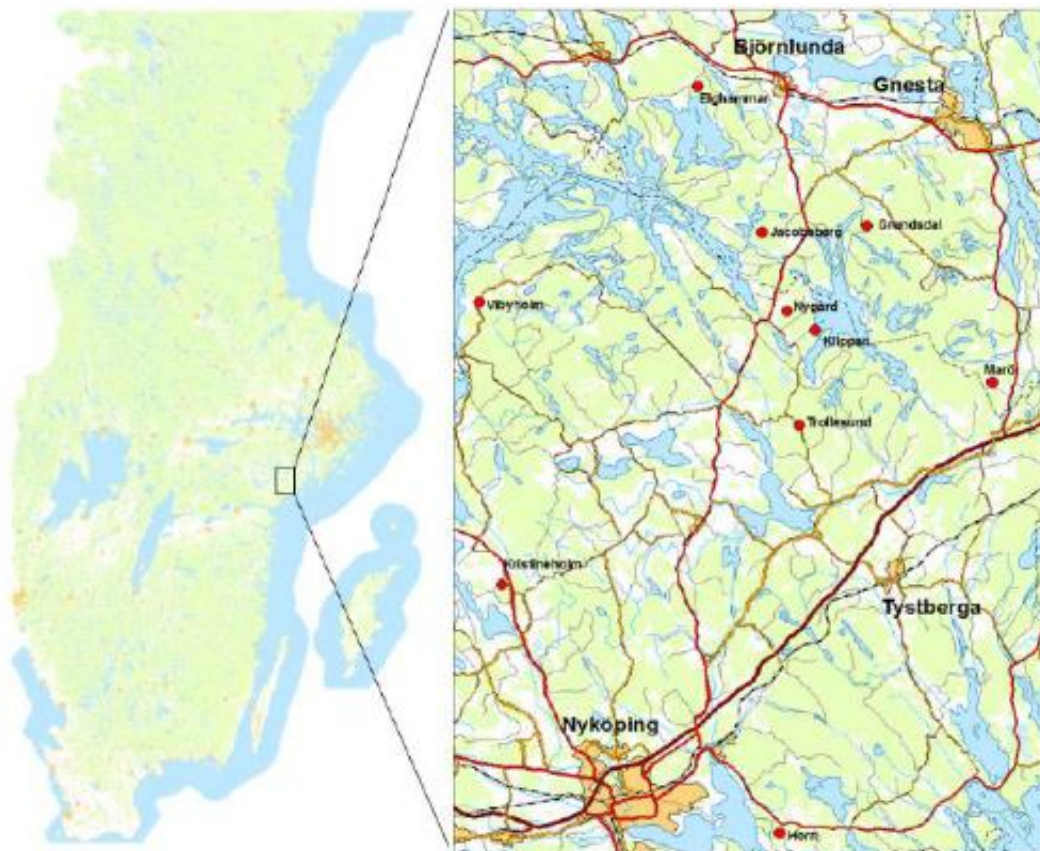


Figure 1: Location of the study area 'Öster Malma', Sweden with its ten study sites marked in red (Ånöstam, 2017).

2.1.2. Site Characteristics

The study area consists of ten individual sites (Table 1). Nine of the ten sites were clear cut in 2014 and replanted with Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*) in 2015. Horn was the only site that was clear cut in 2013 and naturally regenerated with pine. The experiment (see description below) started in autumn 2015 and is still ongoing. Today some sites are dominated by

one or two tree species, mainly spruce and pine, while others have much more species diversity, including silver birch (*Betula pendula*), downy birch (*Betula pubescens*), aspen (*Populus tremula*), willow (*Salix*) and rowan (*Sorbus*).

Table 1: Latitudes and longitudes of the ten sites.

Site	Latitude	Longitude
Elghammar	59.06579	-17.0917
Grundsdal	59.00261	-17.2265
Horn	58.73905	-17.138
Jakobsberg	59.00117	-17.1395
Klippan	58.95803	-17.1809
Kristineholm	58.8511	-16.9143
Marö	58.93267	-17.3262
Nygård	58.96657	-17.1577
Trollesund	58.91737	-17.163
Vibyholm	58.97424	-16.9005

Each of the ten sites consists of four exclosures that measure 14x14 m. All exclosures were set up in 2015 before the experiment began. The exclosures have four different treatment conditions: control, closed, summer, and winter. The control exclosures are open all year and are therefore constantly accessible by all animals. The closed exclosures are closed and fenced off all year to prevent animals from entering and accessing the vegetation within them. Summer exclosures are closed and fenced off during the vegetation period (April to October) only and are then opened during the months October to April. The winter exclosures are the opposite and are therefore closed during the non-vegetation period (October to April) and opened during the vegetation period.

2.2. Camera Traps

Each control exclosure is permanently equipped with a camera trap (Reconyx Hyperfire HC500) in the south-east corner all year round. A second camera trap is shared between the summer and winter exclosures, being switched interchangeably during opening months. The cameras are set up to monitor the wildlife using the exclosures with a focus on the four ungulate species; moose, red deer, fallow deer, and roe deer. As the closed exclosure is permanently free from animals, there is no camera covering that area. The cameras have been in place and continuously taking photographs since

they were first installed at the end of September 2015 and are checked regularly to ensure that they are still operating correctly and have sufficient battery power.

A passive infrared sensor triggers the cameras, when the sensor registers a difference in thermal infrared between moving objects and their background in the detection zone, such as the temperature of the background vegetation or soil and a moving animal (Welbourne et al., 2016). Once triggered, the camera takes a series of three images at one-second intervals to capture the event detected (see for an example, Figure 2). Each camera also records a time-lapse image per day at 13:00 to check the camera is still functioning.



