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Linda Zetterkvist

Master's thesis • 30 hp
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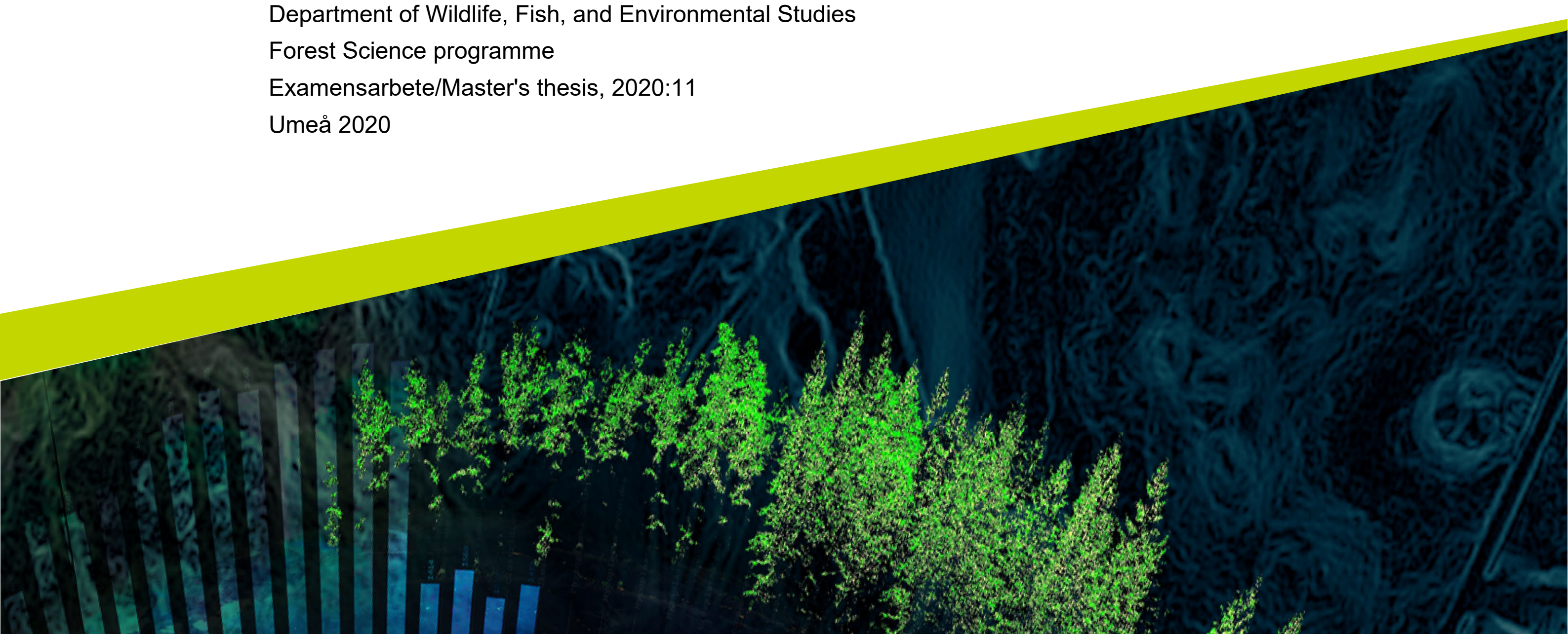

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Abstract

Ungulate management becomes more complex when new species are being introduced and favorable habitats are created by commercial forestry and other forms of land use, resulting in increasing populations. Climate change is also affecting their distributions by altering their ability to spread from their historical range. Management to prevent forest damages, crop damages, vehicle collisions, meet hunting interests and successful conservation programs needs further understanding of how these new emerging ungulate communities function and how they affect their environment.

Speed of movement as a measure of activity has been used in previous studies to understand animal behavior, habits or responses to different habitat, climatic or anthropogenic disturbances. In this work I investigate speed as a measure of ungulate activity in response to other species densities and habitat features in an area located in northern Sweden consisting of a heterogeneous landscape of agricultural land, urban area and coniferous forests.

I used telemetry data originated from GPS-collars fitted to moose, roe deer and red deer to model speed in response to season of the year, habitat type, species density and time of day using linear mixed models (LMM). Density maps were developed from pellet counts and camera trap data in the study area. Habitat features were obtained from the Swedish Surveying Agency (Lantmäteriet). Modeling the different species' daily activity revealed that roe deer and red deer had similar morning and evening activity regardless of season and habitat. Moose however were more active during evening hours regardless of season and habitat. Roe deer were more active in areas with low and medium densities of moose whilst no significant results of moose and red deer activity being affected by densities of other species were observed. Furthermore, red and roe deer were more active during night in contrast to moose who were less active. Season of the year had an effect on all species activities and wetland had an effect on roe and red deer activity. In contrast, moose were more active in open areas and clear cuts.

Keywords: Telemetry, pellet count, camera trap, linear mixed model, ungulate management, red deer, roe deer, moose

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1. Introduction

Animal activity is affected by several climatic, anthropogenic and/or inter-/intraspecific factors (Sprem et al. 2015). These include temperature, daylight, body size, season, among others.

Previous studies have looked at the activity pattern of mammals (Pereira 2010; Ensing et al. 2014; Loe et al. 2007; Kamler et al. 2012; Owen-Smith & Goodall 2014) reptiles (Vermunt et al. 2014) and also in predator and prey interactions (Eriksen et al. 2010).

Speed as a measure of activity amongst ungulates has been used in several different studies (Evavold 2020; Ensing et al. 2014). Speed can be linked to multiple behaviors amongst all moving animals. These include feeding, resting, predator avoidance, nursing, migrating and hunting (Fryxell et al. 2008; Ensing et al. 2014; Evavold 2020;). Moreover, habitat features (Fattebert et al. 2018) and climate plays an important role in animals' ability and desire to move around in their surroundings (van Beest et al. 2012).

Ungulate activity patterns have been of interest due to their increased conflict with humans (Neumann et al. 2012; Ezebilo et al. 2012). As ungulates in Europe are increasing in both number and species diversity, effective management is of great importance to minimize human-wildlife-conflicts (Barrueto et al. 2014). With the advantage from human provided food subsidies and favorable management regimes and climate change, European ungulates are spreading north of their previous range (Ensing et al. 2018).

In Sweden, the composition of ungulate communities goes from three species (moose, roe deer and reindeer) in the far north to multi-species communities in the south. The border between single/two- to multi-communities is moving further and further north as climate change is creating more favorable conditions for other species than moose (*Alces alces*) and roe deer (*Capreolus capreolus*), as well as human-induced influence by introducing new species (Jarnemo et al. 2018).

This may create both direct and indirect negative impacts on biodiversity and also conflicts with human interests such as forestry, agriculture and hunting/game management (Spitzer 2019; Ezebilo et al. 2012).

Wildlife management agencies aim to manage ungulate populations to prevent and reduce possible human-wildlife-conflicts (Spitzer 2019; lansstyrelsen.se). One of these conflicts is ungulate vehicle collisions which are increasing as populations are rising (Hothorn et al. 2015). Indirect and direct competition emerging between sympatric species is becoming more frequent, leading to browsing damage on forest stands as an indirect consequence from interspecific competition (Spitzer 2019).

Direct conflicts over resources across species may cause population impacts such as decreased fecundity and fitness (Richard et al. 2010). Indirect conflicts rising from diminishing resource availability can lead to one species being forced to feed on second choice forage. Spitzer (2019) concluded that browsing damages on Scots pine (*Pinus sylvestris*) by moose increased with high densities of other ungulate species. These density responses may further be analyzed by investigating activity patterns in response to species densities. By understanding activity patterns of ungulates, various conflicts may become easier to predict and prevent. In specific, how ungulates activity is affected by another ungulate species density.

Ungulates are affected by several different biological, temporal and anthropogenic variables and variables every day. Variations in temperature, daylight and snow depth across seasons affect ungulate activity in the northern parts of Scandinavia. These dramatic shifts in living conditions affects the ability to find food and shelter.

Food availability affects ungulate activity by driving animals to move long distances in search of forage (Singh et al. 2012; Allen and Singh 2016). Moose in the northern part of Scandinavia are known for their long migrations between summer and winter home ranges in search for forage (Allen et al. 2016; Rolandsen et al. 2017). Forage is further found in different habitats during different times of the year, also having effect on activity pattern depending on when/if these different habitats are available or not for ungulates (Jarnemo et al. 2018).

Moose, roe deer and red deer (*Cervus elaphus*) are three ungulate species common in the Swedish landscape, in particular, southern Sweden (Jarnemo et al. 2018). As roe deer and red deer are spreading north, moose is now coexisting with these species in the northern part of Sweden as well. This poses new management situations, as the species assemblage is getting more complex. These species differ in both feeding strategy and territorial behavior. Moose is a known browser adapting its demand according to seasonal changes where its preferred source of food is rowan (*Sorbus aucuparia*), sallow (*Salix ssp.*) and aspen (*Populus tremula*) during summer and lingonberry (*Vaccinium vitis-idaea*) and bilberry (*Vaccinium myrtillus*) during spring and autumn (Wam et al. 2010; Spitzer 2019). Roe deer is also a browser, however, having a bigger requirement of high-quality food consisting of young shoots, sprouts and shrubs (Putman 1996; Spitzer 2019) adapting their home range according to availability of recourses, intraspecific competition and seasons (Kjellander et al. 2004). Red deer is a mixed feeder in demand of high-quality forage, browsing on various different plants, shrubs and herbs (Putman 1996; Spitzer 2019). Mires and wetlands are especially selected for by red deer during winter and autumn (Zetterkvist 2020).

Both moose and roe deer live the majority of their life solitary where mature roe deer bucks are highly territorial during spring and summer, whilst moose are less territorial regardless of sex (Jarnemo et al. 2018). Red deer is a more social species usually gathering in herds or groups which are often separated between sexes (Jarnemo et al. 2018).

Interspecific competition adds to the different species' ability to find recourses, especially in areas with high browsing/grazing pressure from other species with similar forage (Spitzer 2019). If more time is required to find resources, activity will shift towards being more active in areas where resource competition is occurring between species, or species needs to settle for less desirable forage (Spitzer 2019). Moose in southern Sweden may be facing high pressure from other sympatric species to choose second choice food, in this case pine (Spitzer 2019). This has led to increased conflicts with forestry where pine is of high commercial value for forest owners and companies.

