The impact of fallow deer (*Dama dama*) grazing on the biodiversity of a Dutch coastal dune system

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Abstract: In the coastal dune system of Amsterdamse Waterleidingduinen (AWD), the Netherlands, numbers of the once introduced fallow deer (*Dama dama*) increased exponentially during the late 1990s and early 2000s. Thereby grazing pressure also increased. By the spring of 2016, the density was an estimated 190-220 deer/km². Several studies show that increased grazing pressure has resulted in loss of biodiversity. This was based on long-running monitoring networks of plant and animal species (including citizen science by volunteers), databases for sightings of plant and animal species, vegetation mapping, data modelling, small-scale field experiments and judgements by independent (inter)national experts. Studied species included mammals, birds, reptiles, butterflies, micro and macro moths, bees, bumblebees, hoverflies, butterflies and plants, as well as vegetation and habitats. Temporal comparisons were used in order to detect changes within the area over time, spatial comparisons for differences between AWD and other, comparable dunes systems with little or no fallow deer grazing. This review summarizes all published papers and reports on this subject up to 2024. These reports are all in Dutch, and therefore this review also makes the conclusions of these publications available for a wider audience. The correlation between increased deer numbers and strongly decreasing numbers of many species (groups) is such that it is justified to conclude that a high grazing pressure has led to significant biodiversity loss, and that strictly protected Natura 2000 habitats are under pressure. Partially based on the impact on biodiversity, the responsible authorities have granted permission for population control of fallow deer since 2016.

Keywords: fallow deer, *Dama dama*, Amsterdamse Waterleidingduinen, deer grazing, overgrazing, biodiversity loss, cascading effects.

Introduction

In temperate climates, large herbivores influence their ecosystems in multiple ways (Côté et al. 2004). They facilitate many plant and animal species, but can also disrupt the habitats they occur in when grazing pressure is too high. By grazing, they have an impact on the biomass and the vegetation height and structure, they produce degradable manure and treading disturbs the soil by either loosening or compacting it. This speeds up or slows down nutrient cycles, decreases litter accumulation and changes the microclimate. As a result the vegetation composition changes. Finally, they compete with, or facilitate other herbivores. Fallow deer (*Dama dama*) were first recorded in the coastal dune reserve of Amsterdamse Waterleidingduinen (AWD), the Netherlands, in the early 1970s. Their numbers increased significantly during the 1990s and 2000s. The increased grazing pressure lead to concerns about their impact on biodiversity. Therefore, a series of studies was set up in order to quantify the impact (if any). This paper reviews the findings of these studies up to and including 2024 and covers habitats, vegetation, plants, mammals, birds, reptiles and insects.

Site description

AWD (3390 ha) is a coastal dune reserve on the border between the provinces of Noord-Holland and Zuid-Holland (Figure 1). This mainly lime-rich, parabolic dune system was formed between 1200 and 1600 AC. At its widest point, it measures a little over 5 km and at its smallest point it is no more than 1.5 km wide. AWD is owned by the city of Amsterdam (12 km away between the nearest points) and managed by drinking water company Waternet. It serves as a vital source for drinking water. With a production of 70 billion litres a year, the area provides up to 70% of the drinking water for Amsterdam and its surroundings. The second main objective is to maintain and – whenever possible – improve the area's natural habitats and biodiversity. The impact of the water production is therefore brought back to a minimum. Roughly, half of the area comprises open habitats, 30% is half open and 20% is closed. From west to east, the habitats of the system change from the sandy beach and the sparsely vegetated foredunes dominated by marram grass (*Ammophila arenaria*) to dune grasslands and wet dune slacks, to dune scrub dominated by common sea buckthorn (*Hippophae rhamnoides*) and finally to dune woodlands. Furthermore, the area is interspersed with waterbodies like unpaved canals and small lakes that are part of the drinking water production facilities, with their own natural values. Coastal dunes support a high and partially endemic biodiversity, but have disappeared in much of Europe as a result of coastal development. It is a relatively rare ecosystem and therefore AWD is protected under the Habitats Directive of the European Union. The Natura 2000 area of Kennemerland-Zuid protects 8170 ha of coastal dune habitats, and AWD covers most of the southern part of the reserve. The Natura 2000 area has been designated to preserve eight habitat types and four species, of which respectively seven and two occur in AWD (Table 1). AWD is furthermore of importance for coastal security (natural sea wall), historical land use (with historical and cultural artefacts) and, with well over a million human visits a year, recreation. From an ecological point of view, issues besides high grazing pressure by deer include fixation of the outer dunes as a safety measure against the sea (turning a once dynamic system into a more static one), high levels of atmospheric deposition (most notably nitrogen), alien invasive plant species and past planting of e.g. pines for timber wood and against sand drift. In order to cope with these issues, sand drift is now being stimulated rather than prevented on a small scale by the removal of top layers in both the outer and inner dunes. An intensive program in order to eradicate alien invasive species has been largely successful. Cattle (cows, sheep) grazed in the area since 1986, but numbers were first lowered before cattle was finally banned in 2017 when grazing pressure from deer became too high.

History of fallow deer in AWD

Based on fossil records, fallow deer were native to the northern part of Europe (including the Netherlands) during the interglacial of the Pleistocene, and went extinct during the Last Glacial Maximum. Despite populations occurring on all continents except Antarctica, it is now considered native only to Turkey where only one undoubtedly natural population survives in the Düzlerçami Game Reserve. Hence, all populations outside Turkey originate from captive stock. It was already introduced across Europe by Phoenicians, Romans and Normans, but most populations are the result of later introductions, many from the 20th century (Masseti & Mertzanidou 2008). Around AWD, fallow deer were first introduced in the nearby Kennemerduinen (within the same current Natura 2000 reserve) around 1958, with about 20 animals present in 1974 (Lever 1985). The first sightings in AWD were in 1973. Fallow deer are not just browsers like the native roe deer (*Capreolus capreolus*), but are also grazers.

