



Temporal patterns of humans and ungulates at bridges

Co-existence or disturbance?

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TRIEKOL report, 30 Dec 2019

Introduction

Fencing combined with crossing structures is widely accepted to be an effective solution to reducing wildlife-vehicle accidents and barrier effects of transportation corridors on wildlife (Clevenger et al. 2001, van der Ree et al. 2015, Huijser et al. 2016). To address the growing pressure towards an open and accessible landscape for both humans and wildlife, and to improve cost-effectiveness of crossing structures, there is an increased tendency to permit human use of wildlife crossing structures, or to construct human and wildlife co-use structures (van der Grift et al. 2011).

The effectiveness of crossing structures and non-wildlife passages to provide habitat connectivity may depend on many different factors, such as dimensions, substrate and vegetation, location and surroundings, and human disturbances (Rodriguez et al. 1997, Clevenger & Waltho 2000, Ascensão & Mira 2007). Human disturbance is usually quantified as the abundance of humans or distance to housings, but the effect of human activity or human-use of crossing structures on the use of crossing structures by wildlife is rarely quantified (see van der Grift et al. 2011, van der Ree & van der Grift 2015). Humans can have a big influence on the behavior of animals, not least of hunted species (Paton et al. 2017, Gaynor et al. 2018). Human use of structures may impact the frequency and the temporal pattern of the use of crossing structures by wildlife (Singer 1978, van der Grift et al. 2011, Barrueto et al. 2014, van der Ree & van der Grift 2015, Trocme & Krause 2019). Results from these studies are inconsistent, as animal use of structures increases (Ng et al. 2004), decreases (Rodriguez et al. 1997, Clevenger & Waltho 2000, Grilo et al. 2008) or remains consistent (Rodriguez et al. 1996, Gloyne & Clevenger 2001, van der Grift et al. 2011, van der Ree & van der Grift 2015) with increasing human use or proximity to human infrastructure. Thus, local studies are required to evaluate the relationship between human use and wildlife use of crossing structures.

To investigate the temporal patterns of animal use and human activities at crossing structures, we compared crossing structures build either for wildlife or for humans, but used by wildlife with different frequencies of human use and evaluated the influence that human presence had

on when and how often ungulates used the crossing structures. We addressed the following questions: 1) When do humans and ungulates use the crossing structures? Furthermore, is there a distinctive pattern of usage? 2) Is there a variation in the usage, when comparing the months, weeks and hours? 3) Is the crossing behavior of ungulates influenced by the human usage?

We expected humans to use structures primarily for recreational purposes, thus mainly in the later afternoon (between 2 and 8 pm) and on the weekends. Following this we expected ungulates to show a clear crepuscular usage pattern, if human usage is high. At undisturbed sites we expected them to show a more evenly distributed usage pattern throughout the day. We focused our study on ungulates; moose (*Alces alces*), roe deer (*Capreolus capreolus*), and the semi-domestic but free-ranging reindeer (*Rangifer tarandus*) in Norrbotten and additionally wild boar (*Sus scrofa*) which only occurred at Borås. The selection of species was made for practical reasons, since these were the ungulate species most frequently occurring at the crossing structures, and ungulates were the target species for the fauna passages included in this study.

We defined disturbance as ungulates reaction on human usage of the structure that leads to an alteration of their usage pattern or to avoidance of the crossing structure. If the disturbance is too severe, the crossing structure would lose its function to provide habitat connectivity. We hypothesized that the ungulates are disturbed by human usage. This disturbance would have minor effects if the human usage is following a pattern, thus predictable. Furthermore, we expect reindeer not to be as disturbed by human usage compared to wild ungulates, because as semi-domestic animals they are used to be handled by humans and are often additionally artificially fed.

This study functions as a status report and a pilot for further and refined analyses of human (co-)use and other factors impacting wildlife effectiveness of crossing structures.

Methods

Data collection

We collected data of animals and human activities by photo trapping in and around five crossing structures in northern Sweden in the county of Norrbotten and one near Borås in the Västra Götaland county in southern Sweden (Fig. 1). Borås was included as a reference of temporal patterns and species abundance at more southern latitudes. Ungulate species at the underpass near Borås were roe deer, moose and wild boar. Due to the low abundance we were not able to analyze varying conspecific temporal patterns between Norrbotten and Borås for roe deer and moose.

Crossing structures differed in design and dimensions, including both minor and larger, over- and underpasses, built primarily for either humans/traffic or animals (Fig. 2). Motion triggered cameras were placed at each crossing structure to capture animals using the structure, and 5-6 cameras in the immediate area around (within 30 m) the crossing structure (see Appendix 1 for detailed information). Cameras were set up to survey the animals and their behavior whilst crossing. Data from the period 13/11/2018 to 30/07/2019 were included in the study. Each structure was monitored for 18 to 32 weeks, over this time (Table 1). Camera trap data was downloaded approximately every second month. We excluded data from Kåtaträskvägen from the period 15/11/2018 to 03/01/2019 due to a malfunction in the timestamp of multiple cameras at that bridge.