The aim for this thesis is to understand more about how the activity of three sympatric species, roe deer, red deer and moose is affected by four different biological variables in a boreal Scandinavian landscape by answering the following questions:

(1) How do sympatric ungulate species, moose, roe and red deer differ in their activity on a daily scale across season and habitat type?
(2) Do season of the year, habitat type and day vs night affect species activity?
(3) Do densities of sympatric species affect species activity patterns?

I have the following hypothesis:
(1) In general, activity peaks during morning and evening hours are expected for all three species. I expect this due to known increased activity during dawn and dusk (Neumann et al 2012). Similar peaks are expected in different habitats.

(2a) Seasonal differences in activity will be visible for all three species, as previous studies have shown behavioral changes in response to changing temperature (Evavold 2020), snow depth and food availability (Spitzer 2019) across seasons.
(2b) Activity is expected to increase during night for red deer (Ensing et al. 2014).
(2c) I expect differences in activity depending on if these habitats are important as movement corridors or feeding/resting places, resulting in more activity when moving or less activity when feeding/resting/hiding.
(3a) Moose activity is expected to increase in areas with high roe deer densities (Zetterkvist 2020), as moose has displayed selection for lower roe deer densities in previous studies.
(3b) Roe deer is expected to increase its activity if there are direct interactions in areas with high moose density as a response of selection for lower densities of moose (Zetterkvist 2020).

In this study I will use speed as a measure of activity for moose, roe deer and red deer by using telemetry data collected from GPS-collars attached to females. I will use linear mixed models (Bates et al. 2015) to test if activity of these three species is affected by these variables. This knowledge could help wildlife managers, in different work fields, to create management plans with more aspects in consideration where these three ungulate species coexist. The focus will be to investigate if the density of these three ungulate species affect one another's activity pattern and also look at how activity differs depending the following important biological factors: season, habitat type and time of day.

2. Material and method

2.1. Study area

This study was conducted in a northern Swedish peninsula called Järnäshalvön, located in the province of Västerbotten (Figure 1). The peninsula borders towards the Bothnian bay on three sides whilst the fourth sides borders towards a railway and fenced highway. The size of the area is 200 km^2 and is dominated by boreal forest and arable land, human settlements and mires. This area is unique because of its multi-ungulate community at relatively high altitude where four different species coexists, roe deer, red deer, moose and fallow deer (*Dama dama*).

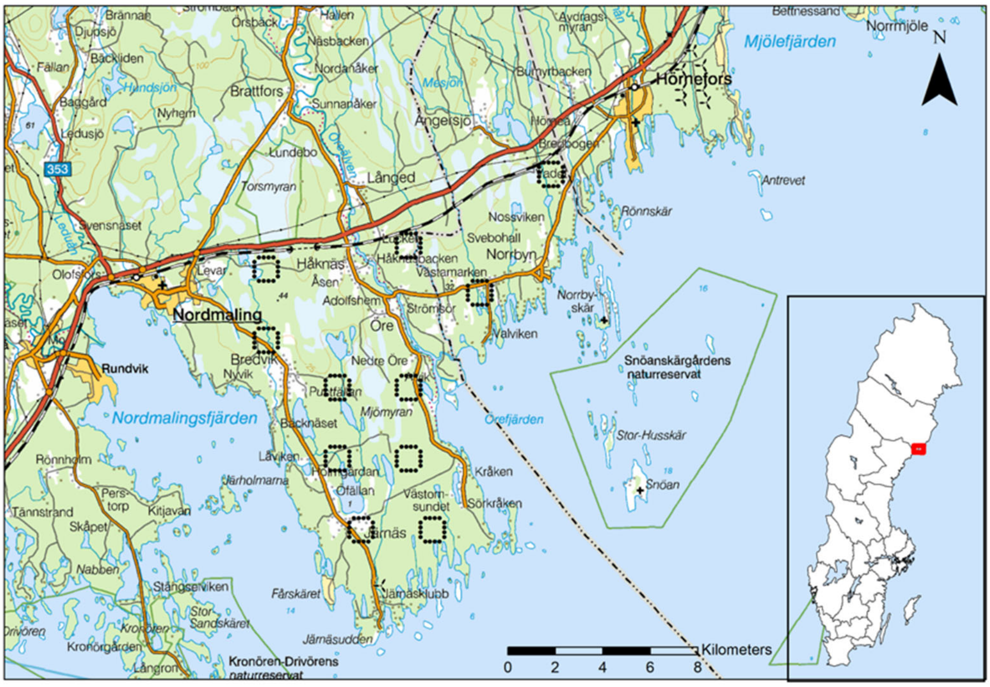

Figure 1. Map over the study area located between Nordmaling and Hörnefors municipalities. Each black dot represents a stationary sampling plot for pellet count. Source: Zetterkvist (2020).

Occasional supplemental feeding of game is practiced in the area, however, the extent of this is unknown since it is carried out voluntarily.

2.2. Data collecting

2.2.1. Telemetry data

Telemetry data on the three species involved in this study was collected through GPS collars. The data gathered from these collars is stored in a data base called WRAM (Wireless Animal Remote Monitoring) at SLU (Swedish University of Agricultural Science). Only females were equipped with collars because females are better suited to wear collars for a longer period of time. The collars used in this study were of the model Vectronic-Aerospace where battery size differed between the species. Batteries of the size 7D was used for moose, 3D for red deer and 1D for roe deer. These collars were also programmed to drop of automatically from the animal when battery ran out. Positioning records fluctuated from 20 min intervals up to 6 h intervals with a mean interval of 30 min for roe deer and 1 h for moose and red deer. Data was collected from year 2017-2019 for moose and roe deer, and 2018-2019 for red deer.

2.2.2. Ungulate density

To be able to create the spatial distribution of ungulate density in the form of raster layers, I used pellet count and camera trap data interpolated using the national Swedish land cover data derived from the Swedish Surveying Agency (www.lantmateriet.se), with the resolution 1x1 km.

Doing so, spatial points were first derived and then fitted to the forest raster, with the function “gstat” in Rstudio (R-version 3.5.1, package “gstat”) , creating a raster containing density information for each species in the form of number of animals per km^2 in each grid of the raster (Figure 3). I divided these density rasters into the four different seasons of the year. I defined the four different seasons as: winter (November-April), spring (May), summer (June-August) and autumn (September-October).

Pellet count

Pellet counts are carried out every year during May-June by SLU staff at stationary sampling plots (Figure 1). Each sampling plot has a radius of 5,56 m (plot size=

100 m^2) and is sampled evenly across the study area. The data in this study was collected during the years 2015, 2016, 2017 and 2018. Each year, pellet groups are removed within the sampling plots and later revisited to count the number of new pellet groups. Species identification is done depending on the size of the pellet groups and individual pellets, later also validated using DNA methods. Furthermore, density of each species over the full area is estimated by the number of pellet groups for each species per day. When using this type of data collection, some constraints need to be taken into consideration such as detectability of pellets and pellet size may affect density estimates (Pfeffer et al. 2018). Moreover, species identification is sometimes difficult in areas where two or more species of similar body sizes are present (Pfeffer et al. 2017; Spitzer et al. 2019). Due to difficulties in distinguishing between fallow deer and roe deer pellets, the number of pellets per pellet group was used to separate the two species. Pellet groups having ≥ 45 pellets were classed as fallow deer and ≤ 45 pellets were classed as roe deer.

Camera trapping

The camera traps were distributed evenly over the study area in 11 squared transects containing 18 locations. Each Camera trap was located at least 100 m apart from the other. It total, 198 camera trap locations were sampled, however, due to camera malfunction, faulty camera placement and fallen tree, 193 camera traps were used for the analysis. A suitable place for a camera to be mounted included a minimum of 10 m of clear view in front of the camera to optimize detectability, and mounting 1 m above ground to avoid large amounts of snow. Furthermore, distances of 5, 10 and 15 m were marked with a red ribbon in front of the cameras' central view. To ensure full functionality throughout the study period, the cameras were programmed to take a control picture every day. All cameras in this study was set to take three rapid-fire shots when triggered, this to ensure full passage of an animal in front of the camera. One downside when using camera trap data is the lack of control of the possible large amount of by-catch data (Hofmeester et al. 2019).

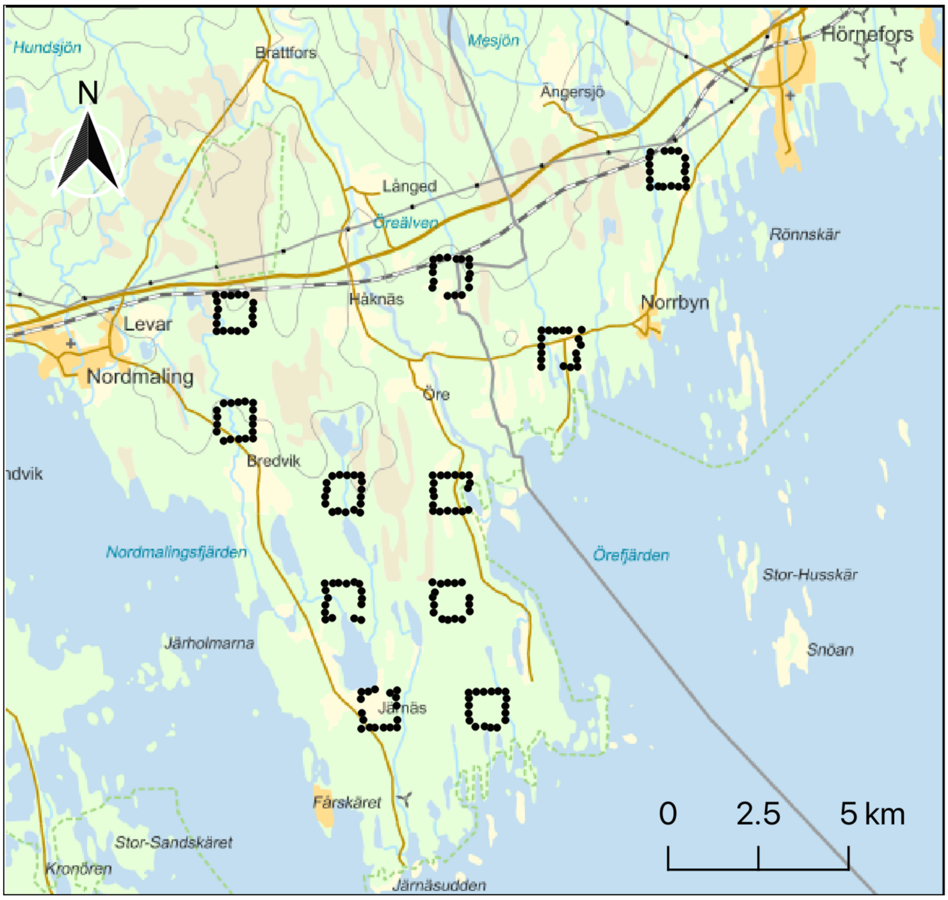

Figure 2. Distribution of camera traps in the study area, Järnänshalvön. Each black dot represents a camera location. Source: Zetterkvist (2020).