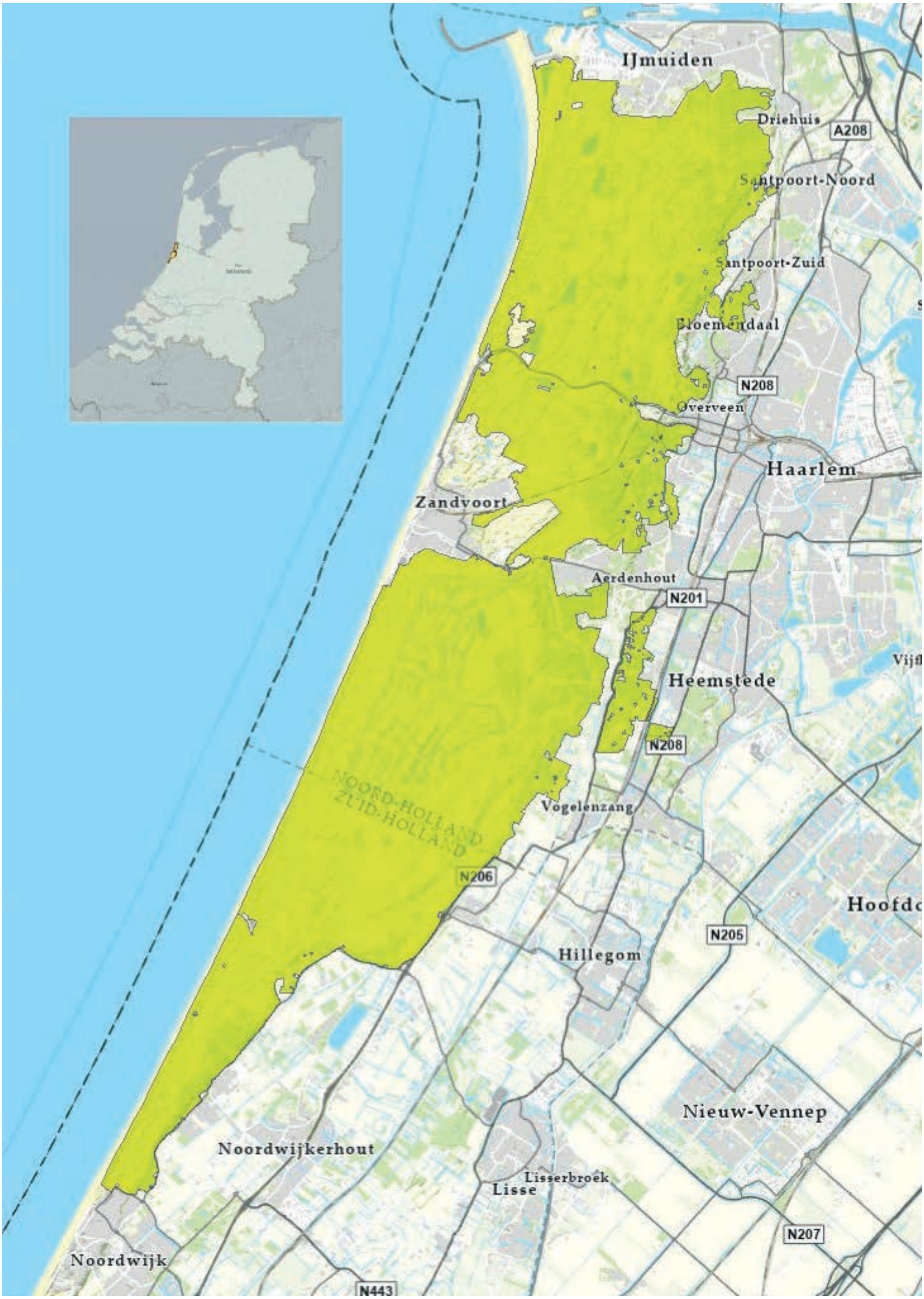

Figure 1. Map of Natura 2000 area Kennemerland-Zuid. Amsterdamse Waterleidingduinen roughly forms the lower half of the reserve. Inlay: position of the area in the Netherlands.

Table 1. Natura 2000 conservation objectives for Kennemerland-Zuid under the Habitats Directive of the European Union (EU).

Habitat types
H2110 Embryonic shifting dunes #
H2120 Shifting dunes ('white dunes')
H2130* Fixed coastal dunes ('dune grasslands' or 'grey dunes')
H2150 Atlantic decalcified dunes Calluno-Ulicetea ('dune heather')
H2160 Dunes with *Hippophaë rhamnoides* ('sea buckthorn scrub')
H2170 Dunes with *Salix repens* ssp. *argentea*
H2180 Wooded dunes of the Atlantic, Continental and Boreal region ('dune woodlands')
H2190* Humid dune slacks ('wet dune slacks')
Species
H1014 Narrow-mouthed whorl snail (*Vertigo angustior*)
H1149 Spined loach (*Cobitis taenia*) #
H1310 Pond bat (*Myotis dasycneme*)
H1903 Fen orchid (*Liparis loeselii*) #

** Habitat types marked with an asterisk (*) have priority*

 # Species or habitat types marked with an (#) occur elsewhere in the Natura 2000 area, but not in AWD

Unlike roe deer, fallow deer have no territorial system that limits population size (Chapman & Chapman 1987). Large predators do not occur in the area, therefore food availability is the main driver behind population densities. With rising deer numbers, collisions with cars in the region increased, and commercial bulb flower fields were damaged by grazing. In order to prevent traffic accidents and economical damage, fences were placed around AWD from 2007 onwards. Since 2012 the entire southern, eastern and northern parts are fenced, cutting the deer off from an important food source: the agricultural land and private estates east of AWD. With both increased numbers and a decreased range for roaming, the browsing pressure within AWD increased significantly. The population peaked with over 3900 counted in 2016. This raised concerns about their impact and therefore Waternet initiated studies and gave assignments to independent NGO's specialized in plant and animal species in order to measure the impact (if any) of deer grazing on the biodiversity of the area. Since 2016 population control within the entire Natura 2000 area (including AWD) was granted by the responsible authorities, partially based on biodiversity loss. The aimed (counted) population size for the AWD after management is determined at 600-800 individuals.

Methods

Studies included: 1. Analyses of existing, long-running standardized monitoring data mostly collected by volunteers (citizen science). 2. Field work in order to collect new monitoring data. 3. Small-scale field experiments. 4. Data modelling. 5. Judgements by independent (international) experts. Most studies in categories 1-4 were initiated by and paid for by Waternet, but were conducted by independent experts.

