Non-grazing vegetation alterations: do the preferences of horses, wisents and cattle make for a trinity of ecosystem managers?

Lotte Schiphof (4241118, Utrecht University)

Leo Linnartz (ARK Natuurontwikkeling)

Merel Soons (Utrecht University)

Abstract

Large herbivores are known to prevent the domination of woody species and increase biodiversity through grazing, but also through non-grazing vegetation alterations such as wallowing and rubbing. The latter two create barren patches, which provide a habitat for plants and arthropods. This study focusses on the different wallowing and rubbing preferences of Konik horses (*Equus ferus caballus*), *Rode Geus* cattle (*Bos primigenius taurus*) and wisents (*Bison bonasus*). These species have been introduced together for their complementary diets in a Dutch nature area called the *Slikken van de Heen*. A field study was conducted in this area, in which wallowing and rubbing patches were recorded. The amount of wallowing patches found was too low for statistical analysis. This was most likely due to the field work being performed during the season in which generally less wallowing occurs. Upon analysing the data found for rubbing patches, it was found that Konik horses prefer to rub in grassy vegetation and patches with a high degree of vegetation cover. Furthermore, they were found to avoid rubbing in tree vegetation and rubbing against roots. Whereas wisents were found to prefer rubbing in tree vegetation and rubbing against roots. Also, they avoided rubbing in grass vegetation and rubbing patches with a high degree of vegetation cover. For *Rode Geus* cattle no significant associations were found due to the low number of rubbing patches used by cattle found. The results of this study show that the rubbing habits of Konik horses and wisents are complementary to each other. It is suggested to consider introducing Konik horses, wisents and *Rode Geus* cattle together in ecosystem management for their complementary non-grazing and grazing vegetation alterations.

Laymen's summary

Large grazers are often placed in nature areas to prevent woody species from taking over. They do this by eating bark and twigs of mature trees or eating young trees. Also, by grazing and trampling they make way for new species and increase biodiversity. Most large grazers make these trampled spots of barren soil by rubbing their bodies against objects and repetitively walking on the ground beneath it. Another way in which large grazer can increase biodiversity is wallowing. This is a behaviour in which an animal lays down on the ground and rolls over. This causes barren patches of soil on which new plants can grow and insects can live, but not all large grazers show this behaviour. European bison (wisents) and horses are large grazers which do wallow.

This research has been performed at the *Slikken van de Heen*, a Dutch nature area in which wisents, Konik horses and *Rode Geus* cattle have been placed to prevent woody species from taking over. These three large grazers were chosen because the eat different plants. This way, they enhance the effect they have on the area. But they also might enhance each other's effect by wallowing and rubbing their bodies. The aim of this research was to find out if these large grazers have different preferences for rubbing and wallowing. The amount of wallowing spots found was relatively low, because the grazers did not wallow often in the months during this research. For the spots beneath rubbing spots it was found that Konik horses prefer to rub in grassy vegetation and prefer a spot with a large amount of vegetation in it. They were found to avoid rubbing in tree vegetation and avoid rubbing against roots. Wisents preferred to rub in tree vegetation and against roots. But they avoided rubbing in grassy vegetation and spots with a large amount of vegetation in it. The amount of spots beneath rubbing objects for *Rode Geus* cattle was too low to draw conclusions from it.

These results show that the rubbing preferences of wisents and Konik horses are complementary, which means that their rubbing behaviour enhances each other's. If the diets are taken into account, the combination of Konik horses, wisents and *Rode Geus* cattle makes for a good combination to use in nature areas.

Introduction

Large herbivores are known to increase biodiversity (Köhler et al., 2016; Cromsigt et al., 2017) and maintain or create open to half-open landscapes, by preventing the domination of woody species. This results mainly from the grazing behaviour of large herbivores on both woody and herbaceous plants (Smit & Putman, 2010). However, other characteristics of large herbivores can also influence the vegetation. For example, through trampling vegetation by repetitively walking beneath rubbing locations.

Animals rub their bodies in order to relieve itching, aid in shedding or spread their odour (Green & Mattson, 2003; Ramos *et al*., 2016). Research on rubbing behaviour has been performed on both herbivores (Coppedge & Shaw, 1997; Ramos *et al*., 2006) and carnivores (Green & Mattson, 2003; González-Bernardo, 2021), but has mainly been focussed on the effect rubbing has on trees. Repetitive rubbing can cause damage to trees especially since rubbing is often accompanied by horning (Coppedge & Shaw, 1997). However, the trampling of vegetation creates barren patches, in which new vegetation can grow. Little research has been performed on these barren patches beneath rubbing locations, but there has been research performed on the barren patches that are created due to wallowing activity (e.g. Coppedge *et al*., 1999; Knapp *et al*., 1999; McMillan *et al*., 2000; McMillan *et al*., 2011; Nickell *et al*., 2018).

Wallowing is a behaviour in which an animal lays down on the ground and rolls toward their back (Reinhardt, 1985). Frequent wallowing on the same location can create a patch with little to no vegetation left (Coppedge *et al*., 1999). Research has shown that, especially inactive wallowing patches, can increase plant (Trager *et* al., 2004; McMillan *et al*., 2011) and arthropod biodiversity (Nickell *et al*., 2018). One of the most researched species regarding wallowing activity is the American bison (*Bison bison*). Several explanations have been proposed as to why American bison wallow. It is suggested that it is a non-social behaviour providing relief from skin irritation during shedding, skin irritation caused by biting insects, defence against ectoparasites. Another explanation provided in literature is that wallowing is a thermoregulatory behaviour. Furthermore, it is suggested that wallowing is a social behaviour associated with group cohesion or with male conflict and rut (McMillan *et al*., 2000). All explanations were found to be not mutually exclusive and it can therefore be argued that wallowing serves all of these purposes (McMillan *et al*., 2000). The American bison is not the only large herbivore to wallow, the lesser known European bison (*Bison bonasus*) also shows this behaviour.

At the beginning of the 20th century this species, also known as wisent, was almost extinct in the wild, but extensive breeding programs with captive individuals and subsequent release has led to wild populations in eastern Europe (Krasinska & Krasinski, 2007). With rewilding in mind, wisents have been released in five nature areas in the Netherlands. Since 1975 wisents have been in *Natuurpark Lelystad*, which mainly focusses on breeding wisents to release them in other nature areas (*Het Flevo-landschap*, 2021). In 2007, a pilot was started in the *Kraansvlak*, in which wisents were shown to open up vegetation and increase the amount of barren patches (Cromsigt *et al*., 2017a). Since this pilot was deemed a success, wisents were also introduced in the *Maashorst* (2016) and the *Veluwe* (2016) (*ARK Natuurontwikkeling*, n.d.) The fifth area where wisents have been released is the *Slikken van de Heen*, a 250 ha. nature area in the southwest of the Netherlands. In order to get accustomed to the area, the wisents have first been introduced in a 25 ha. closed of section since the beginning of 2020. But since September of 2020, the wisents have been allowed into the entire area (FREE Nature, 2020). In this larger area, the wisents have come across the other large herbivore species of the *Slikken van de Heen*, namely Konik horses (*Equus ferus caballus*) and