2.3. Analyses

2.3.1. Linear mixed model

Linear mixed model was used to test whether mean speed (response variable) of each species is affected by four different variables/factors (Bates et al. 2015). These four variables are included in the analysis to test my hypothesis, included as important factors affecting ungulates activity patterns in this northern study area. These factors were treated as fixed effects (predictors), whilst each individual ungulate ID was treated as random effect. The reason why I used linear mixed models is that they help account for data with a complex structure, such in this case, with multiple variables affecting ungulate activity. The response variable was log transformed to become normal distributed and meet the assumption of a linear mixed model.

Models were fitted with the function “lmer” available within the “lme4”- package provided by R-studio (R-version 3.5.1) (Bates et al. 2020). Conclusions of each variables’ interaction with mean speed for each species were then made to connect with results of how activity differs for each species and variable.

Response variable

Speed (km/h) for each species was calculated using a function named speed in the R-package “move” (R-version 3.5.1). As default speed was calculated in m/s, I further changed it to km/h to make it easier to relate to and compare to previous studies.

Predictors

Season of the year was divided according to the same criterion as the species density rasters. Habitat was derived from the same landcover raster used to create species density raster. Each habitat was then further categorized according to relevant habitat features for ungulates within the study area (Table 1).

The habitats were divided into six categories consisting of “forest”, “agricultural land”, “clear cut” (deforested areas with forest height of less than 5 m), “open land” (non-forest open land other than clear cuts), “wetland”, “water” (lakes and sea) and “other” (human settlements and urban areas) (Table 1). Of these six categories, forest, agricultural land, clear cut, open land and wetland were included in the analysis. The reason why I choose these five habitat types is due to known selection overlap in these areas (Zetterkvist 2020), which further can be connected to higher likelihood of density overlap between species.

Density of sympatric species was included in the model to investigate if this factor is significantly affecting the respective species’ activity. Densities of each species were divided into three categories: “high”, “medium” and “low” (Figure 3).

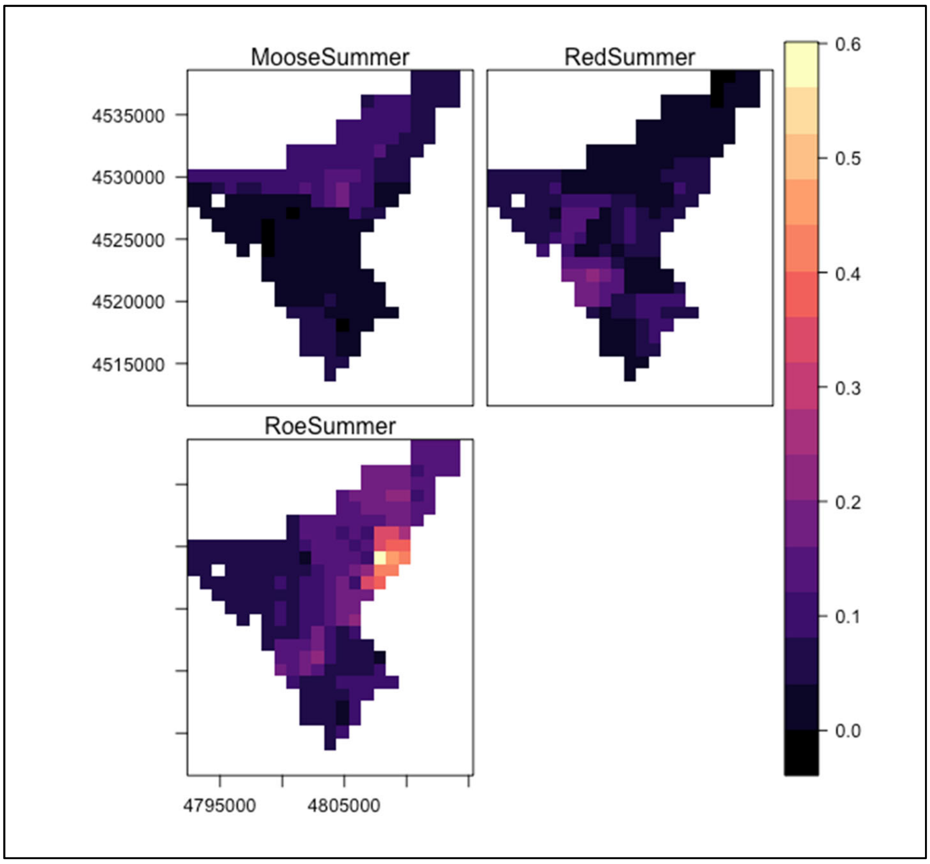

Figure 3. Density for moose, roe deer and red deer during season summer in unit number of animals/km2 on the y-axis to the right. Source: Zetterkvist (2020).

Day and night were calculated by deriving sunrise and sunset with function getSunlighTimes in package "suncalc" available within the R environment (R-version 3.5.1) (Thieurmel and Elmarhraoui, 2019). Mean sunrise and sunset were then derived for each season to furthermore derive day and night for all observations from the telemetry data.

Individual ID was treated as a random factor using a binomial distribution to account for repeated measure nature of the data and variability between individuals. In this study, 27 moose, 23 roe deer and seven red deer was included.

Table 1. Grid codes and classification of the national land cover raster with associated reclassification into the different habitat types included in the study.

Grid code	**Class**	**Reclassified to:**
111	Pine forest not on wetland	Forest
112	Spruce forest not on wetland	Forest

113	Mixed coniferous forest not on wetland	Forest
114	Mixed forest not on wetland	Forest
115	Deciduous forest not on wetland	Forest
116	Deciduous hardwood forest not on wetland	Forest
117	Deciduous forest with deciduous hardwood forest not on wetland	Forest
118	Temporarily non-forest not on wetland	Clear cut
121	Pine forest on wetland	Forest
122	Spruce forest on wetland	Forest
123	Mixed coniferous on wetland	Forest
124	Mixed forest on wetland	Forest
125	Deciduous forest on wetland	Forest
126	Deciduous hardwood forest on wetland	Forest
127	Deciduous forest with deciduous hardwood forest on wetland	Forest
128	Temporarily non-forest on wetland	Clear cut
2	Open wetland	Wetland
3	Arable land	Agricultural land
41	Non-vegetated other open land	Other
42	Vegetated other open land	Open land
51	Artificial surfaces, building	Other
52	Artificial surfaces, not building or road/railway	Other
53	Artificial surfaces, road/railway	Other
61	Inland water	Water
62	Marine water	Water
0	Outside mapping area	Other

Model selection

To answer my hypothesis regarding species activity depending on each variable I built the linear mixed model with speed as response variable and season, habitat type, species density and day/night as predictors in the same model, for each species respectively, and ID as random factor: speed~ season+ habitat+ species density+ day/nigh+ (1|ID). I included all variables in the same model to be able to see the effect of each variable when they interact with each other as to reflect on what these ungulates are exposed to in the wild.

3. Results

Table 2. Number of individuals and observations included in the study derived from the telemetry data.

Species	**Individuals (ID)**	**Observations (Obs.)**	**Mean observations/ID**
Moose	27	125777	4658
Roe deer	23	72451	3150
Red deer	7	18167	2595

3.1. Species daily activity depending on season, habitat and species density

The mean sunrise during winter is earlier than during autumn. This could be because I defined winter as November-April and therefore the early sunrise during November and March-April may influence the mean sunrise to be earlier (Table 3).

Table 3. Mean sunrise and sunset for each season.

Mean sunrise/sunset (time)	**Spring**	**Summer**	**Autumn**	**Winter**
Sunrise	03:20:52	02:55:50	06:49:58	06:29:52
Sunset	21:47:29	22:32:14	18:07:44	17:47:13

Species daily activity depending season

Species activity during different seasons of the year and across the day shows similar pattern across all three species (Figure 4). Moose however display a peak in activity during the day light hours during winter in contrast to the other two species. (These curves are derived from a smoothing method called “geom_smooth” in package “ggplot2” within R-studio with method “loess”). Moose shows the highest peaks in activity of the three species during autumn whilst roe deer have the highest peaks during spring and summer. During winter, roe and red deer have peaks during the evening hours when moose activity is decreasing from its peak during the day.

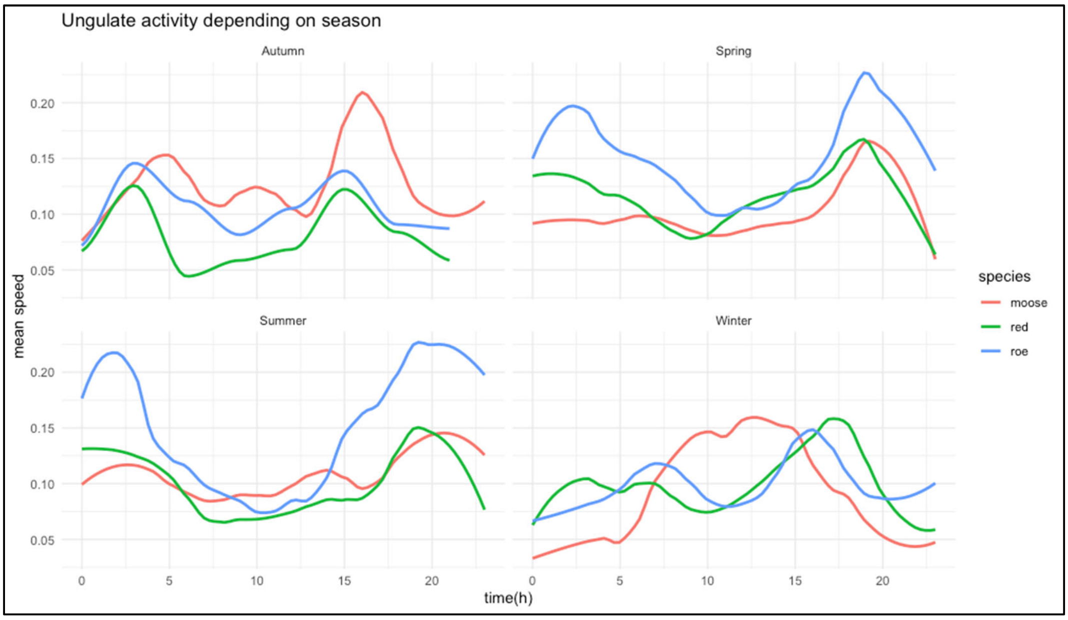

Figure 4. Species daily activity depending on season of the year.

