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In 2013 zijn twee faunapassages aangelegd in Het Nationale Park De Hoge Veluwe. Het doel van deze maatregelen is het vergroten van de landschappelijke cohesie en het faciliteren van uitwisseling van hoefdieren tussen het Park en de naastgelegen natuurgebieden. Migraties van hoefdieren via deze faunapassages kan leiden tot veranderingen in de grootte en structuur van de hoefdierpopulaties, het habitatgebruik door deze soorten en vraatdruk binnen de grenzen van het Park. In deze studie is onderzocht of de faunapassages door hoefdieren worden gebruikt, migraties leiden tot een netto immigratie of emigratie van hoefdieren in het Park, hoe migraties de grootte en structuur van de hoefdierpopulaties beïnvloeden, hoe de al aanwezige hoefdieren reageren op immigranten, hoe migraties het habitatgebruik van de hoefdieren beïnvloedt, welk effect dit heeft op de vestiging, overleving en groei van boomsoorten in het Park en wat de consequenties zijn voor de beheerder van het Park in termen van jachtinspanning om de vastgestelde afschotaantallen te realiseren.

In 2013 two wildlife crossing structures were installed in Hoge Veluwe National Park. The aim of these defragmentation measures is to increase landscape connectivity and facilitate ungulate movements between the Park and adjacent areas. Ungulate migrations via these wildlife crossing structures may lead to changes in ungulate population size and structure, habitat use of these species and browsing pressure within the boundaries of the Park. In this study we assessed whether the wildlife crossing structures are used by ungulates, whether migrations result in a net immigration or emigration of ungulates in the Park, how migrations affect ungulate population size and structure, how resident ungulates respond to immigrants, how migrations affect the intensity at which ungulates use the available habitats, how this affects the establishment, survival and growth of tree species in the Park and what the consequences will be for Park staff in terms of time expenditure to achieve designated cull numbers.

Keywords: habitat fragmentation, defragmentation, wildlife fences, overpass, crosswalk, road mitigation, habitat use, browsing, camera traps, tracking, telemetry, red deer, fallow deer, roe deer, wild boar, mouflon.

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Summary

Background
As a result of the policy plan *Veluwe 2010,* the project "Heart of the Veluwe" was started in 2007, aiming at strengthening natural, recreational and landscape values within the southern parts of the natural area known as the Veluwe in the Netherlands. Important measures concern the restoration of landscape connectivity since these parts of the Veluwe are now highly fragmented by roads and fences. The parties cooperating in this project are the province of Gelderland, the cities of Ede, Apeldoorn and Arnhem, Hoge Veluwe National Park and Vereniging Natuurmonumenten.

Hoge Veluwe National Park is habitat to five ungulate species: red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and mouflon (*Ovis musimon*). To increase landscape connectivity and facilitate ungulate movements between the Park and adjacent areas, two wildlife crossing structures have been installed. At the east side of the Park a wildlife cross-walk facilitates ungulate movements across road N804. At the west side a green bridge facilitates ungulate movements across road N310. Animal migration via these new wildlife crossing structures may lead to changes in ungulate population size and structure as well as alterations in habitat use by these species and browsing pressure within the boundaries of the Park.

Research objective
The objective of our research was to determine whether the wildlife crossing structures are used by ungulates, whether migrations result in a net immigration or emigration of ungulates, how migration affects ungulate population size and structure, how resident ungulates respond to the immigrants, how migration affects the intensity at which ungulates use the available habitats and how this affects plant species associated with these habitats. Furthermore, we wanted to determine the consequences for Park staff in terms of the time needed to achieve designated cull numbers.

Results

What is the intensity of the use of the wildlife crossing structures by ungulates?
Crossing structure Deelerwoud is used by four ungulate species: red deer, fallow deer, roe deer and wild boar. Crossings structure Oud Reemst is used by two ungulate species: roe deer and wild boar. No crossings of mouflon were registered at either crossing structures, which complies with the aim to keep these animals in the Park. At Deelerwoud, red deer and fallow deer cross respectively about 55 and 174 times per year. Roe deer and wild boar cross only occasionally. At Oud Reemst both roe deer and wild boar cross only occasionally.

Is there a nett immigration or emigration of ungulates?
The data suggest a net immigration of red deer and fallow deer at crossing structure Deelerwoud. However, a robust estimate of net migration could not be assessed because the video systems frequently malfunctioned. In the three months that the crossing structures were monitored daily by tracking beds, the migration ratio for all ungulate species at both locations was close to zero.

Do the size and structure of ungulate populations in the Park change as a result of the crossing structures?
Population numbers of red deer, fallow deer, mouflon and wild boar increased after the crossing structures were installed; the roe deer population decreased slightly. Red deer population increase may be (partly) the result of the measured net immigration, but due to the problems with the video systems and the resulting gaps in the data collection, no final conclusions can be drawn. Fallow deer population increase is the result of the measured net immigration as no fallow deer were in the Park before the crossing structures were installed. Fallow deer were observed at crossing structure Deelerwoud soon after it was installed. The first crossings of fallow deer into the Park were about seven months after installation. Currently, only a small group of fallow deer seem to have included

(parts of) the Park in their home range. Roe deer population decrease may be (partly) the result of the measured net emigration, but due to the problems with the video systems and the resulting gaps in the data collection, no final conclusions can be drawn. Mouflon population increase is not the result of net immigration because mouflon did not use the crossing structures. Wild boar population increase is not likely the result of the crossing structures as they used the crossing structures only incidentally, and only indications of a net emigration were found. Between 2011-2016 the structure of the ungulate populations changed only slightly; red deer and wild boar showed a small increase in the male-female ratio, and wild boar showed a small decrease in the female-young ratio.

Do management efforts in the Park change as a result of the wildlife crossing structures?
About a 7 percent increase in culling efforts (red deer, wild boar and mouflon combined) is needed to achieve the designated cull numbers in the years after the wildlife crossing structures were installed. Such higher culling efforts directly relate to the positive trends in ungulate population sizes.

How does the behaviour of the red deer in the Park change, especially in response to fallow deer immigration?
Changes in the behaviour and habitat use of red deer in the Park in response to fallow deer immigration could not be studied as fallow deer immigration numbers were extremely low and no fallow deer were captured and fitted with a GPS radio collar.

Can we accurately measure foraging behaviour with GPS-accelerometer collars in free-ranging deer?
About 70% of the predictions based on accelerometer data on foraging behaviour are correct, but the models often confuse foraging with walking behaviour. Hence, the data from GPS-accelerometer collars used in free ranging deer have only limited value in ecological research.

How does intensity of habitat use by ungulates change?
We found no evidence for any directional changes in patterns of habitat use by the four resident ungulate species - red deer, roe deer, mouflon and wild boar - since the fences were opened. Neither did we detect any consistent trend in the population levels, except for a declining annual trend in the abundance of roe deer.

How do establishment, survival and growth of tree species in the Park change?
Four years of monitoring cannot reveal the full impact of ungulate browsing on the succession of tree species in the Park area. The species composition in the seedling and young sapling layers shows that there is a potential for a diverse tree population in the Park area, but this is reduced by the browsing activity of ungulates. It is, however, not yet possible to draw a conclusion on the long-term impact of browsing on tree species diversity.

Research recommendations
- Continue monitoring the use of the wildlife crossing structures by ungulates for at least three more years.
- Make sure that the video system operates without failures in order to make better inferences about the net immigration or emigration of ungulates.
- Study the impact of the 1.1-meter fence and wild boar gates at the wildlife crossing structures on the use of the structure by the ungulates that are allowed to cross.
- Continue monitoring the fallow deer population in the Park, in relation to their use of the crossing structures.
- Register culling efforts per ungulate species in order to get better insights into (changes) in culling efforts at species level.
- Study year-round behaviour of deer on a spatial scale with accelerometers storing raw accelerometer data supplemented by a third axis.
- Mount a video camera on the collar so that one can see what type of behaviour the animal shows to gather a larger training set to calibrate the accelerometer.
- Use telemetry and accelerometer data to study the effect of culling on (foraging) the behaviour of deer and energy expenditure.
- Maintain the camera network and continue data collection to enable the detection of systematic changes in the abundance and habitat use by ungulates.

- Measure the effective detection area per species across seasons so that capture rates can be corrected for seasonal variations and the data can be used to address many timely questions in ungulate ecology and management, especially if combined with data on food quality and recreational pressure.
- Continue to monitor browsing in the established network and expand the network to replace plots that have grown into the thicket phase with new plots with young plants.
- Enable the establishment of a direct link between browsing and ungulate activity by monitoring tree browsing in front of the camera stations.
- Increase the exclosure network to determine tree species dynamics over the gradient in soil fertility and light availability in the absence of ungulate browsing.

1 Introduction

1.1 Background

As a result of the policy plan Veluwe 2010 (GS Gelderland, 2000) the project "Heart of the Veluwe" was started in 2007, aiming at strengthening natural, recreational and landscape values within the southern parts of the natural area known as the Veluwe in the Netherlands (GS Gelderland, 2007). Important measures concern the restoration of landscape connectivity, as currently these parts of the Veluwe are highly fragmented by roads and fences. The parties cooperating in this project are the province of Gelderland, the cities of Ede, Apeldoorn and Arnhem, Hoge Veluwe National Park and Vereniging Natuurmonumenten.

Hoge Veluwe National Park is habitat to five ungulate species: red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and mouflon (*Ovis musimon*). To increase landscape connectivity and facilitate ungulate movements between the Park and adjacent areas, two wildlife crossing structures were installed. At the east side of the Park a wildlife crosswalk facilitates ungulate movements across road N804. At the west side a green bridge facilitates ungulate movements across road N310. Animal migration via these new wildlife crossing structures may lead to changes in ungulate population size and structure as well as alterations in habitat use by these species and browsing pressure within the boundaries of the Park.

1.2 Research objectives

The objective of our research was to determine whether the wildlife crossing structures are used by ungulates, whether migrations result in a net immigration or emigration of ungulates, how migration affects ungulate population size and structure, how resident ungulates respond to the immigrants, how migration affects the intensity at which ungulates use the available habitats and how this affects the establishment, survival and growth of tree species in the Park. Furthermore, we wanted to determine the consequences for Park staff in terms of the time needed to achieve designated cull numbers.

1.3 Research questions

Our specific research questions were:

1. What is the intensity of use of the wildlife crossing structures by ungulates?
2. Is there a net immigration or emigration of ungulates?
3. Do the size and structure of ungulate populations in the Park change as a result of the crossing structures?
4. Do management efforts in the Park change as a result of the wildlife crossing structures?
5. How does behaviour of the red deer in the Park change, especially in response to fallow deer immigration?
6. Can we accurately measure foraging behaviour with GPS-accelerometer collars in free-ranging deer?
7. How does intensity of habitat use by ungulates change?
8. How do establishment, survival and growth of tree species in the Park change?

1.4 Research approach

To address these questions we monitored the migration of ungulates via the wildlife crossing structures and analysed ungulate population counts and culling efforts (chapter 2), conducted a telemetry study on red deer movement and activity (chapter 3), monitored ungulate abundance and habitat use (chapter 4), and monitored the browsing impact of ungulates (chapter 5).

2 Use of the crossing structures by ungulates

Edgar A. van der Grift, Dennis Lammertsma, Magali Frauendorf, Henk Ruiterkamp & Geert Groot Bruinderink

2.1 Introduction

Hoge Veluwe National Park has been a fenced area for wild ungulates for over 60 years. From April 2013 onwards, however, two wildlife crossing structures have allowed red deer, fallow deer, roe deer and wild boar to migrate between the Park and the neighbouring natural areas. To the west a wildlife overpass across road N310 provides connectivity between the Park and the nature reserve Planken Wambuis. To the east a wildlife crosswalk across road N804 provides connectivity between the Park and the nature reserve Deelerwoud. At both wildlife crossing structures a 1.1-m high fence prevents mouflons from leaving the Park. The deer species can easily jump over this fence and special gates have been installed to let wild boar pass through. The gates for wild boar are supposed to be unsuitable for use by mouflon. In addition, the maximum speed on the N804 was reduced from 80 to 30 km/h.

The wildlife crossing structures may lead to changes in ungulate population size and structure within the Park, especially since ungulate densities are significantly higher in Deelerwoud (~250 red deer/1000 ha), including a large population of fallow deer (~1200 individuals in 2016). Therefore, the Park needed a programme to monitor the consequences of installing the wildlife crossing structures that restored the connectivity with the neighbouring reserves. The Park management wanted to know whether there is a net immigration or emigration of ungulates and how this would affect population size and structure in the Park. Specific research questions were: (1) How intensely do the ungulates use the wildlife crossing structures? (2) Is there a net immigration or emigration of ungulates? (3) Does the size and structure of ungulate populations in the Park change as a result of the crossing structures? (4) Do management efforts in the Park change as a result of the wildlife crossing structures?

2.2 Methods

2.2.1 Collection of data

We monitored the use of the wildlife crossing structures for migration via a video surveillance system installed at the two passages (Figure 2.1). Each system consisted of two cameras, one at the northern entrance of the crossing structure and one at the southern entrance. The systems were designed and installed by a contractor, the Fieldwork Company, under the responsibility of the province of Gelderland. The systems, based on Mobotix cameras, were designed to continuously monitor one of the entrances of each wildlife crossing structure, which was illuminated by infrared lamps at night. The system uses real-time image processing to detect animal activity, compares subsequent images in the target areas it films and generates sequences of stills. Photo sequences of activity were saved on a server under the responsibility of the province of Gelderland. Once a week, the province sent a copy of the photos to a second server, this maintained by Wageningen University & Research. The motion events were annotated by volunteers with the photo processing system of Wageningen University & Research (see Chapter 4).

The video cameras were installed in October 2013. In our analyses we included the data of a 2.5-year period: January 1, 2014 - June 30, 2016. The first months after installation were excluded because this period was used to fine-tune the camera's settings and, consequently, not all days were properly

monitored. During the study period the cameras frequently malfunctioned for a variety of reasons, including power failures and the incomplete storage of footage. These technical problems resulted in an incomplete record of crossing structure use. In October 2014, the cameras at Oud Reemst were vandalised and were down until July 2015.

The cameras at Deelerwoud did not work for 7.4% (north) and 7.5% (south) of the study period due to power failures and vandalism (Annex 1). The cameras at Oud Reemst did not work for 35.4% (north) and 32.7% (south) of the study period due to power failures and vandalism (Annex 1).

The incomplete footage meant that recordings of motion events ended before the animals had left the viewfinder of the video cameras, resulting in inconclusive evidence about a potential crossing. In order to improve crossing rates estimates based on the collected data of the video cameras, we carried out parallel surveys with still cameras and tracking beds over a period of 12 weeks (November 2015-February 2016). The objective was to calculate *correction factors* for the video cameras on the basis of the still cameras and track pad surveys in order better estimate wildlife crossing structure use by ungulates. For a full description of these comparisons of survey methods and an assessment of correction factors, we refer to Frauendorf (2016).

Data on ungulate population numbers and hunting efforts were received from the Park. Deer population numbers are assessed yearly through simultaneous counts by 20-25 people during two nights in early spring (March). Wild boar population numbers are assessed yearly through simultaneous counts by 20-25 people during two nights in early summer (May/June). In these counts species, sex and age group are registered. Hunting efforts are registered by the hunters, including type of hunt (ambush, stalking), time of day (morning, evening), time spent (hours) and number of animals shot, distinguished by species, age group and sex (only for adults).

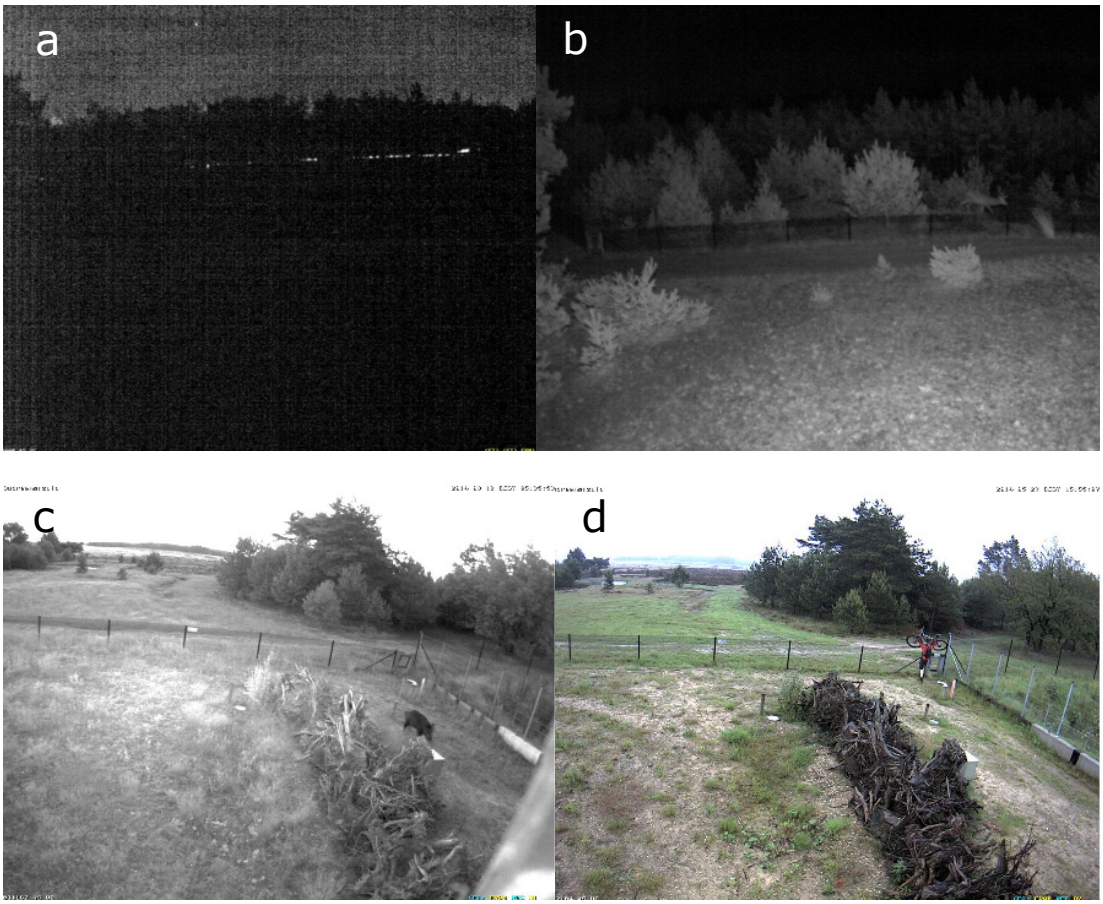

Figure 2.1 *Images from the video systems at the wildlife crossing structures. (a) power failure, (b) red deer jumping the fence, (c) wild boar near the fence, and (d) mountain biker crossing the fence.*

2.2.2 Data analysis

Crossing rates
Yearly crossing rates for each species were calculated by dividing the total number of crossings detected during the study period by the total number of hours that the video system had been functioning during the study period, multiplied by the number of hours in one year. The number of crossings was calculated by adding up the crossing numbers of each camera (north and south), reducing this sum by the number of crossings that had been registered by both cameras (overlap) and multiplying the outcome by the estimated correction factors (Table 2.1). Hereafter we refer to this estimate as 'corrected crossing number'. We defined the overlap as follows: crossings by the same species in the same direction with a maximum of a one-minute time difference. Further, we calculated the number of crossings - incoming and outgoing combined - per ungulate species and wildlife crossing structure over the first six months (2014-2016) and second six months (2014-2015) of each study year to explore possible trends in crossing numbers. We chose to analyse possible trends over six month-periods to ensure the comparability of the data sets between years as no data were available for the last six months of 2016.

Table 2.1 *Estimated correction factors for numbers of ungulates crossing at the wildlife crossing structures in Hoge Veluwe National Park (source: Frauendorf, 2016).*

Species	Deelerwoud	Oud Reemst
Red deer	1.00	na
Fallow deer	2.00	na
Roe deer	na	na
Mouflon	na	na
Wild boar	1.00	na

[1] na = no correction factor could be calculated due to absence of crossings or limited sample size.

Migration ratios
Migration ratios for each species were calculated by dividing the number of animals that entered the Park (incoming) by the number of animals that left the Park (outgoing). Hence, a migration ratio >1 means a net immigration and <1 means a net emigration. Migration ratios were calculated on the basis of the corrected crossing numbers.

Trends in population size and structure
We explored trends in ungulate population size by assessing the growth rates over the six-year study period (2011-2016), i.e. mean increase in population numbers per year, based on the spring counts. We explored trends in ungulate population structure by assessing the mean change per year over the six-year study period of two indexes, based on the spring counts: (1) male-female index, i.e. number of adult males divided by number of adult females and (2) female-young index, i.e. number of adult females divided by number of young.

To explore whether observed red deer migrations affect population numbers we compared the differences between predictions and actual spring counts of stags and hinds before (2011-2013) and after (2014-2016) the wildlife crossing structures had been installed.

The predictions for stag numbers were calculated as follows: summer population size of stags and male yearlings ('spitser') minus culled number of stags and male yearlings. The predictions for hind numbers were calculated as follows: summer population size of hinds and female yearlings ('smaldier') minus culled number of hinds and female yearlings. The summer population size of stags was estimated by adding up the counted number of stags and male yearlings during spring counts. The summer population size of male yearlings was estimated through the number of male calves counted during spring counts. The summer population size of hinds was estimated through adding up the counted number of hinds and female yearlings during spring counts. The summer population size of female yearlings was estimated through the number of female calves counted during spring counts.

We hypothesised that, in the case of a considerable net immigration, actual spring counts of stags and hinds would be significant higher than the predictions based on summer population size in the previous year. We hypothesised that, in the case of a considerable net emigration, actual spring counts of stags and hinds would be significant lower than the predictions based on summer population size in the previous year.

Trends in culling efforts
We calculated the mean number of hours spent on the culling[1] of red deer, wild boar and mouflon before (2011/12 and 2012/13) and after (2013/14, 2014/15, 2015/16) the wildlife crossing structures had been installed. In all of the years the designated cull was never reached; for comparability therefore we extrapolated the numbers to estimate the mean number of hours spent on culling if 100% of the designated cull was reached. We compared the relative difference (in %) in culling hours with the relative difference (in %) between designated cull numbers in the before and after situations. Furthermore, we calculated the mean number of culls per culling hour before and after the crossing structures had been installed. The analysis could not be done for each species separately because the dataset does not provide information on what the target species was for each hunt; hence, culling hours in which no animal was shot could not be limited to one of the species.

2.3 Results

2.3.1 Crossing rates

The video cameras yielded 3,131 (Deelerwoud) and 11,470 (Oud Reemst) image sequences of ungulates during the study period. Of these only 29 sequences were identified as overlap (Table 2.2). Ungulates crossed 368 (Deelerwoud) and 42 (Oud Reemst) times. At Deelerwoud most crossings were by fallow deer followed by red deer (Table 2.3). Roe deer and wild boar crossed at this location only occasionally. Mouflon never crossed. At Oud Reemst only crossings of roe deer and wild boar were registered; however, both species had low crossing rates (Table 2.3). At both Deelerwoud and Oud Reemst the yearly crossing rate estimates increase over time if the estimates over the first or second six months of each study year are compared (Table 2.4). At Deelerwoud this increase is mainly the result of increased crossing by fallow deer. At Oud Reemst this increase is the result of increased crossing by both roe deer and wild boar.