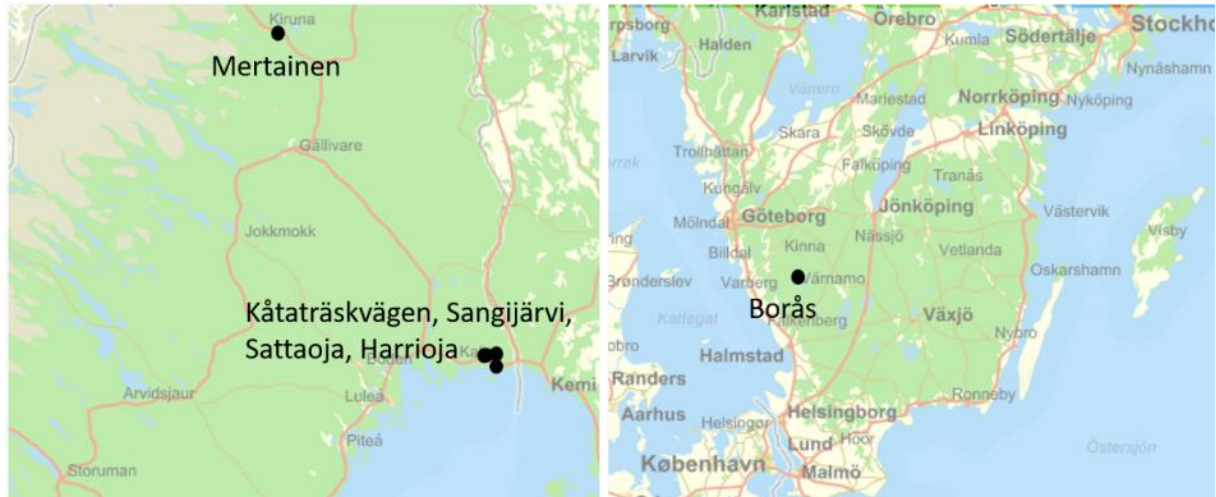


Figure 1: Location of the bridges included in this study. Left map shows the 5 structures in Norrbotten county, and the right map shows the one structure in Västra Götaland county.



Figure 2: Bridges studied; from top left: Mertainen, Harrioja, Kåtaträskvägen, Sattaojavägen, Sangijärvi, Borås. Photos: Trafikverket.

From each photograph, we extracted species present, time of day, temperature etc. We analyzed the timing of events of either humans or animals at the passage site. Human activity was separated in the following types: car, lorry, snowmobile, tractor, motorcycle, other off-road vehicle, other motor vehicle, bicycle, horse, person (be it walking, jogging or skiing), and dog. We defined one event as one or several animals or humans that were photographed by at least one camera in a timespan of a maximum of 10 minutes and behaved similar thus seem to belong to a group of animals or people. Animals of different species were separated into different events, as were human activity of different types. The number of individuals or duration of the event was not considered in the analyses. We summarized the data by the relevant time scale: hour (0-23), weekday (Mo-Su) and month (Nov-July).

Data Analysis

To address temporal patterns in human and ungulate use of crossing structures, we used Poisson-regression models to compare average use (i.e. number of events of humans or each species) by the timescale of interest (i.e. hour, weekday or month).

To quantify if human presence in or near the passage influenced the timing of ungulate use of the passage, we used 2 approaches. First, we divided each day into two periods, following the amount human usage. The period of low human use was defined as 21:00 to 08:59 and high human use as 09:00 to 20:59. The average number of events between the two periods was tested with a t-test and differed significantly ($p < 0.05$). Then, using a Poisson-regression, we compared the number of animal events between the two periods, of each species. The second approach we took, was to compare the time elapsed between 2 conspecific events and events between humans followed by wildlife, using a t-test for uneven variances. We checked for the evenness of the variances beforehand, using an F-Test. We did this first with all observations included. To reduce potential correlation between subsequent events, we also analyzed those events which occurred at least 10 minutes apart.

Microsoft Excel 2016, R Studio (Version 1.2.1335) and the R Commander (Version 2.5-3) interfaces were used for the statistical and graphical analysis of the data. Data collection, data treatment and analyses conducted are described in more detail in Appendix 1.

Results

During the study period, a total of 675 human events were detected at the study sites in Norrbotten and only 15 human events at the underpass Borås. The rate of human use differed between on average 0.07 (Borås) and 2.8 (Kåtaträskvägen) human usage events per day. On average for all Norrbotten bridges combined, 0.54 human events occurred per day. The mean number of humans per event at all Norrbotten structures was 1.62.

Reindeer were the most common visitors at the northern study sites (170 events), followed by moose (149 events) and roe deer (14 events). There was on average 0.12 moose events and 0.13 reindeer events per day for all structures in Norrbotten.

Roe deer crossings dominated at the Borås underpass (267 events), while moose and wild boar were detected only occasionally (7 and 5 events, respectively). This adds up to on average 1.30 ungulate (of which 1.25 roe deer) events per day at Borås.

Temporal pattern of structure use

Diurnal patterns

For all Norrbotten crossing structures combined, more than 90% of the human activity occurred between 9h and 21h (Fig. 3). This pattern was consistent at all study sites. The highest use of humans was in the mid of the day. Human events in Borås were too few (15 events) to be conclusive but followed a similar pattern, with no human activity after 20 h (Fig. 3).