Species daily activity depending on habitat

Mean daily activity patterns in different habitat types are similar across all three species with peaks during morning and evening hours (Figure 5). Moose stand out and are dominantly more active during the afternoon/night in all habitat types except agricultural land where a weak morning peak is visible. Roe deer are most active in agricultural land, open land and clear cuts during evenings (Figure 5). Red deer are more active during the evening than during morning hours in all habitat types. The highest peaks in activity is visible for roe deer in the majority of the habitat types, moose in contrast have the lowest peaks in activity.

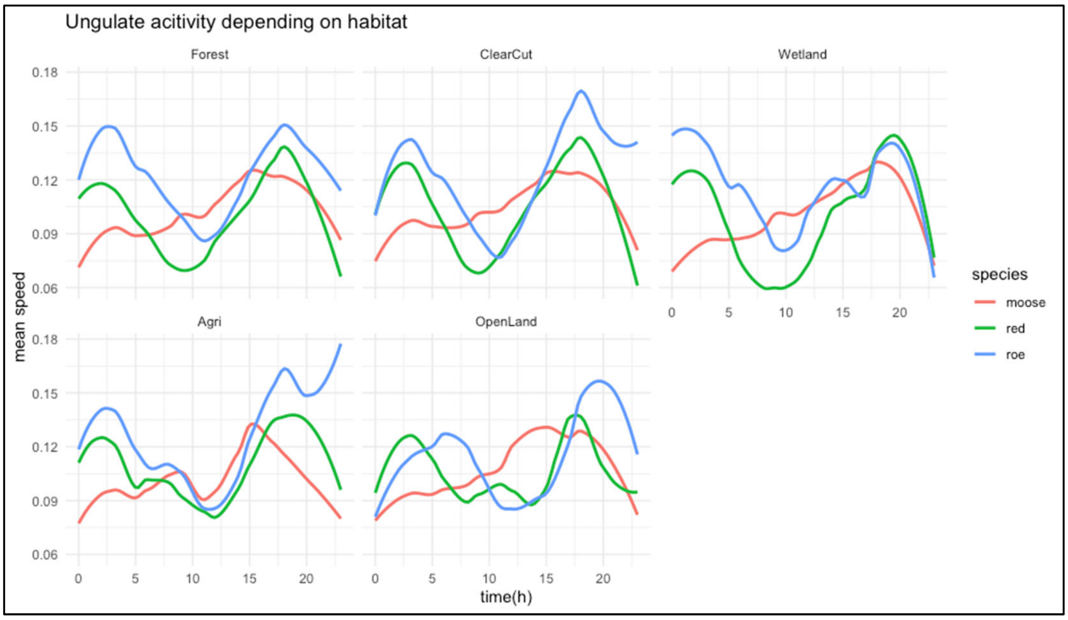

Figure 5. Species daily activity depending on habitat type.

Species daily activity depending on species density

Roe and red deer activity depending on moose density displayed similar morning and evening peaks depending on season of the year and habitat type (Figure 6). However, in high moose density, roe deer display high peaks in activity during morning, midday and evening whilst red deer show lower peaks during morning and evening as in low and medium densities of moose. The trend in roe deer activity seems to increase with moose density.

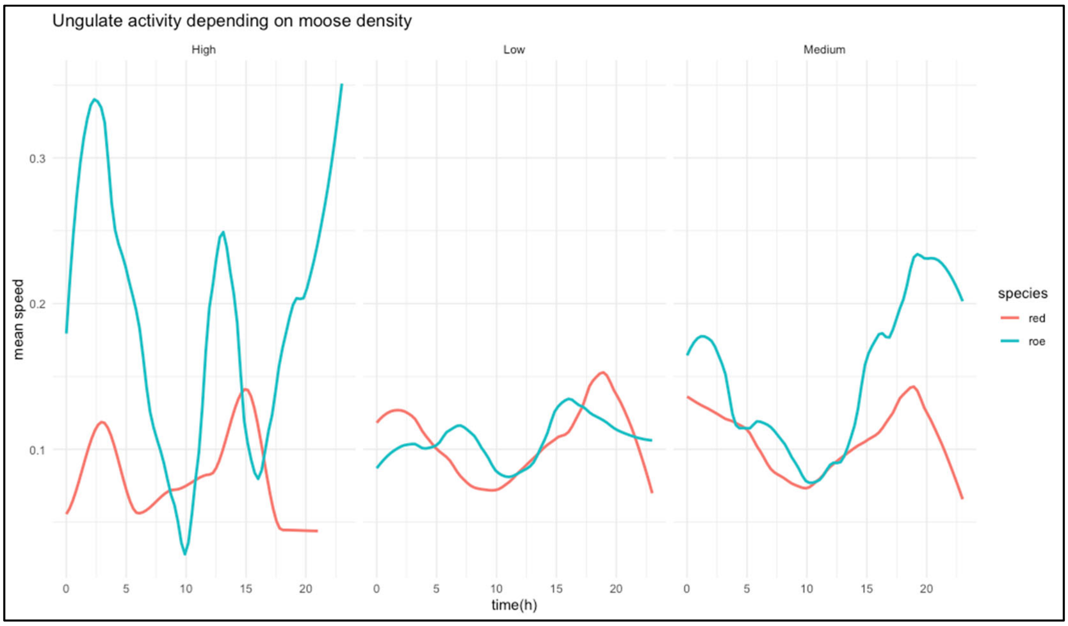

Figure 6. Roe and red deer daily activity depending on moose density.

Moose and red deer activity depending on roe deer density also seems to follow similar morning and afternoon increase in activity as depending on season of the year and habitat type (Figure 7). As for roe deer in response to high moose density, moose display more activity and higher peaks when roe deer density was high (Figure 7). No results regarding daily activity of red deer in response to high roe deer density were possible to derive.

Figure 7. Moose and red deer daily activity depending on roe deer density.

When red deer density was low and medium, roe deer and moose display similar activity pattern as during season of the year and habitat type (Figure 8). However, when red density was high both moose and roe deer showed more and irregularity in activity with morning and evening activity, especially moose.

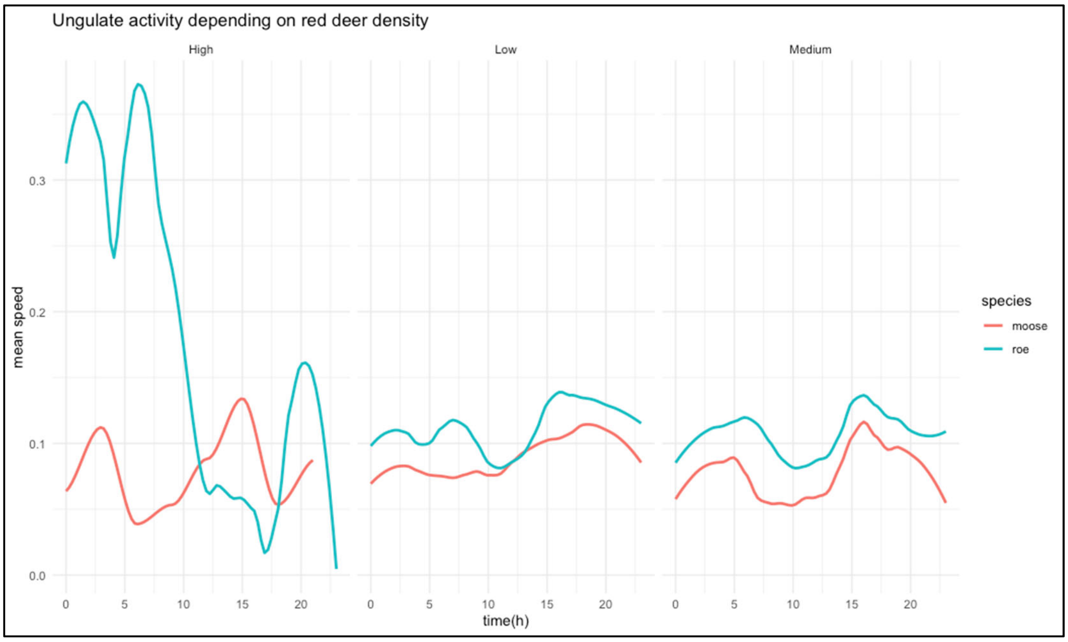

Figure 8. Moose and roe deer diurnal activity depending on red deer density.

Coefficient of variation (CV) for species daily activity

Looking at variation in daily activity for each species across seasons, moose show the highest variation (Figure 9). Roe deer activity variation is slightly higher than red deer and is slightly higher during the day (Figure 9). Red deer display higher variation in activity during autumn and spring and is similar to roe deer's variation in activity during summer (Figure 9). Moose show more variation in activity in morning hours during autumn, summer and winter.

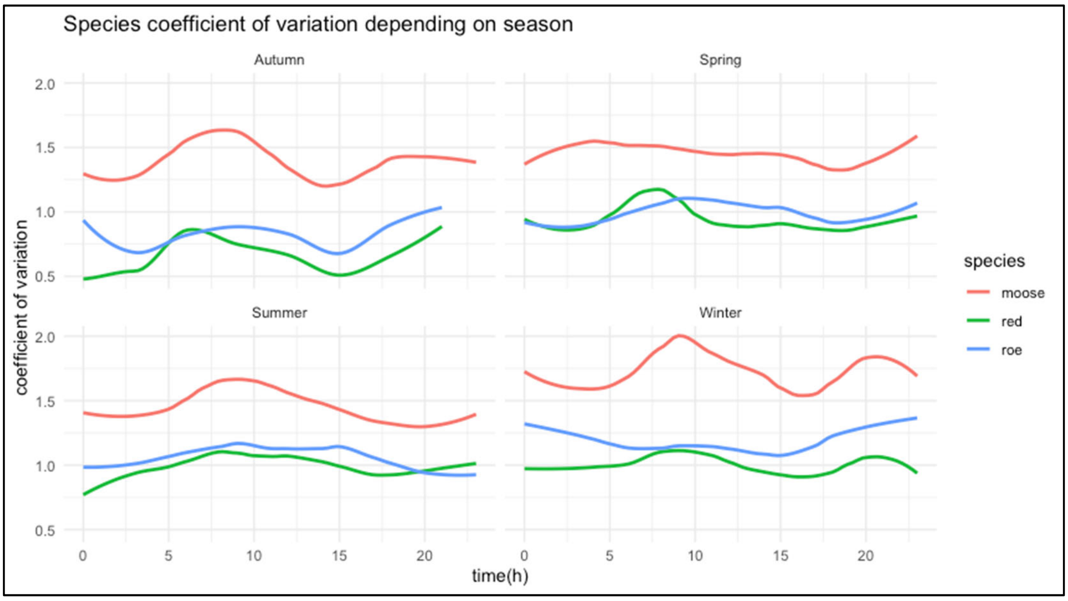

Figure 9. Species coefficient of variation depending on season of the year.