Table 2.2 *Number of single motion events of ungulates recorded by both video cameras (overlap) at the wildlife crossing structures in Hoge Veluwe National Park.*

Species	Deelerwoud		Oud Reemst	
	Incoming	Outgoing	Incoming	Outgoing
Red deer	0	3	0	0
Fallow deer	14	11	0	0
Roe deer	0	0	0	1
Mouflon	0	0	0	0
Wild boar	0	0	0	0
Total	14	14	0	1

[1] Hunting is defined as 'the activity or sport of chasing and killing wild animals'. Culling is a specific type of hunting and can be defined as 'to control the size of (a group of animals) by killing some animals' (Merriam-Webster Dictionary, at www.merriam-webster.com).

Table 2.3 *Estimated yearly crossing rates of ungulates at the wildlife crossing structures in Hoge Veluwe National Park.*

Species	Deelerwoud	Oud Reemst
Red deer	47[1]	0
Fallow deer	174[2]	0
Roe deer	1	10
Mouflon	0	0
Wild boar	4[3]	15
Total	226	25

[1] The yearly crossing rate was estimated with the help of a correction factor (see Table 2.1). As the correction factor for red deer was 1.0, the estimate shown is identical to the non-corrected estimate.

[2] The yearly crossing rate was estimated with the help of a correction factor (see Table 2.1). As the correction factor for fallow deer was 2.0, the estimate shown is twice the non-corrected estimate.

[3] The yearly crossing rate was estimated with the help of a correction factor (see Table 2.1). As the correction factor for wild boar was 1.0, the estimate shown is identical to the non-corrected estimate.

Table 2.4 *Estimated yearly crossing rates of ungulates at the wildlife crossing structures Deelerwoud (A) and Oud Reemst (B) in Hoge Veluwe National Park, calculated on the basis of the data for the first and the second half of each study year. Differences in video camera deployment time are accounted for, and we made use of the correction factors (see Table 2.1).*

A: Crossing structure Deelerwoud

Species	2014		2015		2016	
	Jan-Jun	Jul-Dec	Jan-Jun	Jul-Dec	Jan-Jun	Jul-Dec
Red deer	42	22	29	140	8	na
Fallow deer	5	116	225	296	300	na
Roe deer	0	0	0	2	0	na
Mouflon	0	0	0	0	0	na
Wild boar	0	6	2	4	6	na
Total	47	144	256	441	314	na

B: Crossing structure Oud Reemst

Species	2014		2015		2016	
	Jan-Jun	Jul-Dec	Jan-Jun	Jul-Dec	Jan-Jun	Jul-Dec
Red deer	0	0	0	0	0	na
Fallow deer	0	0	0	0	0	na
Roe deer	0	0	0	0	35	na
Mouflon	0	0	0	0	0	na
Wild boar	0	16	0	27	8	na
Total	0	16	0	27	43	na

[1] na = not applicable; not within study period.

2.3.2 Migration ratio

At Deelerwoud migration ratios could be calculated for red deer, fallow deer and wild boar (Table 2.5). There was a net immigration of red deer and fallow deer, and a net emigration for wild boar. For red deer the number of incoming movements was about 70% higher than the number of outgoing movements. For fallow deer the number of incoming movements was about 30% higher than the number of outgoing movements. The estimated mean yearly net immigration is 12 red deer and 11 fallow deer. For wild boar the number of incoming movements is about 20% lower than the number of outgoing movements, however, the sample size was very small.

At Oud Reemst migration ratios could be calculated for roe deer and wild boar (Table 2.5). Both species showed a net emigration. For roe deer the number of incoming movements was about 20%

lower than the number of outgoing movements. For wild boar the number of incoming movements was about 10% lower than the number of outgoing movements. For both species, however, the sample size was very small.

Table 2.5 *Corrected crossing numbers and migration ratio of ungulates at the wildlife crossing structures in Hoge Veluwe National Park.*

Species	Deelerwoud			Oud Reemst		
	Incoming	Outgoing	Migration ratio	Incoming	Outgoing	Migration ratio
Red deer	69	40	1.7	0	0	na[1]
Fallow deer	228	174	1.3	0	0	na
Roe deer	1	0	na	7	9	0.8
Mouflon	0	0	na	0	0	na
Wild boar	4	5	0.8	12	13	0.9
Total	302	219		19	22	

[1] na = not applicable due to absence of crossings in one or both of the two directions.

2.3.3 Trends in population size and structure

Red deer
In Hoge Veluwe National Park the red deer population has increased steadily over the last six years, with an average growth rate of 9.5 deer per year (Figure 2.2; Table 2.6). The mean difference in population size over the years before and after the crossing structures were installed is 26 red deer. The male-female index showed a small positive trend. The female-young index remained more or less the same.

Table 2.6 *Estimated growth rate over six-year study period, mean population size before and after installation of the crossing structures and mean change in population structure indexes per ungulate species in Hoge Veluwe National Park.*

Species	Growth rate over six-year period		Mean population size		Male-female index		Female-young index	
	mean increase in numbers per year	R^2	Before (2011-2013)	After (2014-2016)	mean change per year	R^2	mean change per year	R^2
Red deer	9.5	0.81	201	227	0.039	0.44	-0.007	0.21
Fallow deer	0.74	0.69	0	2	0.05	0.43	na[1]	na[1]
Roe deer	-1.2	0.02	161	151	-0.05	0.35	na[1]	na[1]
Mouflon	18.1	0.92	232	284	-0.005	0.01	0.006	0.02
Wild boar	17.5	0.51	213	284	0.02	0.02	-0.2	0.31

[1] na = not applicable due to no data.

In 2011-2013 the actual mean spring count of both stags and hinds was lower than predicted (73.0 versus 85.3 for stags; 58.3 versus 77.7 for hinds). Hence, on average stag and hind numbers are overestimated in the predictions by respectively about 12 and 19 individuals. In 2014-2016, after the installation of the wildlife crossing structures, the situation was similar, although the difference between predictions and counts was smaller (79 versus 85 for stags; 80 versus 86 for hinds) (Figure 2.3). As spring counts are lower than the predictions after the passages have been installed, there is no indication for a considerable net immigration of red deer.

Fallow deer

In December 2013, shortly after the crossing structure at Deelerwoud had been installed, fallow deer appeared at the fence. However, crossings into the Park were not registered until May 2014. During spring counts the species was not counted until the spring count of 2015. That year only two males, a stag and yearling, were counted. In 2016 four animals, three stags and one hind, were counted. No recruitment has been registered yet within the Park. One juvenile, registered at the crossing structure Deelerwoud in October 2014, did not cross into the Park. Real population numbers may be higher as species that occur in low densities are likely underestimated.

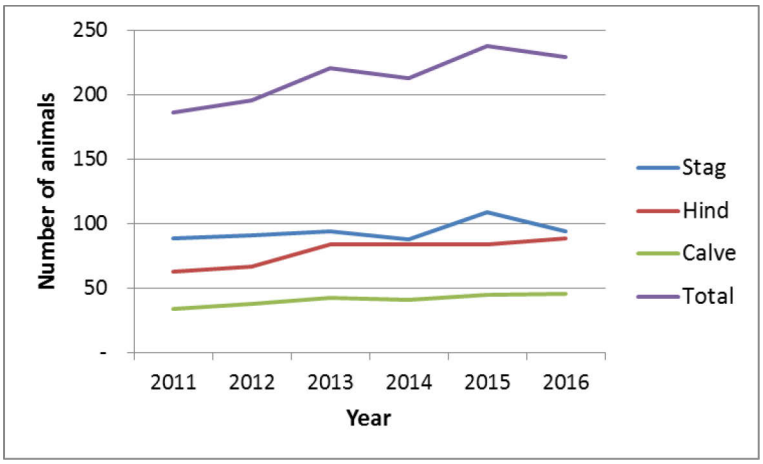

Figure 2.2 *Estimated population size of red deer in Hoge Veluwe National Park between 2011 and 2016, based on spring counts.*

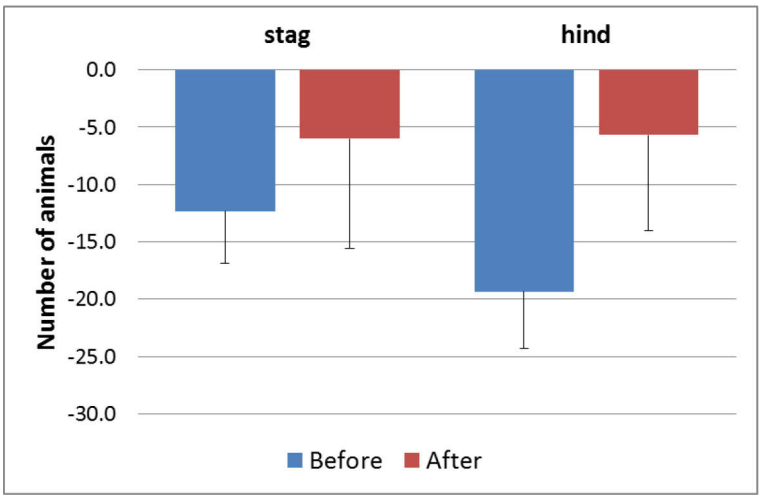

Figure 2.3 *Mean difference between prediction and actual spring count of red deer stags and hinds in Hoge Veluwe National Park before (2011-2013) and after (2014-2016) wildlife crossing structures had been installed. Error bars represent standard deviations.*

Roe deer

In Hoge Veluwe National Park the roe deer population has not changed much over the last six years, with an average growth rate of -1.2 deer per year (Figure 2.4; Table 2.6). The mean difference in population size over the years before and after crossing structures were installed is -10 roe deer. The male-female index showed a small negative trend.

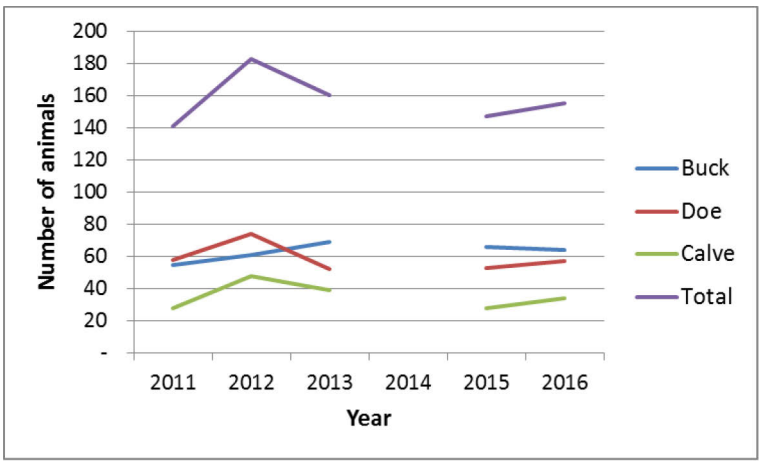

Figure 2.4 *Estimated population size of roe deer in Hoge Veluwe National Park between 2011 and 2016, based on spring counts. No data for 2014.*

Mouflon

In Hoge Veluwe National Park the mouflon population has increased over the last six years, with an average growth rate of 18.1 mouflons per year (Figure 2.5; Table 2.6). The mean difference in population size over the years before and after the crossing structures were installed is 52 mouflons. The male-female index and female-young index remained more or less the same.

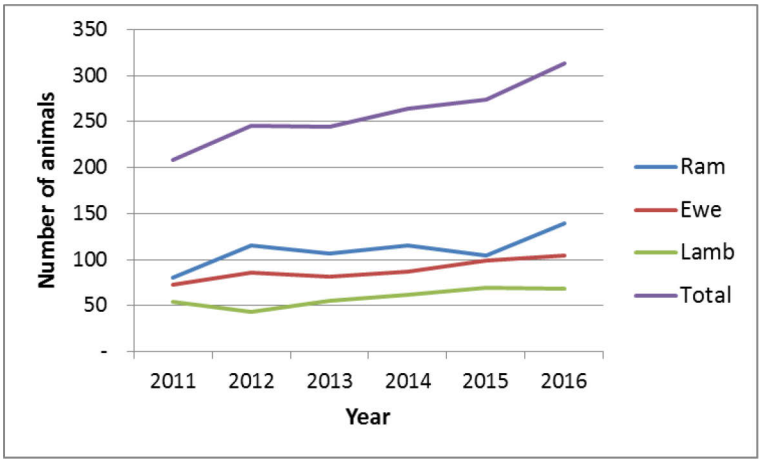

Figure 2.5 *Estimated population size of mouflon in Hoge Veluwe National Park between 2011 and 2016, based on spring counts.*

Wild boar

In Hoge Veluwe National Park the wild boar population has increased over the last six years, with an average growth rate of 17.5 wild boar per year (Figure 2.6; Table 2.6). The mean difference in population size over the years before and after the crossing structures were installed is 71 wild boars. The male-female index showed a small positive trend. The female-young index showed a negative trend.

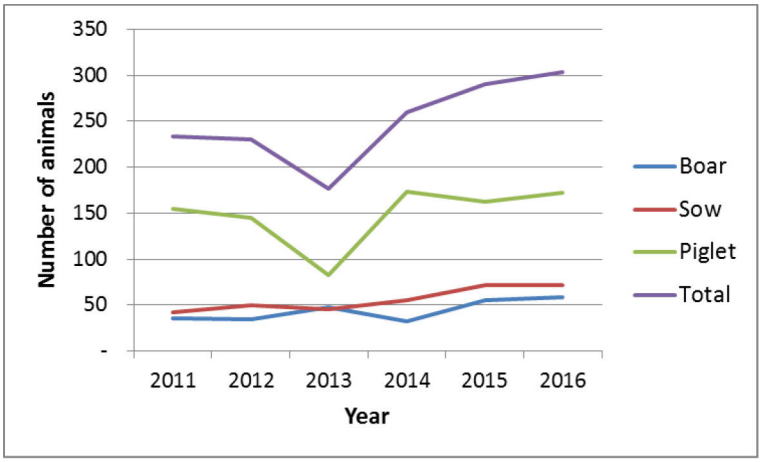

Figure 2.6 *Estimated population size of wild boar in Hoge Veluwe National Park between 2011 and 2016, based on spring counts.*

2.3.4 Trends in culling effort

The estimated mean number of culling hours needed to reach 100% of the designated cull increases by about 7% when the before and after situation are compared (Table 2.7). Simultaneously, the mean number of designated cull increases by about 36%. This indicates that culling became more efficient, as reflected in a 26% increase in the mean number of culls per hour. Note that although designated cull numbers are higher in the years after the installation of the crossing structures, the time spent on culling decreased by about 35 hours per year. Despite a higher efficiency, i.e. higher mean cull numbers per hour, this resulted in a lower percentage of realised designated cull. These findings apply to the three ungulate species combined, for which designated cull numbers were set.

Table 2.7 *Culling efforts (red deer, wild boar, mouflon) before (2011/12, 2012/13) and after (2013/14, 2014/15, 2015/16) the wildlife crossing structures had been installed in Hoge Veluwe National Park.*

Period	Mean designated cull	Mean total culling hours	Mean % designated cull realised	Mean total hours if 100% realised	Mean cull/hour
Before	263	669	75.5	889	0.30
After	357	634	67.0	951	0.38

2.4 Discussion

Except for the moments when video systems malfunctioned, this monitoring method appears to be rather accurate in detecting ungulates. Frauendorf (2016) estimated that there was no significant difference between the detection probability of the video systems when compared to the surveys with tracking beds. The presented crossing rates and migration ratios presented here, however, should be used with care. Because the video cameras frequently malfunctioned, likely a significant number of ungulate movements have been missed. Especially when sample sizes are small, crossing rates and migration ratios lack robustness. Only one or a few additional crossing events could considerably change the estimates of yearly crossing rates and crossing ratios, possibly even resulting in a shift from immigration to emigration or vice versa.

Frauendorf (2016) estimated that the migration ratio for all ungulate species at both locations was close to zero. Although this result also has to be viewed cautiously, as sample sizes were often small

and results were only based on a 3-month monitoring period in winter, it emphasises that our migration ratios should be used with care. That also applies to the correction factors we used for estimating the numbers of ungulates crossing at the wildlife crossing structures in Hoge Veluwe National Park. These factors were based on the study by Frauendorf (2016) that covered a three-month period in winter. If the video systems show differences in detection probabilities between seasons, which is unknown, the correction factors may not be correct for other seasons than winter.

Our estimated yearly crossing rates of ungulates at Oud Reemst are lower than the estimates presented by Emond & Brandjes (2015). They found a yearly crossing rate of about 122 ('once per 3 days') and 37 ('once per 10 days') for roe deer and wild boar respectively. Numbers are hard to compare, however, as their study was limited to two six week-periods in which animal activity is assumed to be high. Furthermore, they considered all animals that passed their still cameras - more or less installed at the central parts of the overpass - as 'crossing', while we focused on whether or not the animals crossed the fence at the eastern entrance. Animals may have walked across the overpass from the west but may have been deterred from entering Hoge Veluwe National Park by the fence. Information on the precise time and direction of the animals' movements may provide more insight, however, these data are not presented by the authors.

Culling became more efficient if the situation before and after the installation of the crossing structures is compared. This may be explained by the fact that culling success simply increases when there are more animals. Despite a higher efficiency, however, we observed a lower percentage of realised designated cull after mitigation. This may be seen as a possible explanation for the positive trends in most ungulate populations.

2.5 Conclusions

We conclude that:

- Crossings structure Deelerwoud is used by four ungulate species: red deer, fallow deer, roe deer and wild boar.
- Crossings structure Oud Reemst is used by two ungulate species: roe deer and wild boar.
- No crossings of mouflon were registered at either crossing structures, which complies with the aim to keep these animals in the Park.
- At Deelerwoud, red deer and fallow deer cross about 47 and 174 times per year respectively. Roe deer and wild boar cross only occasionally.
- At Oud Reemst both roe deer and wild boar cross only occasionally.
- The data suggest a net immigration for red deer and fallow deer at crossing structure Deelerwoud. A robust estimate on net migration, however, cannot be made due to the frequent malfunctioning of the video systems. In the three months that the crossing structures were monitored daily with tracking beds, migration ratios for all ungulate species at both locations was close to zero.
- Population numbers of red deer, fallow deer, mouflon and wild boar increased after the crossing structures had been installed; the roe deer population decreased slightly.
- The increase in the red deer population may be (partly) the result of the measured net immigration, but due to the problems with the video systems and the resulting gaps in the data collection, no final conclusions can be drawn.
- The increase in the fallow deer population is the result of the measured net immigration as there were no fallow deer in the Park before the crossing structures had been installed. Fallow deer were observed at crossing structure Deelerwoud soon after it had been installed. The first crossings of fallow deer into the Park were about seven months after installation. Currently, only a small group of fallow deer seems to have included (parts of) the Park in their home range.
- The decrease in the roe deer population may be (partly) the result of the measured net emigration, but due to the problems with the video systems and the resulting gaps in the data collection, no final conclusions can be drawn.
- The increase in the mouflon population is not the result of net immigration since Mouflon did not use the crossing structures.
- The increase in the wild boar population is not likely the result of the crossing structures since they used the crossing structures only incidentally, and only indications of a net emigration were found.

- Between 2011-2016 the structure of the ungulate populations changed only slightly; red deer and wild boar showed a small increase in the male-female ratio and wild boar showed a small decrease in the female-young ratio.
- An increase in culling efforts (red deer, wild boar and mouflon combined) of about 7% was needed to achieve the designated cull numbers in the years after the wildlife crossing structures were installed. Such higher culling efforts directly relate to the positive trends in ungulate population sizes.

2.6 Research recommendations

We recommend to:

- Continue monitoring the use of the wildlife crossing structures by ungulates for at least three more years. It may take time before animals become fully used to crossing structures; hence, crossing rates estimated here may change over time. The positive trend of crossing events for fallow deer at Deelerwoud already illustrates the variability between years and emphasises the need for longer time series to get better insights into how ungulates accept and use the structures.
- Make sure that the video system operates without failures in order to make better inferences about the net immigration or emigration of ungulates. Test the detection probability of the video systems in different seasons.
- Study the impact of the 1.1-meter fence and wild boar gates at the wildlife crossing structures on how the structures are used by the ungulates that are allowed to cross. Although deer can jump the fence and wild boar can use the gates, the barrier may still reduce structure use if compared with a situation without a fence. We recommend using a BA (before-after) study design to study possible reductions in structure use due to the fence if the current situation is compared with a situation in which the fence is removed from the crossing structures and installed at, for example, 500 m away from the structure entrance. In the latter situation the animals will still have to cross the fence, but this is not combined with entering a narrow habitat strip that crosses a road. We think that, if the fence is situated 500 m away from the structure entrance, the animals will be less reluctant to pass the fence and enter the crossing structure to cross the road. The findings of such a study may help make well-informed decisions on where to place fences at crossing structure elsewhere in the country.
- Continue monitoring the fallow deer population in the Park in relation to their use of the crossing structures. Currently, only a few animals seem to include the Park in their home range and frequently use the crossing structure at Deelerwoud. No mass immigration has yet occurred. Will this situation continue or will there be a steady increase of fallow deer within the Park? Monitoring the population may provide valuable insights into the speed and extent at which the Park is colonised by the species.
- Register culling efforts per ungulate species in order to get better insights into (changes in) culling efforts at the species level.

3 Red deer movement and activity

Dennis Lammertsma, Jan den Ouden, Frank van Langevelde, Geert Groot Bruinderink, Wolbert van den Broek & Edgar van der Grift

3.1 Introduction

The wildlife crossing structures may lead to changes in how ungulates within the Park boundaries use their habitat, not only to help the animals in the Park to enter neighbouring areas but also to allow a possible influx of animals from these neighbouring areas into the Park. The Park management wanted to know how immigrants (in particular fallow deer) would use the Park's habitats, and how resident ungulate species (in particular red deer) would respond to immigrants. Detailed information on habitat use by both red deer and fallow deer could yield vital information for the Park management to assess (potential) the impacts of altered habitat use on nature conservation targets within the Park, e.g., protected Natura 2000 habitats and species. The primary research question we addressed was how the behaviour of the red deer in the Park changed, especially in response to fallow deer immigration.

To address this question we selected an innovative survey technique, i.e. GPS radio collars wilt built-in accelerometers, which can provide accurate around-the-clock data on habitat use, home range, movements and animal behaviour (Löttker et al., 2009; de Weerd et al., 2015; Latham et al., 2015; Hegnes, 2016). A combination of the location of an animal and its behaviour allows for a functional habitat-use map showing not only which parts of the Park are being visited by the animal but also what it is doing there, thereby providing a basis for management decisions (Coulombe et al., 2006; Berger et al., 2014). Hence, a secondary question we addressed was whether we could accurately measure foraging behaviour with GPS-accelerometer collars in free-ranging deer.

3.2 Methods

3.2.1 Collection of data

Two red deer, a stag and a hind, were captured and fitted with a Vectronics GPS Plus collar (Vectronics aerospace GmbH) in autumn 2013 (Figure 3.1). GPS fixes were taken every 15 minutes and stored on the collar. Collars were equipped with a dual-axis acceleration sensor, with the horizontal sensor oriented perpendicular and the vertical sensor oriented parallel to the spine of the deer. Accelerometer fixes were taken continuously for 64 seconds, delivering x- and y-values ranging between 0 and 250. Raw data was subsequently averaged for every 64 seconds and stored on the collar. At least once a month the Park staff located the animals with the VHF radio tag in the collar, and data were downloaded from a distance using a hand-held receiver.

No fallow deer were captured during the study period. Fallow deer immigration numbers turned out to be extremely low (see Chapter 2). In September 2015 the gamekeepers even announced that all fallow deer had left the Park. In October 2015 the Park, in agreement with the research team, decided that no further efforts to capture fallow deer would be made.

Observations to link behaviour to the accelerometer output were made during the winter months of 2013 and early 2014. Visual observations yielded training data for the analysis. Observations were made with binoculars and by video camera. In order to be able to compare behavioural observations with activity values generated by the GPS-collars, observation time was synchronised with the internal clock of the collars. We distinguished four types of behaviour: resting (no movement), foraging, walking (slow locomotion) and running (flight behaviour, gallop). We analysed this data by assessing dominant behaviour during the synchronized 64-second interval.