Figure 2: Example of a trigger event from a camera on-site showing a female fallow deer foraging on a grass species.

2.3. Image Classification

Images captured by the camera traps were classified to create a data set of the animals seen in the area. I classified images taken from September 2017 to September 2018 from eight out of the ten sites (Nygård & Vibyholm were excluded due to time constraints). Images taken between September 2015 and September 2017 were previously classified and therefore included in my analysis (excluding Nygård and Vibyholm). The classification process involved identifying a number of variables including the species present, the number of animals present per species and whether individuals were foraging. Foraging was identified where an animal had its head to the ground or could clearly be seen eating leaves from plants or trees. Foraging behaviour was not separated by species, therefore if there was an image containing two species where one was foraging but the other wasn't, it was classified as a foraging event. Anything else was marked as 'other behaviour'. Species identification could be done due to obvious differences in the appearance of the four ungulate species in question, such as body size and shape. In some instances it was not possible to identify the species present due to blurred images or very dark night images, therefore the animal present was recorded as 'unknown species' and excluded from the analyses. Other details such as gender, age and male antler points

were also recorded. However, these characteristics were not relevant in this study and thus have not been included here for further analysis.

For my analysis, I used passage events as a measure of patch use. A single passage event represents a sequence of continuous pictures triggered by an individual or group of animals. To determine the end of one sequence and the start of a new sequence, I implemented a time gap of 5 mins between two triggers. If the second trigger was taken >5 mins after the initial sequence of images, it was deemed to be a separate passage event.

2.4. Climate Data

I extracted data for daily temperature and snow depth from the webpage of the Swedish Meteorological and Hydrological Institute (SMHI, <https://www.smhi.se/data/meteorologi/ladda-ner-meteorologiska-observationer#param=airtemperatureInstant,stations=all>). Since there has been no weather station located directly in the study area, I extracted daily temperature data from three weather stations surrounding Öster Malma; Floda A, Södertälje and Oxelösund (Figure 3). Based on the data of these three stations, I calculated an average daily temperature for the whole study area. These average daily temperatures were used to extract average values per month and season. Snow depth data was only available from one weather station around Öster Malma, Södertälje (Figure 3). Therefore, I used the snow depth data from this individual station only to calculate monthly and seasonal averages for the study area. To define a season I used each seasons' start and end date (SMHI, <https://www.smhi.se/en/weather/sweden-weather/season-map/>, see also Table 2) and rounded them to receive full months. Rounding to months was done due to a delay in finding the exact start and end dates of each season.

Table 2: Definition of which months form each season.

Season	Months
Spring	March/April/May
Summer	June/July/August
Autumn	September/October/November
Winter	December/January/February

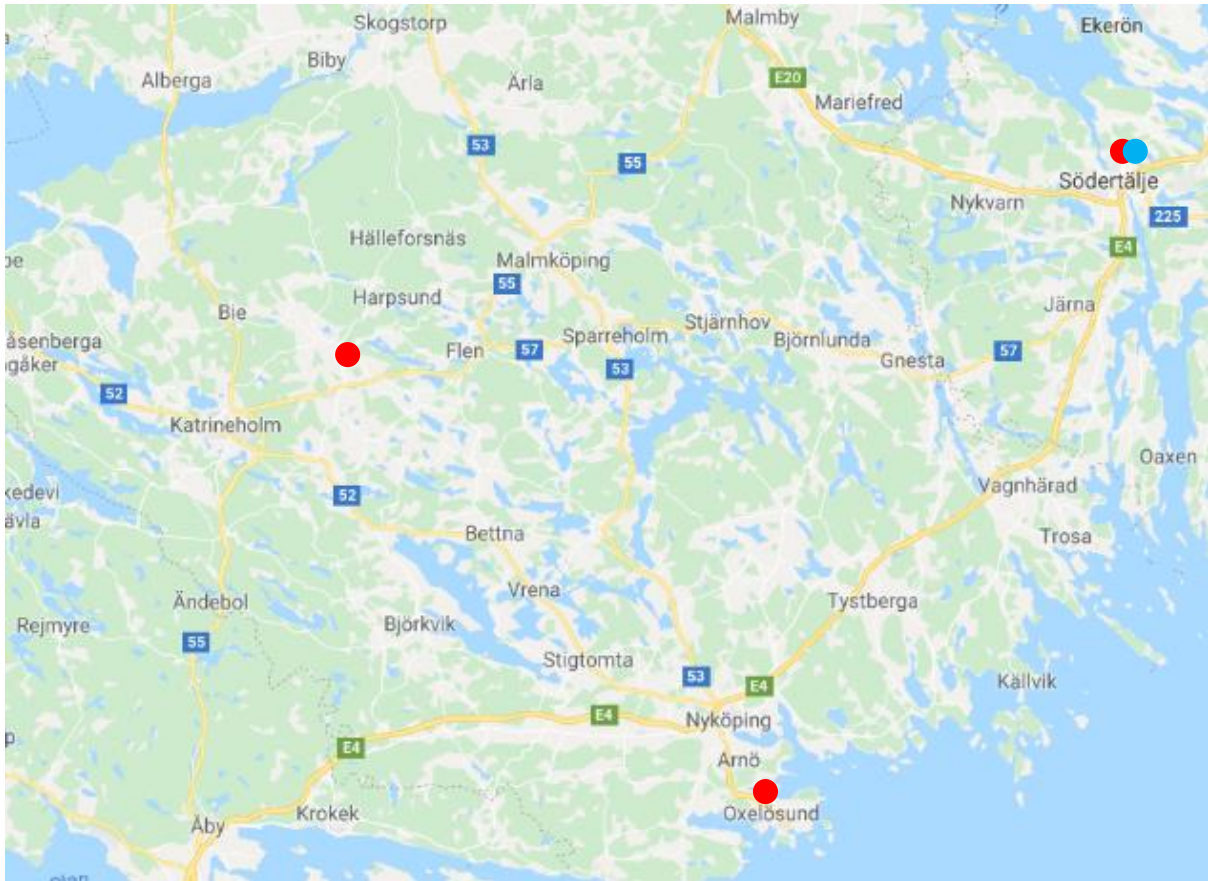


Figure 3: Location of the three SMHI weather stations. Weather stations used for temperature data are marked with red spots while snow depth data is marked with a blue spot (Google Maps., 2019).