Deer monitoring

Numbers of fallow deer and roe deer have been monitored annually since 1969 based on a standardized method, carried out by Waternet during late March or early April, just before the vegetation starts growing (high visibility), but before fawns are born. The area is divided over twelve sections, each covered by one team. The fixed routes cover almost the entire AWD. Whenever possible, each team identifies the age and sex of animals encountered. There are three consecutive counts: around dusk on the first day, and around dawn and dusk on the following day, all within set times. The highest tally of the three counts represents the number for that year. This is a monitoring method that only reflects the bare minimum number of deer present in a year. In order to get more insights into the actual number of deer present, experiments with drones, laser techniques (Lidar) from planes and population data modelling have been carried out. Since 1996, deer have also been counted during standardized transect monitoring of rabbits (*Oryctolagus cuniculus*) during spring and autumn, as part of the governmental national network for ecological monitoring (Netwerk Ecologische Monitoring; NEM). A transect of ca. 25 km divided over 35 parts is crossed after dark by car on a minimum of eight nights in both spring and autumn. All rabbits and deer seen in the headlights of the car are counted. Maximum counts per part are used to determine the maximum counts per season.

Existing monitoring data

Waternet has facilitated standardized monitoring of plant and animal species for nature management purposes for decades. In many cases data have been collected by volunteers (citizen science). Long-term data of plants, mammals, birds, sand lizards (*Lacerta agilis*), butterflies and moths were used. The bird, sand lizard and butterfly monitoring has been standardized within the NEM. Data analysis are being carried out by the Central Statistical Office (in Dutch: CBS). This has resulted in long-term series of data that allow both temporal (population trends and changes in species composition) and spatial analysis (comparisons with trends in other areas). For the latter analysis especially, data from National Park Zuid-Kennemerland (NPZK) were valuable: this roughly forms the northern half of the same Natura 2000 area, with the same habitat types, while fallow deer densities are much lower there. Most analyses were carried out by, or in collaboration with independent not-for-profit organizations that are specialized in specific species groups. Moths were not monitored within the NEM systematics, but a local group has conducted more or less standardized monitoring and they have analyzed their own results. Furthermore, the second form of citizen science was the use of online observation platform waarneming.nl (part of observation.org), that stores mostly unstandardized observation data. These data were used to determine species compositions. In order to monitor Natura 2000 objectives, the vegetation is mapped every 10-12 years. These data allowed comparisons within the area over time.

Modelling

No long-term monitoring data was available for bees, bumblebees and hoverflies, but past observations gave insight in the species composition. Species within these taxonomical groups show a variable amount of dependance on specific plant species, both as larvae (host plants) and imagoes (nectar). With preferred plant species in decline, it was expected that the dependant insects were also in decline. Based on flora monitoring data (Mourik 2015) combined with the ecology of the species, expected trends for bees, bumblebees and hoverflies were modelled.

Field studies

Waternet set up experiments with grazed and ungrazed control plots, using four small (1x1 m) exclosures on four different grasslands where smaller natural grazers like rabbits

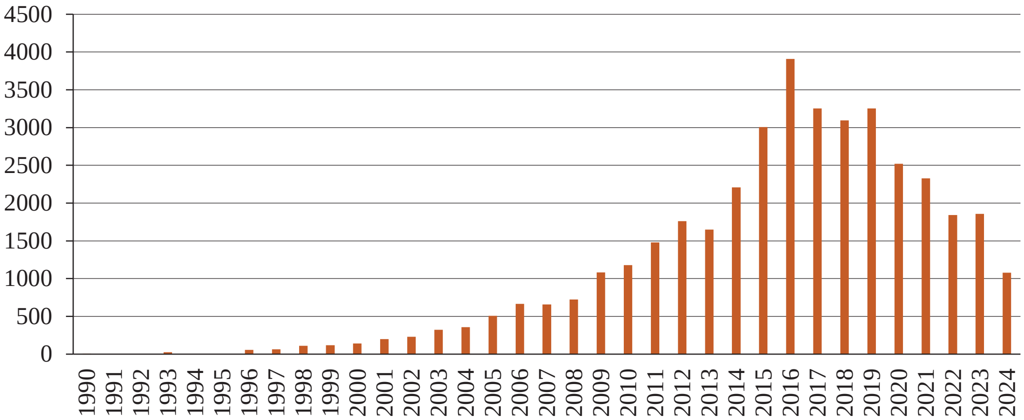

Figure 2. Early spring (pre-reproductive) population trend of fallow deer in Amsterdamse Waterleidingduinen 1990-2024. Population control started from late 2016 onwards.

did have access, but fallow deer did not. The effects on vegetation structure, coverage and species composition in grazed and ungrazed conditions could thereby be measured. In another small-scale experiment, three tiny (0.5 x 0.5m) exclosures were placed in 18 dune grassland plots. Also, several exclosures of different sizes were placed in the area in order to protect vulnerable plant species. Though not set up for a study, these offered an opportunity to measure the conditions of plants in and outside the exclosures. Finally, a past ant survey was repeated.

Expert judgement

The OBN Knowledge Network (OBN Natuurkennis) has ten national expert groups for the natural landscape types of the Netherlands, run by the Ministery of Agriculture, Fisheries, Food security and Nature and the twelve provinces. The OBN Dunes and Coastal Areas Expert Team visited the area twice in order to judge grazing effects by fallow deer. Also, foreign experts from the European Commission have judged nature restoration projects in AWD funded by the EU and carried out by Waternet.

Results

Deer monitoring

Up until spring 2016 there was no population control. For many years deer numbers remained low, but they gradually increased, eventually exponentially (Figure 2). The highest count was in spring 2016, when 3907 individuals were counted. Drone experiments failed to give useful additional insights (Waternet, unpublished data), but according to the Lidar data from 2020 and 2021 ~40% of the deer were missed during the official counts (unpublished data Kavel 10/Waternet). Population modelling showed that up to 48% is missed (FBE Noord-Holland 2024). This means that the population density in spring 2016 was an estimated 190-220 deer/ km². With fawns being born after the counts, the summer population density was even significantly higher. Among the adult deer, does formed the vast majority in 2016 (Figure 3), resulting in exponential population growth each year. Population control from November 2016 onwards focused primarily on the culling of does and fawns, since this lowers the yearly production and thereby is the most effective way to decrease numbers. Between 2016/2017 and 2023/2024, 1440 to 2315 deer

