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Exploring novel techniques to quantify habitat use, diet, and ecological effects of deer, with a focus on fallow deer (Dama dama) in the Elwy Valley, North Wales

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Exploring novel techniques to quantify habitat use, diet, and ecological effects of deer, with a focus on fallow deer (*Dama dama*) in the Elwy Valley, North Wales

A thesis submitted to Bangor University by

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Doctor of Philosophy

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Declaration

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards. I confirm that I am submitting this work with the agreement of my supervisor(s)

Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesishwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy. Rwy'n cadarnhau fy mod yn cyflwyno'r gwaith hwn gyda chytundeb fy Ngoruchwyliwr (Goruchwylwyr)

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SUPERCOMPUTING WALES

Abstract

Ungulate herbivores are key components of terrestrial ecosystems. However, anthropogenic transformation of landscapes has altered how ungulate populations interact with vegetation communities. While many large ungulate species are at risk of extinction, deer (Cervidae) populations have increased rapidly across the temperate zone over recent decades. Overbrowsing from expanding deer populations can reduce the structural complexity of the woodland understory, prevent regeneration, and reduce tree growth, which can be detrimental to woodland wildlife and reduce the profitability of forestry operations. Expanding deer populations present a significant barrier to the goals of the UK and devolved governments to increase forest cover for carbon capture, biodiversity conservation and economic prosperity. Studying the habitat use and diet of individual deer species can provide a better understanding of their effects on woodland environments. This thesis assesses the scientific knowledge regarding the influence of deer on woodland habitats and explores the development of novel methodologies for studying deer behaviour and diet.

A systematic map collated current evidence for the ecological effects of seven deer species – six of which are present in the UK - on woodland and forest vegetation (Chapter 2). The review highlighted discrepancies in coverage between species and geographical regions and showed that many studies have not separated the effects of different deer species on the environment. A field study was conducted in the Elwy Valley, North Wales, a region occupied by a growing fallow deer (Dama dama) population (Chapter 3). Using mobile Terrestrial LiDAR (TLS) and forest inventory surveys, I characterised habitat structural components that may influence deer behaviour (Chapter 4). Horizontal visibility at deer eye-height was significantly reduced with higher densities of smalldiameter tree stems, indicating that woodlands with this type of structure may provide safe refuges for deer under hunting pressure. This visibility metric was applied to behavioural data in a diel occupancy modelling approach (Chapter 5), using motion-activated camera data from a landscapescale study of the Elwy Valley fallow deer. Diurnal occupancy was lower in hunted than nonhunted woodlands, which demonstrated the capability of fallow deer to respond to fine-scale temporal variation in risk. Using DNA metabarcoding to study the seasonal diet of this population (Chapter 6), I revealed that bramble (*Rubus fruticosus agg.*) was a key forage species, especially in winter, while deciduous browse accounted for a high proportion of the diet in the spring, summer

and autumn. Counter to expectations, grasses formed a comparatively small proportion of the diet, indicating that this population mainly relies on woodland resources.

This thesis demonstrates the ability of fallow deer to respond to seasonal variation in resource availability and daily fluctuations in human disturbance, illustrating how their behavioural flexibility has facilitated them becoming one of the most widespread deer species in the world. The UK is lacking an effective landscape-scale deer management plan, with very little information on how individual deer species are affecting vegetation communities and wider ecosystems. This thesis exhibits use of novel technologies to refine the way we study deer herbivory and the ecological role of ungulate species in human transformed landscapes, to focus more on the individual species and design management practices that consider animal behaviour and trophic ecology.

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Table of Contents

Table of Contents	8
List of figures	
List of tables	
Chapter 1	
General Introduction	22
Herbivory	22
The ecological role of ungulate herbivores	22
Ecological effects of the loss of ungulate herbivores	24
When do expanding ungulate populations become "overabundant?"	25
Deer (<i>Cervidae</i>) ecology and population expansion	
Managing impacts of growing deer populations and the importance of deer behaviour	27
Overview of the UK deer species	28
Thesis structure	31
Chapter 2	
A systematic map of the effects of seven deer species on the vegetation of wooded habita	ats33
Introduction	33
Methods	39
Search strategy design	
Article screening	40
Results & Discussion	43