2.5. Data Analysis

I used the data on passage events to calculate a species and site-specific daily index (passage rate per day) as the sum of passages per species, per site, per day. Similarly, I calculated a monthly and seasonal passage rate per species by taking a sum of all passage events divided by the number of days covering those specific time periods, for example, the fallow deer passage rate in June 2018 would be the sum of fallow deer passage events divided by 30 days. I repeated this step for every month between September 2015 and September 2018 and similarly each season from autumn 2015 to autumn 2018. This allowed for a monthly and seasonal passage rate to be calculated for each species for the whole study period as seen below:

$$\text{Passage rate} = \text{number of passages} / \text{number of days camera was active (per month or season)}$$

I first used this dataset to run linear regression tests to identify any relationship between the passage rates of each species separately and the climate variables. My dependent variables were monthly and seasonal passage rates of the four species, where I ran separate models for the monthly and seasonal variables, with two covariates, temperature and snow depth. I then ran general linear mixed effect models in which the passage rate was always the dependent variable. In the initial models, I used the passage rates of all four ungulate species together. I then ran separate models for each species individually to identify species-specific responses to the climate variables, using the passage rate of each individual species as the dependent variable. I included ungulate species as a fixed effect, temperature, temperature² and snow cover as covariates, and site and year as random factors. Again, I ran separate models for monthly and seasonal response variables. I performed all statistical analyses in SPSS Statistics 25.

3. Results

3.1. Climate Variations

Winter 2016/17 was on average approximately 3 °C warmer than the winters of 2015/16 and 2017/18 (Figure 4). The summer of 2018 was on average approximately 3 °C warmer than the two previous summers (Figure 4). Snow depth in the study area varied across the three year study period with winter 2016/17 having the lowest snow depth and winter 2017/18 having the highest snow depth (Figure 4). Summer months always had a snow depth of 0 m, while during spring months (usually in March) there was a very small amount of snow present before it melted to 0 m (Figure 4).

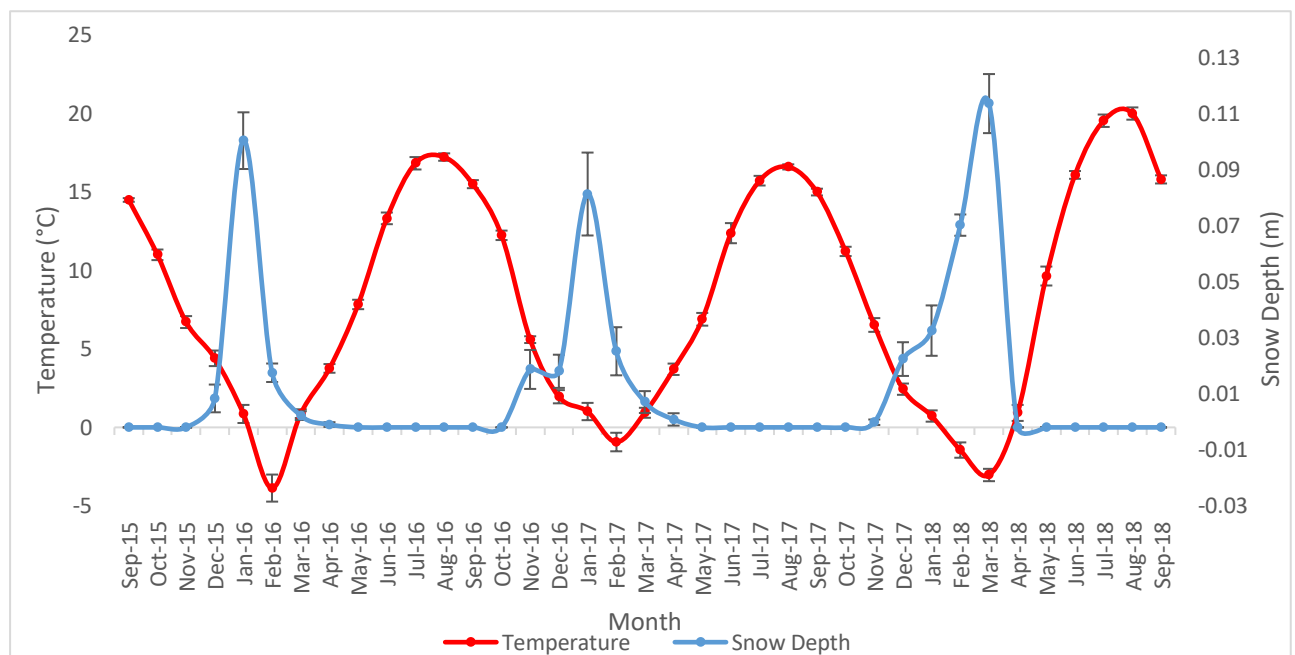


Figure 4: Average monthly temperature variations (in red) and average monthly snow depth variations (in blue) from September 2015 to September 2018 with standard error.