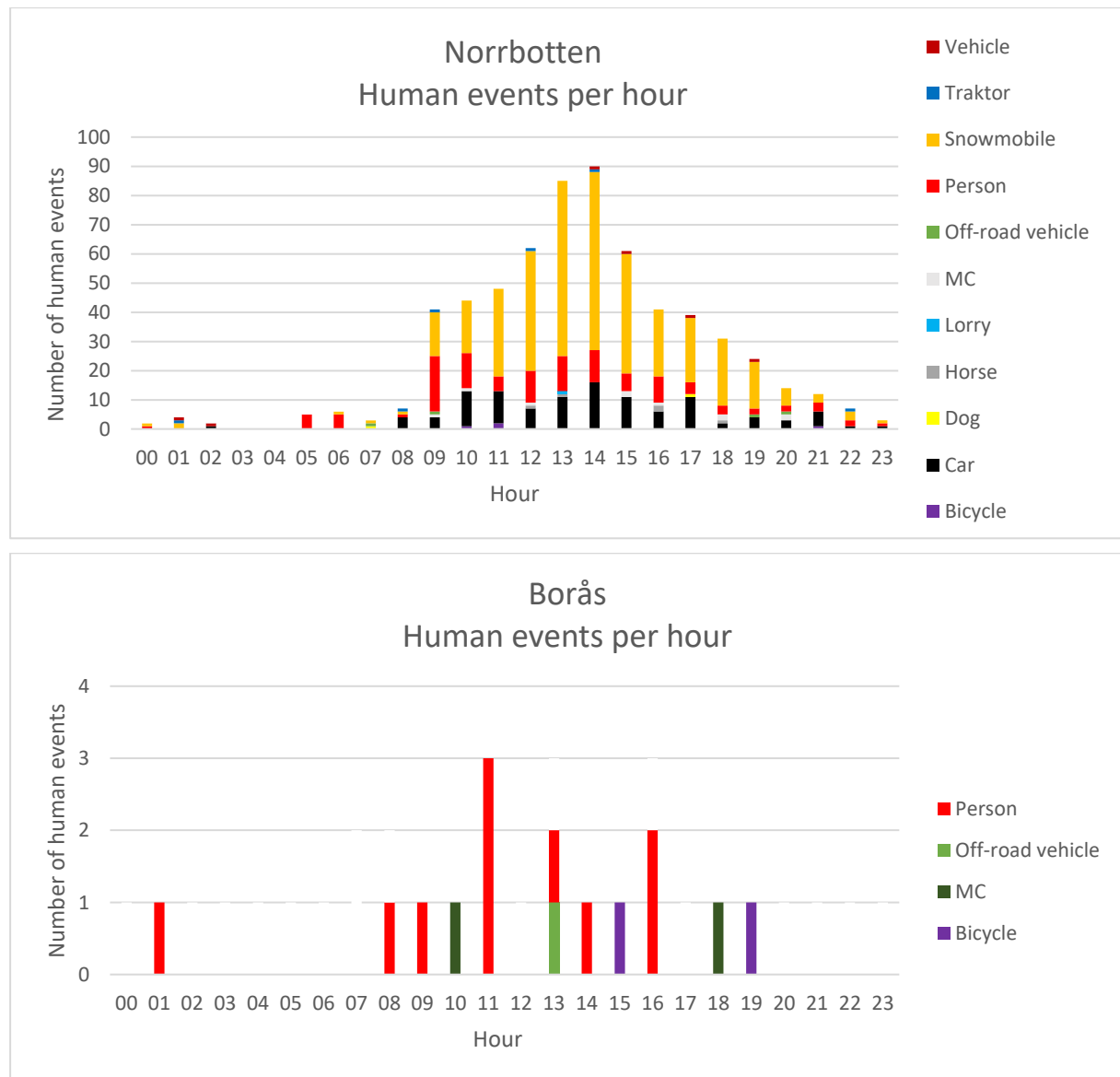


Figure 3: Human events per hour at five crossing structures in Norrbotten and one near Borås.

The diurnal activity pattern of animals at these crossing sites was different between species (Fig. 4). In Norrbotten, reindeer used bridges in daytime, with significantly higher use at 9h, 10h, 12h, 14h, 17h and 18h ($p < 0.05$ for all hours). Moose used bridges more at dusk and at night, with significantly higher use at 17h ($p < 0.05$) and 21h ($p < 0.05$), compared to other hours of the day. The number of roe deer were few and results inconclusive. At Borås, the roe deer had a very

clear diurnal pattern, mainly using the bridge during crepuscular and night-time hours, and the use was thus well separated from the human use which occurred only in daytime (Fig. 3). Other species were rare visitors to the Borås crossing structure, but it can be noted that the few wild boars used it at night.