Rode Geus cattle (*Bos primigenius taurus*) (*Het Zeeuws Landschap, n.d. a)*. Both of these species are also known to use trees for grooming purposes (Inoue & Kaminaga, 1973; Adams, 1975; Köhler et al.,2016). Konik horses are also known to wallow (Feist & McCullough, 1976), whereas *Rode Geus* cattle create patches using their horns during rutting season (Geist & Walther, 1974). The combination of these three large herbivore species was chosen because of their complementary grazing habits on exotic species present in the area (*Het Zeeuws Landschap, n.d. a*). However, little research has been performed on their vegetation altering behavioural habits and if these are complementary. Therefore, this research will focus on the question: *What are the preferences of large herbivores regarding non-grazing vegetation alteration?*

In order to answer this question, two sub questions will be discussed. Namely:

1. What are the characteristics of patches used by wisents, Konik horses and *Rode Geus* cattle?
2. What are the differences between the characteristics of patches used by wisents, horses and cattle?

Previous research in this area has shown that wisents, Konik horses and *Rode Geus* have different preferences regarding their wallowing and rutting patches (Bouma, 2020). Wisents were shown to have a preference for wallowing in areas surrounded by ferns, whereas horses avoided this type of habitat to create wallowing patches. Therefore, it is hypothesized that the characteristics of wallowing patches found differs between the three species. However, this research did not take patches caused by rubbing at trees into account. Therefore, the hypothesis for this part of the study was taken from literature. Since wisents, Konink horses and *Rode Geus* cattle have different habitat uses, it is hypothesized that the characteristics for their tree rubbing patches will differ. Wisents are known to prefer forest habitats (Krasinska & Krasinski, 2007), whereas Konink horses and *Rode Geus* cattle prefer more open habitats (Popp & Scheibe, 2014). Therefore, it is hypothesized that tree rubbing patches of wisents will be more often found in denser vegetation than tree rubbing patches of Konink horses and *Rode Geus* cattle. Literature on the type of object these animals prefer to rub on, the direction of the rubbed surface and the degree of vegetation cover is limited. This might be because the differences between large herbivores regarding these factors are limited. It is therefore hypothesized that large herbivores do not differ in their rubbing preference regarding the type of object to rub on, the direction of the rubbed surface and the degree of vegetation cover.

Methodology

Field site

Field work for this study was conducted between October 19th 2020 and April 16th 2021 at the *Slikken van de Heen* and the *Plaat van de Vliet* (figure 1). These Dutch nature areas are connected through a corridor. The areas are owned by *Het Zeeuws Landschap* and the herds of large herbivores are managed by *FREE Nature*. *ARK*, the organisation under whose supervision this study was conducted, performs research in the areas.

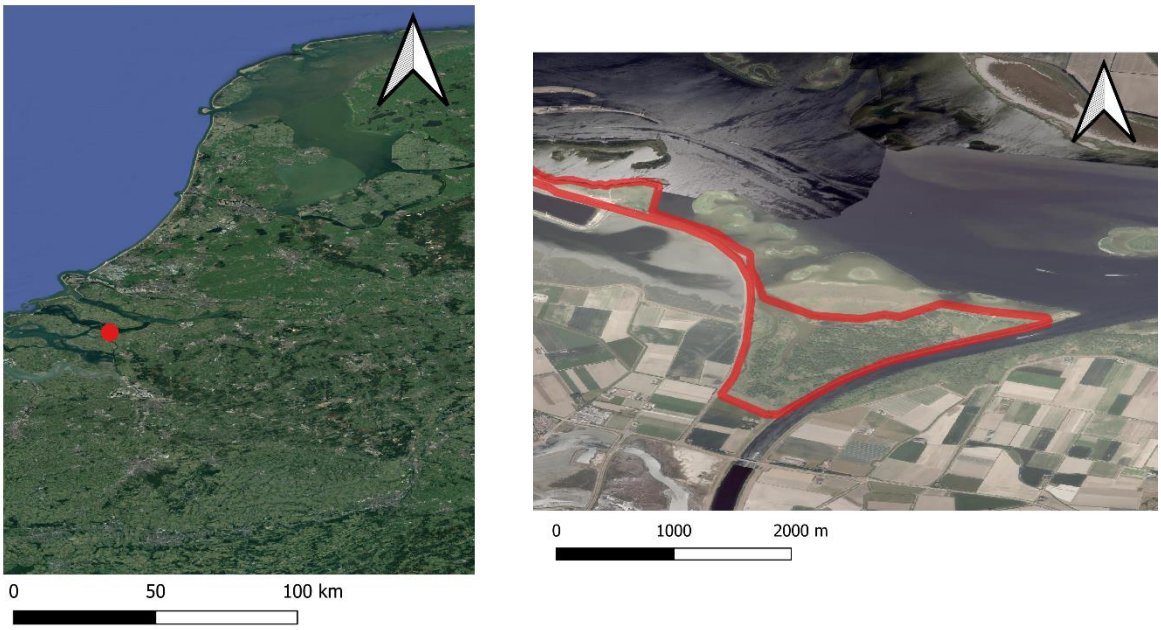

Figure 1. Location of the field work. The field work site was located in the southwest of the Netherlands (left) and consisted of two nature areas, connected through a corridor (right). The large area at the bottom of the right picture is the *Slikken van de Heen* and the area connected through the corridor is the *Plaat van de Vliet*.

Both areas were highly affected by the closing of the *Philipsdam* in 1987. Previously, the areas were surrounded by saltwater with tide, which became a freshwater area without tides after 1987. This history causes for a nutrient rich soil in the areas. In the last decade, the areas (predominantly the *Slikken van de Heen*) have been overgrown by plants such as bracken fern (*Pteridium aquilinum*) and wood small-reed (*Calamagrostig epigejos*), which have caused a dense vegetation (*Het Zeeuws Landschap, n.d. a; Het Zeeuws Landschap, n.d b)*. Furthermore, exotic species such as giant hogweed (*Heracleum mantegazzianum*) and Himalayan blackberry (*Rubus armeniacus*) invaded the area. In order to combat the dense vegetation and exotic species, the large herbivores present were changed. At first, highland cattle (*Bos taurus taurus*) were introduced for year-round grazing, along with summer grazing by agricultural cattle. Although later several Konik horses (*Equus ferus coballus*) were added, this did not accomplish the desired effect, especially since the numbers of both cattle and horses were relatively low. Furthermore, the agricultural cattle introduced medicine in the area via their faeces, which had a detrimental effect on insects and fungi (*Het Zeeuws Landschap, n.d. a; Het Zeeuws Landschap, n.d b*). Therefore, in collaboration with *FREE Nature*, the herd of horses was expanded and the cattle was replaced by *Rode Geus* cattle (*Bos primigenius taurus*). At the beginning of 2020, a herd of wisents (*Bison bonasus*) was introduced to complement the already present large herbivores. The wisents were first introduced into a 25 hectare area to get accustomed to the area, but have been allowed into the entire area since September of 2020. This composition of large herbivores have been chosen for their complementary effects. For example, Konik horses are known to eat wood small-reed, a species rarely eaten by *Rode Geus* cattle and wisents. Whereas *Rode Geus* cattle and wisents eat giant hogweed, which is barely eaten by Konink horses (*Het Zeeuws Landschap, n.d. a; Het Zeeuws Landschap, n.d b*). It has been observed in the field that this combination of large herbivores has a desired effect on the vegetation, however this has not been scientifically proven yet. At the start of this study the herds consisted of 63 Konik horses, 19 *Rode Geus* cattle and 14 wisents. When all field work was conducted, the herds consisted of 60 Konik horses, 22 *Rode Geus* cattle and 13 wisents. These changes were due to births, deaths and removal of animals out of the area.