Systematic search results	43
What is the extent of the literature on impacts to woodland and forest vegetation by the focal species, and to what extent do the species overlap across studies?	43
What is the geographic extent of studies?	47
What are the mechanisms of impact studied?	49
How do studies measure variation in deer activity or numbers?	51
What impacts on vegetation are assessed? What is the coverage of these effects across the focal deer species?	57
Limitations of the review	63
Recommendations for future research	
Synthesis & conclusions	
Chapter 3	68
Woodland study sites in the Elwy Valley68	
Introduction	
Site BHL73	
Site BWN76	
Site EWD79	
Site EWW	
Site HFD	
Site LNH	
Site MRN	
Site PCG92	

Site TCL95	
Site WFR97	
Chapter 4	100
Horizontal viewsheds of large herbivores as a function of woodland structure100	
Author contributions	
Introduction	
Methods103	
Results	
Topographical slope	112
Season	113
Scan consistency	113
Discussion115	
Conclusions	
Chapter 5	119
Woodland habitat use by fallow deer is shaped by human activity and understory structure1	9
Author contributions	
Introduction	
Methods122	
Study site	122
Motion-activated cameras	123
Surveying for environmental covariates	124

Data analysis	126
Diel occupancy modelling	
Results	129
Diurnal occupancy & detection probability	
Crepuscular occupancy and detection probability	
Nocturnal occupancy and detection probability	
Discussion	146
Conclusions	151
Chapter 6	
Woodland plants dominate fallow deer diet across seasons in a woodland-pasture n landscape	nosaic 152
Introduction	152
Methods	156
Study sites	
Field data collection	
Plant resource availability surveys	
Laboratory protocol	
Sample pooling and size selection	
Processing of sequencing data	1.54
	164
Data Analysis	

Sequencing products1	167
Diet diversity1	168
Seasonal variation in diet composition1	173
Resource availability: spatial and temporal variation in plant community composition 1	178
Ground vegetation preference analysis1	179
Tree and shrub preference analysis1	181
Zoo samples1	183
Field blanks1	185
Discussion186	
Methodological considerations1	191
Conclusions193	
Chapter 7 1	194
General Discussion194	
Deer are not a single generic species194	
Advancing deer ecology and behaviour research using novel methodologies195	
Integrating novel methods with ungulate management and policy	
Conclusions	
References	201
Supporting information	273

List of figures

Figure 2.7 Structural matrix showing the number of studies identified by the systematic search that reported the presence of each deer species, and the effects investigated in the identified studies. Note that the total values in this matrix add up to more than the total number of studies (n = 404), as many studies reported more than one deer species present and more than one effect category.......59

Figure 3.1: Map of the Elwy Valley study region in North Wales. The yellow dots show the position of the ten woodlands containing the 71 circular sampling plots surveyed for this study. ...70

Figure 3.4. Photographs from site BHL showing one of the coppiced hazel trees (top) - note the bramble cover - and a mixed stand of red alder and beech (bottom). Photos taken August 2020.....74

Figure 3.6. Photographs of site BWN. The first photo shows the typically open understory of the woodland in a mixed stand of ash and sycamore with some hawthorn. The second photograph shows one of the cherry laurel thickets that provided pockets of dense shelter for the deer......77

Figure 3.11. Map of site EWW. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the

Figure 3.15. Map of site LNH. Note the developed area to the south which comprises a residential area and stables. The surrounding fields were pasture for livestock. The golf course is out of view to the southwest. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Numbers are the plot ID numbers.88

Figure 3.19. Map of site PCG. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the

Figure 3.22. Photographs of site WFR. In the first and second photographs, note the dense holly in the background. In the foreground of the first photograph, there are some knee-high holly bushes that have been stunted from repeated browsing. The second photograph shows a mixed stand with wild cherry, oak, ash and hazel. The third photograph characterises the southeast portion of the site (Plots 2 and 3) which was mostly dominated by ash and sycamore. Photographs taken August 2020.

Figure 4.2. An example curve of percentage horizontal visibility for plot EWW1 one metre above the ground surface. Percentage horizontal visibility (unobscured sightlines) declines with distance from the origin (plot centre) as objects obstruct the view. In this example, the visibility declines sharply between one and three metres from the plot centre. The Viewshed Coefficient (VC) represents the total area under the curve of percentage visibility for each circular sampling plot. 107

Figure 4.4. Predicted values from the global model for Viewshed Coefficient (y) as a function of log small stem density (x). The error around the line represents the 95% confidence intervals.111

Figure 5.2 Number of active camera days across sites, coloured by season. The six survey seasons
correspond to the biological seasons as follows: Post-rut = seasons 1 & 4, Birthing = seasons 2 & 5,
Rut = seasons 3 & 6

Figure 5.8. Model-averaged beta estimates for the effect of each Bioseason on crepuscular detection probability. The biological seasons correspond to the following time periods: Post rut =

January-March, Birthing = May-July, Rut = September-November. Error bars represent 95%	
confidence intervals.	.140

Figure 6.4. Mean proportion of bramble (Rubus fruticosus L. agg.) present in faecal samples per month, split across sites. The error bars represent the standard error for each mean value. The fitted lines represent predicted values from generalised additive models (GAMs). The shaded area around the lines represents the 95% confidence intervals for the predicted values. Colour indicates season.