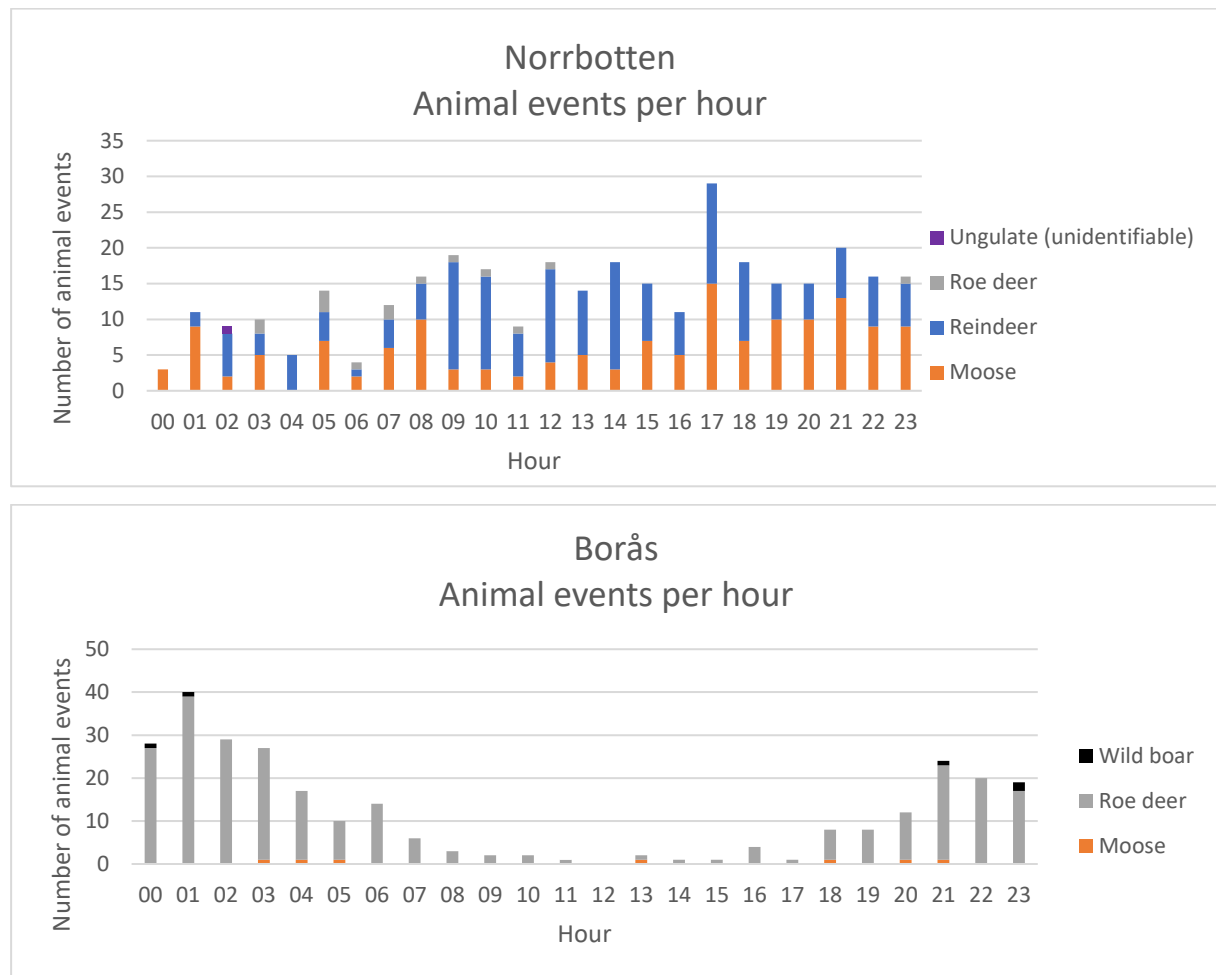


Figure 4: Animal events per hour at five crossing structures in Norrbotten and one near Borås. Results reflect the total number of events at each given hour throughout the study period.

Patterns over the week

In general, humans used the structures quite evenly throughout the weekdays. However, the pattern differed between bridges. In all Norrbotten bridges combined, the human use was higher in weekends (Saturdays $p < 0.001$, Sundays $p < 0.001$), but Mertainen differed from the rest by having less human activity during weekends (Fig. 5). Again, the number of human events in Borås was too low to be conclusive.

On the other hand, the animal use in Norrbotten combined and in Borås showed no variation over the week (Fig. 6). Individual bridges however showed deviating patterns. Mertainen, for example, had a higher animal activity from Friday to Monday (Fig. 6; see results for the other bridges in Appendix 2A).

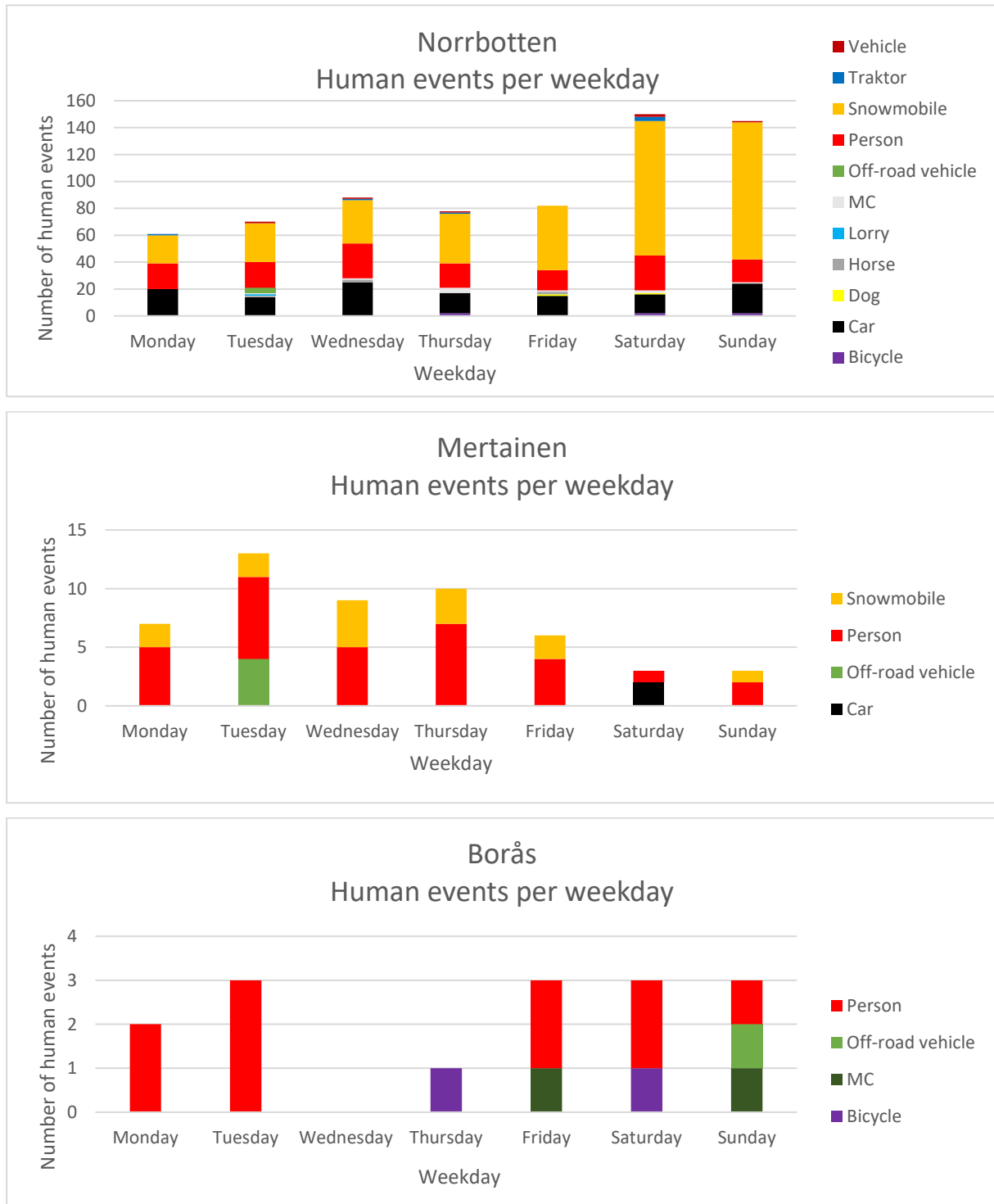


Figure 5: Human events per weekday in all five Norrbotten bridges (top), in Mertainen only (middle) and in Borås (bottom).