The study was in compliance with Dutch legislation on the protection of the welfare of vertebrate animals. Procedures adopted in this study were reviewed and approved by the Animal Ethics Committee (Dierexperimenten Commissie, ALT13.02).

Figure 3.1 *Red deer hind with GPS collar (second individual from the left).*

3.2.2 Data analysis

Both GPS collars yielded approximately 30,000 fixes and 3 million activity records. Obtained training data was limited to 192 observations. Data was skewed on foraging and resting. To supplement the data we calculated the average speed between each consecutive GPS data point. The accelerometer data combined with the average speed in km/h between GPS data points may provide a better model to predict red deer behaviour. To calculate the average speed between GPS data points, we calculated the Euclidean distances, although this is likely to be an underestimation of the actual distances travelled (Pépin et al., 2004; Rowcliffe et al., 2012). Distances travelled <20 m were set to 0 to correct for any inaccuracies of the GPS collar. We tested different models using two methods: (1) classification and regression tree method (CART) and (2) random forest classification (RFC).

The CART method was selected because it offers a relatively straightforward way to classify data by developing a set of hierarchical decision rules (Lewis, 2000). These decision rules classify the data by creating a decision tree, classifying the data in a stepwise process. The decision tree is built up out of nodes in which the data is either classified as a behaviour type or moved to the next node until all data has been classified as a behavior type. The hierarchical decision rules offered by a CART algorithm make the classification relatively easy to interpret and generally contribute to a greater understanding of the classification problem (Prasad et al., 2006; Nathan et al., 2012).

In addition to the CART we used an RFC as suggested by Shamoun-Baranes et al. (2012). This classification method grows n=500 trees, selecting the nodes out of trees which classify the data best. Due to the black box nature of the method it is hard to gain insight into the decision rules applied, but the advantage of this method is that the prediction variance is much smaller than with a CART. The analysis was made using R statistics version 3, using package: "rpart". We tested four statistical models: (1) Model 1: CART using the Y-axis and X-axis data of the accelerometer; (2) Model 2: CART

using the Y-axis, the X-axis data and the average speed; (3) Model 3: RFC using the Y-axis and X-axis data of the accelerometer; (4) Model 4: RFC using the Y-axis, the X-axis data and the average speed.

3.3 Results

3.3.1 Red deer versus fallow deer

Changes in how red deer behaved and used the habitat in the Park in response to fallow deer immigration could not be studied. Fallow deer immigration numbers were extremely low and, consequently, no fallow deer were captured and fitted with a GPS radio collar.

3.3.2 Evaluation of GPS-accelerometer collars

The home ranges of the two red deer were limited to the southern parts of the Park (Figure 3.2). Table 3.1 shows the accuracy of the models in predicting behaviour from accelerometer data. The first CART model (Figure 3.3A) was 82% accurate. It successfully categorised the vast majority of Foraging and Resting behaviour. The second model, adding average speed data, increased accuracy to 83%. The second model (Figure 3.3B), however, failed to categorise Running correctly. Model 1 was more successful in categorising Running (55% correct). In contrast, the second model was more successful in categorising Foraging. The RFC models 3 and 4 performed nearly identically. In this case speed, again, seems to have no value as a predictor value in its current form. Both RFC models had a slightly lower accuracy than the CART models, 75% and 81% respectively. The prediction of Foraging behaviour by all models was about 70% correct.

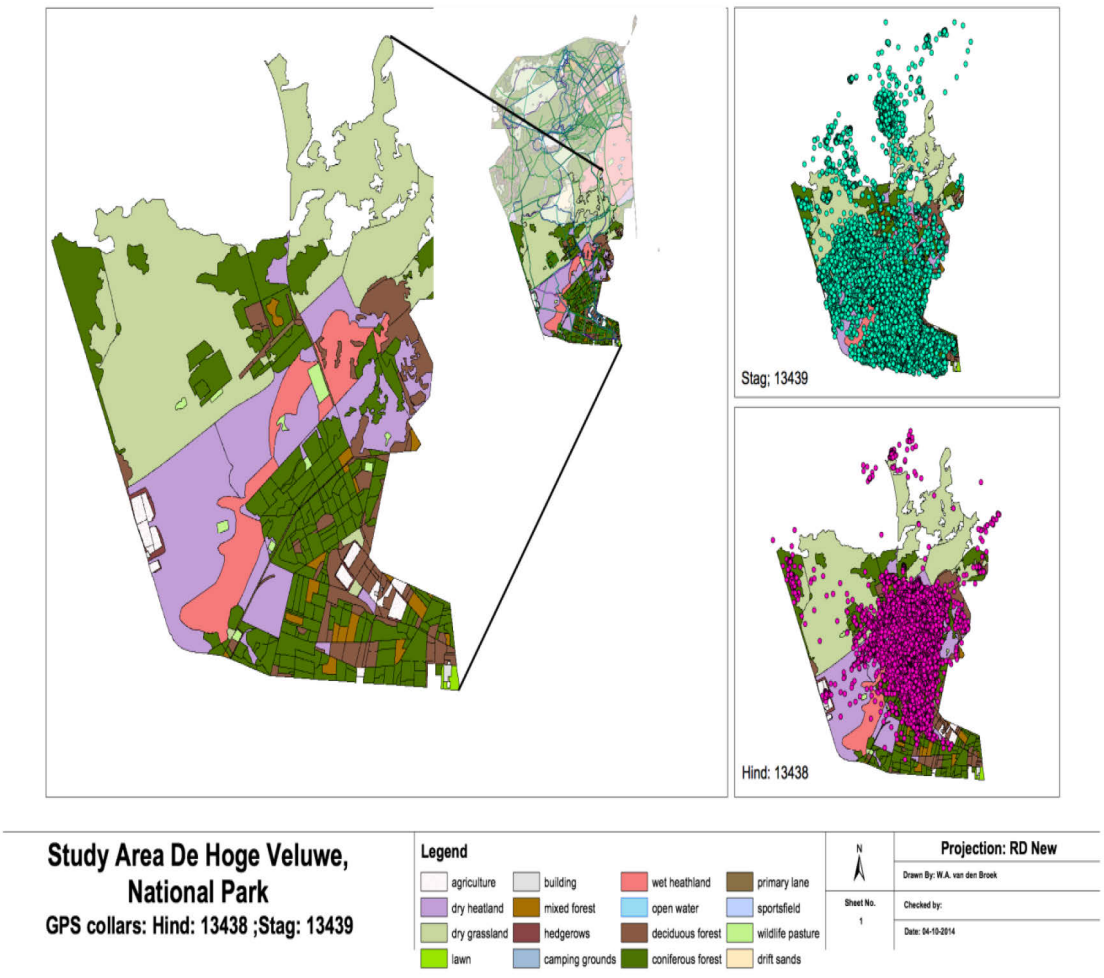

Figure 3.2 *Southern part of Hoge Veluwe National Park, showing the spatial distribution of habitat types and the GPS locations of the hind and stag.*

Table 3.1 *CART and RFC matrix for red deer behaviour. Model 1 is a CART that uses the Y-axis and X-axis data of the accelerometer. Model 2 is a CART that uses the Y-axis, the X-axis and the average speed of the red deer per GPS data point in km/h. Model 3 is an RFC that uses the Y-axis and X-axis data of the accelerometer. Model 4 is an RFC that uses the Y-axis, the X-axis and the average speed of the red deer per GPS data point in km/h. The RFC uses an out-of-the-box error as a measure of accuracy.*

	Model 1 Predicted				**Classification**
Observed	**Forage**	**Rest**	**Run**	**Walk**	**Correct %**
Forage	62	1	1	8	86.1
Rest	2	74	0	1	96.1
Run	3	0	6	2	54.5
Walk	16	0	0	16	50.0
Predicted%	**74.7**	**98.7**	**85.7**	**59.3**	**82.3**

	Model 2 Predicted				
	Forage	**Rest**	**Run**	**Walk**	**Correct %**
Forage	71	1	0	0	98.6
Rest	3	74	0	0	96.1
Run	11	0	0	0	0.0
Walk	17	0	0	15	46.9
Predicted%	**69.6**	**98.7**	**0.0**	**100.0**	**83.3**

	Model 3 Predicted				
	Forage	**Rest**	**Run**	**Walk**	**Correct %**
Forage	54	1	4	13	75
Rest	1	74	0	2	96.1
Run	5	0	5	1	45.5
Walk	21	0	1	10	31.3
Predicted%	**66.7**	**98.7**	**50.0**	**38.5**	**74.5**

	Model 4 Predicted				
	Forage	**Rest**	**Run**	**Walk**	**Correct %**
Forage	60	3	3	6	83.3
Rest	2	74	0	1	96.1
Run	6	0	5	0	45.5
Walk	15	1	0	16	50.0
Predicted%	**72.3**	**94.9**	**62.5**	**69.6**	**80.7**

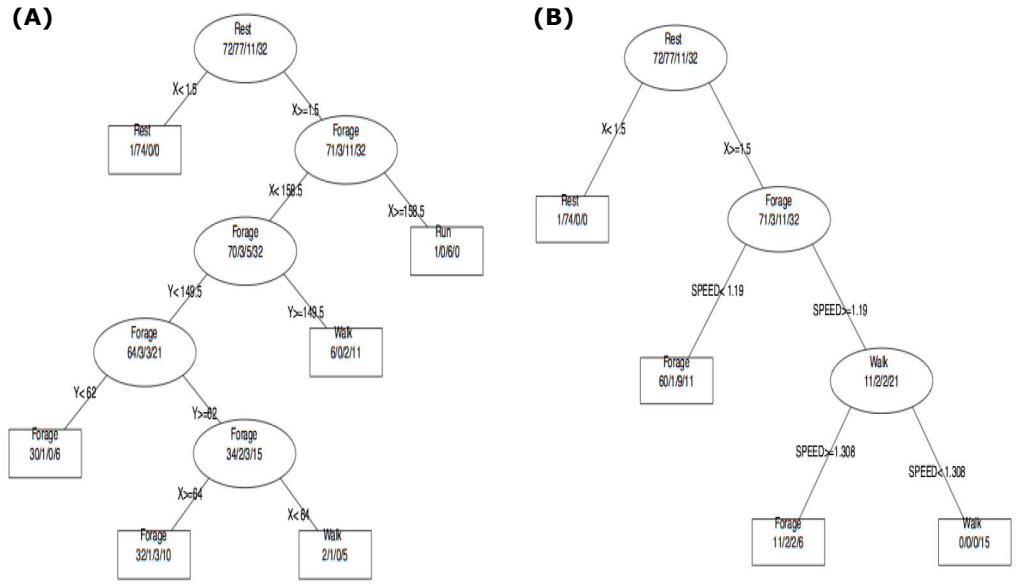

Figure 3.3 *Decision tree for CART model 1 (A) and model 2 (B).*

3.4 Discussion

Our circa 80% accuracy is comparable with recent studies performed on cattle (de Weerd et al., 2015; Hegnes, 2016). Data analysis was hampered by the storage of averaged accelerometer data and insufficient training data. The behaviour of observed red deer varied greatly within the storage interval of 64 seconds, changing constantly from, for example, foraging, vigilance, standing still to walking behaviour. This created a large variance in the recorded averaged data, which does not match with the designated dominant behaviour. Intervals containing only one behaviour tend to have fewer variable activity values than intervals containing more than one behaviour and therefore classify more accurately (de Weerd et al., 2015; Gaylord et al., 2016). As suggested by Bom et al. (2014) a one-second fix, retaining the raw data, provides the highest accuracy. It would greatly increase the usability of the data if the accelerometer could obtain one-second measurements of raw data around each GPS fix, allowing for the accelerometer data to be linked directly to the GPS data. This would provide the maximum amount of information on deer behaviour on a spatiotemporal scale. Increasing the amount of training data and decreasing the skewness of the data could also greatly improve the predictive power of the models.

Much can also be gained by using a different type of accelerometer, one that uses raw accelerometer data supplemented by a third axis (Bom et al., 2014). While the third axis is not strictly necessary it does provide yet another predictor variable that can increase the behavioural classification accuracy, especially for behaviour types where the head is moving up and down (such as foraging). The use of raw data will allow for transforming the data into predictive measures such as static body acceleration, dynamic body acceleration, overall dynamic body acceleration and surge, sway and heave (Nathan et al., 2011; Shamoun-Baranes et al., 2012).

3.5 Conclusions

Our findings indicate that the CART models were the most effective at predicting red deer behaviour. We aspired to use accelerometer data to provide insight into red deer behaviour. Even though the CART analysis provided relatively high accuracy, it is insufficient to guarantee a prediction for all behaviours for both red deer at 57,330 separate locations. Predictions based on accelerometer data on foraging behaviour are correct for circa 70%, but the models often confuse foraging and walking behaviour. Therefore we deem it impossible to classify the data with the current classification models.

3.6 Research recommendations

We recommend to:

- Study year-round behaviour of deer on a spatial scale with accelerometers storing raw accelerometer data supplemented by a third axis. The habitat and weather might affect movement and GPS accuracy (i.e. steep slopes, dense vegetation, open terrain; de Weerd et al., 2015; Gaylord et al., 2016). Also movement may change depending on the season, and the individual fit of a collar can influence recorded activity data. Increased neck circumference of stags during the rut or the weight of antlers might affect the recorded accelerometer data (Gaylord et al., 2016). In order to be able to classify accelerometer data correctly, the amount of training data needs to cover interspersed observations in different habitat types on a year-round basis. This is a considerable disadvantage at the moment. Most classification methods need a training set for every animal used in the study, which requires a large sample size study incorporating multiple species and age-sex combinations. It would be a significant (financial) improvement to find a trustable methodology to validate activity data collected from accelerometers that does not need training data. Mounting a video camera on the collar so that one can see what type of behaviour the animal shows might be an option for gathering a larger training set.
- Use telemetry and accelerometer data to study the effect of culling on the (foraging) behaviour of deer and energy expenditure. Exact information on the position (GPS coordinates) of culling activity, which is not recorded at the moment, would be needed in order to guarantee a proper analysis.

4 Ungulate abundance and habitat use

Patrick A. Jansen, Yorick Liefting & Jan den Ouden

4.1 Introduction

Using a permanent network of camera-trap stations across Hoge Veluwe National Park, we measured the intensity at which ungulates used the various habitats and the relative size and structure of ungulate populations. Our principal aim was to answer two questions: (1) Do the size and structure of ungulate populations in the Park change? (2) Does the intensity of habitat use by ungulates change? In addition, we addressed several other questions as part of MSc thesis projects or pilot studies (e.g., Janssen 2014, Merien 2014, Miguel 2015).

4.2 Methods

4.2.1 Camera-trap network

The monitoring network consisted of 48 stations[2] that were set up in mid-July 2013 in collaboration with Park staff (Figure 4.1). The stations were placed in the six major habitats according to a stratified random design. The points were computer generated in ArcGIS, with the constraint that the distance to the nearest road or trail had to exceed 25 m. Eight stations were set up in each habitat type. Thus, sampling was balanced across habitat categories rather than proportional to habitat area. Moreover, within each habitat, half of the cameras were placed inside the restricted area and half inside publicly accessible areas. Due to a change in policy, the latter areas were also accessible off-trail until January 2016.

Each station consisted of one Reconyx Hyperfire HC500 camera trap inside a steel enclosure, mounted to a steel pole in a solid block of concrete dug into the soil, and with the lens exactly 70 cm above the ground. The cameras had a passive infrared motion sensor that triggered the camera whenever a heat contrast – i.e. a warm-bodied animal – moved in front of the camera within a certain distance. Upon each trigger, cameras took a series of ten photographs at a rate of about 1 per second. This was repeated as long as animals remained in the range of the sensor, yielding image sequences that were a multiple of 10 for each event. Photos were written to a SDHC memory card. Cameras were powered with 12 Eneloop low-self-discharge NiMH AA batteries.

The stations were operated by the game wardens, who visited every station once every 1.5 months to replace the batteries, collect and replace the memory card, clean the camera, check for proper functioning and trim any vegetation that was blocking the view. The memory cards were collected by Wageningen University and Research for processing. We inspected the network was inspected twice a year.

Three cameras were stolen in 2014. Two were replaced, but one very exposed station in forest culture (H5R0-03) was not. After these thefts, the stations were reinforced with a heavier-duty metal pole that was driven deep into the soil and anchored with a solid block of concrete, making theft extremely difficult. Great care was taken to ensure that the cameras maintained exactly the same height and view. Also, cameras were operated with a code lock, which – along with the markings of the case – render the camera useless for trade. There have been no reports of vandalism since, although instances of people investigating the cameras or even tampering with them remain numerous.

[2] Five of the 48 stations and seven additional stations were located at 12 plots at which biodiversity was monitored in a companion project by De Vlinderstichting and Bokdam Advies. Methods used were the same as for the camera-trap network.

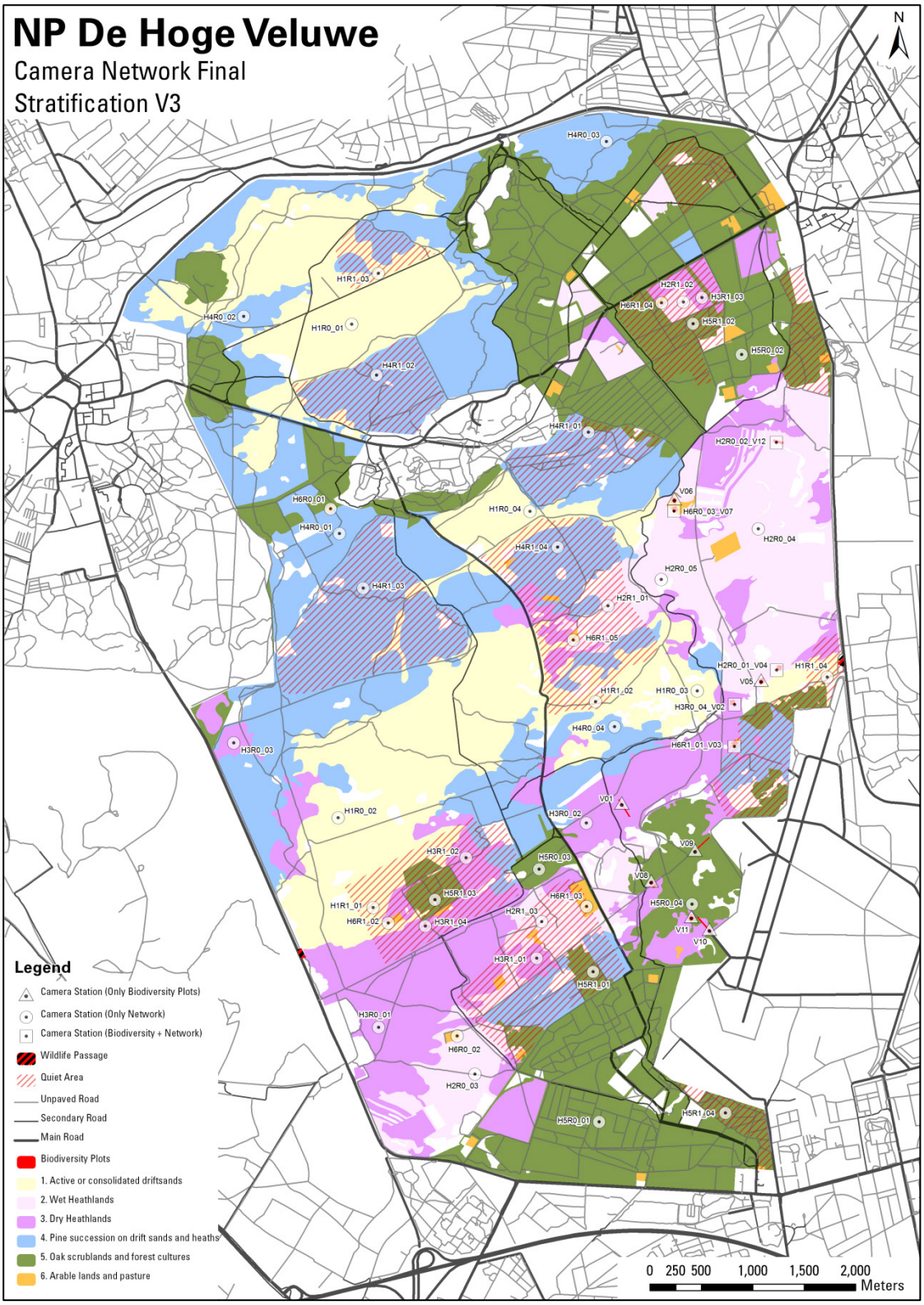

Figure 4.1 *Distribution of permanent camera-trap stations across Hoge Veluwe National Park. The circular dots represent the 48 stations that formed the network for monitoring ungulate abundance and habitat use, stratified by habitat and accessibility to the public. The triangles represent 7 additional stations installed for parallel monitoring of biodiversity plots.*

Overall, the network functioned about 95% of time. For the remaining 5%, recording failed due to a variety of reasons, including camera theft (see above), mistakes during camera setup or image upload and power failure, usually at stations with excessive animal activity. The total sampling effort – the number of days for which photo material was collected from the 48 cameras – between July 2013 and December 2015 amounted approximately to 39,900 days, which corresponds to approximately 109 years.

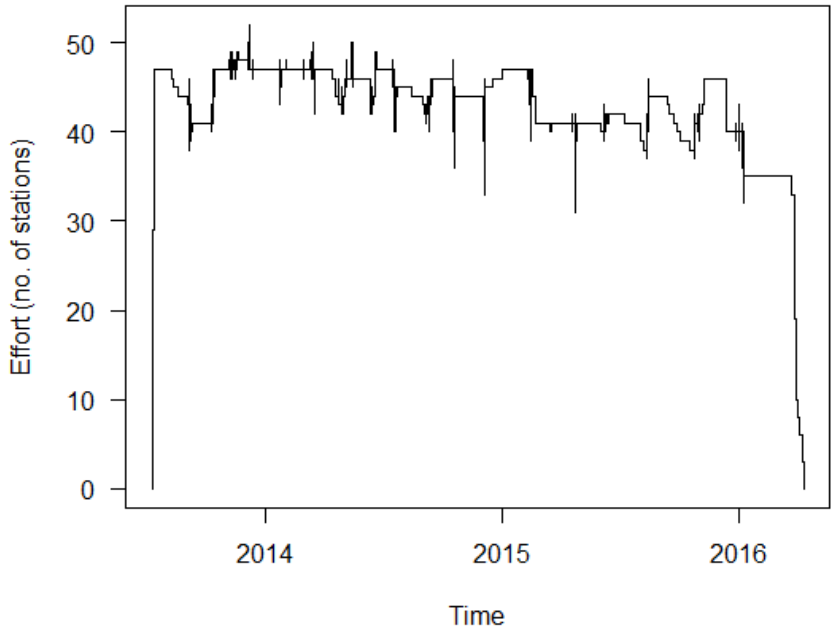

Figure 4.2 *Number of camera-trap stations from which photos were ingested into the database over time. Material collected in 2016 was archived on the server, but has not yet been ingested.*

4.2.2 Photo processing

The cameras yielded massive numbers of photographs. These were all uploaded to a dedicated secure server located in a data centre in Amsterdam and maintained by Wageningen University. A subset of these photos was annotated to obtain observations. The remaining material was archived.

Photo processing was done by a group of 17 volunteers, all members of the Society of Friends of Hoge Veluwe, who had been recruited by the Park management in 2013, as well as by several MSc students of Wageningen University. The Park was going to coordinate the volunteers, but this proved inefficient, so it was done by Wageningen University. The volunteers have been extremely loyal to the project, and some showed tremendous dedication.