Figure 6.5. NMDS plot showing community dissimilarity among fallow deer diet samples, split by month (colour) and the three woodland study sites (shape). Each point represents a sample. 172

Figure 6.7. Ordination of the ground flora survey data for the ten woodland study sites by survey month using NMDS. Deer faecal samples were collected from sites BWN, HFD and WFR. 179

List of tables

Table 2.1. Characteristics of the six UK deer species and North American Elk (British Deer	
Society, 2022; Yellowstone National Park Service (US), 2022)	.38

Table 2.2. Structure of the final systematic search entered into the Web of Science Core Collection including the different components of the main research question, detail on each component and the

search terms used to satisfy each component. The excluded terms were dealt with by specifying "NOT" in the Boolean search string
Table 2.3. Methodologies used to assess or manipulate deer numbers, with example papers from the systematic search. Note that many studies used data from external sources in addition to, or instead of, primary data. Therefore, many studies used a combination of these methods. 53
Table 2.4. The nine categories of effects on vegetation used to classify the 404 studies identified in the systematic search, with examples of metrics and sources included in each category
Table 3.1. Details of the ten woodland study sites in the Elwy Valley
Table 3.2. Woody plant stem size class categories recorded in the woody plant surveys. DBH = diameter at breast height.
Table 4.1. Model estimates and 95 % confidence intervals for each of the variables that featured in the top model ($\Delta AIC = 0$)
Table 5.1 Number of fallow deer detections across each site and survey season. The six surveyseasons correspond to the biological seasons as follows: Post-rut = sum of seasons 1 & 4, Birthing =sum of seasons 2 & 5, Rut = sum of seasons 3 & 6.131
Table 5.2 The top two candidate models (model weight > 0.05) for diurnal occupancy probability (Ψ) with beta estimates and confidence intervals (CI) for each Ψ covariate. p = detection probability, DAIC = delta AIC. See Supplementary S5.4 for the full AIC table and Supplementary S5.5 for the summed Akaike weights for each covariate
Table 5.3 The top scoring model in the AIC table (model weight > 0.05) with beta estimates and covariates for each of the covariates for diurnal detection probability (<i>p</i>) that featured in the model (Hunting and Bramble). Ψ = occupancy probability, DAIC = delta AIC. Significant results are highlighted in bold. See Supplementary 5.6 for the full AIC table of candidate models and Supplementary S5.7 for the summed Akaike weights for each covariate
Table 5.4. Top scoring occupancy models (model weight ≥ 0.05) for investigating effects on covariates on crepuscular occupancy probability (Ψ) with beta estimates and 95% confidence intervals (CI) for each covariate for Ψ that featured in the models. p = detection probability, DAIC = delta AIC. No results were significant. See Supplementary S5.8 for the full AIC table and See Supplementary 5.9 for the summed Akaike weights for each covariate

Table 5.5. Top scoring occupancy models (model weight > 0.05) for investigating effects of covariates on crepuscular detection probability (*p*) with beta estimates and 95% confidence intervals (CI) for each covariate for p that featured in the models. Ψ = occupancy probability, DAIC = delta AIC. Significant results are highlighted in bold. For the Bioseason covariate, the "birthing" season

Table 6.1. Number of surveys per site and month over two years (2019-2020) and number of samples collected per month.
 159

Table 6.2. Timing of sampling occasions for blank pellets, including the dates samples weredeployed in the woodland and later collected, and the codes assigned for each sampling occasion.Samples marked "W" were in the woodland; samples marked "C" were laboratory controls andwere not taken into the woodland.160

Table 6.5. Partial results from pairwise comparison of diversity of ground flora per site across	all
seasons. * = significant at the 95% confidence level	178
Table 6.6. Zoo samples that survived quality filtering for rbcL and ITS2	183
Table 6.7. Field blanks that survived quality filtering for rbcL and ITS2	185