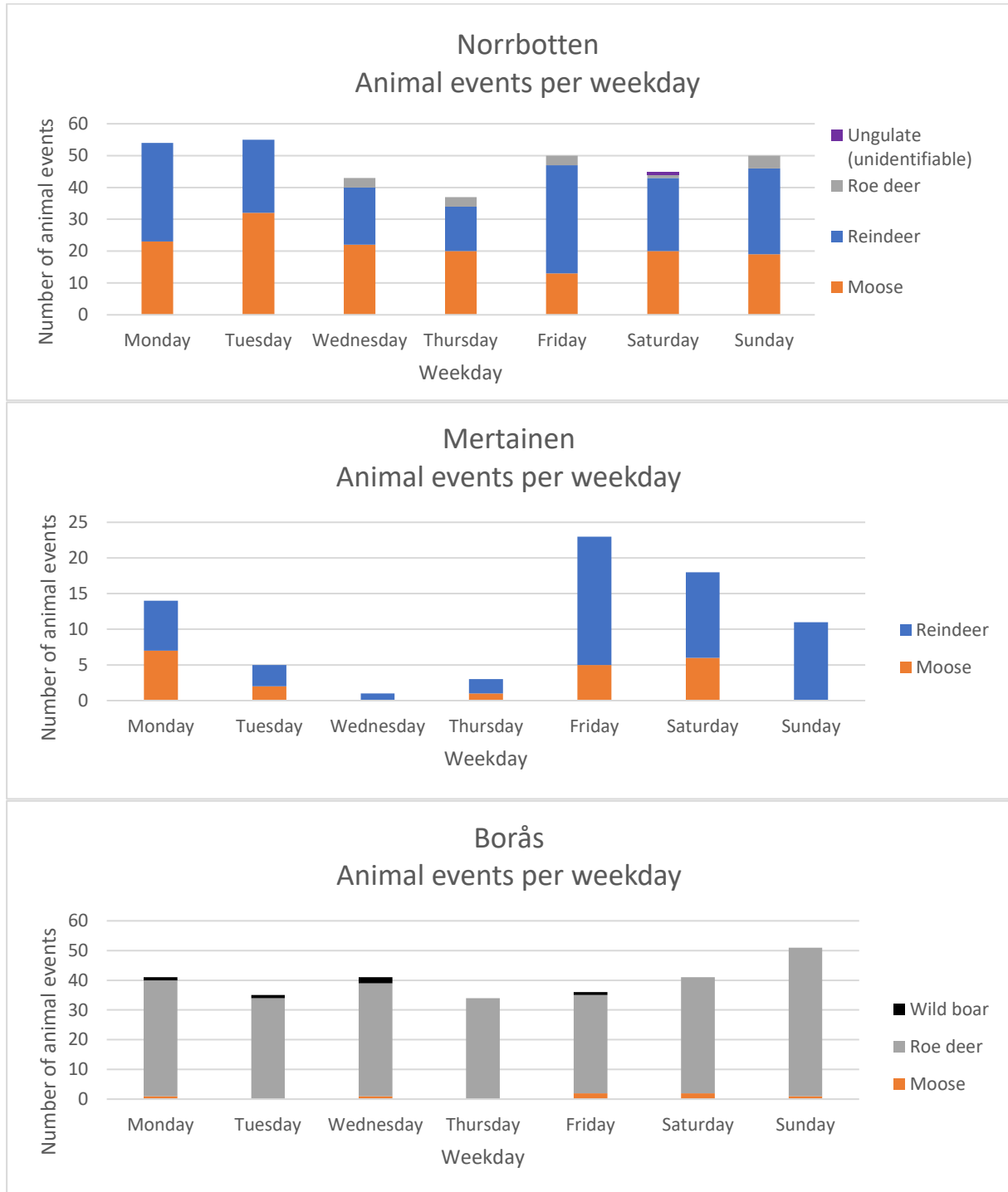


Figure 6: Animal events per weekday in all five Norrbotten bridges, in Mertainen only and in Borås.

The inclusion of the human activity periods (high or low) to answer “question 3) Is the crossing behavior of ungulates influenced by the human usage”, resulted in no significant difference in the general output, but in a few specific cases. Moose showed a significantly lower number of events on Fridays during high human activity ($p < 0.05$) and trends towards a lower use on Saturdays ($p = 0.09$) and Sundays ($p = 0.09$) during high human activity. Reindeer showed a

significantly ($p < 0.05$) lower use rate during low human activity on Sundays, but a non-significant ($p = 0.37$) lower use in general.

Monthly patterns

The monthly use of the Norrbotten bridges over the monitoring period was showing big differences, both bridge-wise (Appendix 2A) and for all bridges combined (Fig. 7). The human activity was the lowest in the early winter (November and December) and peaking in March. Cars were more abundant in early winter and spring; pedestrians were active throughout the winter. From January to April snowmobiles made up the main share of human activity, not least in March.