Experimental design

During the field study, part of the *Slikken van de Heen* and the *Plaat van de Vliet* along with the corridor were scanned for wallowing and rubbing patches. Due to time constrains, only part of the *Slikken van de Heen* could be scanned for patches. Table 1 shows all measurements taken of each patch found, including the units or classifications used. Measurements 12 and 13 were only taken if the patch was classified as a patch used for rubbing a tree. Using the length and width (measurement 4) of the patches, the area was calculated. Since an oval shape resembles wallowing (Polly & Collins, 1984) and rubbing patches most closely, the formula of π*(0.5*length)*(0.5*width) was used.

Table 1. List of all measurements taken of each patch found with its unit/classification. Of each patch, a picture was taken as well. Measurements 12 and 13 were only taken if the patch was classified as a patch used for rubbing a tree.

	Measurement	Unit/classification
1	Picture	n.a
2	Date	n.a
3	Coordinates	Degrees
4	Length and width	Centimetres
5	Part of patch without vegetation	Percentage
6	Type of patch	Wallowing, rutting and rubbing (a nearby tree)
7	Species that last made use of the patch	Horse, cattle and wisent
8	Type of vegetation surrounding the patch	Ferns, moss, grassland and trees
9	Surrounding of the patch	Open vegetation and dense vegetation
10	Location type	Flat ground and sloping ground
11	Distance to nearest tree	Centimetres
12	Type of rubbed surface	Tree stem, tree branch and pole (manmade)
13	Direction of rubbed surface	Horizontal, vertical and sloping

Statistical analysis

R (R core team, 2021) was used to perform all analyses, with package ggplot2 (Wickham, 2016) to create graphs shown. QGIS (QGIS.org, 2021) was used to create maps and to visualize GPS data.

To analyse the data of rubbing patches, each patch used by more than one animal was replicated in the dataset used for analysis. To determine if there was an association between rubbing patches used by a specific animal and other factors concerning patches, Fisher's exact test was used. If this test was found significant ($p<0.05$), standardized residuals were analysed to find which association was contributing to the significance.

Results

During the fieldwork 965 patches were found, of which 925 were rubbing patches and 40 were wallowing patches (figure 2).

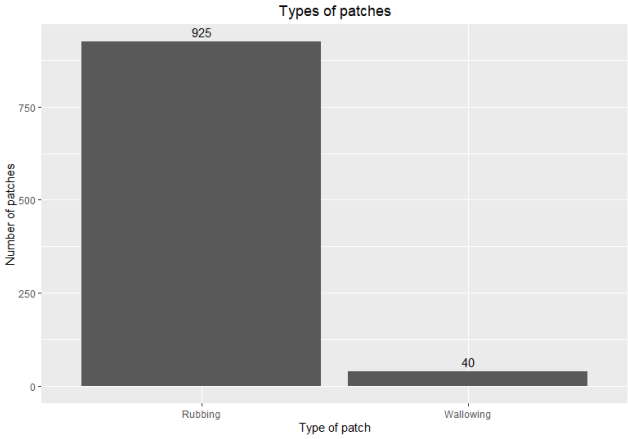

Figure 2. Types of patches (N=965).

Wallowing patches

Since the amount of wallowing patches was insufficient to perform a statistical analysis on, only a visual representation was made. Many of the wallowing patches were at the time of measuring not in use (30). Of the patches that were in use, most were used for wallowing (9) and one was used for rutting (figure 3). Most of the wallowing patches were used by horses (27), few by cattle and one by wisents. For the remaining patches (9) it was not possible to determine which species used the patch (figure 4).

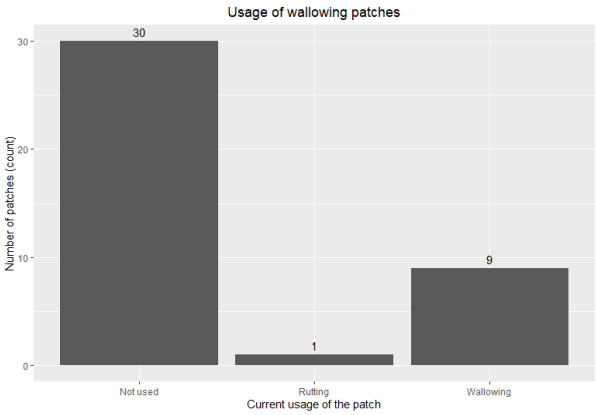

Figure 3. Usage of wallowing patches (N=40).

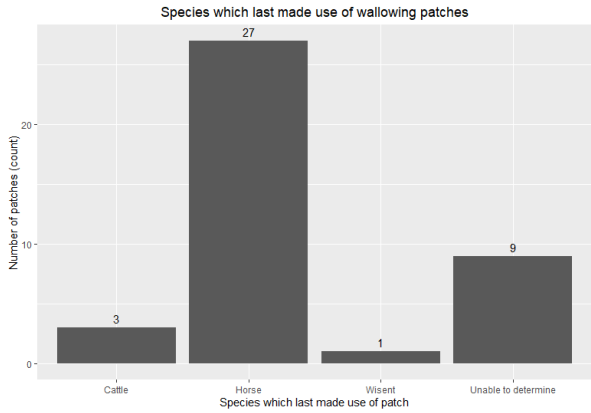

Figure 4. Distribution of wallowing patches over which species has last made use of the patch (N=40).

Rubbing patches

For the rubbing patches, a patch was included more times in the dataset if multiple animals had used it. Therefore, the total number of patches included in analyses of the rubbing patches differs from the total number of rubbing patches. A Fisher's exact test was performed to determine if there is a significant association between the type of animal using a rubbing patch and four different variables. Namely the type of vegetation surrounding a patch, the type of surface that was used for rubbing, the direction of the rubbed surface and the vegetation cover of a patch.

Figure 5 and figure A1 show a visual representation of the rubbing patches of all three different species distributed over four vegetation types. During analysis, a significant relationship was found (p<0.001). Upon further research, a preference of horses was found for rubbing patches located in grass vegetation (std. res.=4.229) and an avoidance for rubbing patches in tree vegetation (std. res.=-3.499). Furthermore, an avoidance of wisents was found for rubbing patches in grass vegetation (std. res.=-5.133) and a preference for rubbing patches in tree vegetation (std. res.=4.571).