Chapter 1

General Introduction

Herbivory

Herbivory plays a central role in the functioning of terrestrial ecosystems (Olff & Ritchie, 1998). The removal of plant tissue influences plant physiological processes (Bryant et al., 1992; Coverdale et al., 2018; Ward, 2016), recruitment (Churski et al., 2017; Hester et al., 1996), growth (Churski et al., 2017; Vila et al., 2003), mortality (Long et al., 2007; Mårell et al., 2018; Parks et al., 1989) and dispersal (Gill & Beardall, 2001; Griffiths et al., 2010). These effects shape competitive relationships among plant populations, scaling up to affect the structure and composition of vegetation communities (Augustine & McNaughton, 1998; Bråthen et al., 2007; Estes & Duggins, 1995; Koerner et al., 2018), nutrient cycling and primary productivity (Leopold & Hess, 2017; Ramirez et al., 2019; Subalusky et al., 2017). Large mammalian herbivores in particular act as a major source of ecological disturbance, which can contribute to the maintenance of habitat heterogeneity and biodiversity (Bakker, Pagès, et al., 2016; Coverdale et al., 2016; Vera et al., 2008; Wisdom et al., 2006). In a world where anthropogenic influence is driving rapid and widespread change in ecological communities, understanding how herbivores interact with and structure their environment is a key aspect of conserving biodiversity and ecosystem function (Abraham et al., 2022; Foster et al., 2014).

The ecological role of ungulate herbivores

Ungulate herbivores are often described as "keystone species" or "ecosystem engineers" because of the transformative effects they can exert on whole ecosystems through top-down pressure on vegetation communities (Apollonio et al., 2017; Forbes et al., 2019; Gordon et al., 2004; Jia et al., 2018; Vera et al., 2008). For instance, excretion of nitrogenous waste and consumption of leaf litter affects the rate of nitrogen cycling and distribution of nitrogen throughout the environment (du Toit & Olff, 2014; Ferraro et al., 2022; Hobbs, 1996; Murray et al., 2013; Pastor et al., 1998). Large

herbivores can also promote carbon "persistence" within ecosystems through defecation and bioturbation of the soil, and consumption of flammable biomass which reduces carbon emissions from wildfires (Kristensen et al., 2022). Ungulate herbivores can reduce the intensity and extent of fires and make them patchier, increasing heterogeneity in the landscape (Johnson et al., 2018; Knapp et al., 1999). In addition, herbivory by ungulates can increase the diversity of herbaceous (Faison et al., 2016; Newman et al., 2014; Perrin et al., 2011) and woody plants (Brüllhardt et al., 2015; Laurent et al., 2017) in forests by suppressing highly competitive species which would otherwise dominate. Selective feeding can alter the composition of plant communities by mediating competitive interactions among plant species differing in palatability (Augustine & McNaughton, 1998; du Toit & Olff, 2014; Kuijper et al., 2010; Strauss & Packer, 2015). Furthermore, browsing and grazing can prevent encroachment of woody vegetation into open habitats, facilitating the persistence of grasslands (Ali et al., 2017; Daskin et al., 2016; Kowalczyk et al., 2021), woodpasture (Augustine & Mcnaughton, 2004; Vera et al., 2008) and tundra (Biuw et al., 2014).

Ungulates can affect the physical structure of plants by influencing their growth form or preventing them from advancing through growth stages (Motta, 2003; Speed et al., 2013). For example, African elephants (Loxodonta africana) can create refuges from herbivory by toppling trees, leading to higher plant species diversity (Coverdale et al., 2016). Ungulate herbivores also affect plant physiology by generating nutrient redistribution within the plant (McNaughton, 1984; Ward, 2016) or upregulation of defences (Ohse et al., 2017; Rhodes et al., 2018; Vourc'h et al., 2001). The influence of ungulates on vegetation structure, composition and physiology has cascading effects on other animals (Foster et al., 2014) such as small mammals (Bush et al., 2012; Putman et al., 1989), amphibians (Baruzzi & Krofel, 2017), birds (Chollet & Martin, 2013; Fuller, 2001) and invertebrates (Berman et al., 2018; Lilleeng et al., 2018; van Klink et al., 2015). A study at the Mpala Research Centre in Kenya found that lizards preferentially occupied elephant-damaged trees and vacated trees when refuges created by elephants were removed, illustrating how ungulate herbivore activity can benefit other wildlife through increased structural complexity of habitats (Pringle, 2008). Ungulates have a crucial role in the functioning of dynamic ecosystems, however changes to their population abundance, density or behaviour can affect how they shape the landscape (Apollonio et al., 2017; Reimoser & Putman, 2011).