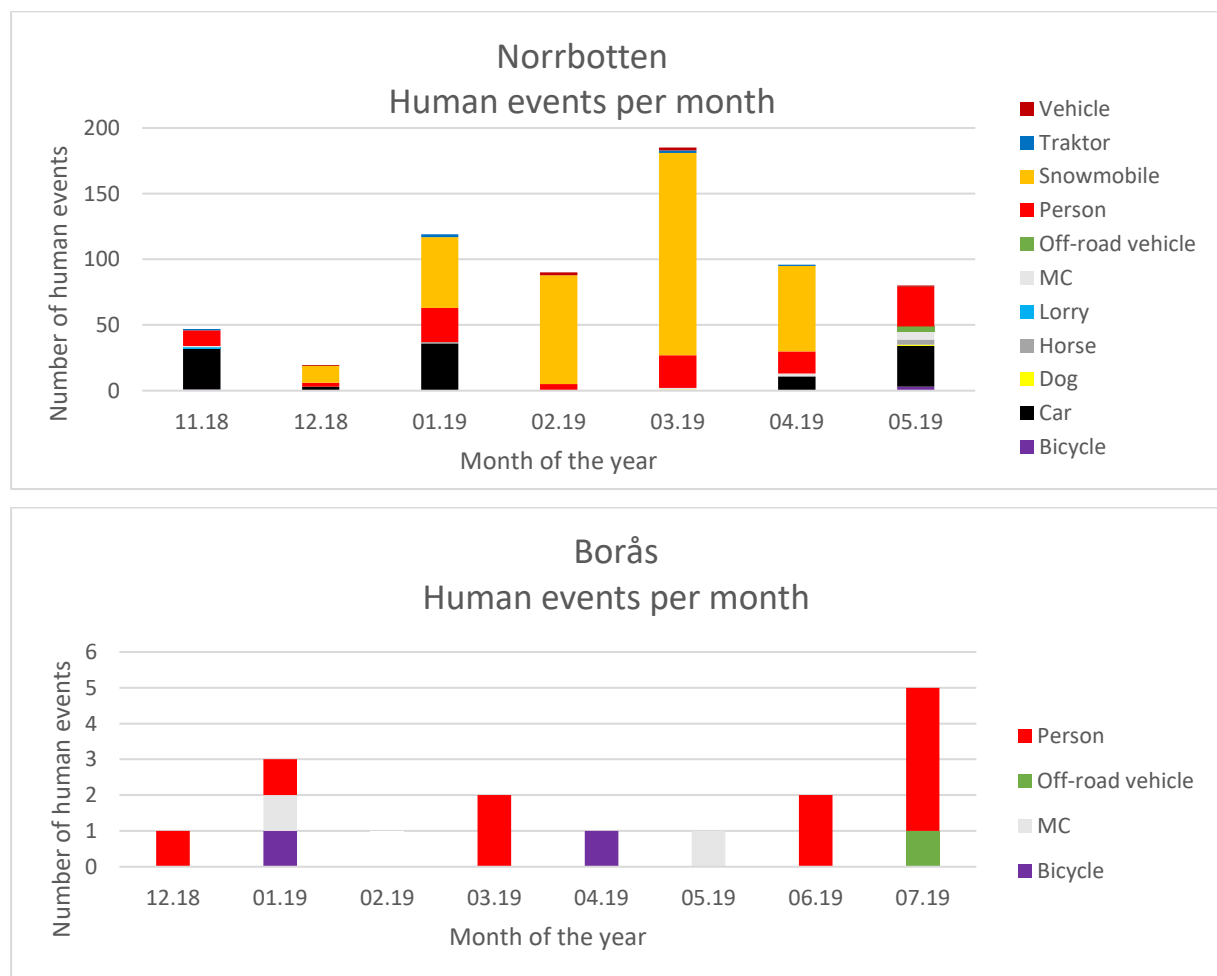


Figure 7: Human events per month in all five Norrbotten bridges and in Borås.

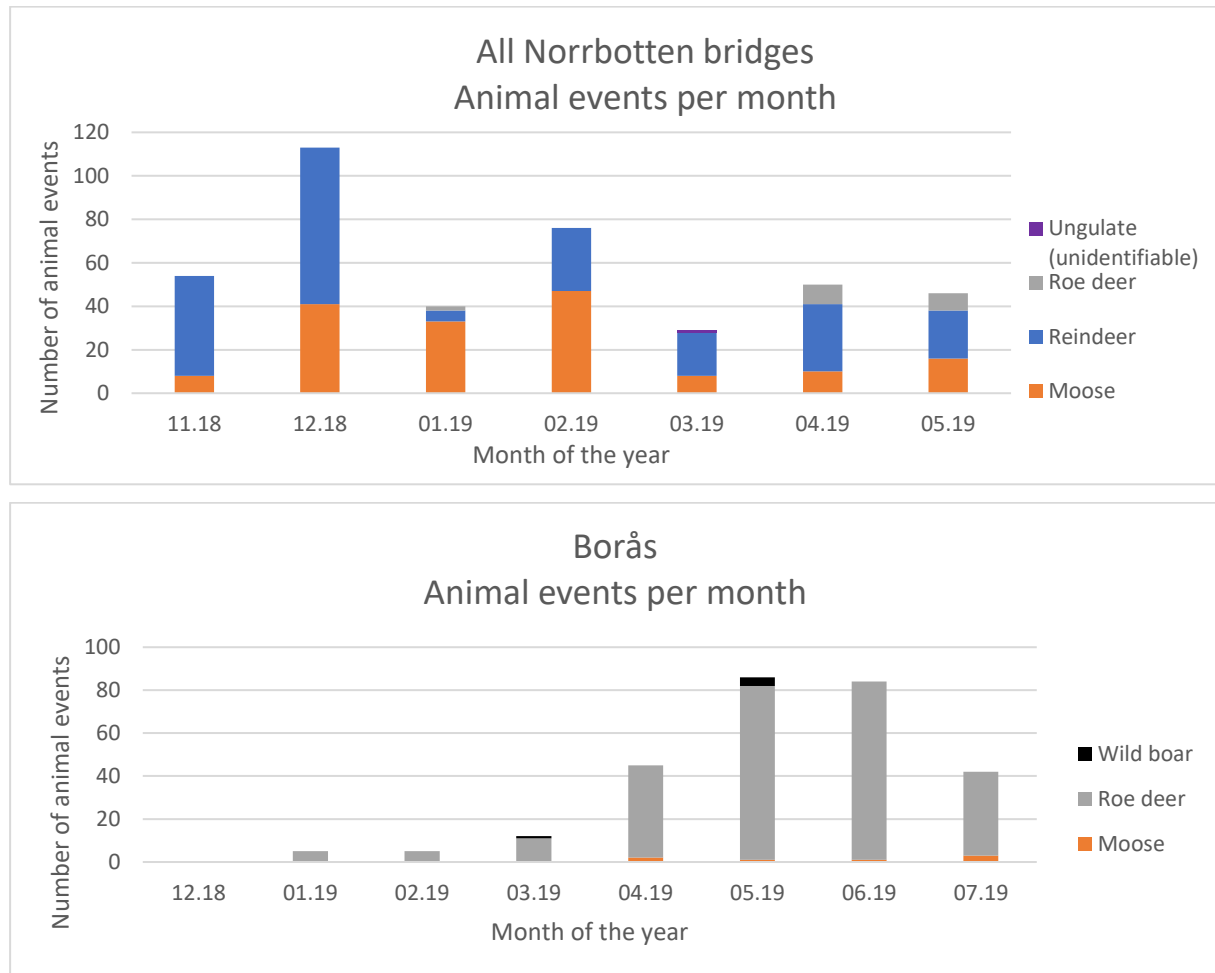


Figure 8: Animal events per month in all five Norrbotten bridges and in Borås.