3.2. Monthly Passage Rates per Species

During the study period, fallow deer and roe deer strongly dominate the visits to the sites, followed by red deer and then moose. The passage rates for all four species, and in all years, dropped strongly during mid-winter. Overall, there appears to be a general trend towards passage rates of fallow deer and roe deer declining slightly over the years. There also seems to be a general trend towards moose and red deer passage rates increasing slightly over the same time period.

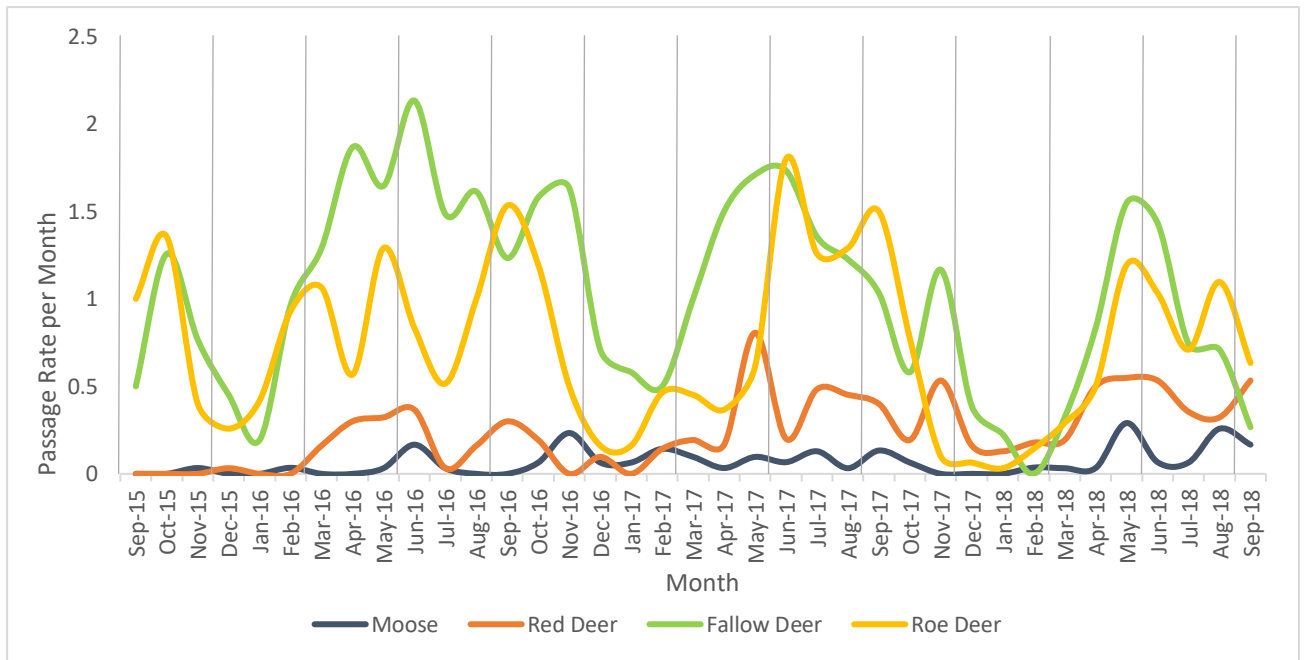


Figure 5: Monthly passage rates of moose (blue), red deer (orange), fallow deer (green) and roe deer (yellow) from September 2015 to September 2018. Grey vertical lines represent seasons.

3.3. Monthly Passage Rates per Species & Temperature

Temperature and temperature² had a strong effect on the dependent variable, monthly passage rates ($p = <.001$) (Table 3). Ungulate species also had a significant effect on the dependent variable ($p = .002$). However year and site, the two random factors did not have a significant effect on monthly passage rates ($p = .169$; $p = .732$) (Table 3). Among the four species, roe deer had the highest R^2 value (0.3817) (Table 4). When looking at the influence of temperatures on the monthly passage rates of the four species individually, it can be seen that temperature had a positive effect on the monthly passage rates of roe deer (estimate = 0.005; $p = <.001$) (Table 4). Moose, red deer and fallow deer however, were not significantly influenced by temperature (estimate = $<.001$, $p = .124$; estimate = $<.001$, $p = .235$; estimate = $<.001$, $p = .616$) (Table 4).