Activity variation depending on habitat type shows that the variation in activity of moose is consistently high (Figure 10). Red deer have similar pattern in activity variation as roe deer in forest and agricultural land, however, with higher peaks. Roe deer activity varies more in morning hours across all habitats, an increase in activity variation is also visible in the evening in forested, clear cut and agricultural areas (Figure 10).

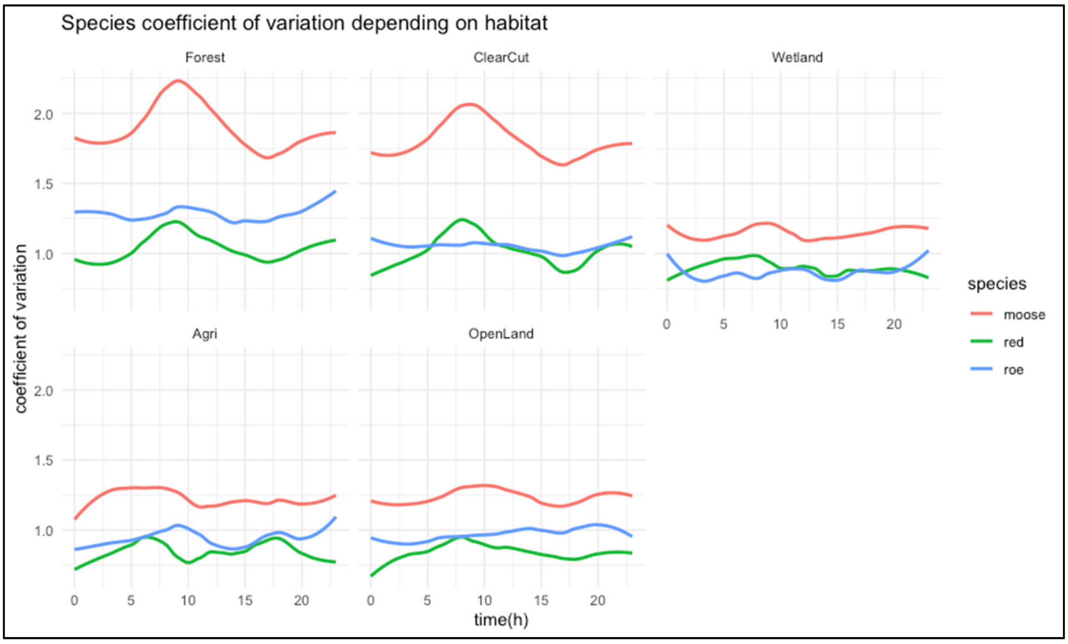

Figure 10. Species coefficient of activity depending on habitat type.

Overall, moose have the highest coefficient of variation in activity of the three species regardless of season and habitat. Roe and red deer have similar coefficient of variation in activity, but roe deer have slightly higher than red deer in the majority of the seasons and habitat types.

3.2. Mixed model analysis results

Using linear mixed model analysis to investigate how different biological important factors affect ungulate activity resulted in six different models for each species (Appendix 10). The models are presented as univariate when only including one of the factors, and multivariate when including all factors in the same model. The model that performed best in explaining the effect of these variables on species mean speed (activity) was the full model (all factors included) for moose and roe deer. For red deer however, the model only including season of the year as fixed effect explained the difference in red deer mean speed best (Appendix 10). This shows the positive effect of including all variables in the same model to explain species activity better by accounting for important biological variables affecting activity in the wild.

3.2.1. Univariate models

Overall, multivariate models explained species activity best for moose and roe deer (lowest AIC), results from the univariate models are attached in appendix (7-9). For red deer, the model only including season had the lowest AIC-value, and therefore highest ranking of the models (Appendix 10) which indicates that season of the year has the highest explanatory factor affecting activity than all factors combined.

Moose

When only using season of the year to explain moose activity in the mixed model, moose showed less activity during spring and winter and more activity during autumn (Appendix 7). Summer did not yield any significant results for moose activity.

Only including habitat as factor affecting moose activity, open land was the only habitat giving significant results showing an increase in activity of moose relative to forest (Appendix 7).

Moose were more active in areas of high roe deer densities and less active in areas with low roe densities (Appendix 7).

Moose were less active in areas with low and medium densities of red deer (Appendix 7).

Moose were less active during night compared to during the day (Appendix 7).

Roe deer

Roe deer were more active during spring, summer and winter compared to autumn (Appendix 8).

Wetland areas made roe deer more active whilst agricultural areas made roe deer less active compared to forest (Appendix 8).

Roe deer displayed less activity in areas of high moose density and more activity in areas with low and medium densities of moose (Appendix 8)

Roe deer were more active, in areas with low and medium red deer density (Appendix 8), and less active in areas with high red deer density when only including red deer density on the model.

Roe deer were more active during the night than during day (Appendix 8).

Red deer

Red deer were more active during spring and less active during winter (Appendix 9).

Red deer displayed less activity in wetlands (Appendix 9).

Red deer activity was not significantly different in response to other species densities (Appendix 9).

Red deer showed more activity during the night than during day (Appendix 9).

3.2.2. Multivariate models

Moose

For moose, autumn (intercept), spring and winter yielded significant results on moose activity. Moose are less active during spring, summer and winter compared to autumn (Table 4).

Overall, moose move faster in clear cut and open land, in contrast to the univariate model which only derived significant results for open land (Table 4).

None of the species densities resulted in significant results in the full model, however, the univariate models did (Table 4; Appendix 7).

Factor time of day displayed less activity during night, the same as in the univariate model (Table 4).

Table 4. Fixed effects for moose activity (speed), full multivariate model. Autumn is the intercept for season, forest is the intercept for habitat, high density of roe deer and red deer is intercept for species density and day is intercept for time of day.

Factor	**Moose**	**Estimate**	**SE**	**t-value**	**p-value**
Season	Intercept	0.28	0. 10	2.78	0.0057*
	Spring	-0.11	0.012	-9.13	<0.0001*
	Summer	-0.10	0.012	-8.19	<0.0001*
	Winter	-0.56	0.012	-47.80	<0.0001*
Habitat	Clear-cut	0.011	0.0058	1.99	0.047*
	Wetland	-0.014	0.017	-0.80	0.42
	Agri.	-0.044	0.048	-0.92	0.36
	Open land	0.053	0.014	3.80	0.00015*
Roe deer density	Roe low	0.020	0.079	0.26	0.79
	Roe medium	-0.016	0.080	-0.20	0.84
Red deer density	Red low	0.097	0.061	1.61	0.11
	Red Medium	-0.085	0.061	-1.40	0.16
Time of day	Night	-0.19	0.0061	-31.65	<0.0001*

Roe Deer

Roe deer were more active during spring, summer and winter as compared to autumn (Table 5). These results are the same as in the univariate model (Appendix 8).

Roe deer were more active in wetlands (Table 5). In contrast to the univariate model this was the only result derived from roe deer activity depending on habitat type (Appendix 8).

Roe deer were more active in areas with low and medium densities of moose compared to the intercept (high density) (Table 5). These results are the same as in the univariate model only including moose density (Appendix 8).

No significant results were derived regarding roe deer activity in response to red deer densities (Table 5), in contrast to the univariate model (Appendix 8).

In contrast to moose, roe deer displayed a significant increase in activity during night (Table 5), the same results were derived in the univariate model (Appendix 8).

Table 5. Fixed effects for roe deer activity (speed), full multivariate model. Autumn is the intercept for season, forest is the intercept for habitat, high density of moose and red deer is intercept for species density and day is intercept for time of day.

Factor	Roe deer	Estimate	SE	t-value	p-value
Season	Intercept	-0.44	0.059	-7.43	<0.0001*
	Spring	0.075	0.022	3.43	0.00060*
	Summer	0.24	0.020	12.23	<0.0001*
	Winter	0.32	0.020	16.089	<0.0001*
Habitat	Clear-cut	-0.020	0.012	-1.72	0.086
	Wetland	0.063	0.025	2.54	0.012*
	Agri.	-0.027	0.021	-1.30	0.19
	Open land	0.024	0.017	1.45	0.15
Moose density	Moose low	0.091	0.027	3.35	0.00082*
	Moose medium	0.13	0.028	4.52	<0.0001*
Red deer density	Red low	0.061	0.043	1.42	0.15
	Red Medium	0.00027	0.043	0.006	0.99
Time of day	Night	0.12	0.0078	15.066	<0.0001*

Red deer

Red deer were more active during spring compared to autumn (Table 6). No other significant results were derived for factor season. However, since the model that got the best ranking results were univariate model season (Appendix 10), looking at these results, red deer displayed less activity during winter (Appendix 9).

Of the habitat types, red deer were less active in wetlands (Table 6). The same results were derived in the univariate model (Appendix 9)

During night, red deer d became more active (Table 6) which were the same results derived from the univariate model (Appendix 9).

Table 6. Fixed effects for red deer activity (speed), full multivariate model. Autumn is the intercept for season, forest is the intercept for habitat, high density of roe deer and moose is intercept for species density and day is intercept for time of day.