The photo processing was done using a custom-built online application called Agouti via a dedicated portal (http://hv.cameratrapping.net) that we customised for photo processing by Dutch-speaking volunteers. A manual was written in Dutch, volunteers were trained in photo processing at Wageningen University and there was one training meeting halfway through the project.

After the technical coordinator has assigned image sequences to individual volunteers, the volunteers then annotated each of their sequences with one or more observations, including species, sex, age class, behaviour and number. Date, time and location were automatically pulled off the image metadata. All observations were stored on the server along with the associated photographs.

We assessed the quality of the observations by re-inspecting a subsample of the annotated sequences. We found that age class, sex and behaviour were not consistent across analysts. Species identification and counts, however, were sufficiently accurate (see Miguel, 2015).

The total number of photos collected (all 55 cameras) amounted to 2,386,777, of which 2,295,465 were photos based on triggers, and 91,312 were time-lapse photos (taken automatically at noon and midnight to check for proper functioning). The photos were grouped into 65,966 sequences that mostly showed passages of one or more individual animals or people. From these, one month worth of images per season, i.e. one-third of the year, was processed and annotated by the volunteers in accordance with the original planning. In addition, all remaining photos from the first 1.5 years were processed as well to give a detailed year-round pattern for one year. In total, volunteers annotated 52,584 sequences (80%), and 13,382 sequences were archived (Figure 4.3).

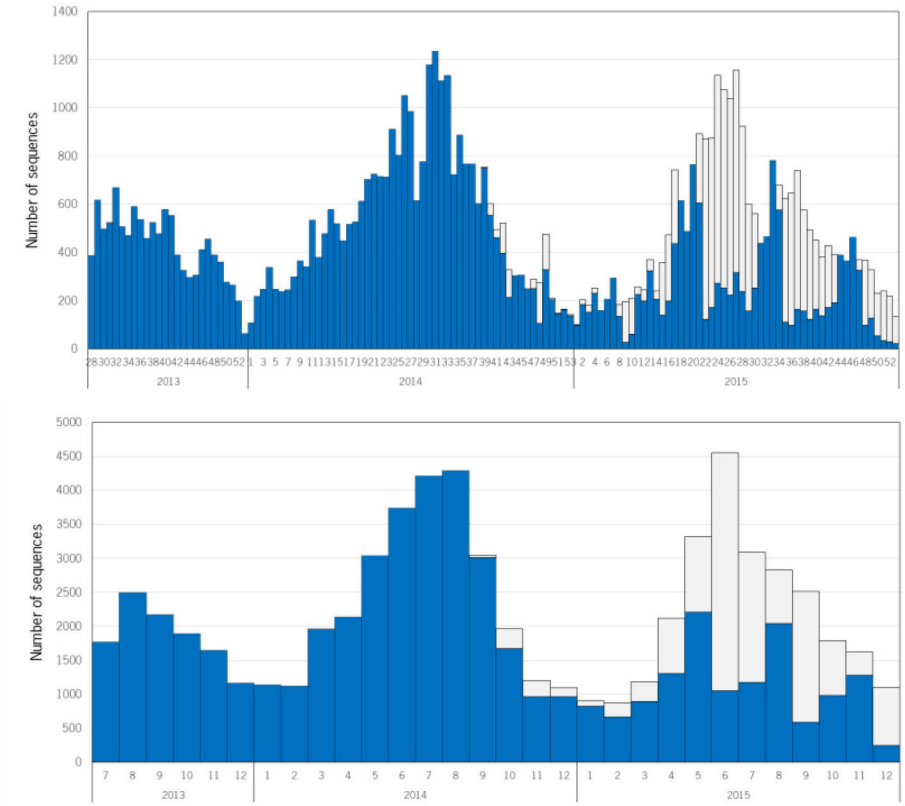

Figure 4.3 *Number of annotated (blue) and archived (grey) photo sequences by week and by month for all 55 cameras including the 48 stations that formed the monitoring network.*

4.2.3 Trend analyses

The number of photo sequences collected by the camera network varied massively over time (Figure 4.3), and showed a clear seasonality, ranging from about 1100 mo^{-1} during the winter to about 4200 mo^{-1} in summer: almost four times as many (Figure 4.5). This variation results from a mix of factors that cannot be easily disentangled, including seasonal differences in the number of camera traps operating, the number of animals, activity levels, detection distance of the camera traps in relation to the weather and the detection distance in relation to animal coat, metabolic rate and peripheral temperature. The low number of photos during winter, for example, is likely related to energy-saving behaviour, coat and metabolism. Red deer, for example, substantially reduce their metabolic rate during winter and engage in nocturnal hypometabolism associated with peripheral cooling (Arnold et al., 2004). Reduced activity in combination with reduced body temperature will obviously result in a much-reduced per-capita likelihood of animal detection by any camera trap.

Given this variation in effective sampling effort, extracting seasonal patterns of abundance and activity requires translating photographic rates into capture rates per camera per unit of time and per unit of effective detection distance, i.e. accounting for differences in sampling effort. In this report, we account only for variation in the number of camera traps, hence variation in rates across seasons should be interpreted with great caution.

To study changes in abundance and habitat use by ungulates over time, we selected one four-week period of observations from the 48 network stations for each of the four seasons per year, ten periods in total. The seasons distinguished were winter (January 21 – February 18), spring (April 23 – May 21), summer (July 24 – August 2), and autumn (October 23 – November 20). The eleventh period – the winter of early 2016 – was not included, as the management regime (off-trail access to visitors) had changed significantly in January 2016. The total sampling effort covered by this dataset amounted to 12,490 days (34 years) and was fairly evenly distributed across habitats (mean 1,249 days, range 1,148–1,322) and seasons (mean 2,082 days, range 2,003–2,157) (Figure 4.4).

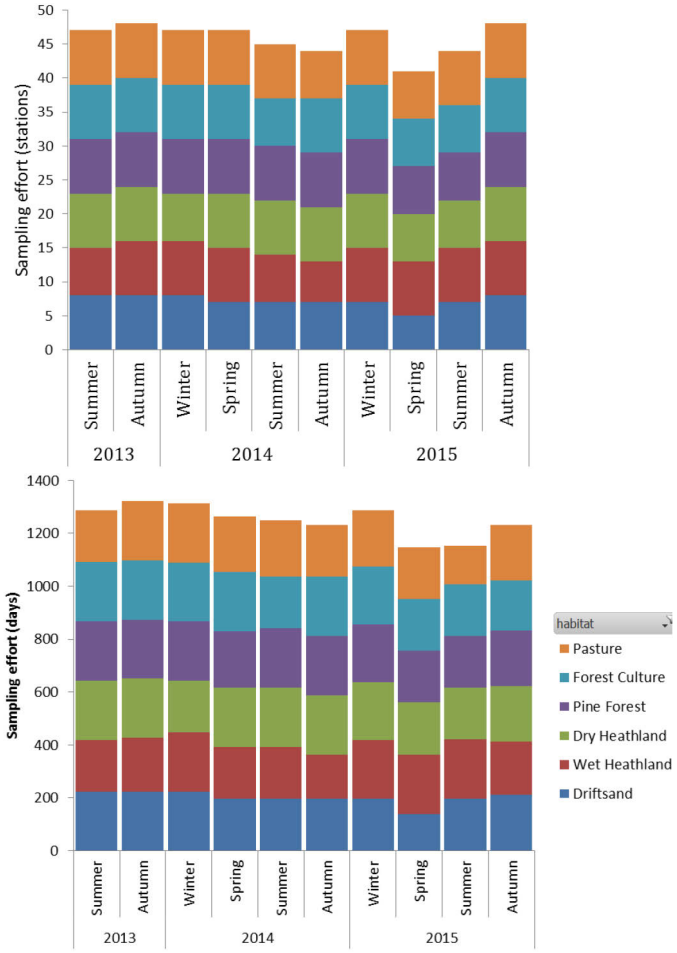

Figure 4.4 *Sampling effort for assessing trends across the study period in terms of number of active stations and number of sampling days.*

4.2.3.1 Habitat use

From the viewpoint of resource selection studies, the camera-trap network represents a Type I design sensu Thomas & Taylor (1990) and Manly et al. (2002), in which measurements are made at the population level rather than at the level of individual animals. The habitat types represent six discrete resource categories; in each type, the camera-trap stations sampled eight randomly located plots.

For each station and sampling period, we calculated the capture rate as the total number of animal detections per effective sampling day (i.e., discounting any time without sampling). This is a measure of the visit frequency of the patch, which is similar to the rate associated with the Number of Visits ς(*i*) to patch *i* in animal tracking (Benhamou & Riotte-Lambert, 2012). The difference with ς(*i*) is that capture rate refers to the absolute number of visits by a given species rather than to one particular tagged individual.

For comparisons across species, habitats and time, the size of the patch monitored by the camera must either be constant or be accounted for. The problem, however, was that the detection distance of the infra-red sensor of camera traps varied between habitats (vegetation density), species (size and insulation), and season (insulation, metabolism, weather conditions), as explained before (Rowcliffe et al., 2011; Hofmeester et al., 2016). This implies that the effective size of the sample plots was highly variable in our study in ways that could not yet be quantified. Methodology for solving this bias is being developed but was not yet available for our report.

We overcame this bias for the analyses of habitat use by averaging capture rates across stations within species and seasons and then comparing relative rather than absolute rates within species, habitats and seasons, which always adds up to 100%. The rates remained slightly biased towards more open habitat types, such as drift sand, because these have greater detection distances (Hofmeester et al., 2016).

First, we calculated the **capture rate** c_j, the number of animal detections per day, for each habitat type *j* as: $c_j = \frac{N}{t}$, where *N* is the number of detections and *t* is the sampling effort in days. **Habitat use** p_j, the proportion of activity in habitat type *j*, was estimated for each species and season as follows. First, we calculated $u_j = \frac{c_j * a_j}{a_t}$, where a_j is the area of habitat *j*, and a_t is the total area. Habitat use is then calculated as: $p_j = u_j / u_t$, where u_t is the sum of all values u_j over all six habitat types.

To quantify the degree to which ungulates distributed their activity uniformly over the six habitat types, we then standardized Levins' (1968) measure of habitat breadth. **Levin's niche breadth B** was calculated as, $\hat{B} = \frac{\left(1/\sum(p_j)^2\right)-1}{n-1}$, where *n* is the number of habitat types (in our case, *n*=6). If *B*=1, then all habitat types get the same amount of activity (i.e., a sixth of the total), regardless of the fact that some habitats are more common than others. If *B*=0, then all activity is concentrated in a single habitat. A decline of B implies an increase of specialization.

To quantify the degree to which ungulates distributed their activity evenly over the total area, we calculated Smith's (1982) measure of habitat breadth. Unlike Levin's measure, Smith's measure weighs the availability of habitat. **Smith's niche breadth FT** was calculated as, $FT = \sum_{j=1}^{n} \sqrt{(c_j/c_t)(a_j/a_t)}$, where c_t is the capture rate summed over all habitat types. If *FT*=1, then all habitat types are used equally intensely (i.e., a sixth of the total). This would mean that all stations have exactly the same capture rate, and the animals uniformly distribute their activity over the total area, regardless of habitat type. If *FT*=0, then one habitat type is used, all other habitat types are ignored. A decline of FT implies an increase of specialization.

To quantify the tendency of ungulates to concentrate activity in a certain habitat type, or 'preference', we calculated an adapted affinity index (Cairns & Telfer, 1980), $\frac{c_j/c_T}{a_j/a_T}$, where c_T and c_T are the summed capture rates and areas across all habitats. An index value of 1 again means that the habitat type is used in the proportion that it occurs, suggesting lack of preference, where index values near 0 indicate that certain habitats are used more heavily than others.

To determine whether and how habitat use and habitat preference changed over time, we calculated these three measures for each of the ungulate species and each of the ten 4-week periods.

4.2.3.2 Abundance

To assess how the abundance of ungulates changed over time, we first considered raw capture rates across stations during the first full year. This revealed that capture rate was too variable across the year to be explained only by variation in abundance (which is also suggested by Figure 4.3). Thus, capture rate was heavily biased by temporal variation in the daily distance travelled and in the effective detection distance of camera traps (i.e. the size of the habitat patch effectively surveyed), as explained under 4.2.3.

To nevertheless assess abundance trends across the entire study period, we used an index approach. First, for the ten 4-week periods across 2013-2015, we averaged capture rates over stations for each species, for each combination of habitat type and season, and multiplied these by the amount of area of each habitat area. To obtain an index, we scaled the values of the first season – summer 2013 – to 100. Differences in the index between the same season of subsequent years suggest differences in abundance. Note that differences in index values between seasons do not reflect relative abundance due to the biases mentioned above.

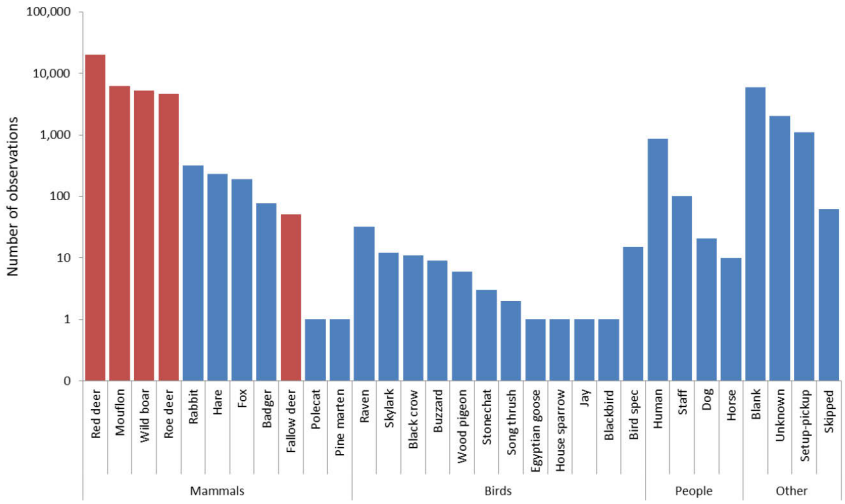

Figure 4.5 *Number of observations per species. The focal ungulate species are in red.*

Table 4.1 *Number of observations and number of individuals counted per species / event type. The focal ungulate species are printed in bold.*

Group	Species		Observations	Individuals
Mammals	**Red deer**	*Cervus elaphus*	20,343	40,265
	Mouflon	*Ovis ammon musimon*	6,267	28,238
	Wild boar	*Sus scrofa*	5,223	10,257
	Roe deer	*Capreolus capreolus*	4,649	4,996
	Rabbit	*Oryctolagus cuniculus*	319	427
	Hare	*Lepus europaeus*	230	249
	Fox	*Vulpes vulpes*	192	196
	Badger	*Meles meles*	78	93
	Fallow deer	*Cervus dama*	51	57
	Polecat	*Mustela putorius*	1	1
	Pine marten	*Martes martes*	1	1
Birds	Raven	*Covus corax*	32	36
	Skylark	*Alauda arvensis*	12	13
	Black crow	*Corvus corone*	11	17
	Buzzard	*Buteo buteo*	9	9
	Wood pigeon	*Columba palumbus*	6	9
	Stonechat	*Saxicola rubicola*	3	3
	Song thrush	*Turdus philomelos*	2	3
	Egyptian goose	*Alopochen aegyptiacus*	1	2
	House sparrow	*Passer domesticus*	1	1
	Jay	*Garrulus glandarius*	1	1
	Blackbird	*Turdus merula*	1	1
	Bird spec		15	20
People	Human		867	1,172
	Park Staff		101	108
	Dog		21	25
	Horse		10	17
Other	Blank		5,959	6,095
	Unknown		2,054	2,789
	Setup-pickup		1,097	1,223
	Skipped		62	69
Grand Total			**47,619**	**96,393**

4.3 Results

4.3.1 Species recorded

Over the entire period of 2013-2015, we accumulated 47,619 observations (Figure 4.5; Table 4.1). Of these, 37,354 (78%) showed mammals (84,780 individuals of 11 species; Figure 4.6), and 94 showed birds (115 individuals of 11 species). Some mammal species known to exist in the Park were rarely recorded, such as pine marten (*Martes martes*), or even missed, such as red squirrel (*Sciurus vulgaris*) and common hedgehog (*Erinaceus europaeus*). These species were too small to be detected by the sensors because of the height (70 cm) at which the camera traps were mounted. For the same reason, the cameras rarely captured birds (Table 4.1).

The four resident ungulate species dominated the dataset (77% of the observations), with red deer as the most commonly recorded (48%). The immigrant species, fallow deer, was recorded just 51 times (0.1%). This implies that there was no evidence for a major influx of fallow deer from the adjacent protected area 'Deelerwoud'.

Figure 4.6 *Selection of images of mammals caught by the network of camera traps across Hoge Veluwe National Park.*

Figure 4.6 *Selection of images of mammals caught by the network of camera traps across Hoge Veluwe National Park.*

4.3.2 Habitat use

The dataset for the ten 4-week periods across 2013-2015 contained just four observations of fallow deer. Thus, a meaningful analysis of habitat use was not possible for this species. For the other four ungulate species, the frequency at which stations were visited differed greatly between habitats (Figure 4.7). The red deer population was most uniformly distributed across the six habitat types (average Levin's *B'*=0.55), meaning that each habitat type received close to $1/6^{th}$ of activity. The other three species showed greater deviations from uniformity (*B'*=0.43–0.46).

The intensity at which the six habitat types were used was far from uniform for all species and all seasons (Figure 4.8). Red deer (Smith's FT=0.56) and wild boar (FT=0.65) clearly used particular habitats more intensely than others, more so than did mouflon (FT=0.72) and roe deer (FT=0.81). On average, roe deer activity was almost evenly spread over the area, meaning that this species shows the most generalism.

Temporal variation in both measures of habitat breadth was large for all four species, but most of this variation was seasonal rather than across the years. For example, wild boar concentrated activity in the forest during autumn and winter. Mouflon and wild boar avoided wet heathland during the summer but not in autumn and winter. Only red deer showed a tendency to become more specialised across the study period, but even this trend was not statistically significant (linear regression: $F_{1,8}$=1.34, P=0.28).

All four species showed a strong preference for pasture, as reflected in the affinity index (Figure 4.10). While this preference fluctuated over the years, no habitat type was ever preferred more by any species at any time. This was also reflected in the relatively high activity levels in pastures for all species and throughout all seasons and years (Figure 4.7). This habitat type is greatly important to ungulates at the Park. Again, there were no clear changes across the years in habitat affinity.

Overall, while habitat use, habitat breadth and habitat preference varied dramatically across the study period (Figure 4.6-4.10), there was no indication of year-to-year changes in any of these variables for any of the four ungulate species.

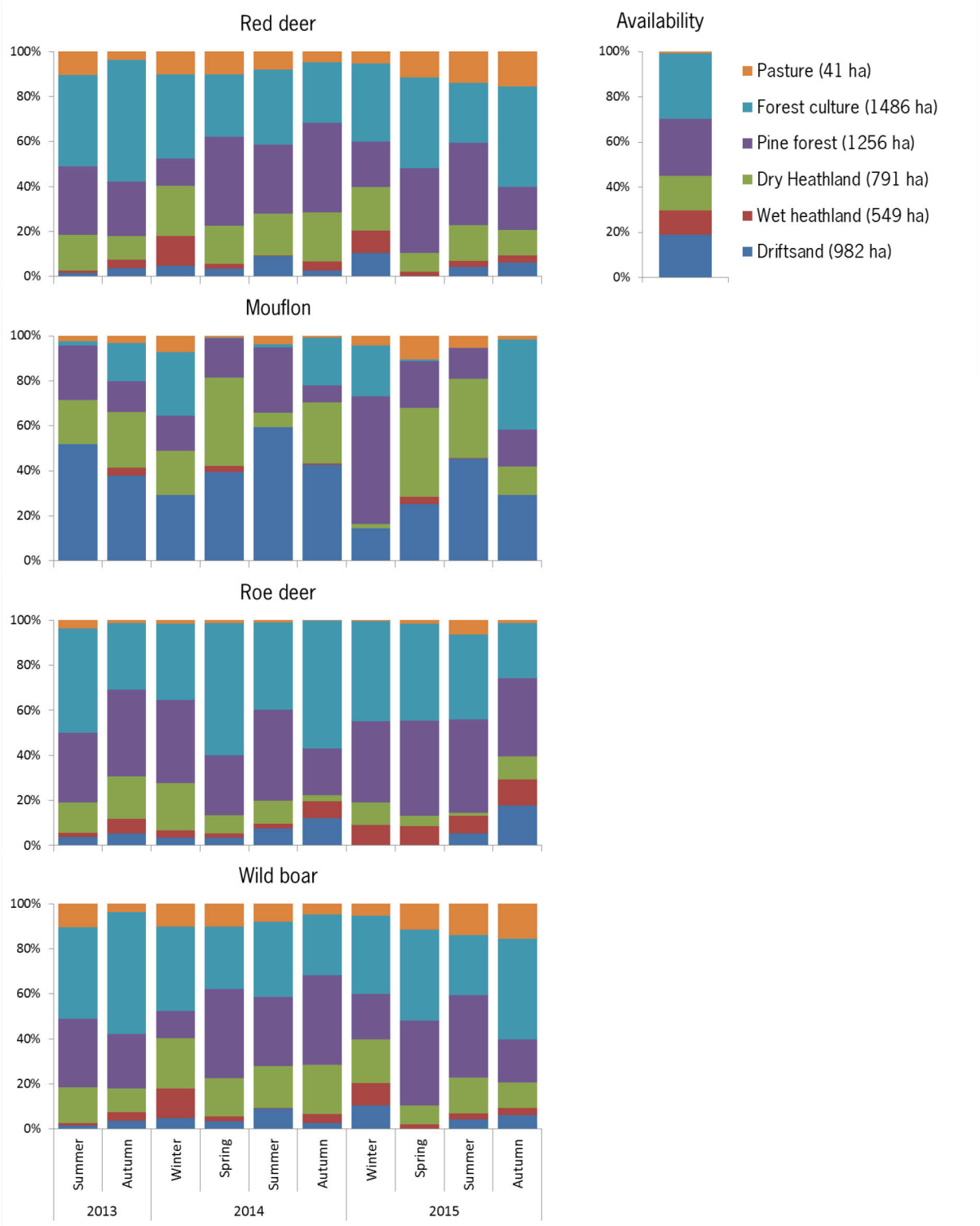

Figure 4.7 *Temporal variation in habitat use by four ungulate populations in Hoge Veluwe National Park as reflected by the distribution of activity over the six major habitat types over 2.5 years. The activity distribution was estimated by extrapolating relative capture rates at camera stations to the available area of each habitat.*