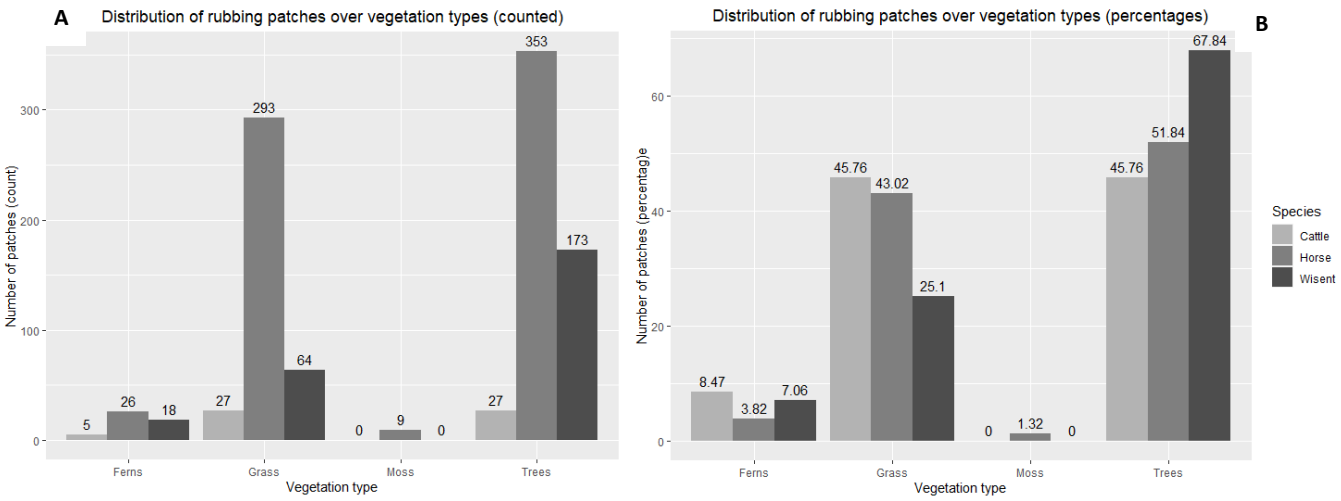

Figure 5. Distribution of rubbing patches of cattle, horses and wisents over vegetation types (N=995). A shows the distribution over the vegetation types in absolute values. B shows the distribution over the vegetation types in percentages, where all values for each species account for 100%.

Figure 6 and figure A2 show a visual representation of the rubbing patches of all three different species distributed over four types of surfaces against which was rubbed. A significant relationship was found (p<0.01). horses were found to avoid rubbing at roots (std. res.=-5.044), whereas wisents preferred rubbing at roots (std. res.=5.160).

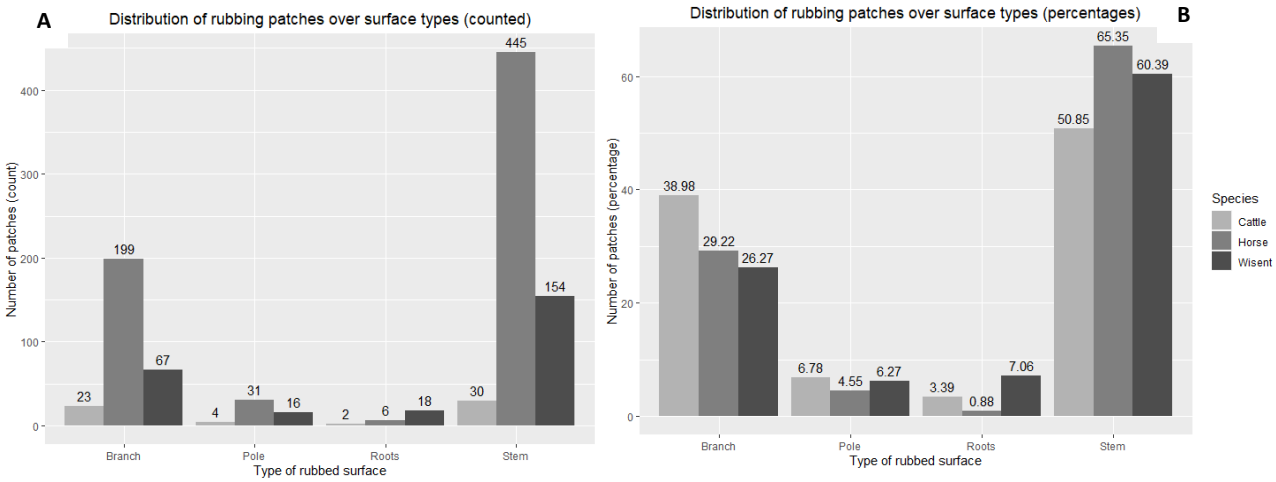

Figure 6. Distribution of rubbing patches of cattle, horses and wisents over the types of rubbed surface(N=995). A shows the distribution over the types of rubbed surfaces in absolute values. B shows the distribution over the types of rubbed surfaces in percentages, where all values for each species account for 100%.

Figure 7 and figure A3 show a visual representation of the rubbing patches of all three different species distributed over three directions of rubbed surfaces. When this was analysed, no relationship was found (p=0.119). However, a trend can be observed for all species to prefer rubbing at sloping surfaces.

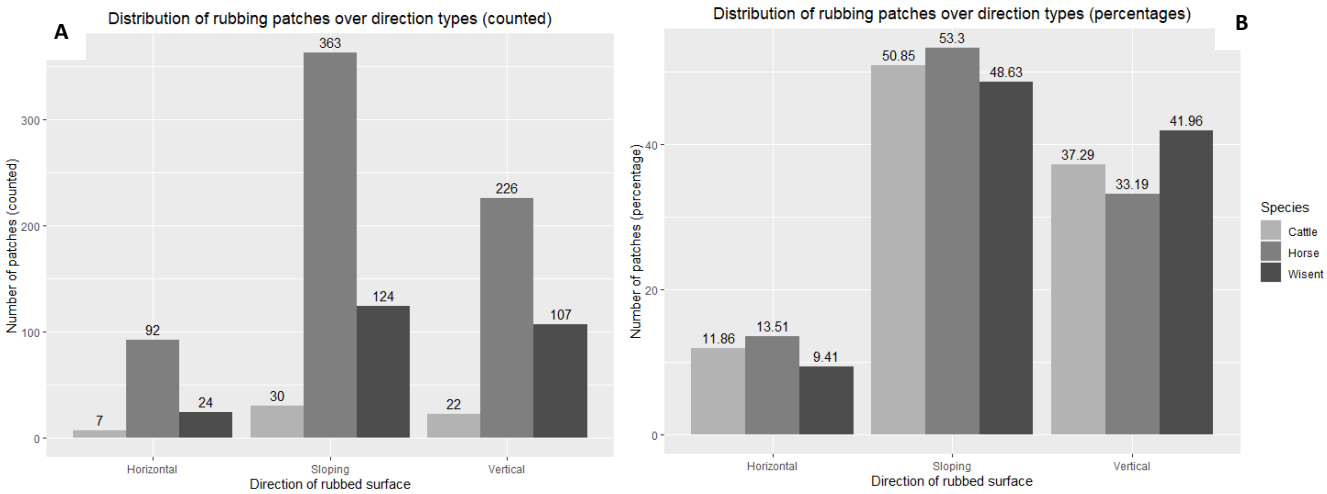

Figure 7. Distribution of rubbing patches of cattle, horses and wisents over the directions of rubbed surface (N=995). A shows the distribution over the types of rubbed surfaces in absolute values. B shows the distribution over the types of rubbed surfaces in percentages, where all values for each species account for 100%.