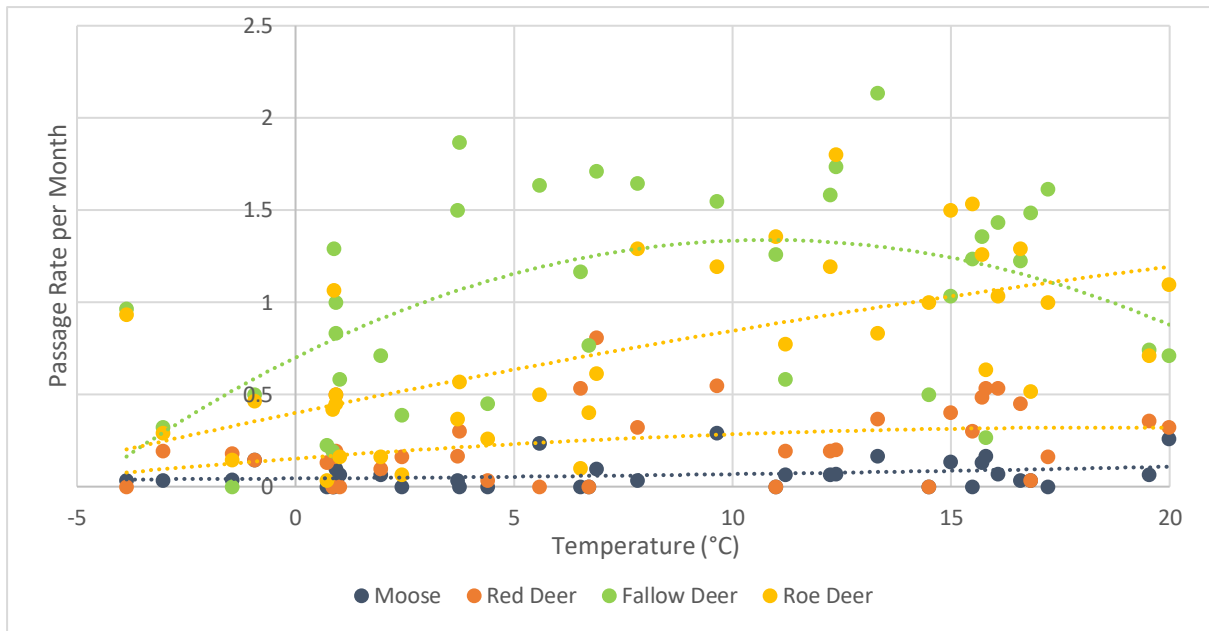


Figure 6: Monthly passage rate of moose (blue), red deer (orange), fallow deer (green), and roe deer (yellow) in relation to temperature. Dotted lines indicate polynomial regressions.

Table 3: Univariate statistical analysis for the effect of temperature, temperature², species, year and site, on the dependent variable, monthly ungulate passage rates.

Explanatory Variables		df	f	p
Temperature	Hypothesis	1	32.310	.000
	Error	1010		
Temperature ²	Hypothesis	1	12.687	.000
	Error	1010		
Ungulate Species	Hypothesis	3	6.538	.002
	Error	22.236		
Year	Hypothesis	3	2.033	.169
	Error	10.755		
Site	Hypothesis	7	.623	.732
	Error	22.374		

Table 4: Regression coefficient estimates, standard error, significance (p) and R² for the effect of temperature on the monthly passage rates per species.

Species	Estimates	Standard Error	t	p	R ²
Moose	.000	.000	1.542	.124	0.0908
Red Deer	.001	.001	1.190	.235	0.1215
Fallow Deer	.001	.002	.502	.616	0.1299
Roe Deer	.005	.001	3.846	.000	0.3817

3.4. Monthly Passage Rates & Snow Depth

Snow depth had a strong effect on the dependent variable, monthly passage rates ($p = <.001$) (Table 5). Ungulate species also had a significant effect on the dependent variable ($p = .002$). Year and site did not have a significant effect on monthly passage rates ($p = .197$; $p = .732$) (Table 5). Fallow deer had the highest R² value out of the four species (0.3214) (Table 6). The individual analysis of the effect of snow depth on the monthly passage rate of each species shows that snow depth had a strong effect on fallow deer monthly passages (estimate = -1.289, $p = .001$) (Table 6). Moose, red deer and roe deer were not significantly influenced by snow depth (estimate = .004, $p = .952$; estimate = -.202, $p = .342$; estimate = -.354, $p = .249$) (Table 6).

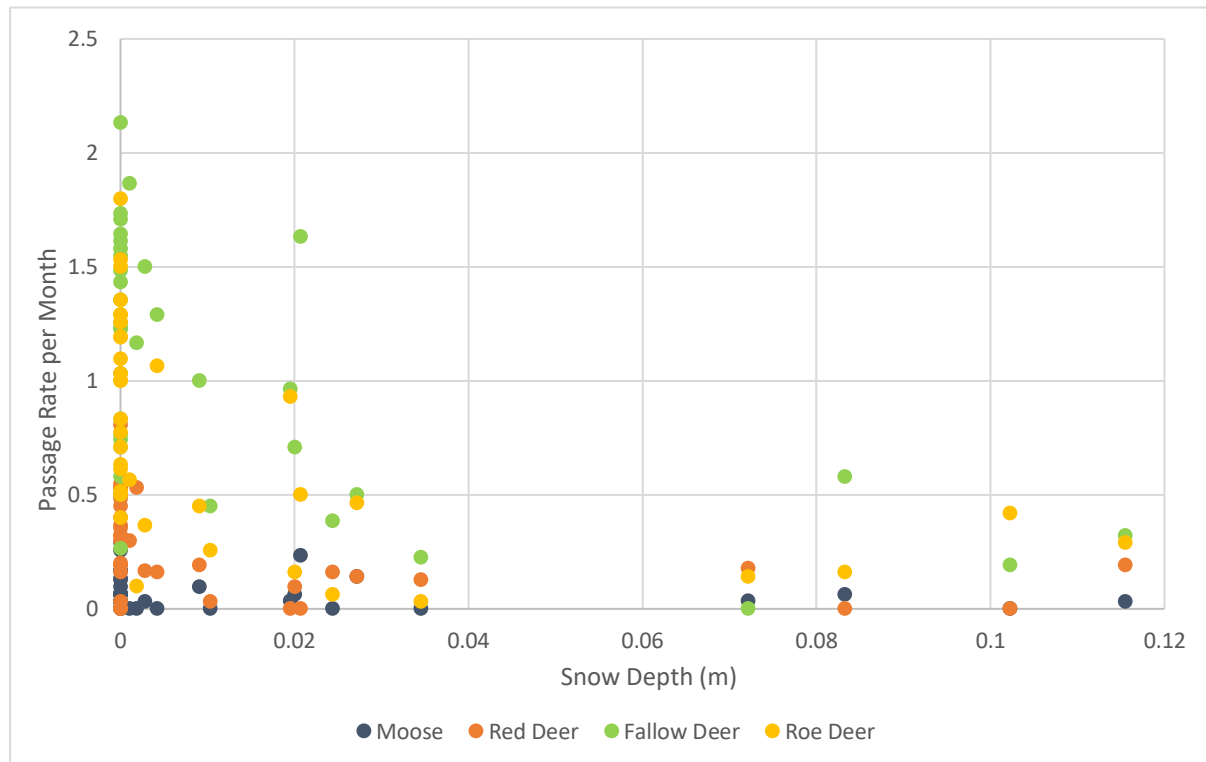


Figure 7: Monthly passage rate of moose (blue), red deer (orange), fallow deer (green), and roe deer (yellow) in relation to snow depth.