Factor	Red deer	Estimate	SE	t-value	p-value
Season	Intercept	-0.12	0.16	-2.012	0.46
	Spring	0.23	0.057	5.74	<0.0001*
	Summer	0.052	0.057	2.91	0.36
	Winter	-0.086	0.059	2.59	0.14
	Clear-cut	0.021	0.017	0.95	0.21
Habitat	Wetland	-0.063	0.030	-0.80	0.036*
	Agri.	-0.0078	0.038	0.86	0.84
	Open land	0.031	0.031	0.51	0.31
Roe deer density	Roe medium	0.081	0.14	0.96	0.56
Moose density	Moose low	0.0069	0.14	0.66	0.96
	Moose medium	-0.043	0.14	0.35	0.76
Time of day	Night	0.086	0.18	4.29	<0.0001*

Individuals of each species were treated as random factors in all models to account for individual variation in activity. Roe deer had the largest variation and standard deviation (SD) (Table 7), which also is reflected in the individual variation in activity graphs (Appendix 2&5). Red deer had the lowest variation and SD in activity even though red deer data contained fewest individuals (Table 7). Red deer, as in these results (Table 7), display lowest variation in activity depending on season and habitat (Appendix 3&6). Moose have as a slightly higher individual variation where some individuals stands out in the seasonal variation during autumn and summer (Appendix 1&4).

Table 7. Random effects for each full model and species with standard deviation.

Random effect	Moose	Roe deer	Red deer
Variance	0.013	0.031	0.012
SD	0.12	0.18	0.11

4. Discussion

Inter- and intraspecific competition is a complex task ungulate management is facing further across Sweden. Many conflicting interests need to be met in order to fulfill goals from government level to private peoples' recreational interests. Therefore, I studied how moose, roe deer and red deer activity is affected by each other's density, combined with other biologically important factors in their environment. My study showed that roe deer and red deer had similar daily activity when compared to moose. It also displayed that when combining season of the year, habitat type, species density and time of day as factors affecting species activity, moose and red deer activity were not significantly affected by another species density. Roe deer were affected by moose density and were more active in areas with low moose densities.

4.1. Daily species activity

This study showed that daily activity of moose, roe deer and red deer differed between seasons of the year, habitat type and species density, in particular for moose.
Moose were most active during autumn and winter, whilst roe deer were most active during spring and summer (Figure 4). Overall, roe deer and red deer had distinct peaks in activity during morning and evening hours, regardless of season or habitat type. Roe deer activity was slighlty skewed towards later morning activity compared to red deer. These results are confirming hypothesis (1) that peaks in activity will be visible for all three species during morning and evening.

Moose were most active during evening hours, depending on season and habitat, except during winter where activity peaked during the day (Figure 3). One theory of why moose activity during winter peaks during the day could be that moose minimize energy loss by being active during the warmer hours of the day (Beest & Milner 2013). Alternatively, groups of individuals/this particular year (Appendix 1) it was more favorable to be active during the day when migrating or moving between feeding places due to for example severe cold or high snow depth. A reason why moose showed more activity mostly during the evening hours, except during winter, could be a reflection of their heat sensitivity (Evavold 2020; Ditmer et al. 2018), and because of that, spending more time being active in the cooler evenings to avoid heat, especially during summer (van Beest et al. 2012; Beest & Milner 2013).

Red deer were least active during the day in forest, clear-cut and wetlands (Figure 4). This could be a reflection of these areas being selected for shelter, resting, feeding or processing food, as these behaviors require low activity. Wetlands are known to be preferred by red deer for feeding resources (Putman 1996). Roe deer and red deer had the most alike daily activity across seasons and habitat types (Figure 3 & 4). Even though these two species differ in territorial behavior, their daily activity seems similar. This could indicate higher chance of these two species crossing paths.

In areas with high moose density, roe deer activity displayed high peaks, whilst red deer had similar peaks in activity as in areas with low and medium densities of moose (Figure 6). Moose displayed similar pattern as roe deer, where moose showed high peaks in activity in areas with high roe deer density (Figure 7). Red deer displayed similar peaks in activity regardless of roe deer density. In areas with high red deer density, roe deer had high peaks in daily activity as for high moose density, compared to roe deer activity in areas with medium and low densities of red deer (Figure 8). Moose displayed no high peaks in areas with high roe deer density. High peaks in roe deer activity in areas with high moose density could indicate avoidance of moose or lack of observations in these areas resulting in these high peaks. The same theory could be true for moose.

The coefficient of variation in activity was highest for moose regardless of season or habitat type and fairly similar between roe deer and red deer. Roe deer's CV, in general, was slightly higher (Figure 5 & 6). One reason could be the way these three ungulates differ in social/herding behavior (Putman 1996; Ensing et al. 2018). Moose and roe deer live solitary throughout most of the year whilst red deer live in groups or herds. This influences the individual variation in the data and therefore, activity. Another reason could be that moose are a partially migrating species, which could influence the results if some of the individuals involved in this study are more or less migrating during winter and spring (Rolandsen et al. 2017).

4.2. Linear mixed model results

The univariate linear mixed models for each factor affecting species activity had higher AIC-values than the multivariate models for moose and roe deer. The multivariate model therefore explains better the observed behaviors for these species (Appendix 10). This was not the case for red deer, where the model only including season had the lowest AIC and therefore the highest performance. The major differences between the multivariate and the univariate models was that for species activity depending on species densities, results were possible to derive for both moose and roe deer in contrast to in the multivariate model, where results only were possible to derive for roe deer activity in response to moose density. This could indicate that species densities are a more important factor affecting roe deer activity than it is for moose and red deer where no significant results were possible to derive in the full model. Roe deer were more active in areas with low and medium densities of moose than in areas of high moose density (Table 5), which is not in line with hypothesis (3) regarding roe deer. This could be as a response to moose and roe deer selecting for different habitats during the majority of the seasons (Zetterkvist 2020). If I would have looked at activity in response to species density depending on season of the year, the results might have looked different and more reflected on the seasonal differences in habitat selection. Both high and low peaks in activity were visible for roe deer in areas with high and medium densities of moose even though the results from the mixed model showed more activity in low and medium densities (Table 5; Figure 5). This could be because the high and low peaks, on average, results in less activity of roe deer in high moose density areas than in medium and low density areas.

Furthermore, spring, summer and winter resulted in moose being less active whilst it resulted in roe deer being more active. Red deer were more active in spring. However, it was not possible to derive significant results for all species and habitat types. Moose displayed more activity in clear cuts and open areas whilst roe deer showed more activity in wetlands. Moose being more active on clear cuts could indicate that they use these areas for passing between habitat patches. Another theory could be that since these areas are lacking good shelter, moose keep themselves in movement to avoid being detected. It could also be that moose are more active on clear cuts during the day whilst less active during night and spread across the whole year, they appear more active on clear cuts. However, this requires further analysis. Roe deer being more active on wetlands could also indicate that this area is primarily used as a passage area. Red deer were less active in wetlands, possibly as an indication of red deer spending time on resting and feeding in these areas (Putman 1996). This could be an indication that different seasons have a bigger influence on species activity, and/or lack of observations in all habitats for each species, in particular for red deer which had the lowest amount of observations/individual (Table 2). Moose as a partially migratory species (Singh et al. 2012) can move long distances between winter and summer areas and therefore moving out of the study area during spring, which might explain the lack of significant results in habitat affecting activity in this particular area. However, since roe deer are more stationary and significant results still were lacking from habitat types, my first theory is more likely:seasons have the greatest impact on species activity.

Red deer were more active during night, which confirms hypothesis (2). Roe deer also were more active during night, this could be of the same reason as for red deer, to avoid anthropogenic disturbances in areas close to human settlements. In my previous study on ungulate habitat selection, roe deer selected for clear cuts, agricultural land and open areas over forested land. These areas are open areas and lack good shelter, which could be the reason why roe deer is more active during night to avoid exposure. In contrast, moose were less active during night (Table 4).

Species daily activity did not differ extremely when looking at seasonal or habitat scale. This could indicate that the time of day is a bigger driver of influencing activity than season of the year or habitat type since the daily activity looked very similar regardless of species body size, feeding behavior or habitat selection (Figure 4-8).

Roe deer have the highest individual variation despite the rather low sample size. This could be due to their solitary and territorial behavior, even amongst females who are less territorial (Ensing et al. 2018), which leads to larger individual variation depending on the area the individual lives in. The microclimate within each territory affects the individual's behavior and activity depending on for example closeness to human settlements, water, food recourses, predators and shelter (Ensing et al. 2018; Putman 1996; Fattebert et al. 2019). Since moose had the second highest individual variation, with its less territorial behavior but still being solitary throughout the majority of the year (Ensing et al. 2018), this theory could be true. Red deer with the lowest individual variation, though the lowest number of individuals in the study, shows the effect of group/herd behavior vs territorial behavior on the individual variation. This could also be a good indication that data and results are representable for these three species. Connecting back to the CV for each species, moose had the highest value.

Even though the ability of roe deer to move is restricted by high snow depth (Ossi et al. 2015), results from the mixed model still showed that roe deer are more active during winter. This could be due to these roe deer who were collared spent time at feeding stations and in closeness to human settlements where roads and yards are being cleared from snow. The same theory could be true for red deer who also were more active during winter, in contrast to moose.

From my previous study on ungulate habitat selection (Zetterkvist 2020), moose selected for open areas and clear cuts over forested areas during winter. These areas are often covered in the highest amount of snow due to lack of forest canopy. The large body size and long legs od moose give them the advantage to move in these areas during winter, in contrast to roe deer. The mixed model analysis showed that moose are less active during winter, which could be to conserve energy by moving less and feed in one place for a longer period.

This study analyzed data from several years with different snow cover, temperature sum as well as habitat alterations such as clear felling of forest. Roe deer activity is highly affected by deep snow (Ossi et al. 2010), restricting its roaming ability to areas close to human settlements or under forest canopy. This could have an effect on the results since telemetry data only were derived from three year for moose and roe deer, and two years for red deer. With climate change, these fluctuations in snow cover and temperatures between years might become less predictable and could potentially be wise to add as a random factor (Davis et al. 2016) in future models of ungulate activity. Disturbances from habitat alterations caused by humans might also have an effect on species activity within a species home range. Clear felling of a forested area creates young forests stands which contains more forage than old mature forest stands (Bergqvist et al. 2018). This ultimately changes ungulates behavior in this area on habitat level in response to available forage (Spitzer 2019). If such a disturbance happened during the period of data recording, sudden change in the animal's behavior within its home range might quickly alter its overall activity.

Results from the full model did not yield significant results regarding species densities effect on moose activity, however, univariate models did. One reason for this could be other variables such as season and habitat have a bigger influence. Furthermore, species densities might not affect red deer activity, as red deer are living in groups/herds in combination with being a mixed feeder and therefore being more adaptable in their forage (Spitzer 2019; Putman 1996). The lack of an effect might also be simply because there are not high enough species densities to have affect moose and red deer activity in this area.