Timespan between events

The Students T-Test of the timespan between the animal's use and the human's use showed significant differences in the duration between usage events ($p < 0.05$). Moose were using the crossing structures after a shorter time period if the foregoing event was another moose (29.05 hh.mm), compared to events when the foregoing user was a human (78.35 hh.mm). The result (33.48 hh.mm) remained significant ($p < 0.05$) if periods lower than 10 minutes were excluded. There was no significant difference in reindeer use with previous reindeer events (mean = 28.55 hh.mm, $p = 0.070$; respectively mean = 32.03 hh.mm and $p = 0.104$ with periods <10 minutes excluded) to foregoing human events (mean = 62.21 hh.mm). See also Appendix 2B for more detailed results presentation.

Discussion

Our results show that both ungulates and humans can exhibit activity patterns at crossing structures. Humans show clear patterns on the weekday and hour basis. Ungulates show species-specific differences in their usage patterns, with higher activity at daytime (reindeer) or at crepuscular hours and in the night (roe deer and moose). Furthermore, the usage of both ungulates and humans is un-evenly distributed over the observed months. The comparison of

the sequence of ungulate usage with foregoing human/conspecific event is indicating avoidance behavior in moose, but not in reindeer.

The diurnal activity pattern described by wild ungulates in our results are in line with previous studies (Eriksson et al. 1981, van der Grift et al. 2011, Ericsson et al. 2017a, 2017b). Moose were using bridges primarily in the dusk and night-time. Moose activity at dawn was not significantly different to the activity in daytime. According to Ericsson et al. (2017a, 2017b), moose in northern Sweden show clear crepuscular activity in spring and late summer, but activity around the clock in the summertime.

Reindeer used bridges primarily in the daytime, which agrees with activity periods found in the literature; reindeer are classified as primarily diurnal, but with some activity phases in the night-time and with round the clock activity in summertime (Eriksson et al. 1981). This activity pattern contrasts with Colman et al. (2001) and van Oort et al. (2007) who found weak circadian activity patterns in semi-domestic reindeer in Norway and on Svalbard. However, the reindeer activity may depend on temperature, with the highest activity in the cooler parts of the day (Franke et al. 2004).

The roe deer diurnal pattern at Borås is the most distinctive one; they show peaks of activity from dusk till dawn and little activity in the mid of the day. The roe deer activity at Norrbotten is too low to be conclusive. Roe deer activity patterns at Borås are in line with results of other studies (Pagon et al. 2012, Krop-Benesch et al. 2013, Bonnot et al. 2019).

The diurnal pattern of human activity was comparable to that in other studies (van der Grift et al. 2011 for the Netherlands, Trocme & Krause 2019 for Switzerland). The human daytime use was consistent within all bridges, and was similar to other studies that measured the number of humans using passages (Rodriguez et al. 1997 for Spain, Mata et al. 2005 for Spain) or lower (Clevenger & Waltho 2000 for the USA, van der Grift et al. 2011 for the Netherlands).

The analysis of the daily usage pattern generally showed little variation in the ungulate's usage over the week. Humans on the other hand generally showed higher activity in the weekends, which is comparable to other studies (van der Grift et al. 2011, Trocme & Krause 2019). These patterns suggest no human disturbance on the weekday timescale. However, usage patterns both for humans and ungulates at one of our bridges (Mertainen) indicated contrary results.

Human usage at Norrbotten differed extremely between the months, peaking in March. Animals on the other hand showed highest crossing rates in December. However, heterospecifics showed different peaks, resulting in highest reindeer crossing rates in December, moose in February and roe deer in April and May. The huge differences in the animal use rates over different months could be explained by the partially seasonal migration of both moose and reindeer (Ball et al. 2001) and the lower general activity and movements of ungulates during winter especially when snow impedes movements (Georgii 1981, Rissenhoover 1986, Luccarini et al. 2006, Richard et al. 2014). Human usage is most likely related to the working days, thus higher in the weekend if related to recreational activities.

The result of our comparison of the durations between single crossings is indicating that animals could be disturbed by human presence at the site. This is also indicated by the results of other authors that show low ungulate activity during high human activity phases (Singer 1978, Clevenger & Waltho 2000, van der Grift et al. 2011, Ciuti et al. 2012, Seidler et al. 2018, Trocme & Krause 2019, Bonnot et al. 2019). Van der Grift et al. (2011) observed for a crossing structure in the Netherlands, that roe deer would use the structure later in the day if the human activity was high, but this delay disappeared after midnight. However, they did not find any variation in the total number of roe deer crossings. This is contrary to results presented by Olsson (2007), showing a negative relationship of roe deer's preference for structures with high human use in Sweden. However, the wildlife crossing structure use of roe deer described by van der Grift et al.

(2011) may not be comparable to the structures we observed due to extreme differences in the amount human usage. In contrast to our results, they measured 165 and 500 human crossings per day. In our case the rate of human users differed between on average 0.07 (Borås) and 2.8 (Kåaträskvägen) human usage events per day. The mean number of humans per event at all Norrbotten structures was 1.622. The analysis by van der Grift et al. (2011) suggests no difference in the number of roe deer using the passage, but differences in the time of use. Our results suggest similar temporal niching behavior in moose in Norrbotten and roe deer at Borås. Moreover, the comparison of moose crossing during periods of high and low human usage is indicating that the number of moose using the crossing structure could be negatively affected by a higher number of human users.