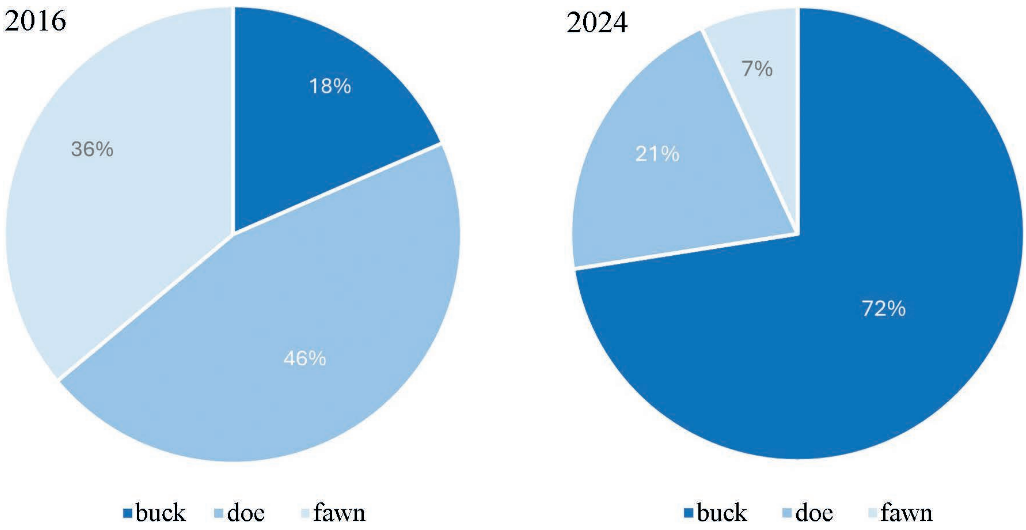

Figure 3. Ratios of bucks, does and fawns of fallow deer in Amsterdamse Waterleidingduinen in 2016 and 2024.

have been shot each winter. This strategy has resulted in both a population decline and a significant shift in the doe-to-buck ratio (Figure 3).

Effects of grazing on habitats, vegetation and plant species

In general, as explained into more detail below, the picture painted by Oosterbaan et al. (2018) and Oosterbaan & Mourik (2020) is that overgrazing has led to a huge impact on the vegetation and vegetation structure of the area. When deer numbers peaked, dune grasslands (H2130) and terrestrial parts of humid dune slacks (H2190) lost their structure and flower richness. Edible plants were grazed off to ground level, creating monotonous grassy lanes of the same height, with only small herbs still flowering. Thickets and shrubs had fallen apart on a large scale due to trampling. There was no rejuvenation in the forests (H2190). The lower layers of herbs and scrub were rare at best but absent in most forested areas.

Natura 2000 habitats

Oosterbaan et al. (2019) conclude that trampling greatly influenced Natura 2000 restoration projects. At sites where sod-cutting had been applied as a nature management measure, the vegetation did not recover. The same applied for the edges of restored pools. While not substantiated, the directorate of the European Commission that judges the execution of EU funded nature restoration projects noted that: *"The management of the site is very well done but overgrazing by fallow deer seems to jeopardise the favourable conservation status of the targeted priority EU habitat 2130 (Fixed coastal dunes with herbaceous vegetation - grey dunes) and the EU habitat 2160 (Dunes with Hippophae rhamnoides)."* (Anne Burrill, DG Environment European Commission, September 2015). Based on expert judgement, the OBN Dunes and Coastal areas Expert Team concluded that grazing had become too intensive and that this contributed to a negative impact on the natural quality of the area. With the grazing pressure at the time, they expected plant species to disappear (VNBE 2018). These expert judgements were later confirmed by data. Based on vegetation mapping, qualifying Natura 2000 habitats decreased significantly between 1997 and 2017. In 1997, 82.5% of the area was assigned to a Natura 2000 habitat type. In 2007, this had decreased to 77%, and in 2017 to 52.8% (Figure 4). The authors mention fallow deer grazing as the most important cause of the decline (Oosterbaan et al. 2018).

Vegetation and plant species

Oosterbaan & Mourik (2020) showed that, based on flora and vegetation mapping in 1997, 2007 and 2017, high density fallow deer grazing has had an effect on three vegetation levels: 1. Biomass. 2 Vegetation forms. 3. Characteristic flora species. In this paper, level 4, 'Physical condition of plants' is added.

1. *Biomass*. The highest scale level is of the total amount of above ground biomass. This seems to have decreased significantly after 2007, correlating with increasing deer numbers. Forest rejuvenation (H2190) had been absent for a long period of time and plant height of all herbs and grasses combined decreased with 33%. This is supported by an additional small-scale field study by Aggenbach & Clevers (2020). Based on field work in 2018 and 2019 with tiny (0.5 x 0.5m) exclosures on 18 dune grassland plots (H2130), they concluded that after only one growing season without deer grazing, the plant biomass, the cover and height of flowering herbs was higher within the exclosures than in control plots.
2. *Vegetation forms*. Oosterbaan & Mourik (2020) grouped similar plant forms together in nine groups (Table 2). On this intermediate scale level, grasses, the poisonous species and mosses increased significantly in coverage (the latter nearly completely caused by one species: the neat feather-moss (*Pseudoscleropodium purum*)), whereas small scrub (H2160), large herbs and lichens steeply decreased. Trees and larger shrubs were unaffected by grazing and increased.

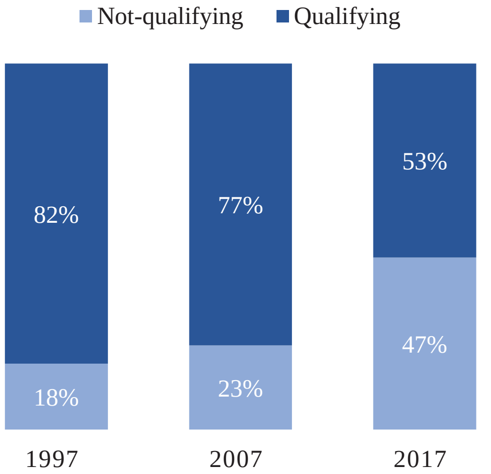

Figure 4. Qualifying Natura 2000 habitats in Amsterdamse Waterleidingduinen in 1997, 2007 and 2017, based on data from Oosterbaan et al. (2019).

Table 2. Vegetation groups and difference in coverage in Amsterdamse Waterleidingduinen between 1997 and 2017 (based on Oosterbaan & Mourik 2020).