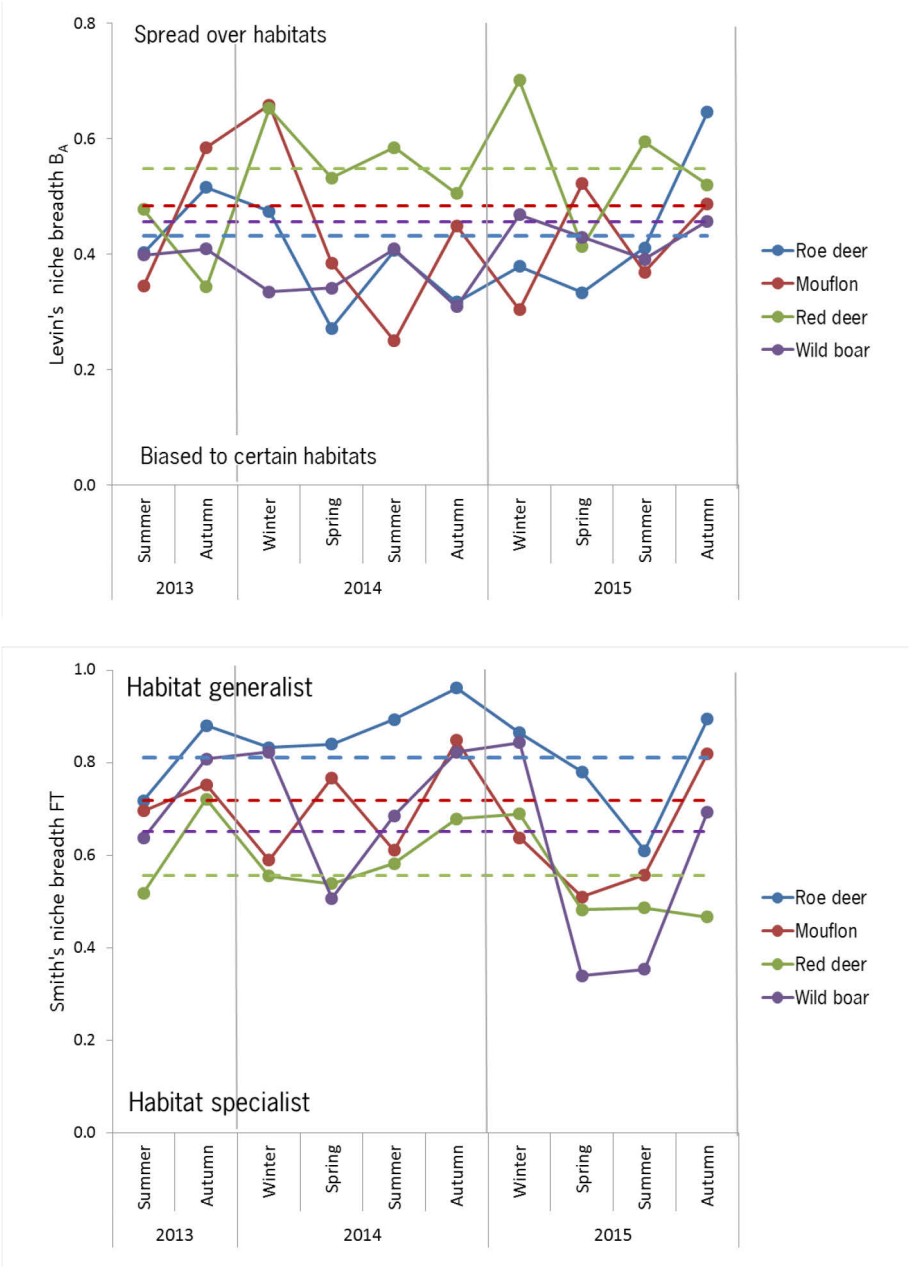

Figure 4.8 *Temporal variation in habitat breadth – the uniformity in which habitat types were used – of four ungulate populations at Hoge Veluwe National Park over 2.5 years, using two alternative measures. Levin's BA shows the uniformity of the distribution over the six habitat types; Smith's FT does the same but takes into account how much of each habitat is available. The dashed lines show habitat breadth averaged over the entire study period.*

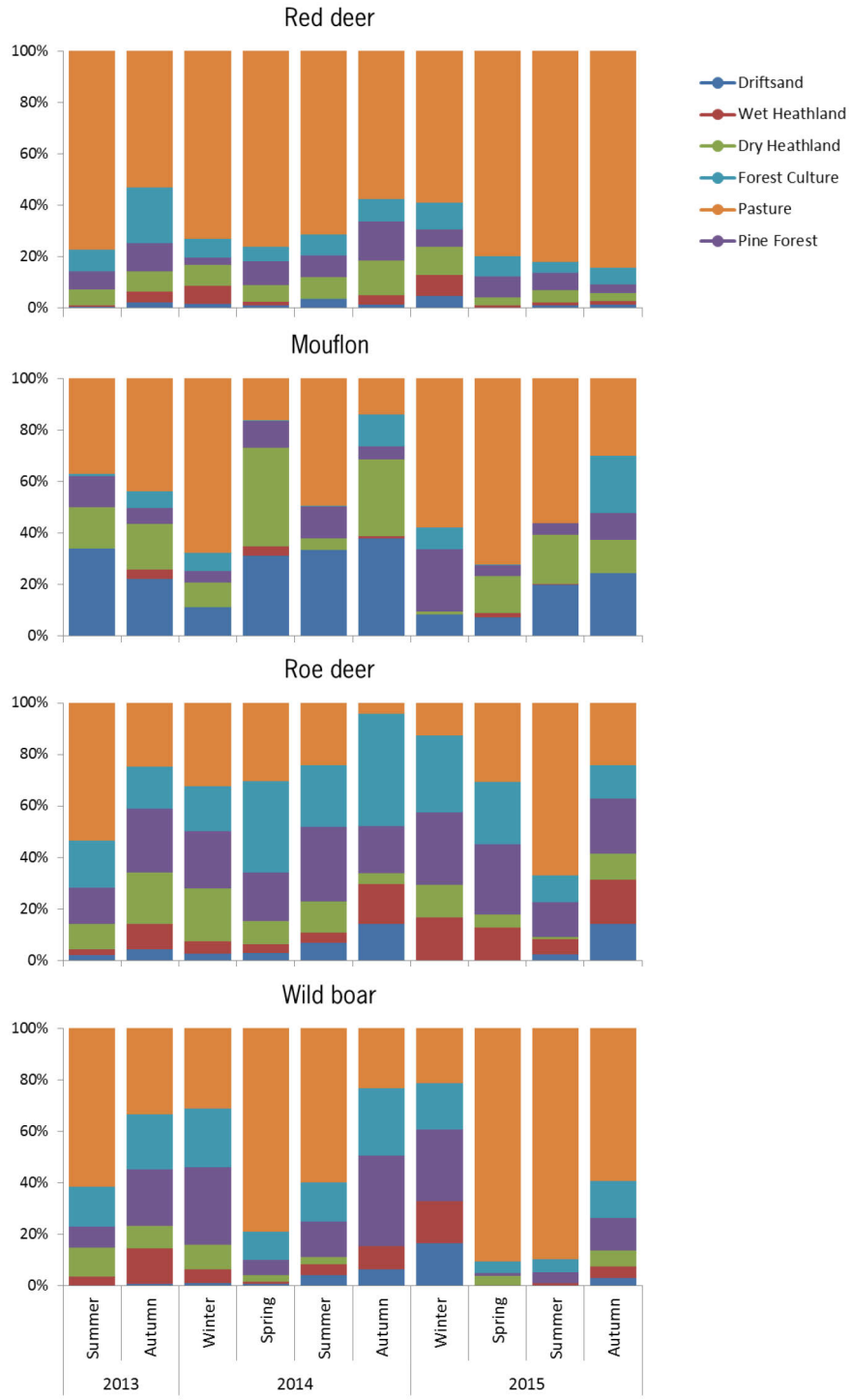

Figure 4.9 *Temporal variation in the intensity of use – an indicator of preference – of six major habitat types in Hoge Veluwe National Park for four ungulate species over 2.5 years. Intensity of use was estimated by averaging capture rates across stations per habitat type. Intensities for all habitat types were then standardised to add up to 100%.*

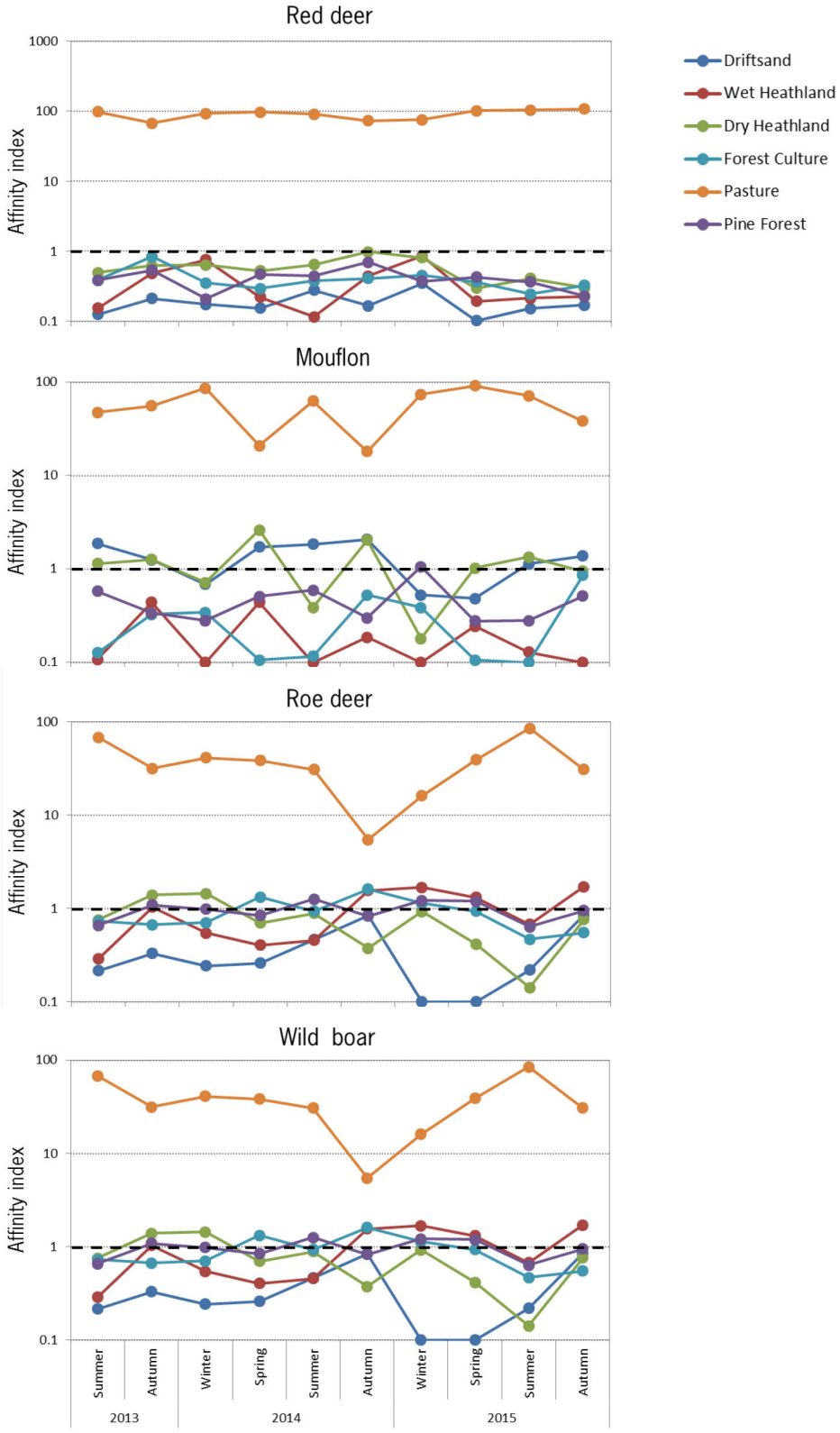

Figure 4.10 *Seasonal variation in habitat 'preference' of four ungulate species in Hoge Veluwe National Park over 2.5 years based on the visit frequency to patches recorded by camera traps. Plotted values are the adapted affinity index (Cairns & Telfer, 1980) based on capture rate per habitat and habitat availability (area). Values >1 indicate preference, and values <1 indicate avoidance. The dashed line at 1 marks where habitat use is proportional to its occurrence. Note the log_{10}-scale. Index values of 0.1 were used when the species was not observed.*

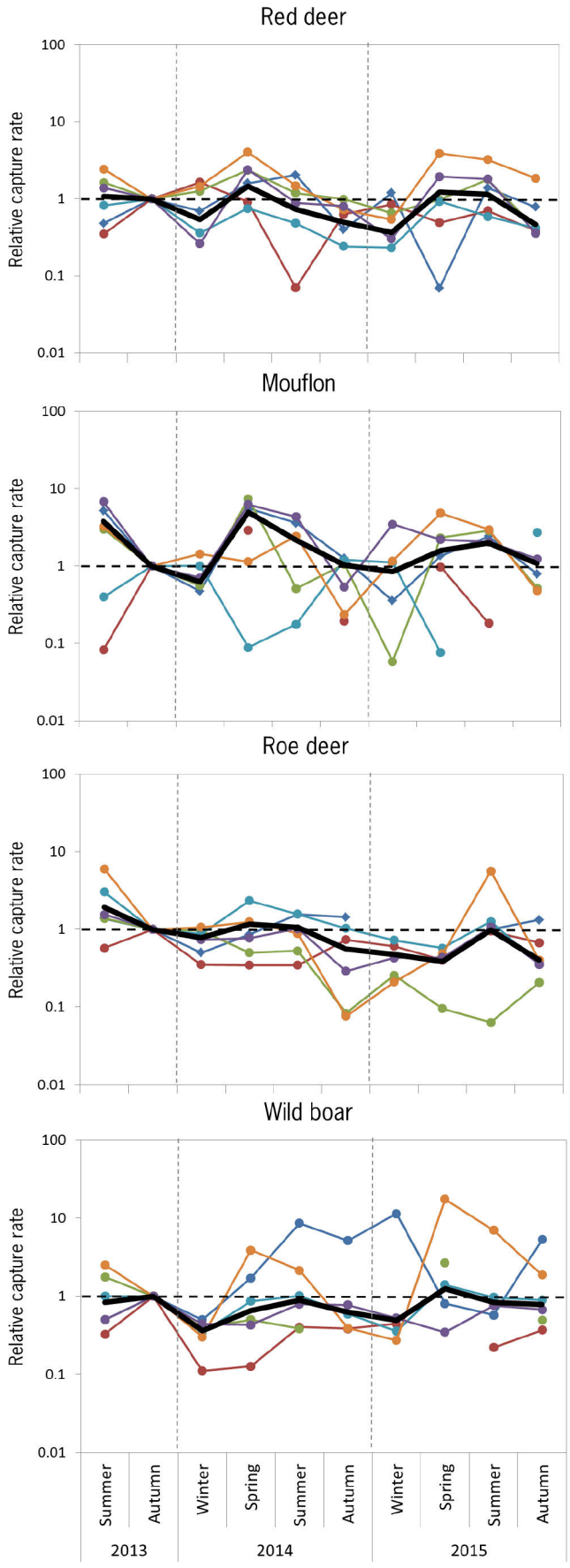

Figure 4.11 *Relative abundance index of four ungulate species at Hoge Veluwe National Park over the study period as estimated from capture rates of camera traps, where the reference (Autumn 2013) is set to 1. Coloured lines show the abundance index for the six habitat types (legend as in Figure 4.10), and the bold black line refers to the entire Park.*

4.3.3 Abundance and structure

To assess whether the abundance and population size of ungulates had changed since the fences were opened, we calculated trends in the abundance of the four ungulates over time using the same 10-season dataset as for the analysis of habitat use (Figure 4.4). The assumption is that the capture rates across the eight stations located within each habitat type were representative for the habitat type and could thus be extrapolated to the entire surface. As point of reference, we used two different periods: summer 2013 and autumn 2013. These fall just before and just after the opening of the fences, respectively. Comparison between the same season of subsequent years solves the problem of variation in detectability.

For each species, the index values were highly variable over time, especially within habitat types (Figure 4.11). Trends in index values depended on the reference point used. Using autumn 2013 as a reference point (Figure 4.11), there was a signal of decline from autumn 2013 to autumn 2015 in red deer (-53%), roe deer (-60%) and wild boar (-22%), but not in mouflon (+7%). Using summer 2013 as a reference point, there was a signal of decline from summer 2013 to summer 2015 in roe deer (-49%) and mouflon (-47%), but no major change in capture rate for red deer (+7%) and wild boar (-1%). Thus, trends were inconsistent and dependent on the period of reference in all species except roe deer.

4.4 Discussion

The camera-trap network yielded a massive number of photographs, most of which were annotated by a group of dedicated volunteers to yield observations, which can be translated to capture rates (also known as photographic rates). We have used these capture rates to assess trends in habitat use and the relative abundance of ungulates at Hoge Veluwe National Park after the opening of wildlife crossing structures.

The fact that fallow deer appeared on the images more than 50 times shows that this species has entered the Park, likely via the wildlife passage from Deelerwoud, where this species is abundant. However, the number of records is an extremely small proportion of the total collection, indicating that the population never exceeded more than a handful of individuals. Also, the intensity at which this population used the habitat patches that we monitored was too small to expect any ecological impact on the other ungulate species.

We found no evidence for any directional changes in patterns of habitat use by the four resident ungulate species, red deer, roe deer, mouflon and wild boar. Although we found very large fluctuations in habitat breadth and preference across the sampling period, this variation was primarily seasonal. Clearly, the four species differ in their habitat breadth and habitat preferences, and, within species, their preferences fluctuate throughout the year. Our survey is rather unique in that it allowed us to capture these preferences in numbers.

Among other things, the numbers demonstrate that the pastures maintained by Hoge Veluwe National Park are very important for sustaining wildlife. The pastures are used many times more intensely than any other habitat type, and the amount of animal activity located in this habitat type is thus extremely disproportional to the amount of area it represents. In general the cameras yielded valuable data on the intensity at which habitat patches are used by wildlife, which may be useful for quantifying browsing pressure or for assessing effects of experimental treatments.

We detected a declining trend in the abundance of roe deer across the study period. The reasons for this decline are unclear. Roe deer is the single ungulate species that is not culled in the Park, and direct counts over the past decades show high year-to-year variability (Leidekker, pers. comm.), which may explain the pattern observed. We found no consistent trend for the other three species. That is, trends observed in these species depended on whether the comparison was across summers or autumns. No trends were expected in these species as they are culled annually to maintain the population at predetermined levels. One possibility is that the sensitivity of camera traps declined over time due to the wear of the cameras despite the protective enclosures. This, however, would have produced declines in the capture rate of all species, not just roe deer.

4.4.1 Limitations

A proper comparison across species, habitats or seasons requires that spatio-temporal variation in sampling efforts is accounted for. We did this by accounting for effective sampling time, so that observations could be expressed as rates. However, we did not fully account for a less obvious set of corrections: interspecific and spatio-temporal variation in the detection distance of camera traps. This variation arises from the fact that commercial camera traps – including our mode – use a passive infrared (PIR) sensor to detect wildlife. PIR sensors detect movement of temperature contrasts as fluctuations in the amount of infrared received.

The problem is that these contrasts are highly variable. For example, the level of contrast of animals depends on ambient temperature (low contrast when hot), the amount of infrared emitted depends on animal body size (large animals are detected over greater distances) and infrared transmission depends on humidity (signal declines as air becomes more humid) and vegetation density (vegetation diffuses the signal).

In our analyses of habitat use, we have partially circumvented this problem by standardising response variables within species and seasons, but differences in effective detection distance between habitat types remain. For example, we likely overestimated the intensity of use for drift sand and pasture, habitats where it is less likely that vegetation limits the range of the PIR sensor. Likewise, we probably underestimated the intensity of use for wet heathland, where grasses limit the range of the sensor. However, while these biases affect the absolute values of the measures that we calculated, they do not influence the trends across the study period.

The patterns of relative abundance are especially vulnerable to differences in detection distance. If this produces inflated capture rates in open habitat types such as drift sand, the contribution of animal activity to the abundance index varies with the habitat in which it occurs. Another possibility is that stochasticity of capture rates at stations in the larger habitat types, such as the two forest types, has a relatively large influence on the index. In addition, the use of a four-week period as baseline makes the abundance trends sensitive to the choice of the reference period. One solution is to use a longer reference period, for example 3 months, to obtain more accurate capture rates, i.e., based on more observations per station. However, capture rates fluctuate so strongly between months that this introduces new biases.

At any rate, future studies should measure the effective detection area per species across seasons and also over the lifetime of cameras so that capture rates can be corrected for this variation (for example, using the methods described in Rowcliffe et al. (2011) or Hofmeester et al. (2016)). Capture rate would thus be expressed as the number of events per unit sampling time and per unit effective detection distance. Once this issue is solved, more powerful analyses become possible.

A final limitation of the analyses in this report also disregarded the differences in utilization by wildlife that exists between restricted areas and publicly accessible areas within the same habitat. As we assigned half of the camera stations to each category while restricted areas made up – on average – just 20% of each habitat, we have thus oversampled restricted areas. Knowing that animal activity may be biased towards using these 'safer' areas, especially when recreational pressure is high, this may have influenced the patterns that we observed.

4.5 Conclusions

We found no evidence for any directional changes in patterns of habitat use by the four resident ungulate species since the opening of the fences. Neither did we detect any consistent trend in the population levels. We found evidence for the colonisation of Hoge Veluwe National Park by fallow deer, but the species was so rare compared to the other four ungulates that its population may still be ecologically irrelevant.

This study has yielded a wealth of material that gave insight into the way in which ungulates use the strikingly different habitats in the Park. When the problems of seasonal variation in detectability are accounted for, the data can be used to address many timely questions in ungulate ecology and management, especially if combined with data on food quality and recreational pressure.

4.6 Research recommendations

- Detection of systematic changes in the abundance of ungulates and their habitat use requires a data series that is longer than the 2.5 years covered in this report. We therefore recommend that the camera network is maintained and data collection continued to make it possible to detect these trends. Continuation, however, requires that the approach for processing photo material be reviewed as the burden on volunteers was and their returns too low. One possibility that may be explored is involving the public in photo analysis. Multiple recent examples show that such crowd sourcing of photo processing can be successful, both in producing reliable data and in generating public involvement.
- A second pertinent problem to solve is of variation across seasons and cameras in sensitivity to wildlife, and the integration of data collected at stations to the level of the Park. Solving this problem demands a major research effort involving the collection of field data on effective detection distance across habitats and seasons as well as mathematical modelling. Results from such an exercise would be of high value to camera-trap-aided monitoring in general.
- The data collected in this camera-trap survey are suitable for addressing for a wide range of additional ecological questions, both fundamental and applied. The sampling design makes optimal use of several features of the Park that facilitate the research of spatio-temporal patterns of habitat use by wildlife. These include the fencing of the Park, which constrains the options for wildlife to choose which habitats to use at what time; the relatively sharp boundaries between habitat patches, ensuring that choices are categorical; the subdivision of each habitat category into restricted and public areas, which can function as an experimental treatment; and the fact that public access is regulated by strict opening hours.
- One type of research that is very suited to this combination of circumstances is on the impact of recreation on the spatio-temporal activity patterns of wildlife. The scheduled shifts in opening hours and the change in the level of off-trail access per 2016 offer a unique opportunity to investigate the impact of recreation in Before-After designs, or even Before-After Control-Impact designs. This is especially interesting when combined with studies of wildlife impact on vegetation, which can be achieved by creating overlap between the browsing studies and the camera trapping.

5 Monitoring ungulate browsing

Jan den Ouden & Patrick A. Jansen

5.1 Introduction

Ungulate browsing on woody species has been monitored in Hoge Veluwe National Park since 2012. Woody species are an important dietary component of large herbivores, and leaves, buds, small twigs and bark make up a significant part of the daily food intake of deer, affecting the growth and survival of the browsed individuals. This has an effect on the density and the composition of the regenerating woody species.

The objectives of this monitoring programme were to establish baseline data on the incidence and variation in top shoot browsing by ungulates on trees and shrubs and to determine whether changes in ungulate densities result in changes in the amount of browsing. The monitoring was performed by students and interns under supervision of Hoge Veluwe National Park and Wageningen University.

The results from the browsing plots have already been presented in a number of student reports (Kuipers et al., 2012; Wonders, 2014; Ortiz Diaz & Garcia Sanchez, 2015; Verbeek, 2016).