For each patch, it was measured which percentage of the patch was covered with vegetation. Of these percentages, three degrees were used. Namely low (0-33%), medium (34-67%) and high (68-100%). Figure 8 and figure A4 show a visual representation of the rubbing patches of all three different species distributed over the three degrees vegetation cover. A significant relationship was found for this factor (p<0.01). Horses showed a preference for patches with a high degree of vegetation cover (std. res.=4.113). Wisents were found to avoid patches with a high degree of vegetation cover (std. res.=-4.570).

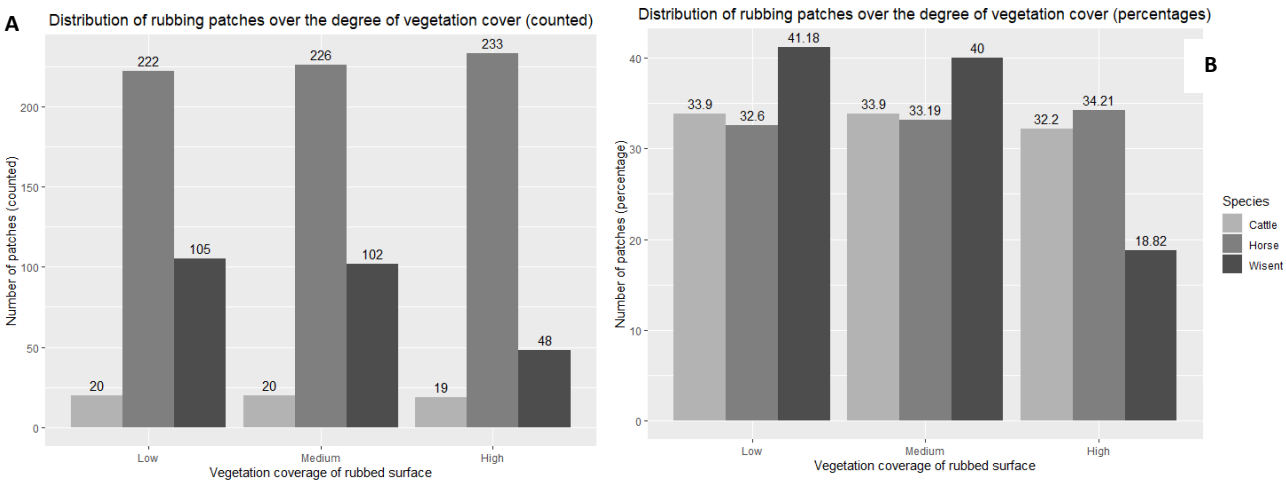

Figure 8. Distribution of rubbing patches of cattle, horses and wisents over the degree of vegetation cover of a patch (N=995). A shows the distribution over the degree of vegetation cover in absolute values. B shows the distribution over the degree of vegetation cover in percentages, where all values for each species account for 100%.

Discussion

This research focussed on the preferences of large herbivores regarding non-grazing vegetation alteration. In this research, two types of non-grazing vegetation alteration can be distinguished. Namely, patches of barren soil created by wallowing activity and patches of barren soil created by rubbing activity against objects.

Wallowing

The amount of wallowing patches found was too small to perform statistical analysis on. However, a trend can be seen in the gathered data. Many of the wallowing patches were not in use (figure 9) and most were used by Konik horses (figure 4). Previous research in the area by Bouma (2020) also found that most wallowing patches found at the Slikken van de Heen were used by Konik horses. This could be explained by the large herd size of the Konik horses compared to the other large herbivores in the nature reserve. However, in this previous research an increase in wallowing patches by wisent was observed between March and May. The difference in wallowing activity could therefore be explained by seasonality, since wallowing activity of wisents is observed to be less in winter than in spring and summer (Reinhardt, 1985; Coppedge & Shaw, 1997; Krasinksa & Krasinski, 2007). Furthermore, wisents were only present in the research area since the end of summer, explaining the low number of wisent wallowing patches. Research on the American bison (*Bison bison*) has shown that there are several explanations for wallowing behaviour, which are not mutually exclusive (McMillan *et al*., 2000). These explanations include relief from skin irritation during shedding, thermoregulatory behaviour, relief from skin irritation caused by biting insects and defence from ectoparasites. These factors that contribute to wallowing behaviour increase during spring and summer when shedding starts, temperature increases and biting insects and ectoparasites become more active (Mooring & Samuel, 1998). Since fieldwork for this study was conducted during October and April, it could be argued that wallowing activity is expected to be lower in these months. Literature on wallowing activity in horses was not found, but the explanations for their wallowing activity could be argued to be similar as well as the explanations of the decreased absence of wallowing patches used by horses. The rutting patches used by cattle also increase in numbers during rutting season. Since rutting takes place during spring/summer, this could explain the low numbers of rutting patches used by cattle.

Figure 9. An unused wallowing patch, clearly showing the absence of vegetation.

Another explanation for the decreased number of wallowing patches could also be the difference in transects and habitat availability for wisents. In the previous study by Bouma (2020), wisents were only allowed in a 25 ha. area of the nature reserve. During this study, they were allowed access to the entire area. During this study, the previous wisent area was omitted due to time constrains. This area consists of several barren spots with sandy soils, which are known to be the preferred soils by wisents for wallowing (Cabon-Racynska *et* al., 1987; Coppedge *et al*.,1999). Therefore, it could be possible that the wisents did create wallowing patches, but not in the researched areas. This explanation cannot be used to explain the low numbers of wallowing and rutting patches used by Konik horses and cattle, since the transects for horses and cattle of the previous study were also covered in this research (Bouma, 2020).

Rubbing patches

Horses

For the rubbing patches, enough data was gathered to perform statistical analysis on. This analysis shows a positive association between patches used by horses and patches located in grass, vegetation as well as a negative association between patches used by horses and patches located in tree vegetation (figure 5). Despite the absence of literature on the rubbing preferences of Konik horses, studies on exmoor ponies and Shetland ponies showed a preference of horses to grass vegetation in general (Lamoot *et* al., 2004; Popp & Scheibe, 2014). The study on exmoor ponies also showed a preference for resting in closely wooded areas (Popp & Scheibe, 2014).