Vegetation group	1997	2017	Difference	
	ha	ha	ha	%
Trees	295	441	145	+49%
Large scrub	185	268	83	+45%
Small scrub	494	289	-205	-41%
Grasses	872	1086	214	+25%
Large herbs	414	213	-202	-49%
Small herbs	97	79	-18	-19%
Poisonous herbs	35	61	26	+26%
Mosses	779	1229	450	+42%
Lichens	171	34	-137	-80%

increase
decrease

Grasses and mosses benefited from shrub complexes like sea-buckthorn (H2160) falling apart by trampling, covering the newly created open spaces. Also, they benefited from the disappearance of species like European dewberry (*Rubus caesius*) and burnet rose (*Rosa pimpinellifolia*) that normally occur in dune grasslands (H2130). A steep decline of lichens was largely caused by trampling. Large herbs declined due to grazing, and as a result, poisonous herbs benefited from the lack of competition. The latter was already shown in several earlier studies. Based on half a century of standardized flora monitoring, Mourik (2015, 2017) showed that only very small or poisonous species, some grasses and older trees and larger scrub with thick barks survived. No less than 66% of all common non-poisonous flowering plants measuring over 15 cm in height had decreased strongly between 2000 and 2013-2014. Species with large leaves or inflorescences decreased more than smaller species (that are less vulnerable to grazing). As expected beforehand, poisonous species did not decrease. Oosterbaan et al. (2019) state that based on flora mapping for the Natura 2000 monitoring system, virtually all plant species had been negatively affected by fallow deer grazing accept for the poisonous and very odorous ones.

3. *Characteristic flora species*. On the third scale level, Oosterbaan & Mourik (2020) concluded that coverage of characteristic dune plants had decreased in alarming rates. Out of 177 species mapped between 1997 and 2017, 72% decreased whereas only 24% increased. For species depending on pollination, even 76% decreased and only 19% increased.
The effects of grazing on larger flowering herbs were already studied before deer numbers peaked. In a small-scale field experiment, using 16 1x1 m exclosures spread over four dune grassland sites, Reussien (2013) and Aldershof (2014) showed that deer grazing had a negative impact on flower richness and the occurrence of host plants for butterflies. In control plots, species normally very common in the dunes like viper's bugloss (*Echium vulgare*), common bugloss (*Anchusa officinalis*), common evening-primrose (*Oenothera biennis*) and greater mullein (*Verbascum thapsus*) were nearly impossible to find. If present, usually only rosettes were found, whereas these species grew abundantly within the small exclosures (Figure 5). In the control plots, only poisonous, very smelly and/or thorny species like common ragwort (*Jacobaea vulgaris*) and hound's tongue (*Cynoglossum officinale*) flowered. Mourik (2017) showed that the steep decline of 78 species between the 1996-2005 and 1996-2015 decades was much stronger than expected based on national trends, correlating with the strong increase of the deer population, and that the decrease intensified during the final years of the study (with deer numbers still growing). This also affected rarer species. For instance, in 2006-2014 there were still 54 sites with the nationally rare round-leaved wintergreen (*Pyrola rotundifolia*), but in 2015-2016 only six sites were left. A similarly alarming trend was seen in the localized *neerlandica* subspecies of the orchid broad-leaved helleborine (*Epipactis helleborine*), with 49 sites found in 2006-2014, but only two in 2015-2016. Wild basil (*Clinopodium vulgare*) decreased from 168 sites in 2002 to 15 in 2015-2016 (Mourik 2017). Oosterbaan & Mourik (2020) mentioned that due to an increase of small-scale sand drift caused by ecological restoration projects, pioneering species should have benefited, but didn't. These also decreased as a result of deer grazing.

4. *Physical condition of plants*. The fourth, smallest scale, that was not specifically categorized as such by Oosterbaan & Mourik (2020), is the physical state of plants. Many plants are still present, but do not or barely flower (Mourik 2015). Edible plants that have not (yet) been grazed off to the ground, are in a poorer physical state than those protected within exclosures. Oosterbaan et al. (2019) state that this even applies to normally very common species. During flora mapping, many were encountered in a vegetative state only. On transects used for standardized butterfly monitoring, the number of flowers (and thereby: nectar supply) strongly decreased. In 1992-1996 (hardly any fallow deer), 2007-2008 (mod-

Figure 5. In a field experiment with small exclosures (Reussien 2013, Aldershof 2014) unfenced control plots were grazed off to the ground, whereas inside small exclosures (1m x 1m) larger flowering herbs grew abundantly, in this example dominated by viper's bugloss (*Echium vulgare*), Amsterdamse Waterleidingduinen, 8 June 2016 (Vincent van der Spek/ Waternet).

erately high numbers) and 2015-2016 (peak numbers) the number of flowers along butterfly monitoring transects were counted. Between 2007-2008 and 2015-2016, the number of flowers suitable for butterflies decreased by 77%. Compared to 1992-1996, this was even 98% (Wallis de Vries 2017). Van der Spek & van der Voet (2018) used broad-leaved helleborine as an example species in order to measure the physical state of edible plants. The orchids within two 7x4 m exclosures were on average more than twice as large, the size of the leaves was nearly twice as long and the number of flowers was more than twice as high as in helleborines in the control plots. The number of flowering plants within the exclosures was 131, whereas only twelve were found in the control plots within the same humid dune slack (H2190). Oosterbaan et al. (2019) confirmed this by concluding that 95% of the broad-leaved helleborines inside exclosures flowered, opposed to only 5% outside the exclosures.

Effects of grazing on fauna

Mammals

The population of roe deer in AWD was at a maximum between 1996 and 2002, with up to 250 counted. With increasing numbers of fallow deer, roe deer rapidly declined and eventually disappeared altogether (Figure 6). Nowadays they are only very seldomly seen, whereas they do occur regularly in surrounding estates without fallow deer (personal observation). Rabbits are the other mammalian grazers of the area, but populations in the Netherlands including AWD have dwindled, in many places to near-extinction, due to the outbreak of variants of Rabbit Hemorrhagic Decease. Potential positive or negative effects in relation to fallow deer could therefore not be studied.