5.2 Methods

5.2.1 Collection of data

A network of permanent sampling plots was established between 2012-2015 (Figure 5.1). In 2012, 40 plots were created, and in subsequent years 10 new plots were added to the network each year. Plots were created in locations with recent tree regeneration, areas where the Park management wanted to establish new forest regeneration. Plots were distributed over the entire Park area. A small number of plots were located in animal retreat zones, and some located in exclosures not accessible to deer (Table 5.1). Most plots were located in recently cleared areas or under an open canopy of mature trees. Thus, the density and composition of the plots do not represent he average regeneration status in the Park. Over the years, several plots were lost due to severe damage by logging or the activity of volunteers removing conifers. Such plots were used to assess individual browsing, but were not used to analyse patterns in browsing or plot dynamics over several years.

Table 5.1 *Number of browsing plots available for analysis over the four years of monitoring.*

	Census year			
	2012	2013	2014	2015
Total no. of plots	40	50	57	66
plots in exlosures	4	4	4	5
plots in animal retreat	9	9	9	10
Park section:				
Hoenderloo	16	22	24	27
Kemperberg	10	10	12	15
Wildbaan	14	18	21	24

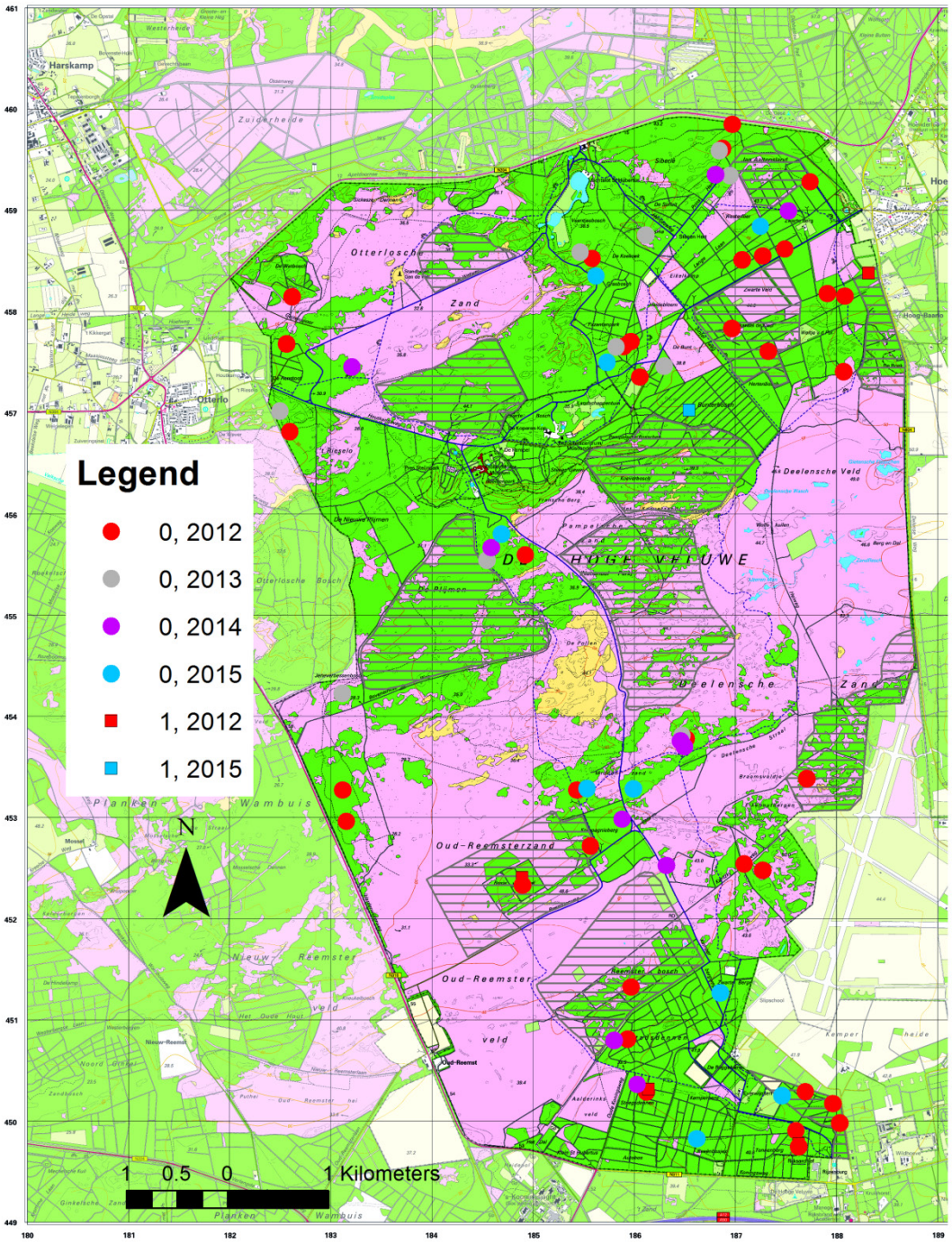

Figure 5.1 *Map of the Park with locations of the browsing plots (0, circles) and plots in exclosures (1, squares) by year of creation.*

Plots consisted of permanently marked transects (3x24 m), subdivided in 6 subplots (3x4 m). Plots were marked by a wooden stake at the start and end points of the transect, and transects were laid out by running a measuring tape between the two stakes and recording plants 1.5 m to the left and right of the central line. Transects were oriented north-south, with the start of the transect at the northern stake. For each individual woody species larger than 10 cm, species identity, height class (Table 5.2) and browsing damage were recorded. Plants <10 cm were not inventoried to avoid large numbers of young seedlings. Also any damage by fraying or bark peeling was recorded. Plots were inventoried in September/October prior to leaf fall.

Table 5.2 *Height classes used for determining plant size.*

Height class	Height (cm)
1	10-40
2	40-80
3	80-120
4	120-160
5	160-200
6	>200

Browsing damage was recorded as a browsed top shoot of the current year (indicating browsing during the growing seasons) and as a browsed top shoot of the previous year (indicating the accumulated browsing on the previous growing season and following winter/early spring, see Figure 5.2). In 2012, browsing was only recorded for the current shoots in ten plots. After evaluating the distinctions made in the field between the current and the previous year's shoots, the compensatory growth after the current shoots had been browsed caused too many mistakes in assessing the correct browsing category. Therefore, we restricted the analysis of browsing to the records on the current year's shoots only.

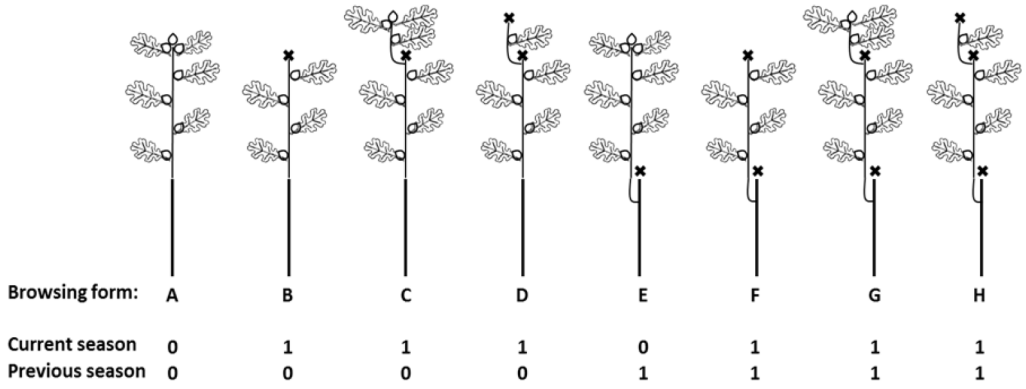

Figure 5.2 *Differentiation between browsing by ungulates in current and previous year. Distinction between years was made based on the presence of buds and leaves on the current year's shoots. Only browsing on the current year's top shoots was analysed.*

Browsing was only recorded when this was caused by ungulates. Browse marks were identified by the morphology of the cutting fringes. Frayed edges indicated ungulate browsing, and clean and straight bite marks indicated rodent or lagomorph browsing. In the latter case (occurring very infrequently) the shoot was recorded as 'not-browsed'.

The habitat features of each plot location were characterised by estimating the percentage cover of the most dominant vegetation layers in a 25 m radius circle around the plot. Estimates included canopy cover of mature trees, cover of the shrub layer between 50-500 cm, cover of *Vaccinium myrtillus*, and cover of grasses (most frequently *Molinia carulea* and *Deschampsia flexuosa*). Cover was estimated to the nearest 5% when cover was >10% and to the nearest 1% when cover was <10%.

5.2.2 Data analysis

We used a browsing index to estimate the intensity of browsing at plot level. The index was calculated as the percentage of broadleaved saplings <1.6 m browsed in a plot relative to the total number of broadleaved saplings <1.6 m present. The browsing index was calculated for each plot for each year separately. Data on temporal variations in browsing and vegetation dynamics were calculated for the subset of plots that were available for analysis over the entire four-year period and that were not affected by management. Data on habitat features on each plot location were averaged over the entire period that the plot was monitored and then classified into a cover category (Table 5.3).

Table 5.3 *Categories used to characterise habitat features for individual plots.*

	Cover class		
Cover type	**1**	**2**	**3**
Tree canopy	<25%	25-50%	>50%
Shrubs	<25%	25-50%	>50%
Vaccinium	<5%	5-25%	>25%
Grasses	<25%	25-50%	>50%

An index was derived for alternative food availability for ungulates using the cover of *Vaccinium* and grasses. Categories used were: low = *Vaccinium* <5% and grass <25%, medium = *Vaccinium* 5-25% OR grass 25-50%, and high = *Vaccinium* 5-25% AND grass 25-50%, or *Vaccinium* >25% OR grass >50%.

The preference of ungulates for browsing a species *i* in a plot was calculated using the selectivity index (S_i) developed by Jacobs (1974):

$$S_i = (C_i - B_i) / (C_i + B_i - 2 * C_i * B_i)$$

where C_i = the relative browsing of species *i* in the plot, calculated as the proportion of species *i* in the total of browsed individuals in the plot, and B_i = the relative availability of species *i*, calculated as the proportion of species *i* in the total of individuals present. S_i was calculated using the individuals <1.6 m (height classes 1-4). The selectivity index S_i was averaged over the total number of plots in which a species occurred. Plots where no browsing occurred were not included. S_i can vary between -1 and 1, where a value around 0 indicates indifference. Species with a positive index are preferentially browsed, and species with a negative index are avoided.

5.3 Results

We found a total of 26 woody species in the plots over the four-year monitoring period (Table 5.4). *Pinus sylvestris* and *Betula pendula* were by far the most abundant species, both occurring in over 90% of the plots. Broadleaved and coniferous species were present in approximately the same number of individuals over the years. *B. pendula* was highly overrepresented within the broadleaved group; over 80% of all broadleaved individuals were birches. The coniferous individuals were slightly more evenly distributed over the species, with about 60-70% of the individuals being *P. sylvestris*.

Table 5.4 *Frequency of occurrence of all species encountered in the browse plots in the four census years and the mean occurrence and mean number of individuals in the subset of plots that were monitored over the complete four-year period. Species in bold typeface occur on average in >40% of the plots and with >100 individuals.*

	Frequency (% occurrence in plots)					Mean no. individuals
	2012	2013	2014	2015	`12-`15	`12-`15
No. of plots:	*40*	*50*	*57*	*66*	*36*	*36*
Species:						
Abies grandis	8	4	5	8	6	181
Acer pseudoplatanus	5	4	4	3	3	2
Aesculus hippocastanum	3				1	0
Amelanchier lamarckii	45	46	63	55	54	377
Betula pendula	90	78	82	85	91	2943
Betula pubescens	58	64	65	55	61	182
Carpinus betulus	3				1	0
Castanea sativa				5	1	0
Fagus sylvatica	18	16	23	21	17	17
Ilex aquifolium	0	4	7	8		
Juniperus communis	0	2	2	2		
Larix kaempferi	40	42	37	45	44	732
Picea abies	13	6	18	20	14	17
Picea sitchensis	3	10	2		4	3
Pinus nigra	0	2	2	8	2	1
Pinus strobus	3				1	0
Pinus sylvestris	93	88	88	85	91	3238
Prunus serotina	40	34	42	44	47	193
Pseudotsuga menziesii	43	36	42	41	44	886
Quercus robur	55	66	70	65	62	233
Quercus rubra	28	36	32	32	33	67
Rhamnus frangula	40	52	44	52	44	297
Sorbus aucuparia	60	64	63	62	64	920
Thuja occidentalis				2		
Tilia cordata	5	4		3	4	4
Tsuga heterophylla	23	16	16	17	20	60

5.3.1 Exclosures

The species composition in exclosures varied greatly between plots (Figure 5.3). Two plots were located in exclosures where a young tree layer >2 m had already developed when plots were created in 2012. This layer was dominated by broadleaved species and *P. sylvestris* (plot 23) or by *B. pendula* and *P. sylvestris* (plot 34) and hardly changed over the four-year monitoring period (Figure 5.3). The plots in the two other exclosures were located in recently established regenerations, dominated by *Sorbus aucuparia* (plot 15) and *P. sylvestris* (plot 39). In plot 15, *S. aucuparia* grew up to dominate the tallest height class over time. In plot 39, the growth of the young trees was remarkably slow, with most individuals remaining in the small height classes. In 2015, *B. pendula* established itself in the dense pine sapling layer. In all exclosures, browsing occurred in some years on a small number of trees, indicating that exclosures are occasionally visited by ungulates (species unidentified).

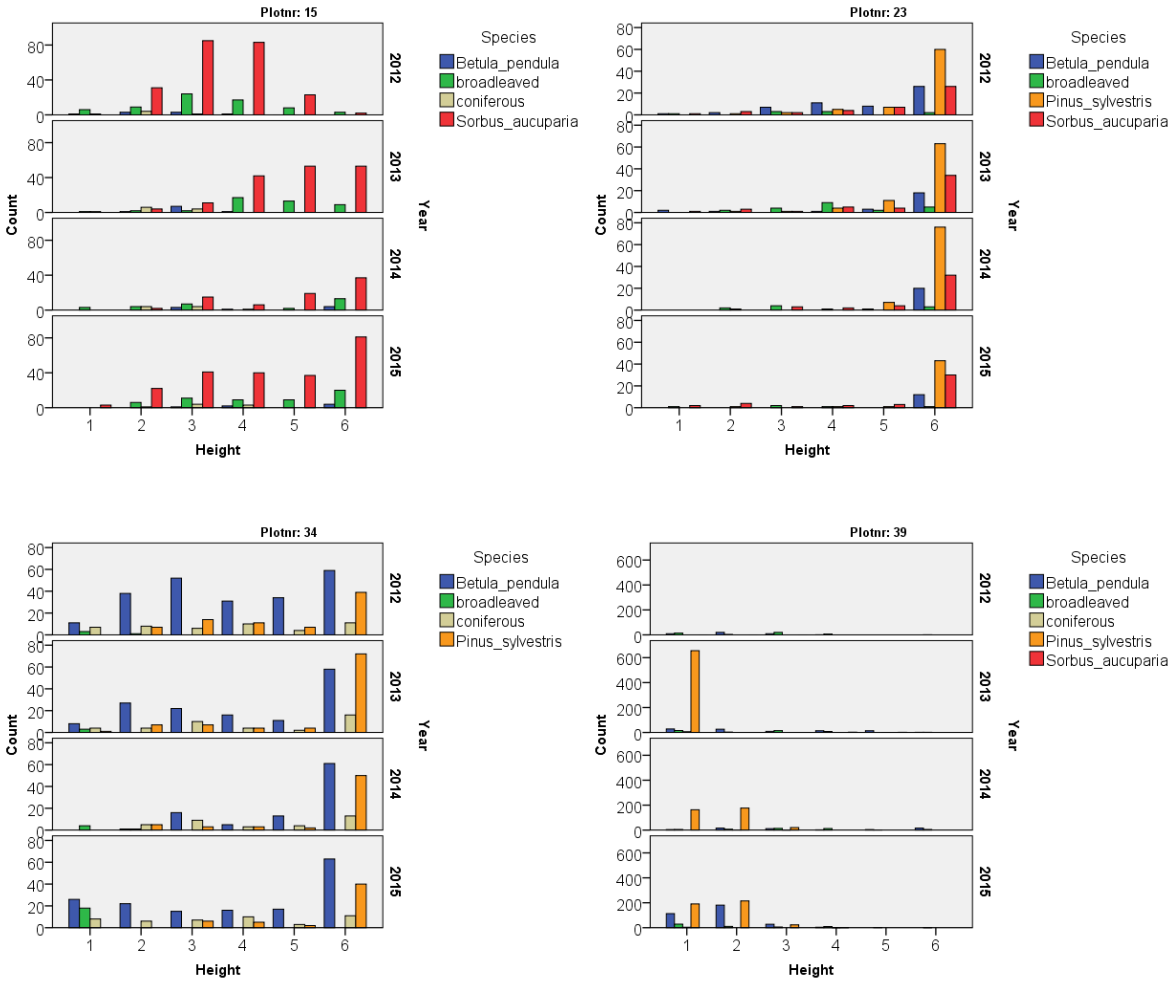

Figure 5.3 *Changes in species composition and height class distribution in the four exclosures that were monitored over the period 2012-2015.*

5.3.2 Browsing preference

Conifers were clearly avoided (Figure 5.4). *Fagus sylvatica*, *Quercus rubra* and *Q. robur* all had a negative selectivity index, suggesting they were browsed less than would be expected based on their relative abundance in the plots. Note that in one of the census years (2014), both *F. sylvatica* and *Q. rubra* had a selectivity index value of -1, suggesting they were strongly avoided by ungulates, while in another year (2012) *Q. rubra* was selectively browsed. On average, *B. pendula*, *Prunus serotina* and *Amelanchier lamarckii* were browsed indifferently (Figure 5.4). *Rhamnus frangula*, *B. pubescens* and *Sorbus aucuparia* were selectively browsed, with median selectivity index values >0 in all census years.

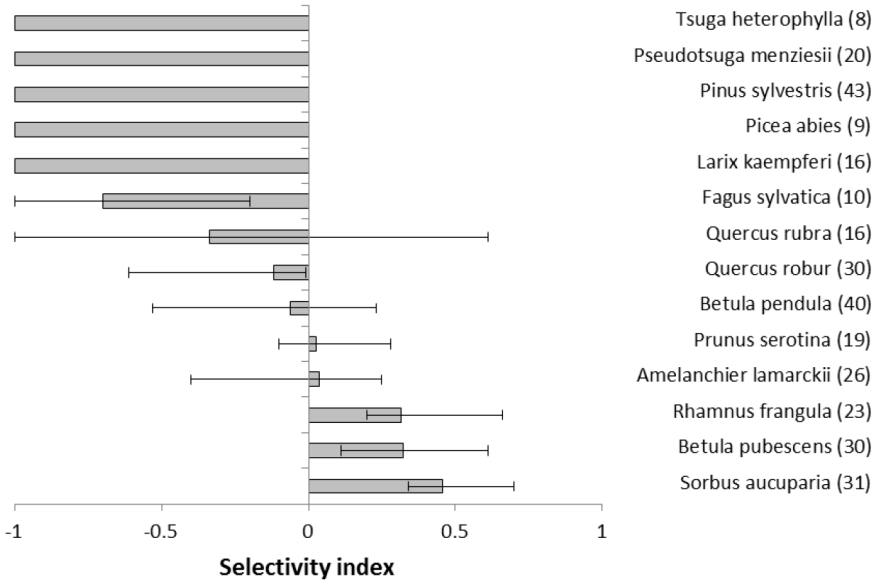

Figure 5.4 *Selectivity indices for the most frequent tree species (occurring in more than six plots within a given census year). Bars represent the average median selectivity indices over the four census years, weighted by the number of observations per year. Error bars show the highest and lowest median values per species for a given census year. The average number of plots containing the species is shown between brackets behind species names. Only data from freely accessible plots are included.*

For some tree species, selectivity in browsing by ungulates was related to the availability of alternative food in the plots (Table 5.5). When the cover of *Vaccinium myrtillus* or grasses increased, ungulates browsed on the two *Betula* species significantly less selectively in the plots. Selectivity in browsing on *S. aucuparia* also decreased when grass cover in a plot increased (Table 5.5). Conifers were always avoided, regardless of the presences of alternative food sources.

Table 5.5 *Selectivity in browsing on the most frequent broadleaved species in relation to cover of Vaccinium myrtillus (top) and grasses (bottom) in and around the plot. Data are median values per cover class over all plots available for analysis and pooled across the census years (maximum four years). Cover was determined as mean value over the censused years in a plot. Test statistics from the non-parametric Kruskal-Wallis test, with df=2.*

	***Vaccinium myrtillus* cover classes**				
Species	**< 5**	**5-25**	**> 25**	**χ^2**	**P**
Amelanchier lamarckii	0.32	-0.01	0.00	5.84	0.054
Betula pendula	0.23	-0.26	-0.47	12.04	0.002
Betula pubescens	0.60	0.13	0.07	9.47	0.009
Fagus sylvatica	-0.57	-1.00	-0.20	0.74	0.691
Prunus serotina	0.23	-0.27	-0.05	1.21	0.546
Quercus robur	0.03	-0.79	-0.05	3.00	0.223
Quercus rubra	-0.15	-0.33	0.24	0.67	0.717
Rhamnus frangula	0.28	0.29	0.28	0.11	0.946
Sorbus aucuparia	0.57	0.45	0.25	2.85	0.240

	Grass cover classes				
Species	**< 25**	**25-50**	**> 50**	**χ^2**	**P**
Amelanchier lamarckii	0.20	-0.08	0.21	3.21	0.201
Betula pendula	0.60	-0.01	-0.10	13.24	0.001
Betula pubescens	0.76	0.13	0.21	6.40	0.041
Fagus sylvatica	-0.57	-1.00	-1.00	0.34	0.845
Prunus serotina	-1.00	-0.31	0.21	0.99	0.609
Quercus robur	-1.00	-0.15	-0.03	0.76	0.685
Quercus rubra	0.32	-1.00	-0.12	2.82	0.244
Rhamnus frangula	0.76	0.43	0.23	5.84	0.054
Sorbus aucuparia	0.81	0.56	0.33	7.39	0.025

5.3.3 Browsing height

Browsing on top shoots was related to the height of the trees (Figure 5.5). Most browsing occurred in the first two height classes (10-80 cm), where on average 45% of all broadleaved individuals were browsed. As the height of the individuals increased, browsing percentages decreased. Tree saplings larger than 1.60 m (height classes 5 and 6) were much less browsed: on average 5.7% of the browsed broadleaved individuals were in these two height classes (Figure 5.5). In conifers, this percentage is slightly higher: 6.4% of the browsed individuals were larger than 1.60 m.

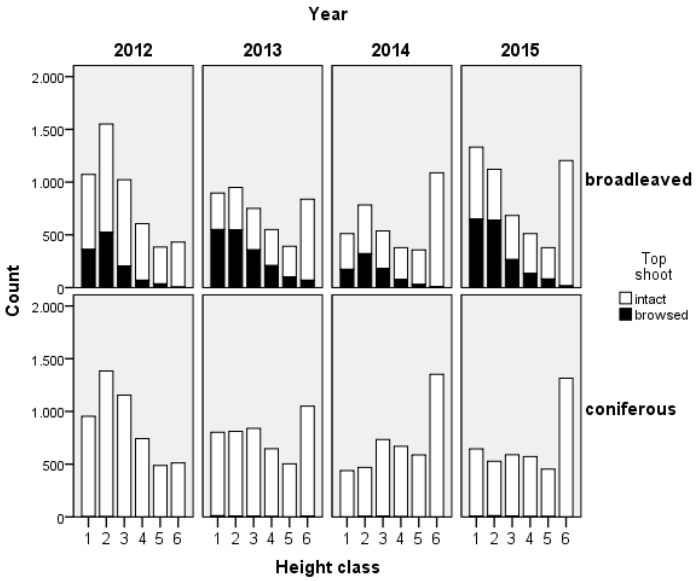

Figure 5.5 *Height distribution and browsing on broadleaved and conifers in the four census years. Only plots accessible to ungulates and measured in all census years are included. Data pooled over all plots (n=32).*

Coniferous species are hardly browsed at all, and of all saplings larger than 1.60 m only 0.1% was browsed (Table 5.6). Two of the most preferred species, *R. frangula* and *S. aucuparia*, had a considerable amount of browsed individuals in the larger height classes (Table 5.6). The percentage browsed in broadleaved saplings >1.60 m was significantly correlated (Spearman's rho=0.817, df=9, p=0.007) with the selectivity index (Figure 5.6).