The positive association between rubbing patches of Konik horses and rubbing patches in grass vegetation could be explained by a preference for grass habitat in general (Lamoot *et* al., 2004; Popp & Scheibe, 2014). But the negative association between Konik horses and rubbing patches in tree vegetation does not agree with the available literature on exmoor ponies (Popp & Scheibe,2014). An explanation for this could be that horses of the same genus do not share the same habitat preference. Another explanation could be that habitats preferred for resting are not preferred for rubbing. Further research on this topic could provide an explanation for the negative association between rubbing patches used of Konik horses and rubbing patches in tree vegetation.

Furthermore, a negative association was found between rubbing patches used by horses and patches for which roots are the rubbed surface. Figure 6 also shows a preference for rubbing patches for which stems are the rubbed surface. This preference can be explained by the presence of this surface types. The availability of stems and branches was relatively higher in comparison to poles and roots. However, compared to the other species horses did more often avoid rubbing against roots. This might indicate a dislike of horses to rub against the roots of fallen trees. Future research is needed to provide scientific literature for the assumption that horses indeed have preferences and dislikes when it comes to the type of rubbing surface.

No significant association was found between rubbing patches used by horses and the direction of the rubbed surface. However, a preference for rubbing surfaces with a sloping direction is seen (figure 7). This could be explained by the fact that sloping surfaces provide the opportunity to choose the perfect height to rub a belly or back. Horizontal surfaces are only fit for one height, suggesting that the observed trend is correct. Also, in other nature areas a preference for sloping surfaces has been observed, but not published (L. Linnartz, personal communication, July 2021). In future research, a different approach could be used to strengthen this field observation. Instead of counting the amount of rubbing patches in the entire area, a plot could be made in which all available rubbing locations are counted and determined used or unused by a species. The percentage of used horizontal, vertical and sloping rubbing locations could provide a better insight in the preferences of the species regarding direction.

A positive association was found between rubbing patches used by horses and rubbing patches with a high degree of vegetation cover (figure 8). This could indicate that horses do not regularly return to rubbing patches and often create new rubbing patches. This has been observed in the field (L. Linnartz, personal communication, July 2021), but has yet to be scientifically proven. This finding on rubbing patches is contradictory to the findings on wallowing patches by Bouma (2020). The results of this previous study showed that horses regularly return to the same patches to wallow. This would suggest that horses have different preferences regarding their grooming behaviours.

Wisent

For rubbing patches used by wisents, a positive association was found with rubbing patches in tree vegetation and a negative association with rubbing patches in grass vegetation (figure 5). This is in compliance with the habitat preference of wisents found in literature. Wisents are essentially a grass-eating animal, but have adapted to make use of a forest habitat (Krasinska & Krasinski, 2007). This adaptation may have been driven by human pressure and the increasing replacement of open grass habitats by forest habitats in their native environment. In literature, it is theorized that wisents have acted as a refugee species when they converted from their optimal habitat (grass habitat) to their suboptimal habitat (forest habitat) (Kerley *et al*., 2012). However, recent studies on the diet of wisents in another Dutch nature area (*Kraansvlak*) have shown that their foraging behaviour best resembles the foraging behaviour of a species that prefers a mixture of grass and forest habitat (Cromsigt *et al*., 2017b). The preferences of wisents for rubbing patches in tree vegetation found in this study match both explanations, since both habitat types contain large amounts of trees.

Another positive association was found between rubbing patches used by wisents and rubbing patches for which roots were the rubbed surface (figure 6 & figure 10). No literature was found on the preference of wisents for a particular surface type, but studies on the North-American bison did show that bison had a preference for certain species of tree (Coppedge & Shaw, 1997). Since rubbing is often accompanied by horning (Coppedge & Shaw, 1997), which causes damage to trees, it can be suggested that this behaviour accompanied by a preference for certain species can alter the composition of woody species (Beschta *et al*,. 2020). Since this preference has only been established in the North-American bison, future research should reveal if wisents have the same effect on vegetation, since this was beyond the scope of this research.

Figure 10. Roots of a tree which wisents and horses used for rubbing. Through repetitive trampling a barren patch has been created.

For the direction of the rubbed surface, no significant associations were found with rubbing patches used by wisents. As mentioned before, the preferences for sloping surfaces has been observed in other areas (L. Linnartz, personal communication, July 2021), hence the higher bars shown in figure 7. However, no literature was found to support this trend.

A negative association was found between rubbing patches used by wisents and rubbing patches with a high degree of vegetation cover (figure 8). This would indicate that wisents do not often create new rubbing patches. In another Dutch nature area (*Kraansvlak*) it was found that the amount of barren spots and sandy spots increased after the introduction of wisents. It was unclear if wisents created these new patches, but it was clear that these patches were maintained and liked by wisents to rest and wallow on (Cromsigt *et al*., 2015). Furthermore, field observations on wallowing patches used by wisents show that wisents tend to expand barren soil created through molehills to wallowing patches (L. Linnartz, personal communication, July 2021). These findings are in agreement with the results found on rubbing patches in this study. If wisents are avoiding patches with a high degree of vegetation cover, they are most likely maintaining patches already in existence. Future research focussed on the amount of rubbing patches created by wisents and/or if wisents regularly return to rubbing patches, could further strengthen these findings.

Another interesting find is the amount of rubbing patches used by wisents. 995 patches in total were found, 59 of which were used by cattle, 255 by wisents and 681 by horses. When this is compared to the herd sizes at the beginning of this study (19 *Rode Geus* cattle, 14 wisents and 63 Konik horses), it can be calculated that wisents make relatively more rubbing patches per individual (3,1 per cattle, 18,2 per wisent and 10,8 per horse). This would suggest that wisents rub relatively more often than Konik horses and *Rode Geus* cattle. The relatively few rubbing patches per Konik horse could be explained by the allogrooming behaviour of horses, during which horses groom each other (Feh & De Mazières, 1993). Furthermore, cattle are known to use their own horns to rub themselves (Knierim *et al*., 2015). Wisents do not show any behaviour in which they groom each other or use their own horns. The absence of these kinds of behaviours could explain the relatively large number of rubbing patches found per wisent. Further research would be needed to test this assumption.