Birds

The nightingale (*Luscinia megarhynchos*) is on the Dutch red list of threatened birds. Nationally the numbers have declined, but

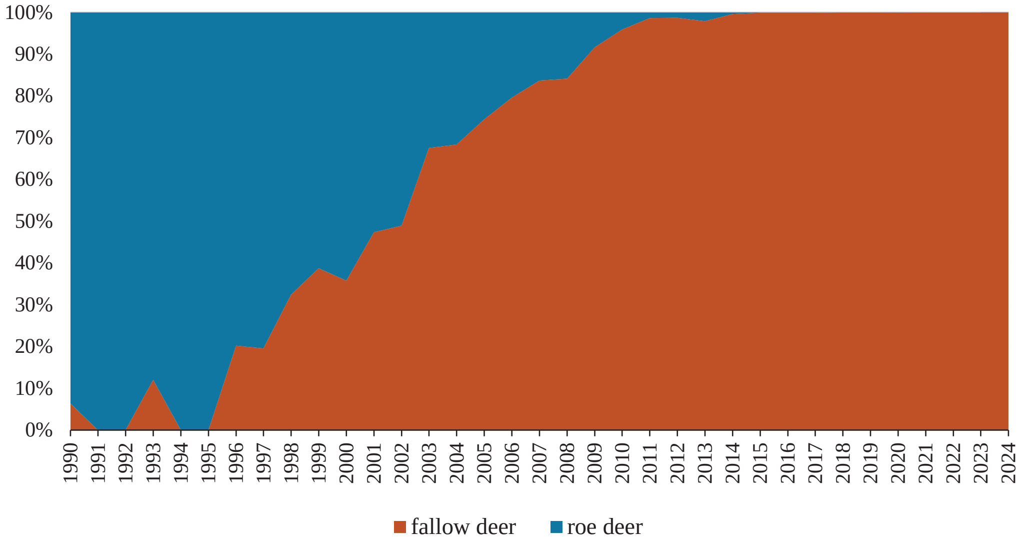

Figure 6. Ratio of roe deer (orange) vs. fallow deer (blue) during deer counts at Amsterdamse Waterleidingduinen 1990-2024. Roe deer have been outcompeted by fallow deer: they virtually disappeared after 2014.

the calcareous coastal dunes form the national stronghold, and densities are still high there. AWD however forms the exception. Noordzij & van der Spek (2017) showed that there is a significant negative correlation between deer and nightingale densities. The higher the deer densities, the steeper the declines. In 2015, the lowest number of nightingales since the start of the standardized breeding bird censuses in 1985 was reported. In Meijendel, province of Zuid-Holland, a geomorphologically similar dune system without fallow deer (save a few stragglers), the nightingale densities slightly increased during the same time span. In order to eliminate other causes, only areas without past large-scale nature restoration measures like removal of the invasive alien black cherry (*Prunus serotina*) or sod cutting were used in this study. Browsing and trampling by deer resulting in more open scrub with less cover was believed to be the determining factor for the declines within AWD (Noordzij & van der Spek 2017). Another example species dependant on scrub (H2160) for breeding is the dunnock (*Prunella modularis*). De Groot (2024) showed that based on breeding bird censuses between 1984-2022, the species declined steeply after 2010, whereas similar declines were not nearly as strong both in comparable areas just outside AWD and nationally. Based on aerial photographs, De Groot (2024) concluded that scrub with e.g. sea buckthorn and wild privit (*Ligustrum vulgare*) had declined and the quality of remaining scrub deteriorated (H2160), caused by fallow deer trampling and grazing.

Reptiles

Sand lizard is the only reptile species of the area. Coastal dunes form an important habitat for this strictly protected species under the Habitats Directive. Based on long-term monitoring the population in AWD increased between 1994 and 2012 (Ehrenburg & Janssen 2014). However, the population has declined between 2012 and 2023. Nationally, the population also declined since, so more factors seem to be at place, but Molenaar et al. (in press) showed that the population in AWD declined earlier, and that the decline was steeper, also compared to similar areas nearby with less or no fallow deer. They showed that the habitat within lizard monitoring plots had changed and that habitat structure, which is of vital importance for sand lizards, had declined as a result of grazing.

Butterflies

Three studies based on long-term monitoring show that the butterfly population (all species combined) decreased by 76% between 2005 and 2016 (Wallis de Vries 2015, 2017, 2019). Fifteen out of the 23 species (65%) that are common in AWD declined. These declines were statistically significantly stronger than in the neighboring NPZK, where deer densities were much lower. The declines in AWD were also statistically significantly stronger than in comparable coastal dune systems without fallow deer elsewhere in the Netherlands. The declines intensified in 2015-2016, with deer numbers still on the rise, compared to 2014. Declines were strongest in species that, based on their ecology, *a priori* were classified as moderately to very vulnerable for grazing, whereas species marked as not vulnerable for grazing did not show such marked declines. This was further demonstrated by the fact that areas with higher deer densities showed stronger decreases. According to the author, this shows that the relationship between increasing deer numbers and declining butterfly population are causal. Finally, after the number of deer also increased in NPZK, species vulnerable to grazing also started to decline there.

Moths

For the macro moths, Wallis de Vries (2015) calculated that a larger number of species declined in AWD (30% out of 393 species) than in neighboring NPZK (13% out of 420 species). As in butterflies, the decline in species *a priori* marked as vulnerable for grazing was strongest. Moth monitoring between 2006-2019 showed that especially a group of species dependant of dune grasslands was in decline. Six out of seven of these species show more positive trends nationally, whereas they declined in AWD. Therefore the causes were thought to be local and the author links this to grazing by fallow deer (Kruijsen 2021).

Bees, bumblebees and hoverflies

With edible flora decreasing (see above), population declines of species dependant of plants as hosts or for nectar were expected. Smit (2015) calculated that out of 85 species of bees and bumblebees known to occur in AWD between 1980 and 2014, 65 must have decreased based on their ecology (dependance on nectar) in relation to long-term plant monitoring data (Mourik 2015). For ten species the decline was over 50%. In some species of hoverfly the larvae use specific host plants. Out of 105 species known to occur in AWD between 1980 and 2014, eleven species were thought to have shown a strong decline, whereas only two had increased. The estimated trends for bees, bumblebees and hoverflies were based on the absence or occurrence of plant species per km^2 grids and not on the actual numbers of plants, let alone the physical state of individual plants. Smit (2015) therefore stated that the actual declines must have been much stronger than calculated.

Ants

Ants are the only group studied for which negative effects that can be correlated with fallow deer were not found (Noordijk & van Loon 2015). Based on expert judgement however, the authors did raise concerns about scarce species with nests above the ground, since trampling by deer could disturb these.

Narrow-mouthed whorl snail
(Vertigo angustior)

This tiny snail is a Habitats Directive species (H1014) and it therefore is of high nature management importance. Population sizes or trends are unknown, but in general grazing has a negative impact. Expert judgement by independent authorities on mollusks came to the conclusion that grazing pressure by fallow deer has created a 'savannah-like' habitat (low vegetation with larger bushes), with a large impact on the structure and composition of the vegetation and the structure of the soil. Therefore a strong decrease of snails in general, including the narrow-mouthed whorl snail, was suspected (Boesveld & Gmelig Meyling 2018).