This study highlights the importance to incorporate several features affecting species activity to get a wider perspective of ungulate activity, and also that activity might not give the best indication of direct interspecific competition. For moose, and possibly also red deer, other factors than species densities seem to have a greater effect on activity. However, for roe deer, moose density had an effect on its activity even when involving other factors. This shows that the effect of other species densities varies between species and if the effect is going just one or both ways. Spitzer (2019) showed that roe deer increased its browse on *Vaccinium ssp*. in areas with high ungulate densities, which becomes an indirect effect in response of other species. Therefore, simply looking at these factors affecting species activity might not give the whole picture, but still an indication of what affects species activity. Red deer activity depending on species densities did not yield any significant results, this is most likely due to lack of data (Table 2) and possibly red deer's different social behavior in contrast to the other two solitary species, in combination with its dietary plasticity enabling it to adapt its forage according to current food availability (Spitzer 2019). To better understand these factors affecting activity responses to species density one could combine each factor with species density in the analysis to understand how these factors together affect species. For example, during summer and autumn, these three species have the greatest overlap in selection of habitat (Zetterkvist 2020),- Looking at how species activity is affected by species densities within each season and habitat might give a better understanding in the complexity of interspecific competition.

4.3. Conclusion

With the increased complexity in species management, in particular ungulate management, where numbers are increasing alongside with changing species assemblages, multi-species management is in the need to understand better these complicated systems. This study could contribute in this matter by highlighting the importance to consider habitat, season, species density and time of day in affecting ungulate activity in a boreal forest landscape. Combining the knowledge from this study with other similar studies of multi-species communities will give a better understanding of what affects these species when new and more species are introduced in a system. This study also shows the advantage in using several data collection methods to display and understand more about species activity.

This study could be applicable in other species management perspectives and work fields such as predator management which in many places in Sweden and the rest of the world is becoming more complex as successful conservation programs lead to these species increasing in number. Humans effect on species activity, behavior and ability to find places to live is another aspect that could be used with similar analysis and method of data collecting (Buuveibaatar et al. 2016). Studies like this can also be useful where management is less successful or lacks knowledge to better grasp which methods are best to use in a management situation.

For further studies, looking at how daily activity of sympatric species differ and/or overlap, could help broaden the understanding of underlying differences and similarities across species. Using overlap analysis is a tool that could be used to measure the extent of these differences and possible similarities between species to get a better grasp of the possible extent of interspecific competition to further connect with density responses. Adding information such as body mass, fawn body mass, home range size could also help understand secondary responses of species densities. Richard et al. (2010) found a negative correlation between roe deer fawn body mass and red deer density. This shows that density responses might not be visible in changed activity but through other biological responses.

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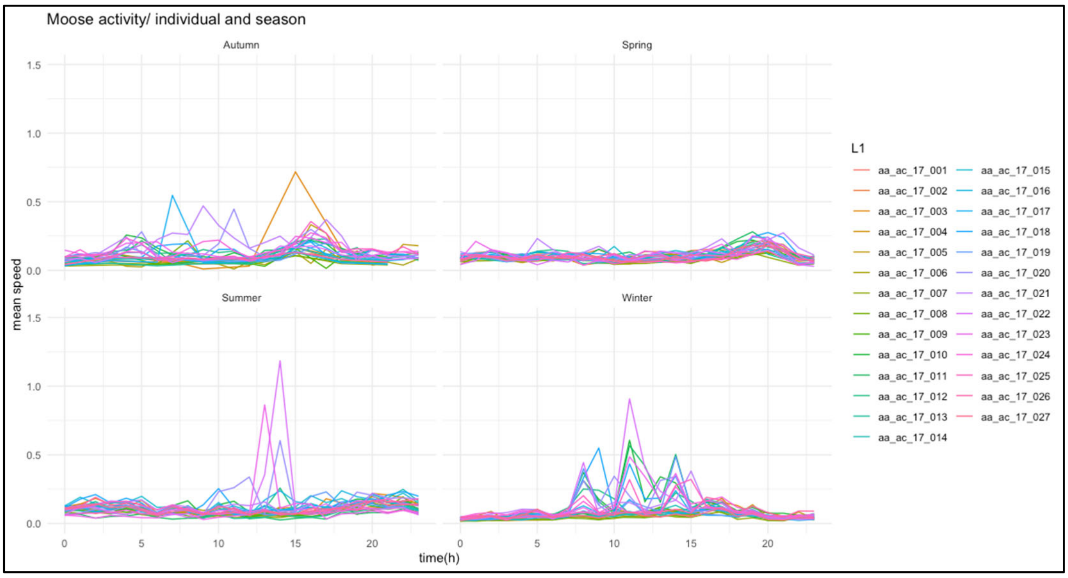
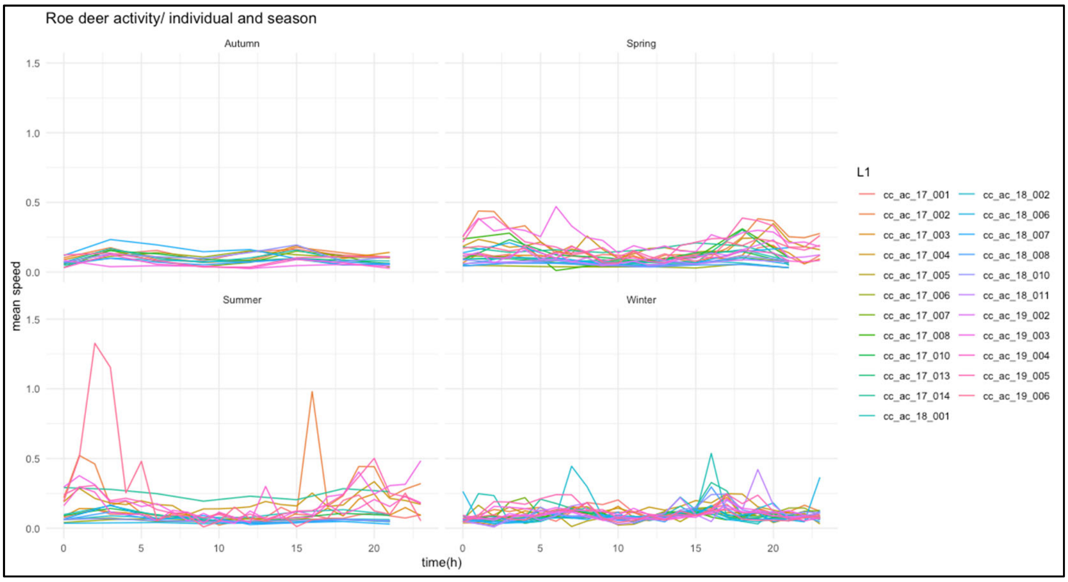
Appendix 1



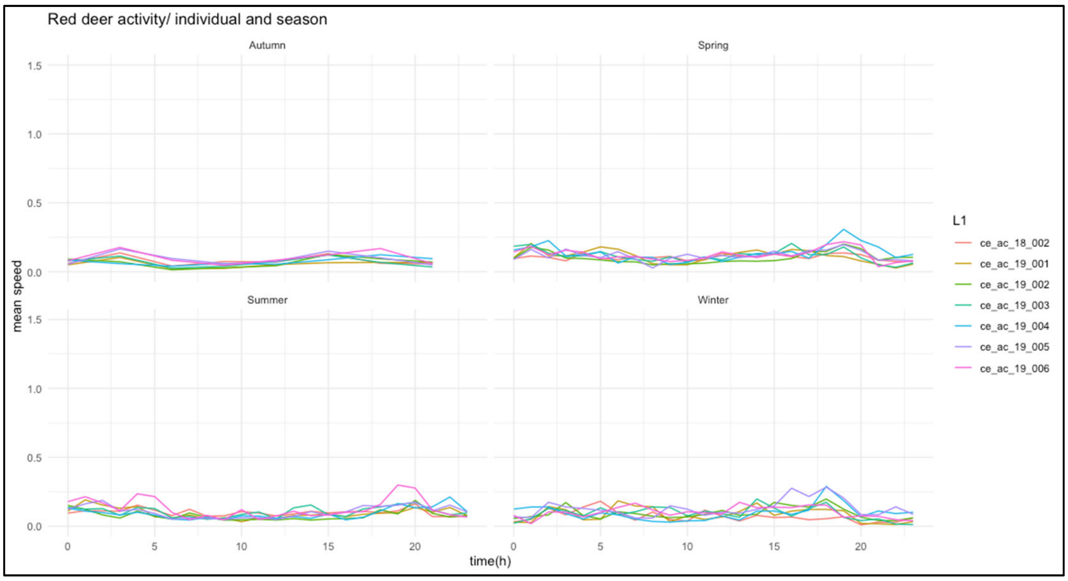
Appendix 1. Moose activity per individual and season, displaying individual variability in activity pattern throughput the day and season. L1 stands for individual ID.

Appendix 2



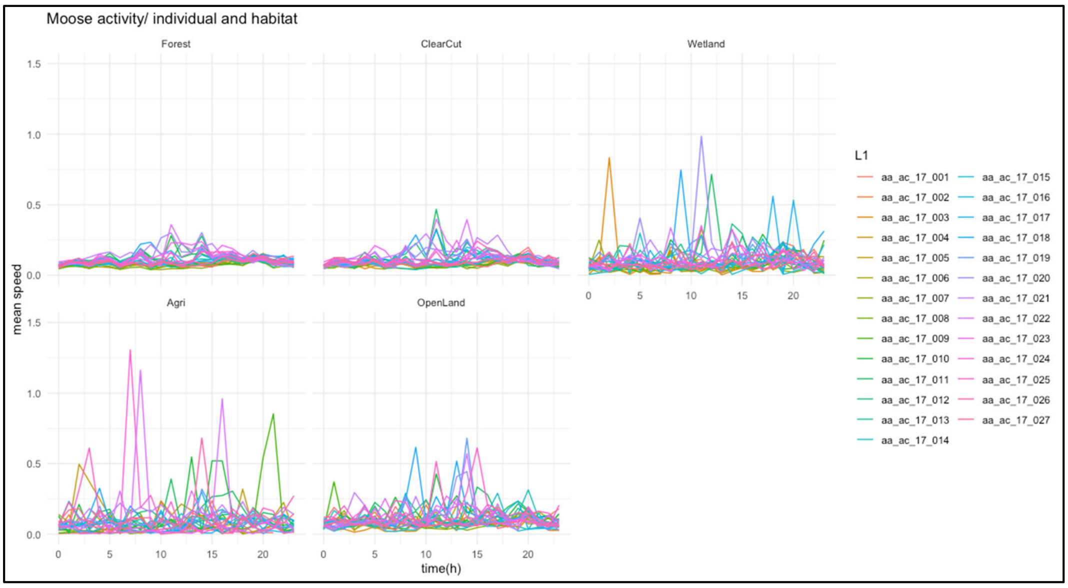
Appendix 2. Roe deer activity per individual and season, displaying individual variability in activity pattern throughput the day and season. L1 stands for individual ID.