Cattle

For cattle, no associations were found between any of the variables mentioned before (vegetation type, type of rubbed surface, direction of rubbed surface and vegetation cover). Literature on rubbing behaviour of cattle is very limited. There have been studies on agricultural cattle and the enriching effect of putting trees for rubbing in pastures (Kohari *et al.*, 20007). However, these types of studies did not examine the preferences of cattle in regards to rubbing location, surface and direction. Furthermore, research has shown that cattle can damage trees by rubbing at them as well as by foraging on trees (Adams, 1975). The effect of their dietary habit of foraging on trees has been better researched than their rubbing behaviour. It has been found that cattle, like wisents, include woody species in their diet (Cromsigt *et al*., 2017a). Cattle is known to browse on twigs, whereas wisents are more prone to eating bark (Cromsigt *et al*., 2017b). However the main portion of their diet consists of grass-like vegetation (Lamoot *et al*., 2004). This is in compliance with research on their habitat preferences, which showed a preference for grass vegetation with tendencies to spent their time partially in tree vegetation (Lamoot *et* al., 2004; Voeten & de Graaf, 2012; Popp & Scheibe, 2014). This would suggest that cattle are adapted to semi-open habitats (Popp & Scheibe, 2014). Despite not seeing any significant associations, figure 5 does show the preference for cattle to rub in grass and tree vegetation to be equal. This is in agreement with the previously stated literature on the habitat preferences of cattle. Figure 6 shows that cattle were most likely to rub on stems and branches, which can be explained by their higher abundance in comparison to poles and roots as previously stated. The preference to rub on sloping surfaces (figure 7) has been observed in other nature areas (L. Linnartz, personal communication, July 2021). Analysis on the degree of vegetation cover shows that all degrees were equally favoured by cattle (figure 8). The absence of significant results could be explained by the low number of rubbing patches found used by cattle (59) compared to patches used by horses (681) and wisents (255). In future research, a higher amount of rubbing patches used by cattle should be included. This could be achieved by increasing the field work area to the entire area of the *Slikken van de Heen*.

Species comparison

In the analysis of rubbing patches, several differences were found between the characteristics of Konik horses and wisents. Their associations found regarding vegetation, surface and degree of vegetation cover preferences were opposite of each other. These complementary characteristics together with their complementary diets (Cromsigt *et al*., 2017b) makes for a suitable combinations of large herbivores to use in ecosystem management.

Future research

In the text above, several adjustments or future research suggestions have been proposed. However, there are some other research ideas that could further expand the knowledge on the characteristics of non-grazing vegetation altering behaviour. This research was performed with the assumption that rubbing patches created by large herbivores have similar environmental effects as wallowing patches. However, this assumption has only been theorized and not researched. Further research would be needed to confirm this idea. Future research could also expand the factors which were studied to be characteristics or preferences of large herbivores when considering wallowing or rubbing patches. These could include noise pollution, distance to water for drinking or thermoregulation, etc. These suggested follow-up studies would enhance knowledge about large herbivores and their non-grazing vegetation characteristics.

Conclusion

From this study it can be concluded that the preferences of large herbivores regarding non-grazing vegetation alteration differ. Especially Konik horses and wisents were found to have complementary preferences. Cattle was not found to have any significant preferences. However, their dietary preference of eating giant hogweed makes for a desirable third species in this combination for ecosystem management. Therefore, for future introductions of large herbivores for ecosystem management, it is highly recommended that this trinity is considered.

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Appendix A

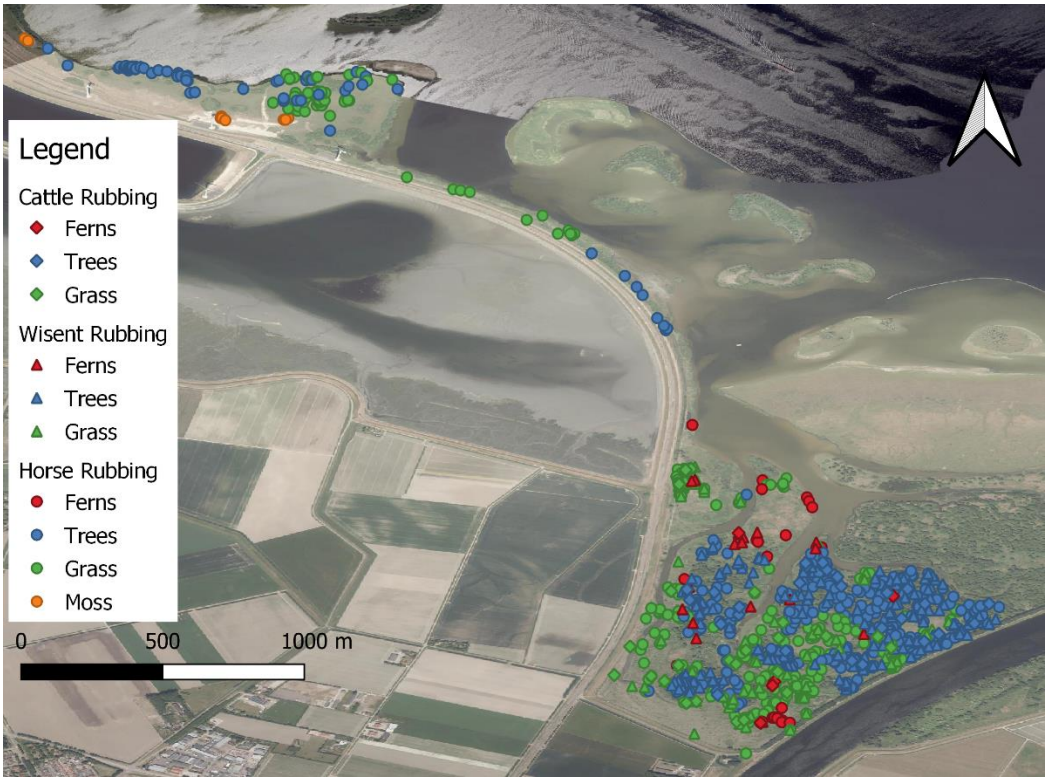

Figure A1. Visual representation of the distribution of rubbing patches used by cattle, horse and wisent distributed over four vegetation types underneath a rubbing post (N=995).

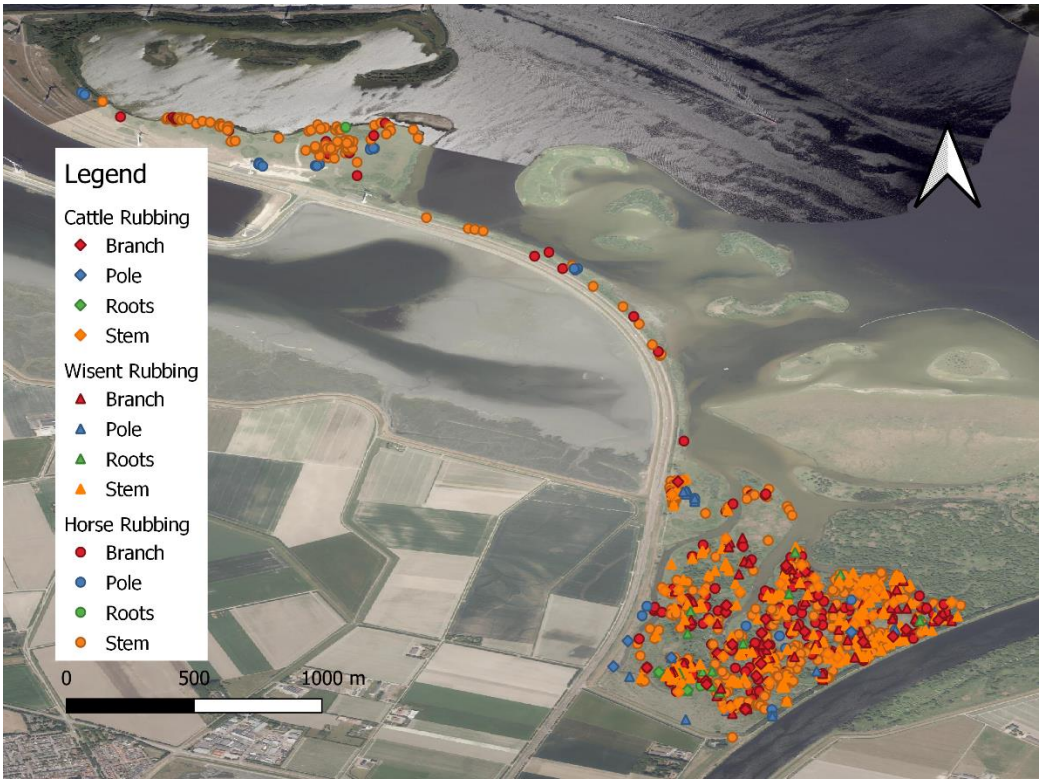

Figure A2. Visual representation of the distribution of rubbing patches used by cattle, horse and wisent distributed over four types of rubbed surfaces (N=995).