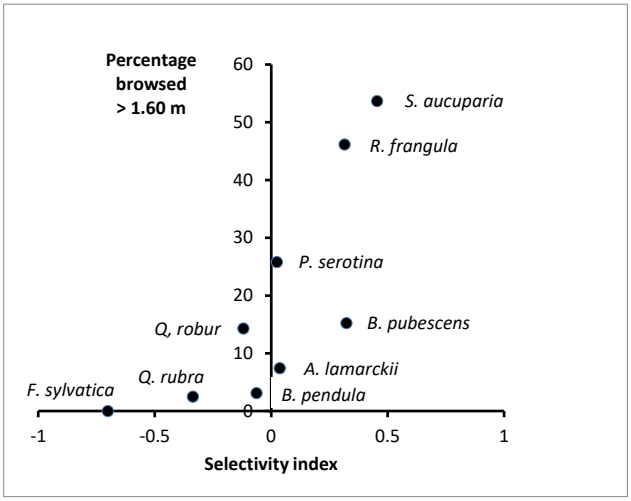

Figure 5.6 *The correlation between the percentage of trees >1.60 m browsed and the selectivity index for browsing on the most abundant broadleaved species.*

Table 5.6 *Total number of individuals (N) and the percentages top shoots browsed (%) per species and per height class. Data were pooled over all plots in the 2012-2015 censuses, excluding plots in exclosures. Within species, the height class with the maximum percentage browsed is indicated in bold.*

	Height class (cm)											
	10-40		40-80		80-120		120-160		160-200		> 200	
Species	N	%	N	%	N	%	N	%	N	%	N	%
Pinus sylvestris	3291	1	2671	**1**	2288	1	1866	0	1451	0	3013	0
other conifers	1564	1	2524	0	2127	**1**	1525	0	1043	0	1916	0
Amelanchier lamarckii	830	51	1031	**59**	458	45	239	20	162	12	162	2
Betula pendula	1699	**21**	3782	18	2956	18	1897	14	1277	9	3240	1
Betula pubescens	499	42	373	**54**	127	45	56	30	23	22	23	9
Fagus sylvatica	126	13	147	**31**	73	25	31	13	25	0	36	0
Prunus serotina	339	43	268	78	176	**86**	64	70	21	48	41	15
Quercus robur	592	41	415	65	121	64	21	**67**	2	50	5	0
Quercus rubra	377	47	572	**62**	568	42	275	9	154	5	206	1
Rhamnus frangula	1920	61	1225	83	355	**86**	187	79	158	64	180	31
Sorbus aucuparia	1855	69	1533	**81**	744	79	396	78	152	67	66	23
other broadleaved	112	20	111	**42**	40	25	13	38	3	0	1	0

Given the prevalence of browsing in the lower height classes and on the very low browsing percentages in conifers, evaluation of browsing incidence (browsing index) is based on calculations of average browsing percentages on broadleaved individuals less than 1.60 m in height.

5.3.4 Bark stripping and rubbing

Physical damage to the tree stem by bark stripping and antler rubbing hardly occurred in the plots (Table 5.7). Damage to bark from rubbing antlers was more frequent than from bark stripping, but never exceeded 1% of all the plants. Bark stripping occurred in many tree species, most frequently on *B. pendula* (40%) and *P. sylvestris* (20%). As birch is normally not stripped by deer (Vospernik, 2006) this is probably a misidentification of damage type and should be considered as fraying damage. Antler rubbing occurred in similar proportions in coniferous and broadleaved individuals. As in bark stripping, rubbing was most prevalent in *B. pendula* (39%) and *P. sylvestris* (28%). In the field, it was difficult to discern rubbing damage from bark stripping, especially on smaller individuals, which may underlie the contrasting trend in the percentages of rubbing and stripping recorded in the different censuses (Table 5.7).

Table 5.7 *Incidence of bark stripping and rubbing in the four census years. All available data pooled except plots in exclosures.*

Year	% trees with stripped bark	% trees with rubbed bark
2012	0.01	0.72
2013	0.04	0.27
2014	0.09	0.17
2015	0.11	0.06

Larger saplings were preferentially rubbed and stripped (Figure 5.7). Most bark was rubbed or stripped at a height of 50-100 cm on the stem (Figure 5.7).

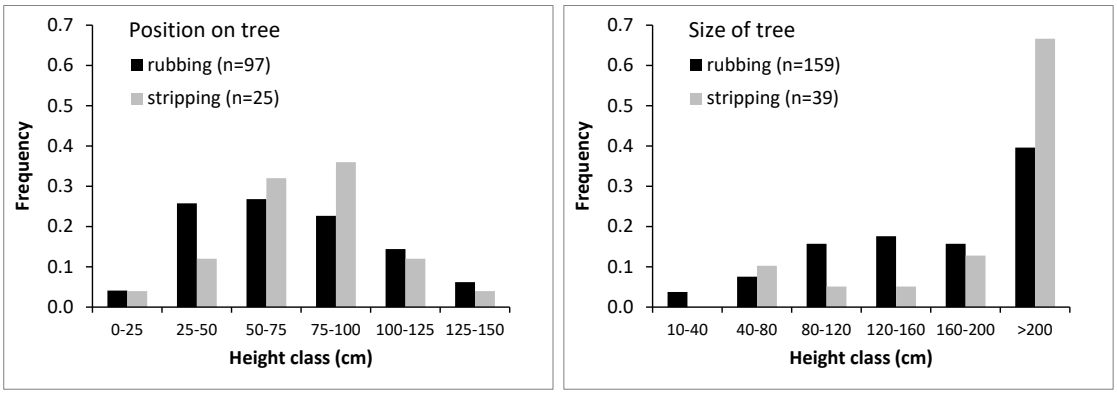

Figure 5.7 *The distribution of damage by antler rubbing and bark stripping in trees over the height within the trees (left) and the size of the trees (right). Data pooled over all four census years.*

5.3.5 Browsing

The browsing index (percentage of top shoots browsed from broadleaved species shorter than 1.60 m in a plot) varied over the years and over the Park area (Figure 5.8). When comparing data in the subset of 25 plots that were available for a comparison over the full four years and that had at least 20 broadleaved individuals (n=25), the median browsing index was highest (52.5%) in 2013, while it was lowest (17.4) in the preceding year (Table 5.8). Differences between years were significant (Kruskal-Wallis, χ^2=12.0, p=0.007), but these were due to fluctuations between years rather than resulting from a trend (Table 5.8, Figure 5.8).

The browsing index was consistently lower in the Kemperberg area as compared to the Hoenderloo and Wildbaan areas (Table 5.8). When pooling the data for the four census years, this difference in median browsing index between Park sections was highly significant (Kruskal-Wallis, χ^2=24.4, p<0.001).

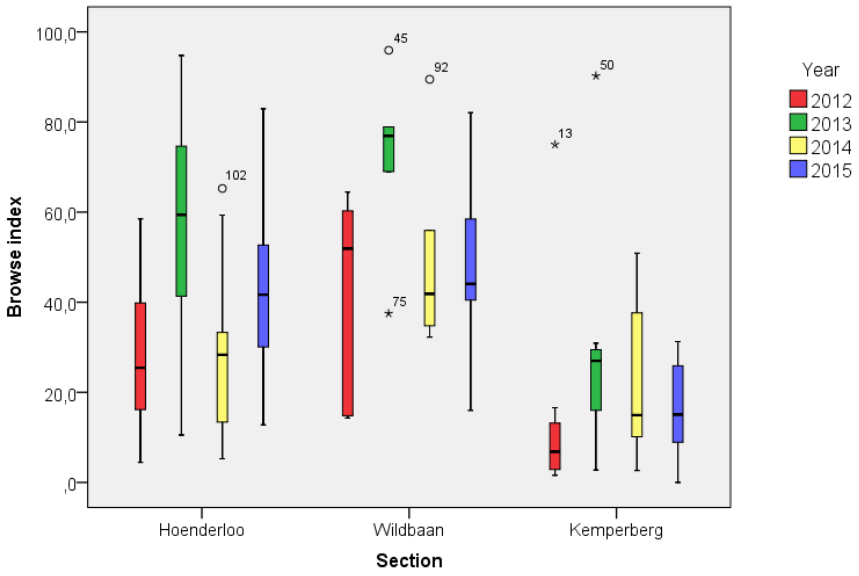

Figure 5.8 *Variation in browsing over the four census years in the three Park sections. Only plots that were censused in 2012-2015 and that had at least 20 broadleaved individuals less than 1.60 m tall are included (n=25).*

Table 5.8 *Median browsing index per year and per Park section. Data calculated for those plots that were censused completely over the 2012-2015 period and that had at least 20 broadleaved individuals less than 1.60 m tall are included.*

		Year				
Section	No. plots	2012	2013	2014	2015	Total
Hoenderloo	12	25.4	59.4	28.3	41.7	34.5
Wildbaan	5	51.9	76.9	41.9	44.1	53.9
Kemperberg	8	6.8	27	15	15.1	15.4
Total	25	17.4	52.5	28.9	33.3	

When considering all available data from the censused plots in the period 2012-2015, we see that the differences in the browsing index between areas remained. In the Kemperberg area (southern part of the Park) trees were less browsed as compared to the other areas in the Park (Table 5.9). When pooling the data over all censuses, the effect was very strong (Kruskal-Wallis, χ^2=25.6, p<0.001). When tested for the individual years, this effect was significant for 2013 and 2015 (Table 5.9). There were no significant differences in browsing between plots located in or outside a wildlife retreat area in any of the census years (data not shown).

Table 5.9 *Median browsing index (percentage of broadleaved tree saplings <1.60 m high with browsed top shoots) in the four census years in the three Park sections. Number of plots indicated between brackets. Only plots with more than 20 broadleaved saplings were included. The results from the Kruskal-Wallis test refer to differences in median browsing index between Park sections within the years.*

Year	Park section			Kruskal-Wallis	
	Hoenderloo	Wildbaan	Kemperberg	χ^2	p
2012	24 (13)	34 (6)	7 (8)	5.42	0.067
2013	60 (19)	78 (8)	27 (8)	10.40	0.006
2014	31 (21)	39 (13)	15 (10)	2.81	0.245
2015	47 (23)	42 (15)	13 (13)	12.29	0.002

Several vegetation characteristics significantly influenced the amount of browsing in the plots (Table 5.10). Tree canopy cover did not affect the amount of browsing. The browsing index was lower when pots were located in areas with a high shrub cover, but browsing was higher when plots located in areas with a high cover of *Vaccinium myrtillus* or grasses (Table 5.10 and 5.11). The cover of these last two were combined into a single indicator for the availability of alternative food in the plots, which significantly affected the browsing index (see Figure 5.9).

Table 5.10 *Test statistics on the differences in browsing index between plots differing in cover by tree canopy, shrubs, Vaccinium, grasses and alternative food sources. Differences were tested with Kruskal-Wallis non-parametric tests.*

Cover type	χ^2	P
Tree canopy cover	1.458	0.482
Shrub layer	13.744	0.001
Vaccinium myrtillus	6.505	0.039
Grasses	19.487	0.000
Alternative food available	7.514	0.023

Table 5.11 *Median browsing index of plots in the four census years by cover percentages of the tree canopy cover, shrubs, Vaccinium myrtillus and grasses (mainly Molinea carulea and Deschampsia flexuosa). Number of plots between brackets). All censused plots are included, except for plots that contained less than 20 broadleaved individuals. Availability of alternative food is calculated from Vaccinium and grass cover, with low = Vaccinium <5% and grass <25%, medium = Vaccinium 5-25% OR grass 25-50%, and high = Vaccinium 5-25% AND grass 25-50%, or Vaccinium >25% OR grass >50%.*

		2012	2013	2014	2015
Tree canopy cover	< 25 %	17 (11)	50 (14)	31 (15)	40 (19)
	25-50%	20 (13)	69 (15)	34 (16)	37 (18)
	> 50%	15 (3)	57 (6)	32 (13)	37 (14)
Shrub cover	< 25 %	65 (1)	53 (3)	37 (7)	59 (12)
	25-50%	24 (10)	68 (15)	37 (19)	40 (20)
	> 50%	15 (16)	55 (16)	18 (16)	27 (17)
Vaccinium cover	< 5%	24 (15)	68 (17)	32 (23)	32 (28)
	5-25%	14 (11)	55 (14)	28 (16)	41 (17)
	>25%	47 (1)	62 (4)	31 (5)	61 (6)
Grass cover	< 25 %	5 (7)	31 (8)	14 (10)	21 (12)
	25-50%	19 (8)	62 (12)	32 (13)	47 (13)
	> 50%	25 (12)	69 (15)	36 (20)	41 (25)
Alternative food	low	6 (4)	35 (5)	22 (6)	30 (8)
available	med	12 (6)	69 (7)	16 (9)	17 (8)
	high	20 (17)	60 (23)	35 (29)	44 (35)

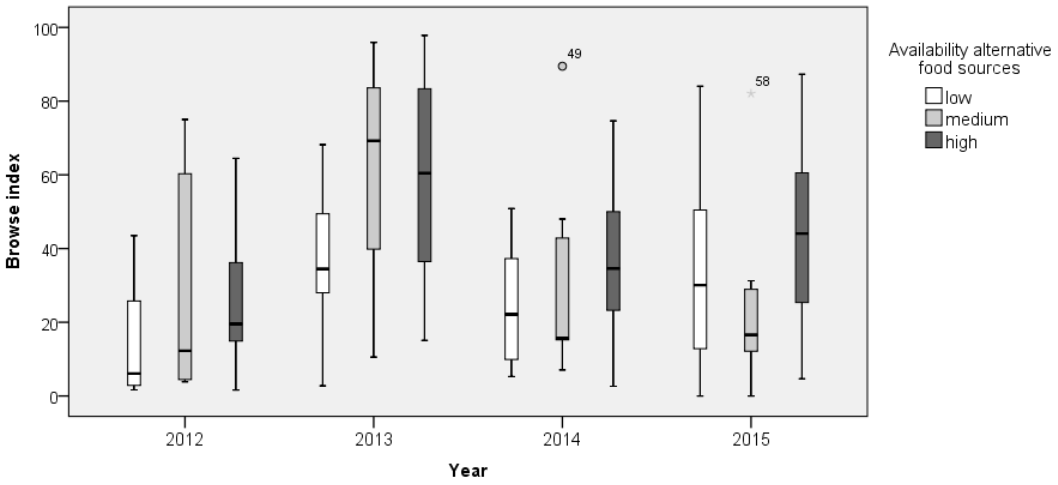

Figure 5.9 *Browsing index (percentage of broadleaved tree saplings <1.60 m tall with browsed top shoots) in the four census years in plots with varying alternative food available for ungulates. See Table 5.11 for the definition of low, medium and high alternative food availability.*

In the Kemperberg plots, the availability of alternative food was slightly lower as compared to the plots in the other sections in the Park. In the Kemperberg, 54% of the plots had a high alternative food availability, against 67% and 81% in Hoenderloo and Wildbaan respectively.

On the species level, most species were represented with too few individuals in the plots to do an analysis on differences in the browsing index between years. Only *B. pendula* and *S. aucuparia* occurred in sufficient numbers (that is with at least 20 individuals <1.6 m in height in a plot). Browsing on *B. pendula* was considerably lower than on *S. aucuparia* (Figure 5.10). Browsing on both species was significantly higher in 2013 (Kruskal-Wallis: *B. pendula*: χ^2=24.4, p<0.001; *S. aucuparia*: χ^2=13.3, p=0.004).

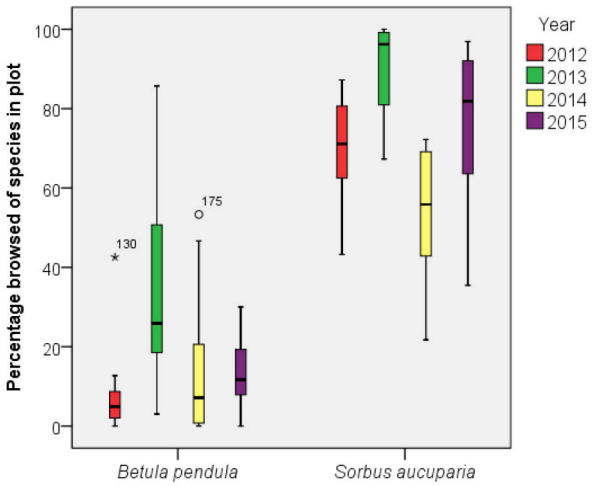

Figure 5.10 *Median browsing index of Betula pendula and Sorbus aucuparia in the four census years. Medians are calculated for plots with at least 20 individuals of a species present <1.6 m in height and in plots that were available for analysis over the entire period.*

The percentages of individuals browsed of *B. pendula* and *S. aucuparia* were not related to the total density of the regeneration in the plot nor to the number of broadleaved individuals, either total number or only individuals <1.6 m high. The percentage of top shoots browsed in *B. pendula* decreased by as the number of individuals of conspecifics increased in the plot, but this correlation was not significant in any year (Figure 5.11). Only in 2015 was there a slight negative correlation between percentage of *B. pendula* browsed and the total number of conifers present in the plot (Spearman's rho=-0.511, p=0.025, n=19).

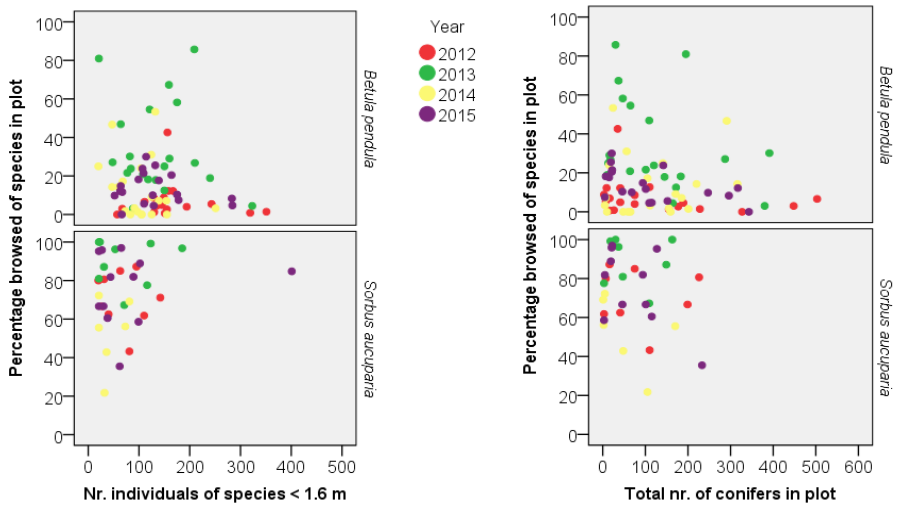

Figure 5.11 *Percentages of plants of Betula pendula and Sorbus aucuparia browsed in the four census years as a function of total number of the species in the plot (left) or total number of conifers in the plot (right). The browsing index per species was calculated for plots with at least 20 individuals of a species present <1.6 m in height and in plots that were available for analysis over the entire period.*

Based on the browsing index data of the four censuses, it is possible to calculate the required sample sizes that would enable the detection of a given percentage difference in browsing (Figure 5.12). These sample sizes were calculated using the formula given by Eckblad (1991):

$$N=t^2 * \text{variance} / (\text{accuracy} * \text{mean})^2$$

where t=t-value from t-distribution with α=0.05 and appropriate df, variance and mean of the browsing index of the census year, and accuracy as the proportion deviation from the estimated mean.

On average, the current network of 70 plots would allow observers to note a difference of about 15-20% in the browsing index.

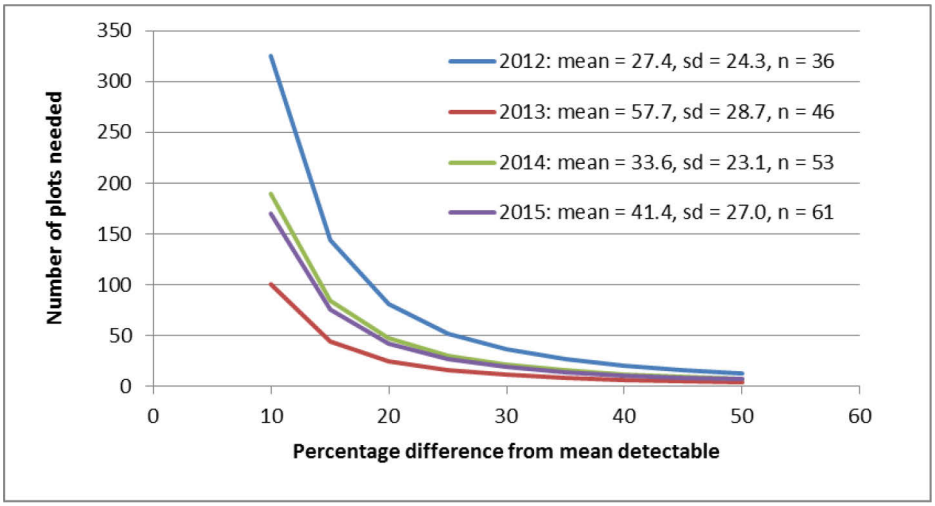

Figure 5.12 *The number of plots required to note a difference of 10-50% from the estimated mean percentage browsed in the plots in 2012-2015. Calculations are based on the assumption that a 2-sided t-test is performed to test the difference in the browsing index between censuses, with α=0.05.*

5.3.6 Changes in species composition

No large changes in species composition were detected over the four-year monitoring period. *P. sylvestris* and *B. pendula* dominated most of the plots and were able to grow into the large height classes. Other conifers like *P. menziesii* and *L. kaempferi* were able to maintain themselves in the plots and continued to grow into the larger height classes (Figure 5.13).