Table 5: Univariate statistical analysis for the effect of snow depth, ungulate species, year, and site on the dependent variable, monthly ungulate passage rates.

Monthly Passages		Df	f	p
Snow Depth	Hypothesis	1	68.754	.000
	Error	7.224		
Ungulate Species	Hypothesis	3	6.538	.002
	Error	22.236		
Year	Hypothesis	3	1.865	.197
	Error	10.409		
Site	Hypothesis	7	.622	.732
	Error	22.379		

Table 6: Regression coefficient estimates, standard error, significance (p) and R² for the effect of snow depth on the monthly passage rates per species.

Species	Estimates	Standard Error	t	p	R ²
Moose	.004	.072	.060	.952	0.045
Red Deer	-.202	.212	-.951	.342	0.1332
Fallow Deer	-1.289	.392	-3.285	.001	0.3214
Roe Deer	-.354	.306	-1.156	.249	0.2394

3.5. Seasonal Passage Events

Spring and summer passage events of moose and red deer increase from 2016 to 2018, while they declined for fallow deer. Roe deer spring passage events were lower in 2017 compared to 2016 and 2018 (Figure 8), while summer passage events were higher in 2017 compared to 2016 and 2018. Fallow deer and roe deer had almost identical passage events for the years 2017 and 2018 (Figure 8). Trends in autumn passage events of the four species were more variable than in the three other seasons (Figure 8). Winter passage events for the four ungulate species are low compared to the other three seasons with the most regular passage events being made by fallow deer in all three years (Figure 8).

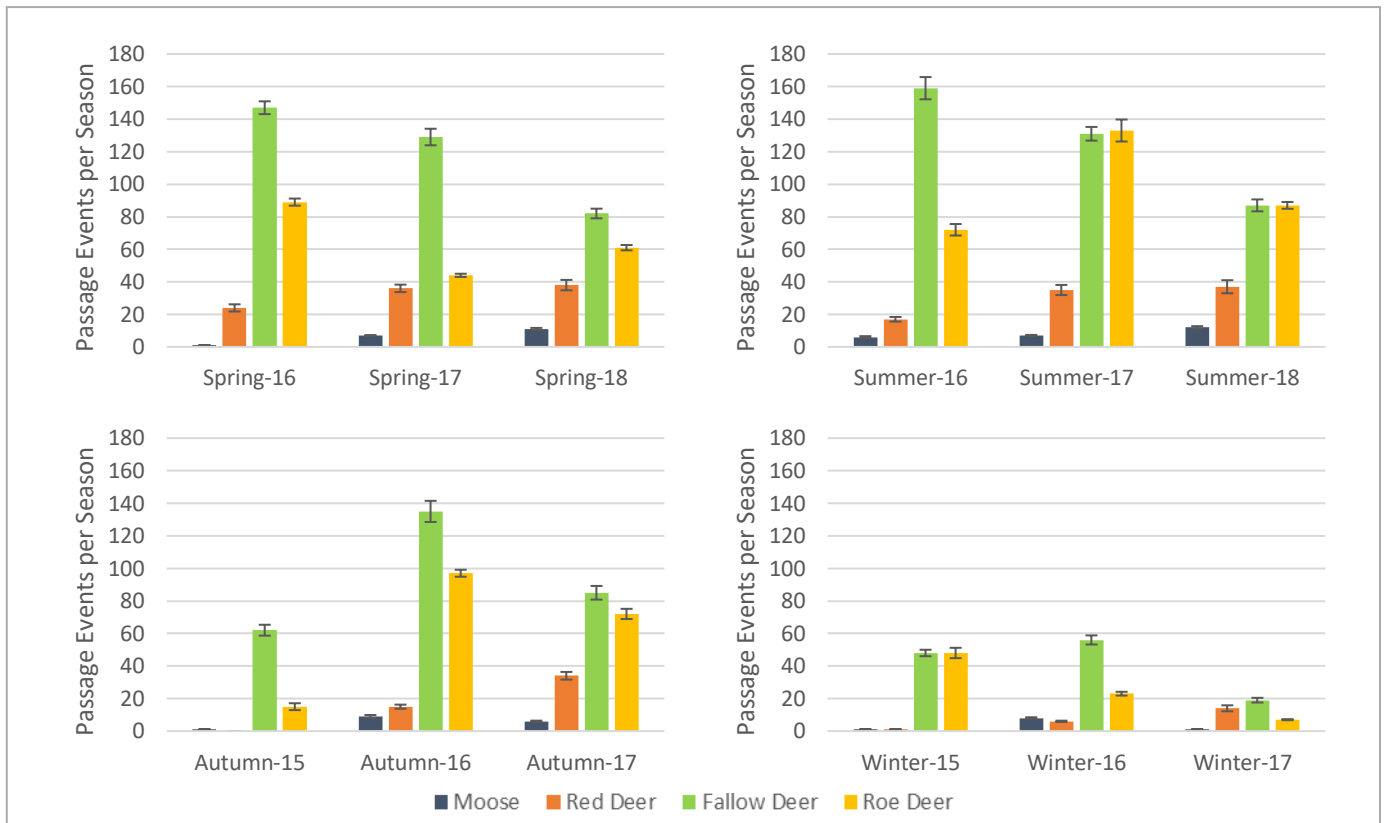


Figure 8: Seasonal passage events of moose (blue), red deer (orange), fallow deer (green) and roe deer (yellow) with standard error.