Discussion

Legal status

The Dutch legal status of fallow deer as a native, protected species can be challenged. Based on fossil records, fallow deer indeed once occurred in the Netherlands naturally. However, it also went extinct naturally under a climate change, and all current Dutch populations are of feral stock.

Population trends and number of deer counted

Using Lidar data for deer counts in a hilly terrain with forests and scrub is very much in its infancy and the value of the results need to be interpreted with caution. Two issues arise: in order to cover the entire area, a plane has to fly a total of 30 flight lines in order to cover the area. In the meantime, deer were expected to have moved around. Determining the number of double counts as well as the number of deer missed was impossible. Aerial photographs were made simultaneously. Artificial Intelligence could detect objects but was far from flawless, and deer had to be manually separated from other large living creatures like cattle, foxes, visitors etc., making it vulnerable to mistakes. Based on expert judgement, the hunters estimate 40-50% of the deer are missed during the official counts, in most years towards the higher end of this estimate. This matches the combined Lidar and population modelling data of 40-48%. The percentage of deer missed in the official counts varies from year to year: varying weather conditions are for instance of influence (Marcel Doornbosch, personal communication, 24 August 2024). Using the mean of the three counts instead of the highest number counted in a year could also be used as method, but the current method is used by all site managers in the region, as prescribed by the local authority responsible for fauna management (Faunabeheereenheid Noord-Holland). The current counts however give a good insight in the long-term population trend. Does are no longer in the vast majority, meaning the population has leveled off and the current numbers imply that the desired counted population size of 600-800 has come within sight. The trend is validated by the number of deer counted during rabbit transactions counts. Despite the numbers being much lower than in the official counts, the trends are extremely similar (Figure 7) and correlate statistically (Spearman's ρ=0.987).

Effects of deer grazing on biodiversity

In order to preserve Natura 2000 habitat types and their rich biodiversity, some degree of grazing is desired, especially as long as nitrogen deposition levels remain too high. Without grazing (and mowing), this leads to grass encroachment. But the exponential growth of the deer population has resulted in an imbalance. Surprisingly perhaps, four centuries ago the impact of fallow deer on the vegetation of a calcareous dune system was already acknowledged. At the start of the 17^{th} century, one hundred fallow deer from England were introduced in the dunes near The Hague, the Netherlands. Twenty years later they were all shot, since the damage to the vegetation was considered too high (Chapman & Chapman 1980). Measuring biodiversity as a whole is practically impossible. The number of species (groups) studied is however believed to be diverse enough to form a good sample. Several studies show the negative effects of fallow deer

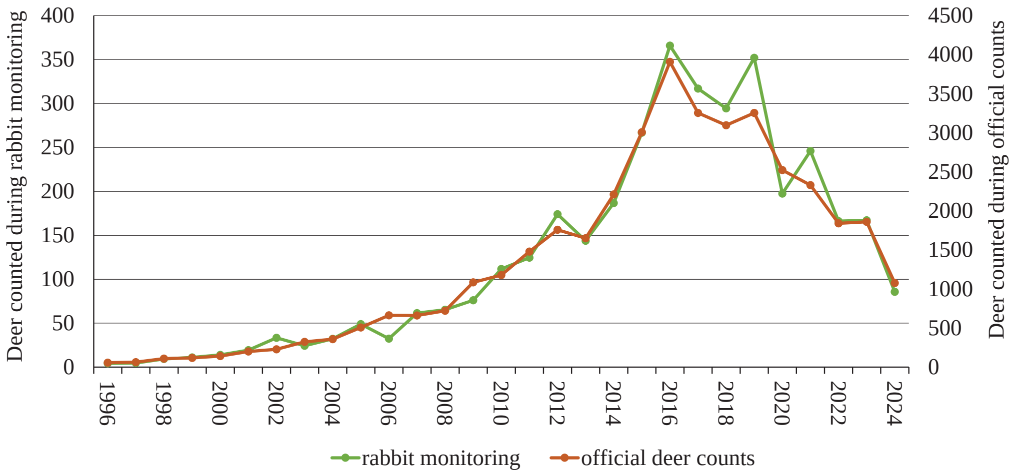

Figure 7. Fallow deer trends in Amsterdamse Waterleidingduinen are being monitored in two ways: 1. During area-wide official deer counts. 2. During transect counts designed for rabbit monitoring. The strong similarity in trends seems to validate both trend monitoring methods.

grazing and trampling on habitats and plant species, and that, as a consequence, there are cascading effects on a wide range of animal species, ranging from invertebrates to vertebrates. Since none of the studies show largely profiting species (groups), it seems justified to conclude that high-pressure deer grazing has caused broad biodiversity loss. Future monitoring will show if deer management was in time and if habitats and their plant and animal species will recover, and if an extinction debt was prevented. With deer numbers currently still being considered too high, signs of recovery have not yet been measured. For instance, the deer counts show that roe deer have not yet returned. Between 2017 and 2022, common nightingales decreased further (Waternet/Sovon, unpublished data), which is perhaps unsurprising since the scrubs where they normally breed in had not recovered from the trampling effects. The next vegetation mapping is scheduled around 2030. This will shed light on the extent of recovery of habitats. In 2024 the flora of the entire area was mapped. The results have not yet been analysed, but based on field impressions recovery of characteristic species was not noticed (Bernard Oosterbaan, personal comment, 7 November 2024). A renewed analysis of the butterflies is scheduled for 2025, but again the impressions from the field are not positive (Mark van Til, personal comment, 7 November 2024). Most of the studies show a correlation between an increase of deer on the one hand and a decrease of a (group of) species on the other. The field experiments with the small exclosures were very informative, but the scale was too small from a scientific point of view. Nonetheless, causal effects between high grazing pressure by fallow deer and biodiversity loss seem likely for two reasons:

1. The amount of studies showing declines of species (groups) and negative effects on habitats over time, that also differ from very similar areas with far lower deer densities or no deer at all; and 2. Many of the conclusions are supported by studies on (fallow) deer grazing elsewhere. In a worldwide review on deer overabundance, Côté et al. (2004) described the effects on the growth and survival of many herb, scrub, and tree species, and how this modified patterns of relative abundance and vegetation dynamics. As a consequence, there are cascading effects on insects, birds, and

mammals, in line with the findings in AWD. Several studies are directly related to specific species (groups) that have declined in AWD. Italian studies show that fallow deer are dominate over roe deer and that they outcompete them (Focardi et al. 2006, Feretti et al. 2011), and that this is not habitat-dependant (Feretti et al. 2012). It is known that high densities of deer in Britain negatively affect the populations of several passerine species (Newson et al. 2011). Palmer et al. (2015) showed when population trends for deer strongly increased (46%), the population trend across deer-sensitive birds dependant on understory vegetation declined much more than the trend for deer-tolerant birds. Causal effects have even been specifically studied in nightingales. An experiment shows that deer browsing reduces habitat sustainability for breeding nightingales. Densities within unbrowsed exclosures were 15 times higher than in browsed control plots (Holt et al. 2010). Invertebrate abundance and species density decreased with an increasing length of browsing history by introduced Sitka deer (*Odocoileus hemionus sitkensis*) on Canadian islands that were compared with neighboring islands without deer (Allombert et al. 2005). In Britain, red deer (*Cervus elaphus*) can negatively affect both the vegetation and invertebrates (Baines et al. 1994), and though depending on the local situation, butterflies can suffer from deer grazing, including by fallow deer (Feber et al. 2001). These are just examples; many more studies supporting the findings in AWD can be found.

Future perspectives

The aimed counted population size of 600-800 fallow deer was determined by the province administration, based on a report that modelled the population size in which fallow deer in AWD could co-exist without mutual competition (Groot Bruinderink et al. 2013). This roughly equals the population size of 2006-2008. This coincided with the fact that for many studied species, this was around the threshold of their declines. With an aimed population size of 600-800 counted deer, the actual density (including the 40-48% of deer missed during the counts) will then be an estimated 34-45 per deer/km². If this is low enough to stop a decline in biodiversity remains to be seen. Effects of deer grazing on open dune habitats have not been extensively studied elsewhere, but there are many studies on deer grazing and their effects on forests, of which over 700 ha is present in AWD. In a field experiment with white-tailed deer (*Odocoileus virginianus*) in the east of the United States, the threshold of a negative impact on forest vegetation was 8 deer/km² (Horsley et al. 2003). Though white-tailed deer are on average moderately larger and heavier than fallow deer, this is much less than the aimed for 34-45 fallow deer/km² in AWD. A British study states that forest regeneration is most likely impossible when deer densities, including fallow deer, are higher than 14 deer/km² (Gill & Morgan 2009). As shown by Oosterbaan et al. (2020), the habitats in AWD were impoverished by years of high-pressure grazing. In a growing population, 600-800 counted deer might have been around the threshold for biodiversity loss, but due to the impoverishment of the habitats, hysteresis might have taken place. Hence, it is likely that 600-800 deer is too many for full biodiversity recovery. A scientific study by University of Amsterdam, Stichting Bargerveen and De Vlinderstichting in collaboration with site managers Waternet en PWN (NPZK) has been conducted since 2020. In AWD 16 larger fenced exclosures covering 40 ha. have been placed, preventing deer from grazing (smaller grazers like rabbits can enter). Unfenced, grazed plots of a similar size in similar habitat serve as controls. Grazing effects on vegetation and invertebrates are being measured. The exclosures were only placed in the second year of the study, in order to carry out baseline measurements in the first year. This allows a comparison in both space and time of the grazed and ungrazed plots. This study will thereby provide insights in causal rather that correlative effects. Furthermore it might give more insights into the question which deer densities are optimal in relation to both Natura 2000 objectives and biodiversity in general. After a population size of 600-800 has been achieved, ongoing analyses and evaluations should lead to adaptive deer management in order to find the right balance.

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Samenvatting

De invloed van begrazing van damherten op de biodiversiteit van een Nederlands duingebied

De Amsterdamse Waterleidingduinen zijn een grotendeels kalkrijk duingebied van bijna 3400 ha op de grens van Noord- en Zuid-Holland. In de jaren 1990 en aan het begin van deze eeuw, nam het aantal damherten (*Dama dama*) er exponentieel toe. De soort was eind jaren 1960 elders in de regio illegaal uitgezet. Met de toename van de herten nam ook de graasdruk in het gebied sterk toe. In het voorjaar van 2016 lag de dichtheid op 190-220 damherten/ km^2, wat op basis van onderzoeken elders zeer hoog is. Uit onderzoeken blijkt dat de toegenomen graasdruk een groot effect heeft op de flora en vegetatie, wat een cascade-effect veroorzaakt en waardoor ook diersoorten sterk afnemen. Dit artikel vat alle gepubliceerde onderzoeken samen. Naast planten en vegetatie zijn effecten gemeten op zoogdieren (reeën zijn geheel verdwenen), struikbroedende vogels, zandhagedissen, vlinders, nachtvlinders (zowel micro's als macro's), bijen, hommels en zweefvliegen. Van de onderzochte groepen werden alleen op mieren geen effecten gevonden. De correlaties (en in een enkel geval causale verbanden) tussen toegenomen graasdruk en afnemende biodiversiteit is gemeten aan de hand van langlopende monitoringsnetwerken van flora en fauna (dikwijls uitgevoerd door vrijwilligers), alsmede databases met losse waarnemingen zoals waarneming.nl, datamodellering, nieuw veldwerk zoals kleinschalige veldexperimenten naar graaseffecten en vegetatiekarteringen, en (internationale) externe expertmeningen. Veel onderzoeken zijn uitgevoerd door onafhankelijke kennisinstellingen. Daarbij zijn zowel vergelijkingen gemaakt in de tijd (voor en na toename van herten binnen het gebied) als in ruimte (vergelijkingen met zeer vergelijkbare gebieden zonder of met veel minder damherten). De onderzoeken wijzen dusdanig één kant op, dat het gerechtvaardigd is te concluderen dat begrazing door grote aantallen damherten leidt tot aanzienlijk biodiversiteitsverlies. Dit sluit aan bij internationale onderzoeken naar (dam)hertenbegrazing. Deels gebaseerd op het aangetoonde biodiversiteitsverlies wordt de populatie sinds het najaar van 2016 middels afschot in aantal teruggebracht. Een lopend wetenschappelijk onderzoek naar graasgedrag moet mede antwoord geven op de vraag welke hertenstand acceptabel is vanuit biodiversiteitsoogpunt.

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