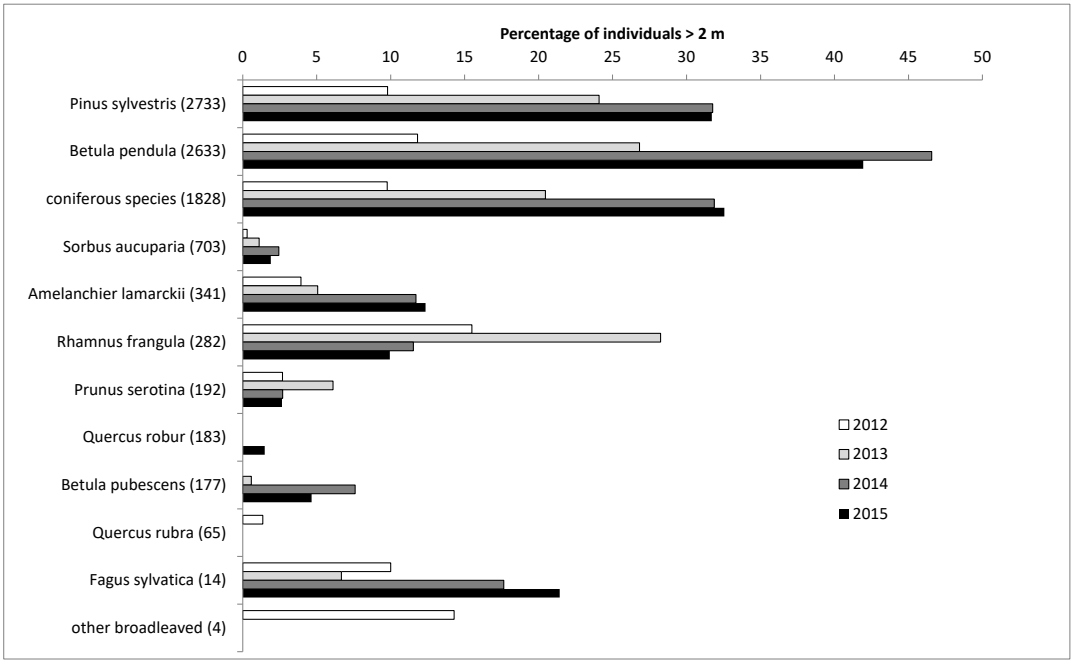

Figure 5.13 *Percentages of individuals larger than 2 m within species by year in plots that were monitored over the entire four-year period. Mean total number of individuals between brackets.*

The smaller size classes contained the highest number of species. On average 6 species were present in a plot in the lowest height class, and the number of species present in a plot decreased as height classes increased (Figure 5.14). Over the years, there was a slight increase in the number of species in the classes over 160 cm.

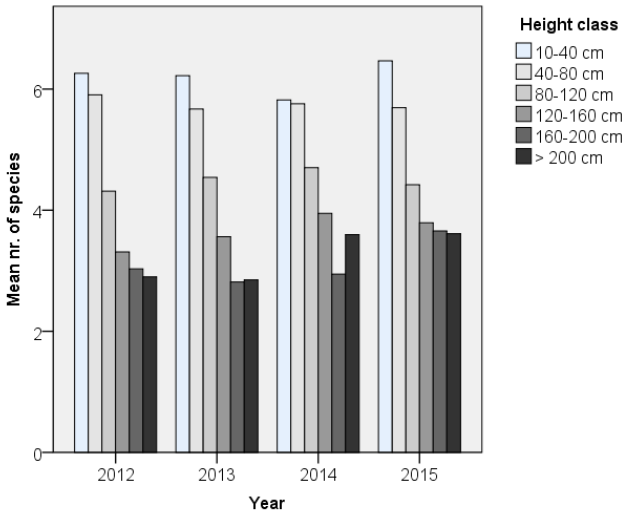

Figure 5.14 *Average number of species per height class per plot over the four-year monitoring period. Data include plots that were monitored over the entire four-year period.*

S. aucuparia was barely able to reach height classes beyond the browsing height of ungulates (Figure 5.15). When *S. aucuparia* was present in a plot, it was mostly confined to the lower height classes and stayed there over the years due to frequent browsing.

When *B. pendula* was present in the plots, it was generally able to grow into the larger size classes (Figure 5.16). Only in a few plots with initial dominance of *P. sylvestris was B. pendula* unable to establish itself in the larger size classes.

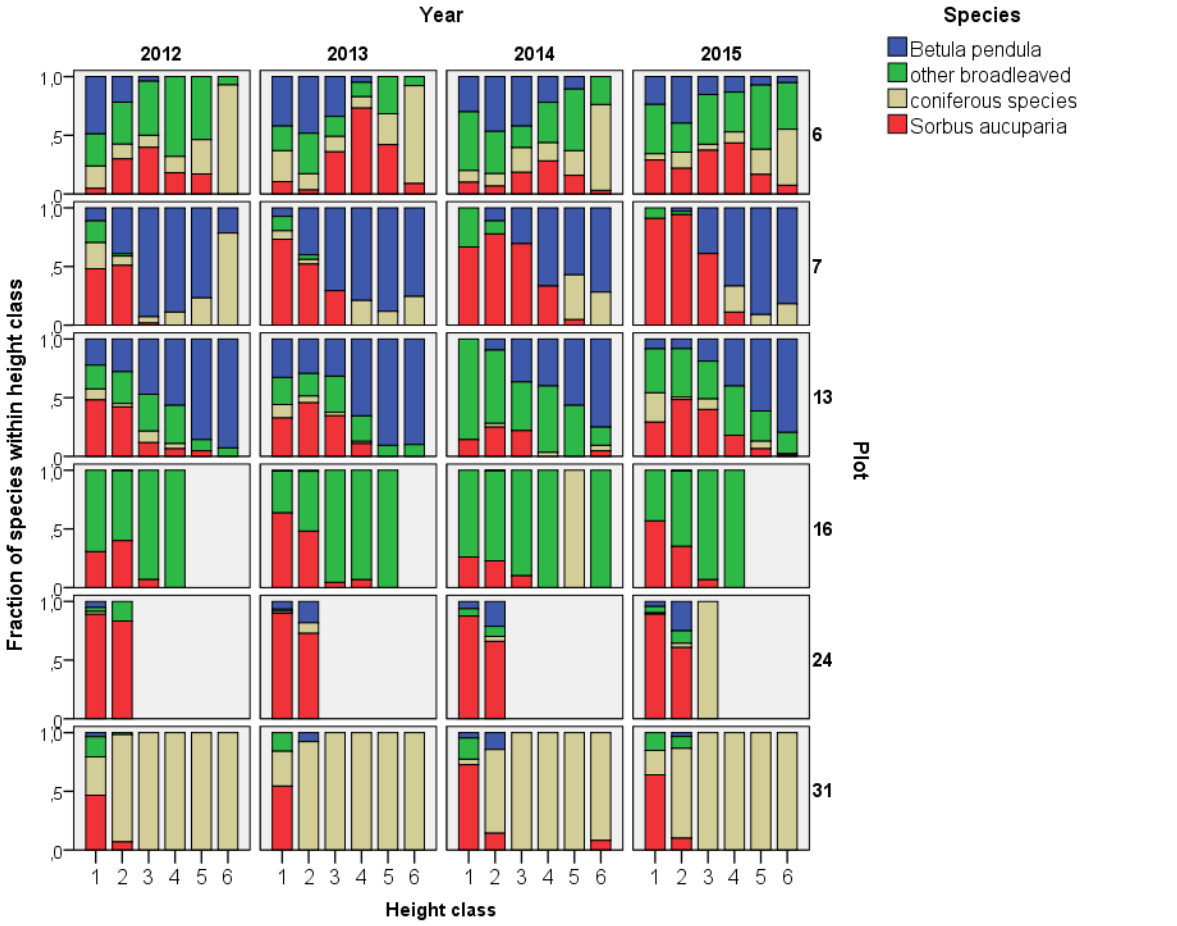

Figure 5.15 *Fractions of species within height class per year and per plot. Only plots are shown that were monitored over the entire four-year period and that contained at least 20 individuals of Sorbus aucuparia.*

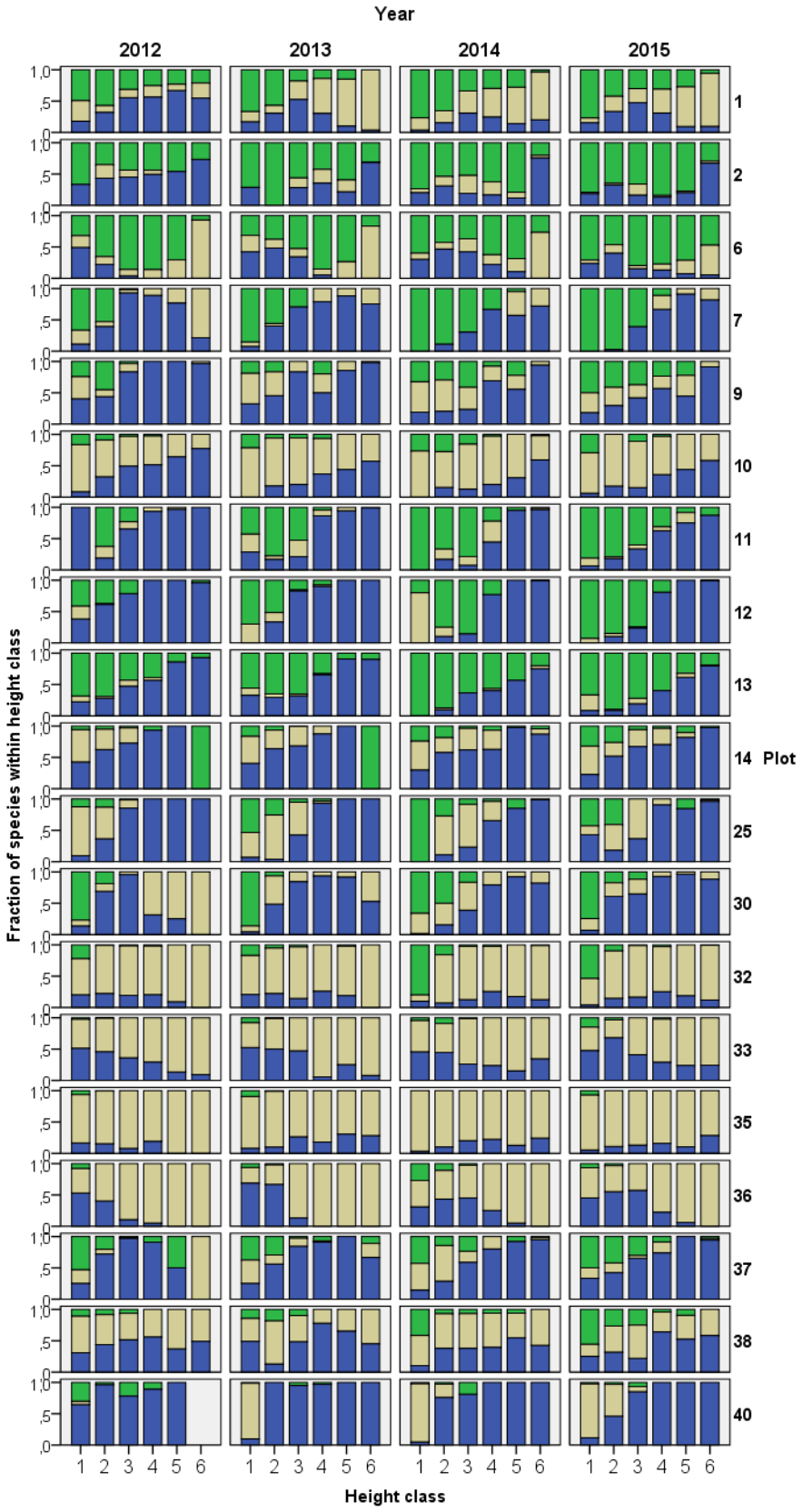

Figure 5.16 *Fractions of species within height class per year and per plot. Only plots are shown that were monitored over the entire four-year period and that contained at least 20 individuals of Betula pendula.*

The mean species diversity increased slightly over the four census years (Figure 5.17). This was not related to the increase in the number of species. The number of species was significantly different (K-W tests within years, all $p<0.01$) between sections, being almost twice as high in the older and more fertile estate areas of Hoenderloo and Kemberberg than in the poorer sites of Wildbaan (Figure 5.17). Diversity increased in Hoenderloo and Kemperberg but not in Wildbaan; however, this increase was not significant between years.

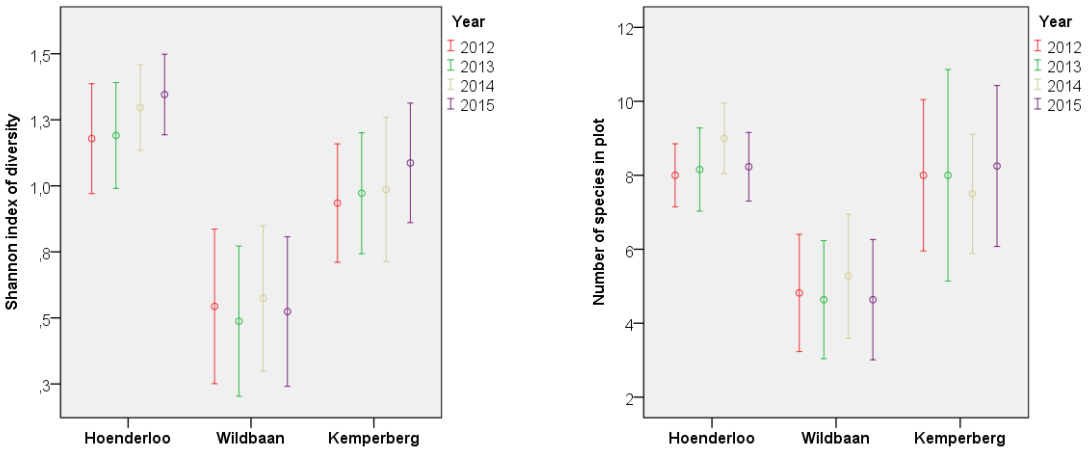

Figure 5.17 *Shannon's index of diversity (left) and mean number of species per plot (right) in the four monitoring years in Hoenderloo (13 plots), Wildbaan (11 plots) and Kemperberg (8 plots). Data include plots that were monitored over the entire four-year period and were accessible to ungulates.*

5.4 Discussion

Browsing varied considerably between years. No consistent increasing or decreasing trend in browsing was detected over the four-year monitoring period. Weather conditions varied considerably between years. The winter 2011/2012 was rather warm, with a short cold period in February with 13 days of snow covering the ground (Figure 5.18). The winter 2012/2013 was exceptionally cold, with low temperatures in January and February, and a relatively deep snow cover persisting into the middle of March (Table 5.12). The following spring was also colder than average. The winter of 2013/2014, however, was exceptionally warm, with no snow at all. The winter of 2014/2015 was normal, with a thin snow cover. It is likely that the high average browsing index in 2013 is due to a prolonged winter and long snow cover in the preceding period. Of course, other factors may also underlie the variation in browsing, such as the availability of an extensive acorn crop. This was not further investigated.

Table 5.12 *The occurrence of a snow cover in the winter periods preceding the censuses. Data from weather station Deelen. Source: www.knmi.nl.*

Winter	Period with snow	Days with snow cover	Maximum snow depth (cm)
2011/2012	30/1 – 13/2	13	3
2012/2013	6/12 - 14/12	8	11
	15/1 - 15/3	38	10
2013/2014	no snow	-	-
2014/2015	17/12 - 9/2	25	5

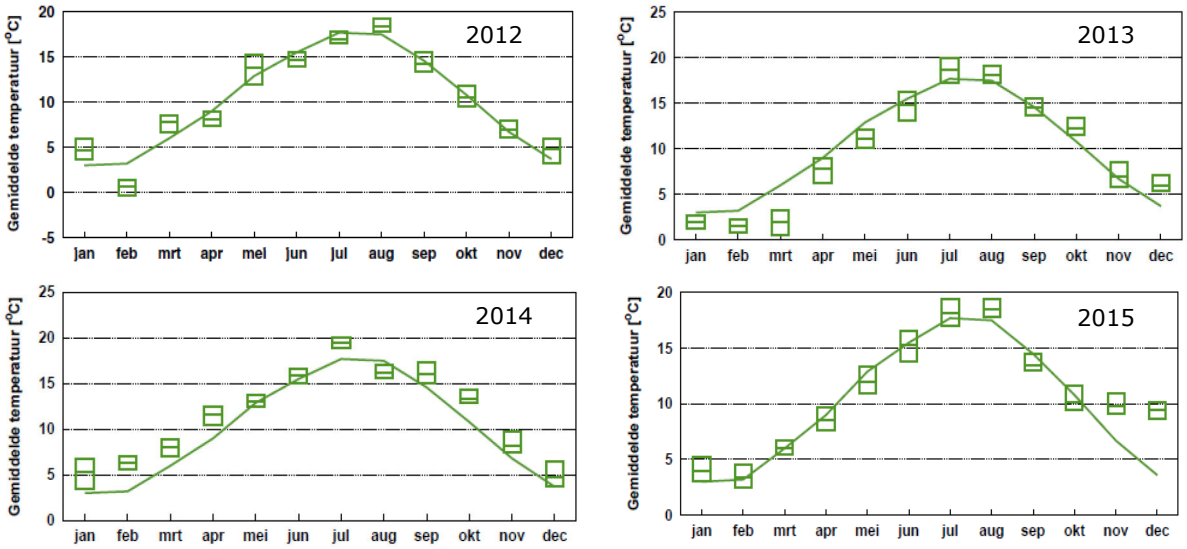

Figure 5.18 *Mean monthly temperatures in the four census years. Boxes indicate the mean, maximum and mean monthly average temperatures measured in the weather stations in the Netherlands. Curve indicates the long-term average temperature. Data from www.knmi.nl.*

Deer clearly prefer to browse certain species. *R. frangula*, *B. pubescens* and *S. aucuparia* are selectively browsed and are hardly able to grow into the highest size classes. The classical 'victim' of browsing, *Q. robur*, is only intermediately preferred by deer, indicating that ungulate browsing cannot solely be held accountable for the lack of oak recruitment, the most preferred species.

Species like *A. lamarckii* and *P. serotina* are moderately preferred by ungulates. These species are also selectively removed from the forest understorey by management. As they are used for browsing, maintaining these species in the forest understorey might deflect some browsing pressure from other species.

Preferential browsing restricts individuals to the smaller height classes. Species like *S. aucuparia* or *R. frangula* are easily dispersed by birds and are very frequent throughout the Park, but occur predominantly in the lower size classes. Excluding ungulates by exclosures enables *S. aucuparia* to grow up with other species.

Red deer also browse on individuals >2 m by breaking or bending the top with their antlers (see e.g. Smit et al., 1998). This means that the total effect of red deer on the growth and survival of trees is larger than what is expressed in the data of this report (where the browsing index was calculated for individuals <1.6 m).

When alternative food sources like grasses or *Vaccinium myrtillus* are available, browsing on tree saplings increases, but at the same time selectivity in browsing decreases. The negative correlation of browsing to shrub cover may indicate that deer avoid areas with dense cover and low visual range.

There is variation in species composition and browsing incidence in the Park. On average, the Wildbaan area has the lowest soil fertility and has a less diverse woody species flora as compared to the Kemperberg and Hoenderloo sections. There is less browsing in the Kemperberg area.

Given the high spatial and temporal variation in browsing, a large number of plots are required to detect significant differences is browsing. The current network of 70 plots allows observers to note a 15-20% change in browsing.

5.5 Conclusions

Four years of monitoring cannot reveal the full impact of ungulate browsing on the succession of tree species in the Park area. The species composition in the seedling and young sapling layers shows that there is a potential for a diverse tree population in the Park area, but this is reduced by the browsing activity of ungulates. It is, however, not yet possible to draw a conclusion on the long-term impact of browsing on tree species diversity. Competitive exclusion of some species by the dominance of fast growing pioneers like *B. pendula*, *P. sylvestris* and *L. kaempferi* will likely reduce the diversity of tree species, even in the absence of browsing. Continued monitoring of the current plots combined with observations in the newly created exclosures will allow future browsing to be evaluated.

5.6 Research recommendations

Based on these results, we recommend the following:

- Continue to monitor browsing in the established network. Expand the network to replace plots that have grown into the thicket phase with new plots with young plants. Plots in the thicket phase can be kept in the monitoring system to study tree species dynamics into the pole phase under the influence of ungulate browsing.
- Enable the establishment of a direct link between browsing and ungulate activity by monitoring tree browsing in front of the camera stations.
- Increase the exclosure network to determine tree species dynamics over the gradient in soil fertility and light availability in the absence of ungulate browsing.

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Annex 1 Video camera deployment time

Table A1.1 *Number of days the video system was operational at wildlife crossing structure Deelerwoud.*

Camera North		Camera South	
Start date and time	**Deployment duration (days)**	**Start date and time**	**Deployment duration (days)**
2-10-2013 11:50	29	2-10-2013 11:50	29
1-11-2013 4:30	28	1-11-2013 8:30	29
3-12-2013 21:30	28	3-12-2013 15:10	28
1-1-2014 1:50	31	1-1-2014 1:10	31
1-2-2014 1:00	28	1-2-2014 2:10	28
1-3-2014 1:40	13	1-3-2014 0:10	14
23-4-2014 14:20	7	22-4-2014 14:50	8
1-5-2014 2:40	31	1-5-2014 6:10	31
1-6-2014 10:30	29	2-6-2014 5:40	29
1-7-2014 0:10	31	1-7-2014 5:50	30
1-8-2014 8:20	31	1-8-2014 12:30	30
1-9-2014 2:20	30	1-9-2014 2:20	30
1-10-2014 0:50	31	1-10-2014 0:50	31
1-11-2014 0:10	30	1-11-2014 0:10	30
1-12-2014 0:20	31	1-12-2014 0:20	31
1-1-2015 8:30	30	1-1-2015 8:30	30
1-2-2015 14:30	27	1-2-2015 17:40	27
1-3-2015 3:40	31	1-3-2015 3:50	31
1-4-2015 6:20	29	1-4-2015 13:20	29
1-5-2015 7:00	30	1-5-2015 6:40	30
12-6-2015 20:00	18	12-6-2015 9:00	18
1-7-2015 1:40	31	1-7-2015 2:50	31
1-8-2015 5:20	30	1-8-2015 5:20	31
1-9-2015 0:00	30	2-9-2015 2:20	29
1-10-2015 1:20	31	1-10-2015 11:20	31
1-11-2015 4:50	30	1-11-2015 11:20	29
4-12-2015 11:40	27	4-12-2015 11:40	27
1-1-2016 15:20	28	1-1-2016 15:20	30
1-2-2016 17:10	28	1-2-2016 5:50	29
1-3-2016 8:40	31	1-3-2016 8:40	30
1-4-2016 0:00	30	1-4-2016 5:00	30
1-5-2016 0:10	31	1-5-2016 1:50	31
1-6-2016 0:00	29	1-6-2016 10:50	29
TOTAL	**843**		**843**

Table A1.2 *Number of days the video system was operational at wildlife crossing structure Oud Reemst.*

Camera North		Camera South	
Start date and time	**Deployment duration (days)**	**Start date and time**	**Deployment duration (days)**
2-10-2013 11:50	29	2-10-2013 11:50	29
1-11-2013 10:10	29	1-11-2013 10:50	29
1-12-2013 6:20	31	1-12-2013 5:00	31
1-1-2014 13:50	30	1-1-2014 13:50	30
1-2-2014 18:20	27	2-2-2014 10:50	26
1-3-2014 11:10	13	1-3-2014 11:10	13
22-5-2014 8:50	10	25-4-2014 23:10	5
1-6-2014 0:40	30	1-5-2014 0:50	31
1-7-2014 4:20	31	1-6-2014 1:40	30
1-8-2014 0:30	31	1-7-2014 4:40	31
1-9-2014 3:50	30	1-8-2014 0:40	31
1-10-2014 2:30	31	1-9-2014 0:10	30
1-11-2014 11:10	22	1-10-2014 2:20	30
24-7-2015 11:00	7	2-11-2014 9:10	21
2-8-2015 8:00	29	24-7-2015 10:50	7
1-9-2015 1:00	29	1-8-2015 0:50	31
1-10-2015 0:30	31	1-9-2015 6:10	29
1-11-2015 0:20	30	1-10-2015 0:30	31
1-12-2015 5:40	30	1-11-2015 1:30	30
1-1-2016 0:10	30	1-12-2015 8:40	30
1-2-2016 3:30	28	1-1-2016 0:10	30
1-3-2016 10:40	30	1-2-2016 1:20	29
1-4-2016 11:00	29	1-3-2016 10:30	31
1-5-2016 6:00	31	1-4-2016 3:40	29
1-6-2016 0:10	30	1-5-2016 2:10	31
		1-6-2016 1:30	30
TOTAL	**589**		**614**

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