3.6. Effect of Temperature on Seasonal Passage Rates

On a seasonal time scale temperature, temperature² and snow depth all have a strong effect on ungulate passage rates ($p = .001$; $p = .015$; $p < .001$) (Tables 7 & 8). In the temperature model ungulate species is also significant ($p = .003$) (Table 6). Neither year nor site, the two random factors, were statistically significant ($p = .553$; $p = .679$) (Table 7). Similarly, in the snow depth model, ungulate species was statistically significant while year and site were not statistically significant ($p = .003$; $p = .533$; $p < .680$) (Table 8).

Individually, none of the four species' seasonal passage rates are significantly influenced by temperature (Table 9). There is a strong effect of snow depth on fallow deer seasonal passage rates (estimate = -2.735, $p = .019$) (Table 10). There is no effect of snow depth on the seasonal passage rates of moose, red deer or roe deer ($p = .334$; $p = .892$; $p = .373$) (Table 10).

Table 7: Univariate statistical analysis for the effect of temperature, temperature², ungulate species, year and site on the dependent variable, seasonal ungulate passage rates.

Seasonal Passages		df	f	p
Temperature	Hypothesis	1	11.613	.001
	Error	274		
Temperature ²	Hypothesis	1	9.951	.015
	Error	274		
Ungulate Species	Hypothesis	3	6.437	.003
	Error	22.582		
Year	Hypothesis	3	.763	.533
	Error	14.125		
Site	Hypothesis	7	.691	.679
	Error	24.520		

Table 8: Univariate statistical analysis for the effect of snow depth, ungulate species, year and site, on the dependent variable, seasonal ungulate passage rates.

Seasonal Passages		df	f	p
Snow Depth	Hypothesis	1	27.562	.000
	Error	275		
Ungulate Species	Hypothesis	3	6.437	.003
	Error	22.582		
Year	Hypothesis	3	.765	.533
	Error	13.313		
Site	Hypothesis	7	.690	.680
	Error	24.552		

Table 9: Regression coefficient estimates, standard error, significance (p) and R² for the effect of temperature on the seasonal passage rates per species.

Species	Estimates	Standard Error	t	p
Moose	.001	.001	1.810	.073
Red Deer	.002	.002	.835	.406
Fallow Deer	-.003	.003	-.891	.375
Roe Deer	.004	.003	1.433	.155

Table 10: Regression coefficient estimates, standard error, significance (p) and R² for the effect of snow depth on the seasonal passage rates per species.

Species	Estimates	Standard Error	t	p
Moose	.206	.213	.970	.334
Red Deer	-.096	.708	-.136	.892
Fallow Deer	-2.735	1.150	-2.378	.019
Roe Deer	-.750	.839	-.894	.373

4. Discussion

4.1. Effect of Climate Variations on Ungulate Passage Rates

I carried out this study to understand the influence climate has on the patch use of a multi-species ungulate community in the south of Sweden. As Sweden's ungulate communities are expanding in both density and range it is important to understand how the climate affects their behaviour. With climate projections showing a strong likelihood of future warming, up to 3 °C warmer by 2100 (IPCC, 2014), understanding the response of ungulates to these factors is important. I investigated the effect of climate on ungulate patch use by using data collected from camera traps to assess whether climate changes were having any influence on ungulate passage rates in southern Sweden. The outcome of this study is that temperature only had a strong effect on the monthly passage rates of roe deer, suggesting that as temperature increases, roe deer visitation increases. Snow depth only had a strong effect on the monthly and seasonal passage rates of fallow deer. Fallow deer passage rates were negatively affected over a monthly and seasonal scale in relation to snow depth, which suggests that their visitation rates decline as snow depth increases.

Hypothesis I, that passage rates will be highest during spring and summer, is supported for red deer, fallow deer and roe deer as their passage rates are highest during spring and summer months (Figure 5). Moose, however, had high passage rates during summer months 2016, winter months 2016/17, and spring months in 2018. During 2017, moose passage rates fluctuated with increases and decreases throughout each season (Figure 5). Therefore the hypothesis is not supported for moose.

My result for moose differs from other studies that have looked at the effect of temperature on moose behaviour. They have found that when the temperature exceeds their critical threshold in summer, they reduce their use of open habitat areas, such as the exclosures in my study, and instead select more sheltered, forest habitats (Dussault et al., 2004; van Beest et al., 2012). My study, however, found that despite summer temperatures regularly exceeding the moose critical threshold, especially during the hottest summer months in 2018, their highest July and August passage rates occurred during this time period, in open habitat areas. This could also be explained by the low density of moose in the study area. Moose are the least common of the four species found in the study area with a density of 6-10 individuals/10km² which is much lower than the fallow deer, the most common species in the study area with a density of 88-107 individuals/10² (Ånöstam, 2017). As moose are the most abundant ungulate species in Sweden (Apollonio, 2010), different results might be found if this study was repeated in an area with a higher density of moose, as it would provide a more representative dataset to assess any trends of how moose patch use is affected by climate variations.