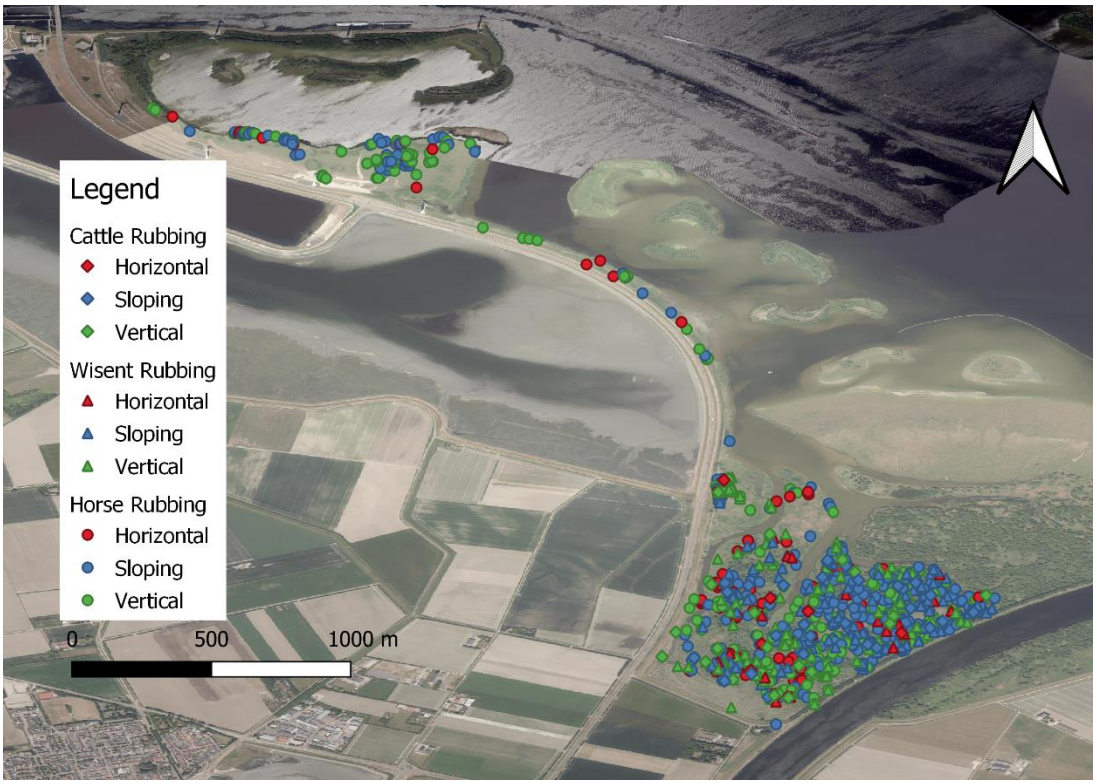

Figure A3. Visual representation of the distribution of rubbing patches used by cattle, horse and wisent distributed over the directions of rubbed surfaces (N=995).

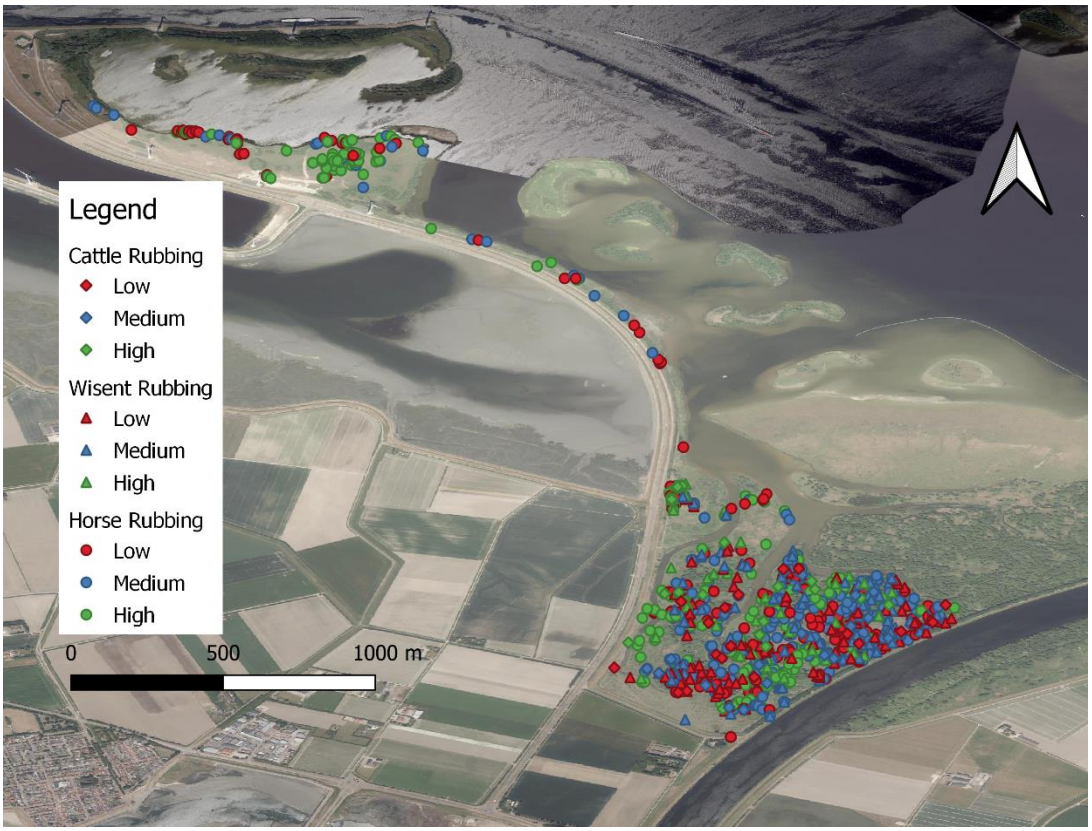

Figure A4. Visual representation of the distribution of rubbing patches used by cattle, horse and wisent distributed over the degree of vegetation cover of a patch underneath a rubbing post (N=995).