It is well known that human activities can stress ungulates and lead to a higher display of vigilance behavior (Stankowich 2008, Ciuti et al. 2012, Paton et al. 2017) due to the perception of a predation risk (Gavin & Komers 2006). This vigilance behavior is also displayed at human transport infrastructure and crossing structures (Ciuti et al. 2012, Seidler et al. 2018) and can influence the success of ungulate crossing attempts (Singer 1978, Clevenger & Waltho 2000). A meta-analysis by Gaynor et al. (2018) showed high influences on animals' temporal patterns due to human activity. Especially during the hunting period animals could change their behavior drastically with possible interferences of other human activities. Paton et al. (2017) found out that elk (*Cervus elaphus*) avoided roads, spent less time feeding, showed more vigilance behavior and used other habitats during spring migration versus autumn migration which overlaps with the hunting period. Not only hunting, but also other human activities can stress ungulates and lead to a changed behavior. The meta-analysis by Stankowich (2008) shows differences in both intra- and interspecies behavioral responses to different human activities. Wild reindeer in Norway seem to be more disturbed by pedestrians than by snowmobiles, measured by their flight distance (Reimers et al. 2003). Semi-domestic reindeer seem to avoid human settlements (Skarin et al. 2008) and hiking trails (Skarin et al. 2010). These results lead to the appearance that semi-domestic reindeer are generally disturbed by humans and exhibiting similar avoidance patterns as wild reindeer, but the strength of this avoidance behavior may differ (Skarin & Åhman 2014). In our case, we hypothesized that semi-domestic reindeer are not as strongly influenced by human activities as wildlife, because the reindeer are handled by humans and in some cases artificially fed. This is in line with our results, that show significantly longer time periods for a moose event following a human event, but insignificantly longer durations for reindeer event following a human event. If roe deer and moose are compared, instead of wild reindeer, to semi-domestic reindeer, our results are suggesting the same as Skarin & Åhman's (2014) results; the wild ungulates roe deer and moose are more disturbed by human usage than the semi-domestic reindeer.

It is also known that animal's response to human activity may depend on the predictability of the human behavior. Animals react on humans that move on a trail with a lower flushing distance than to humans moving off-trails (Miller et al. 2001). This may also be the case in the animal's reaction and shift of their temporal patterns. Moreover, a shift in the ungulates temporal or spatial pattern is only possible if they have alternatives (Gill et al. 2001).

The meta-analysis of Stankowich (2008), the results of Paton et al. (2017) and Trocmé et al. (2019) are underlining this. They found out that the risk perception of the animals measured as the flight distance and the display of predator avoidance behavior of ungulates was dependent on the surroundings, mostly the vegetation. This leads to the suggestion that if a structure for human and ungulates co-use is build, one should focus on an environment that leads to a reduction of the ungulates' predation risks perception.

In general, we do not find our data to be really conclusive. Not all temporal patterns were consistent. We interpret the results of the time difference analysis together with the statistical

results of the human and animals' interaction analysis as slight shifts in ungulate behavior and accordingly a reaction to the human use of the bridges. Furthermore, the data could have been analyzed differently. For example, we could have chosen to use number of individual animals instead of number of animal events, and similarly the "degree" of human activity (number of people or vehicles, time extent etc.) instead of merely human events. This would have resulted in higher numbers of individuals and due to this a bigger dataset. However, we suspect that the numbers gathered with that approach are more likely to be overestimated, compared to our approach using events, because animals are more likely to be counted multiple times when using pictures of several cameras at the same time. Using 10 minutes as a definition of an event was arbitrary, and we did not test the outcome of any other possible definition. However, other authors use similar timespans for defining one animal event (Fiderer et al. 2019). A comparison of the time differences including a bootstrap method would allow a stronger further analysis via creating pseudo samples.

The limited number of bridges used in our study and time period restricts the conclusions that can be drawn. The data was in multiple cases not sufficient to statistically analyzing the single structures. The grouping of all datasets in Norrbotten allowed better statistical analysis but was also evening out patterns at the individual bridges. Further data collection will help this limitation.

We did not include the structures architecture, type and landscape factors, even though it is known that they have a big influence on the animals' use rate (Rodriguez et al. 1997, Gloyne & Clevenger 2001, Ng et al. 2004, Clevenger & Waltho 2005). Landscape factors should be included, since a higher human use of the structure does not necessarily also require a use of the landscape in general. The animals on the other hand could also be influenced by human use of the surrounding or traffic flow at the highway, which is influencing their behavior at the structure, even if the human use is low. This could be the case at Borås, where the human activity is the least in all structures monitored in this study. Here, roe deer diurnal usage patterns may be influenced by human activity in the surroundings rather than directly how humans used the structure, or completely independent of human disturbance.

This report shows the need for a deeper analysis of the possible interference of the human use of crossing structures and the animals' use. A larger set of data should be included in further analysis, furthermore the influence of crepuscular timing and human activity on the animal use and possible differences with regards to the hunting period should be addressed in further studies. To gain more knowledge about possible differences in usage patterns of crossing structures and the usage of the rest of the landscape, both patterns should be compared more detailed. An experimental variation of human use at structures of different dimensions and with different landscape ecological factors would generate a necessary insight to answer the question to what degree human co-use of structures could be acceptable, before limiting the animal use and the ecological function of crossing structures.

Our report shows a possible influence of human appearance on the animal's timing at crossing structures. This influence is however strongly dependent on the species and probably also the timing of the human appearance, the human behavior and the predictability thus consistency of human usage. Furthermore, it is very likely that other factors like the surrounding landscape, general human use of the landscape and architecture of the structures have influences that could interfere with each other and the animal's use. Based on this a possible allowance of human co-use cannot be answered in general but needs a case to case analysis. In the end, the possibility to allow co-use is depending on the target species, type, timing and amount of human activity, design of the structure, possibility for alternative animal crossings and purpose of the structure. In the end one should keep in mind that animals can be influenced negatively due to human use even though it is not obviously visible.

Acknowledgements

The study was conducted within an Erasmus internship by Fabian Knufinke at Universität für Bodenkultur Wien (BOKU), visiting Swedish University of Agricultural Sciences (SLU). It presents preliminary results derived in the research program TRIEKOL III - Applied Road and Rail Ecology (<http://triekol.se/home-eng/>), managed by the Swedish Biodiversity Centre (SLU) and funded by the Swedish Transport Administration.

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