Hypothesis II, that winter passage rates will be considerably lower than summer passage rates, is partly true for all four ungulate species. Both fallow deer and roe deer had a large decrease in passage rates during winter months when compared to summer months while red deer and moose follow the same trend (Figure 5). A previous study carried out in the same study area also found a trend towards lower visitation during winter compared to summer (Ånöstam, 2017). The large decrease in passage rates shown by fallow deer and roe deer in my results could be caused by forage availability in the study area. During winter months the field layer may be covered with a layer of snow, therefore, trees play a more important role in the diets of the ungulate species (Månsson et al., 2015). This could lead to a decrease in the use of open areas during winter months, such as the exclosures in my study. While the exclosures were all replanted following the initial clear cut, they are at different stages of growth, some being quite bare, with few, small trees, while others have an abundance of larger trees. Snow depth could be a limiting factor for ungulate winter passage rates due to the negative impact it has on covering the field layer forage and limiting ungulate movement. Supplementary feeding sites may also influence winter ungulate passage rates, especially fallow deer. Supplementary feeding has been found to maintain higher densities of fallow deer in areas around feeding sites than would normally occur (Felton et al., 2017), therefore suggesting that feeding sites are an important determinant in fallow deer habitat patch selection.

Hypothesis III, that as average monthly snow depth increases, monthly ungulate passage rates will decrease, is only supported by fallow deer as the estimates show that the effect of snow depth on them was found to be significant, their monthly and seasonal passage rates decreasing as snow depth increased (Tables 6 and 10). The reduction in passage rates as snow depth increases has also been reported in other studies, especially in larger ungulates as the movement in snow requires a greater expenditure of energy (Rivrud et al., 2010). Moose, in particular, have been previously found to have their movement limited by snow cover (van Beest et al., 2011) however my results do not support this. Again this could be due to the low density of moose in the area giving a poor representation of how patch use of moose in Sweden is influenced by climate variations.

Hypothesis IV, that passage rates will decrease during hot months, was not supported by these results. Over the years moose and red deer summer passage rates increased while there was a general trend towards decreasing summer passage rates for fallow deer and roe deer (Figure 5). This differs to other studies into the effect of temperature on movement, which have found that high summer temperatures have a negative effect on the movement of cervids (Hayes and Krausman., 1993; Rivrud et al., 2010). A possible explanation for moose and red deer summer month passage rates increasing during the study period could be related to the set-up of the study area. When the ten sites were clear cut and replanted in 2014/2015, grasses and small trees were the dominant species. This would have

suited the smaller species, fallow deer and roe deer, as their dietary preferences are grasses, herbs and small trees. However, during the following years, the trees have grown taller with bigger branches, therefore being more favourable for the larger species, moose and red deer. This would mean that there was higher forage availability for moose and red deer in summer 2018.

4.2. Limitations

A major limitation of this study is the short time period during which the camera traps were taking images at the ten sites. Three years of continuous data was used as this is what was available to me at the time. However, when trying to assess the influence of weather on another variable, in this case, ungulate passage rates, it would be preferential to have at least 30 years of data as climate often refers to average weather patterns during the previous 30 years (NASA, 2017).

The snow depth data is also a limiting factor to this study. Only one weather station around the study area, Södertälje, had snow depth data available for the time period covering this study. This data is collected manually by SMHI either with a ruler, or fixed measuring stick (SMHI, 2013). This measurement is also not always carried out daily. If this is the case then the snow depth from the nearest weather station also recording snow depth is taken. This leads to the possibility of erroneous readings through human error as well as having to rely on the readings of different weather stations that is potentially tens of kilometres away from the study area. The other issue with snow depth data is that snow depth may vary significantly across small scales as it is influenced by the topography of the area, for example, slope or canopy cover (Zheng et al., 2016). As this is not uniform across the study area there will be areas which are deeper or shallower than the SMHI measurements.

Regarding image classification, a limitation arises due to the fact that it has been carried out by at least three different people, including myself. This could lead to human errors such as the misidentification of a species or misinterpretation of behaviour such as foraging (Young et al., 2018). While this is not likely to lead to significant errors that would be detrimental to the study, it is something that future studies should take into consideration. The image classification should be done consistently by the same individual to remove the human error.

The camera traps work with a passive infrared sensor which detects heat differences between the background and a moving object (such as an animal). On extremely hot days the background, such as vegetation and rocks, may heat up to the point where there is no detectable difference between the background and an animal walking in front of the camera (van Berkel, 2014). This is more of an issue with smaller species as they emit less body heat than larger species. Detection distance is another issue related to body size as detection of smaller species could decrease compared to the larger

species the further away from the camera they are (Apps and McNutt, 2018). This would, therefore, mean that some passage events could be missed on an extremely hot day and therefore affect the outcome of the study by giving a false representation of the hottest days. Detectability and passage rates can also be affected by differences in insulation of summer and winter fur. As ungulates grow a winter coat to better insulate themselves during the colder months, there will be a difference in their heat signature in summer and winter, thereby leading to the possibility of being less detectable by the sensor in the camera trap (Hofmeester et al., 2019). This could mean that during winter, the ungulates are more detectable than in summer as there will be a bigger difference in the background temperature and their body temperature which is increased due to better-insulated fur.

5. Conclusion

Understanding the effect of climate variations on ungulate patch use can help to develop management strategies and further our knowledge on how climate change could affect multi-species ungulate communities. Here, I have shown that temperature and snow depth may have an effect on ungulate passage rates but that effects varied widely among species. Temperature was found to strongly affect the monthly passage rates of roe deer while snow depth was found to strongly affect both the monthly and seasonal passage rates of fallow deer. While climate variations have been found to have an effect on ungulate passage rates, it is more likely that other factors had more of an influence on changes to ungulate passage rates, such the setup of the study site and forage availability. After being clear cut and replanted, the smaller species (fallow deer and roe deer) initially benefitted from the vegetation available, However as the tree species in the sites have grown they are now more desirable for the larger species, moose and red deer. While some strong effects of both temperature and snow depth were found in my study there is still a lot of uncertainty and further studies should be carried out to better understand how climate variations affect ungulate patch use.

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