Appendix 3



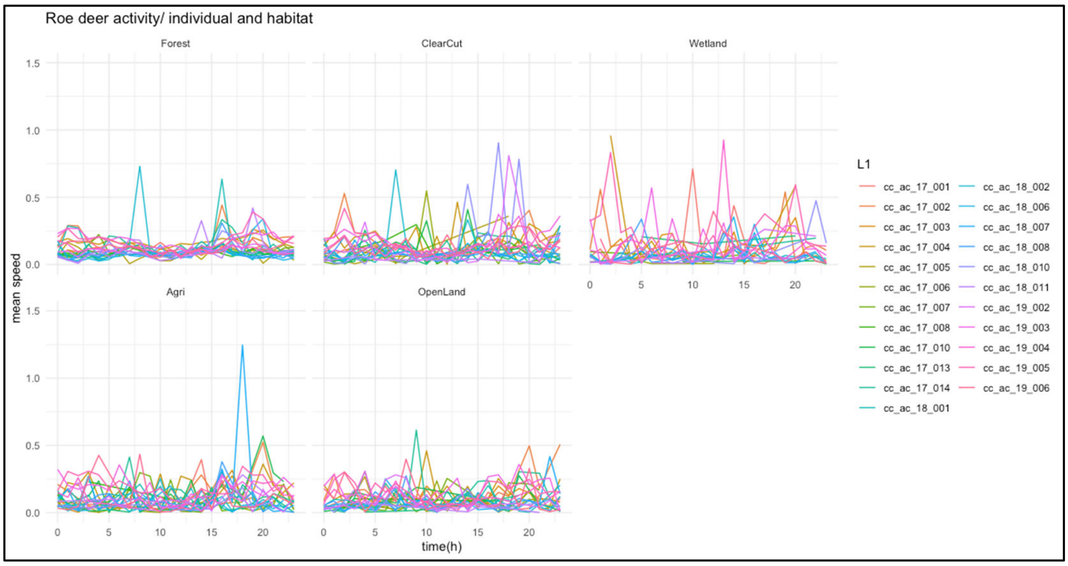
Appendix 3. Red deer activity per individual and season, displaying individual variability in activity pattern throughput the day and season. L1 stands for individual ID.

Appendix 4



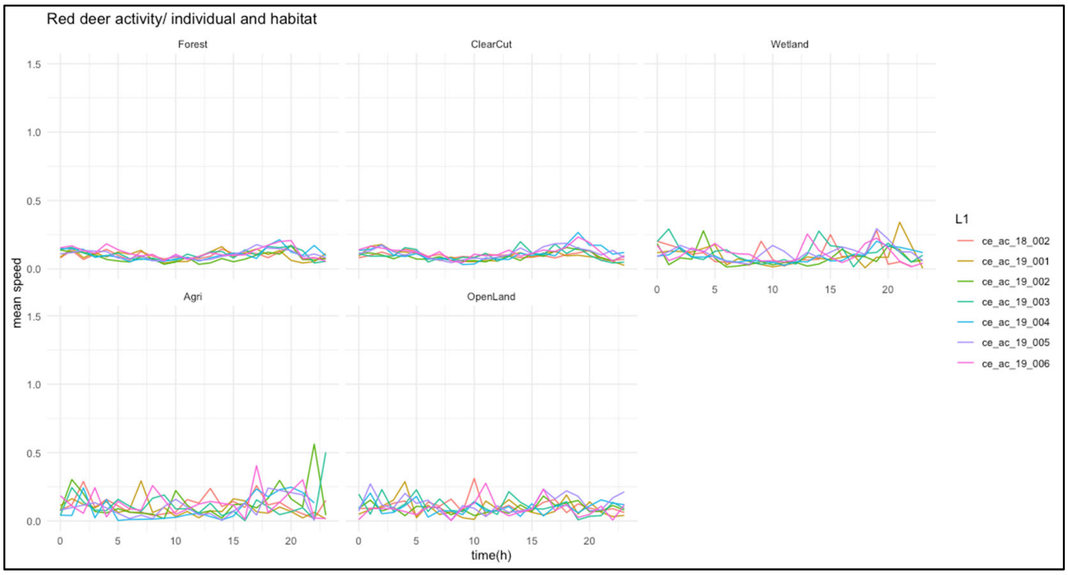
Appendix 4. Moose activity per individual and habitat, displaying individual variability in activity pattern throughput the day and habitat. L1 stands for individual ID.

Appendix 5



Appendix 5. Roe deer activity per individual and habitat, displaying individual variability in activity pattern throughput the day and habitat. L1 stands for individual ID.

Appendix 6



Appendix 6. Red deer activity per individual and habitat, displaying individual variability in activity pattern throughput the day and habitat. L1 stands for individual ID.

Appendix 7

Factor	Moose	Estimate	SE	t-value	p-value
Season	Intercept	0.2641709	0. 03091	8.546	<0.0001*
	Spring	-0.0232235	0.01161	-2.001	0.0454*
	Summer	-0.0004403	0.01128	-0.039	0.9689
	Winter	-0.5208874	0.01101	-47.314	<0.0001*
Habitat	Intercept	-0.065176	0.05131	-1.270	0.218772
	Clear-cut	0.005101	0. 005981	0.853	0.393770
	Wetland	-0.013381	0.01777	-0.753	0.451402
	Agri.	-0.083400	0.04941	-1.688	0.091446
	Open land	0.054922	0.01453	3.780	0.000157*
Roe deer density	Intercept	0.2031	0.09814	2.070	0.040*
	Roe low	-0.2892	0.08776	-3.295	0.001*
	Roe medium	-0.1158	0.08809	-1.315	0.189
Red deer density	Intercept	0.06013	0.07967	0.755	0.45192
	Red low	-0.12454	0.06099	-2.042	0.04117*
	Red medium	-0.18330	0.06230	-2.942	0.00326*
Time of day	Intercept	0.08277	0.04725	1.752	0.0954
	Night	-0.32220	0.005790	-55.650	<0.0001*

Appendix 7. Fixed effects for moose for each univariate model (season, habitat, roe density, red density and day/night. Autumn is the intercept for season, forest is the intercept for habitat, high density of roe deer and red deer is intercept for species density and day is intercept for time of day.

Appendix 8

Factor	Roe deer	Estimate	SE	t-value	p-value
Season	Intercept	-0.28546	0. 03903	-7.315	<0.0001*
	Spring	0.08118	0.01803	4.503	<0.0001*
	Summer	0.25848	0.01675	15.429	<0.0001*
	Winter	0.36394	0.01557	23.381	<0.0001*
Habitat	Intercept	-0.001943	0.04154	-0.047	0.9631
	Clear-cut	-0.018945	0. 01184	-1.600	0.1096
	Wetland	0.059539	0.02488	2.393	0.0167*
	Agri.	-0.041346	0.02084	-1.984	0.0473*
	Open land	0.025151	0.01673	1.503	0.1328
Moose density	Intercept	-0.2813	0.04666	0.755	<0.0001*
	Moose low	0.2875	0.02381	-2.042	<0.0001*
	Moose medium	0.2464	0.02595	-2.942	<0.0001*
Red deer density	Intercept	-0.2929	0.05783	-5.065	<0.0001*
	Red low	0.3180	0.03917	8.119	<0.0001*
	Red medium	0.2292	0.03961	5.786	<0.0001*
Time of day	Intercept	-0.06546	0.03976	-1.646	0.114
	Night	0.14217	0.007424	19.151	<0.0001*

Appendix 8. Fixed effects results for roe deer for each univariate linear mixed model (season, habitat, roe density, red density and day/night. Autumn is the intercept for season, forest is the intercept for habitat, high density of moose and red deer is intercept for species density and day is intercept for time of day.

Appendix 9

Factor	Red deer	Estimate	SE	t-value	p-value
Season	Intercept	-0.040109	0. 0501	-0.704	0.490214
	Spring	0.157003	0.04055	3.872	0.000108*
	Summer	-0.009806	0.03971	-0.247	0.804942
	Winter	-0.105495	0.04269	-2.471	0.013466*
Habitat	Intercept	-0.026740	0.04.476	-0.597	0.5705
	Clear-cut	0.031080	0. 01680	1.850	0.0644
	Wetland	-0.059285	0.03022	-1.962	0.0498*
	Agri.	-0.002674	0.03829	-0.070	0.9443
	Open land	0.037946	0.03073	1.235	0.2169
Moose density	Intercept	0.002497	0.07330	0.034	0.973
	Moose low	-0.044441	0.05941	-0.748	0.454
	Moose medium	0.040850	0.06017	0.679	0.497
Roe deer density	Intercept	-0.01627	0.04291	-0.379	0.718
	Roe medium	0.01033	0.05417	0.191	0.849
Time of day	Intercept	-0.02862	0.04288	-0.667	0.52890
	Night	0.05058	0.01713	2.952	0.00316*

Appendix 9. Fixed effects results for red deer for each univariate linear mixed model (season, habitat, roe density, red density and day/night. Autumn is the intercept for season, forest is the intercept for habitat, high density of roe deer and moose is intercept for species density and day is intercept for time of day.

Appendix 10

4.3.1. Model ranking

The full model explained the variation in activity best for both moose and roe deer with lowest AIC-value (Appendix 10). For red deer, the model containing only season as factor explained the variation in activity best.

Appendix 10. Model ranking using Akaike's information criterion.

Model	**Moose**	**Roe deer**	**Red deer**
	AIC	*AIC*	*AIC*
Full	**347626**	**201835**	51298
Season	348743	202049	**51271**
Habitat	356102	203054	51438
Moose density	-	202894	51398
Roe density	355710	-	51398
Red density	356071	202907	-

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