Ecological effects of the loss of ungulate herbivores

The anthropogenic transformation of landscapes is having a significant effect on ungulate herbivore populations (Linnell et al., 2020). Many large herbivores are at risk of extinction and are declining in range and numbers (Ripple et al., 2015). In addition, with the ever-expanding sprawl of human infrastructure, anthropogenic disturbance can generate avoidance behaviour by ungulate species (Stankowich, 2008). This disrupts ungulate habitat use (Krishna et al., 2016; Oberosler et al., 2017) which may alter their ecological function as herbivores (Maxwell et al., 2019) and impact the health of ungulate populations (Jayakody et al., 2011; Spitz et al., 2019). The extirpation of ungulate herbivores often has profound effects on vegetation communities, with each ungulate species exhibiting differences in their feeding ecology and the pressure they exert on vegetation (Augustine & Mcnaughton, 2004). For example, Burkepile et al., (2016) found that the exclusion of small herbivores such as impala from savanna plots led to reduced plant diversity, possibly because this prevented less competitive plant species from establishing through increased light limitation (Burkepile et al., 2016). In addition, a 10-year experiment on Svanøy Island in Norway found that the exclusion of red deer (*Cervus elaphus*) resulted in lower plant species diversity and evenness, with a few species dominating the ground vegetation (Lilleeng et al., 2016).

Reductions in numbers of ungulate herbivores have complex, indirect and often unexpected effects on ecosystems, such as changes to nutrient cycling (Bardgett & Wardle, 2003). For example, a simulation study of caribou (*Rangifer tarandus*), which are vulnerable to extinction (Gunn et al., 2016), found that deposition of nutrients through defecation and death was important for maintaining landscape heterogeneity in tundra environments (Ferraro et al., 2022). Furthermore, extirpation of large herbivores can alter plant-invertebrate interactions (Pollard & Cooke, 1994; Takagi & Miyashita, 2012). Using the Kenya Long-term Exclosure Experiment, Palmer et al., (2008) found that ten years of large herbivore exclusion led to reduced investment from acacia trees in mutualistic ant provisioning, including shelter and food rewards. This led to competitive exclusion in favour of a different ant species that did not depend on these rewards, resulting in increased beetle infestation and tree mortality in acacias (Palmer et al., 2008). In the same study area, Keesing and Young, (2014) showed that large herbivore exclosure led to the pouched mouse (*Saccosotmus mearnsi*) doubling in abundance, resulting in a three-fold decline in acacia seedling survival. In addition, reduction or absence of ungulates can lead to a decline in large carnivores which rely on ungulate populations as an important food source (Schmidt, 2008; Zhang et al.,

24

2014). For example, Walton *et al.*, (2017) studied how the enforced seasonal migrations of semi – wild reindeer (*Rangifer tarandus*) in Norway affected reproduction and survival in Eurasian lynx (*Lynx lynx*). Lynx did not follow reindeer as they migrated, which led to some lynx lacking reindeer prey in their home range. There was a significant reduction in female lynx reproduction and survival of yearling kittens in areas where reindeer had been absent the previous winter (Walton et al., 2017).

When do expanding ungulate populations become "overabundant?"

Conversely, there are concerns of how "overabundant" ungulate populations can also impact ecosystem dynamics (Bernes et al., 2018). Reduced mortality due to extirpation of large predators, introductions of non-native species and human modification of landscapes have led to expansion of some ungulate populations, especially in the temperate zone (Côté et al., 2004; Ramirez et al., 2018). This may be seen as a victory for conservation in contrast to many endangered large herbivore species (Ripple et al., 2015). Indeed, there is evidence that global herbivore biomass is drastically lower than it was before widespread, intensive anthropogenic habitat destruction and hunting (Fløjgaard et al., 2021). Large herbivores are a crucial natural disturbance mechanism for the health of terrestrial ecosystems, but conflict with human land use objectives in heavily modified landscapes has generated frequent use of the term "overabundant" to describe ungulate populations which may be well below their historic size (Hanberry & Faison, 2023; Carpio et al., 2021). It can be argued that the main goal should be localised management until the desired outcome for human land use is reached, without investing finite resources in population monitoring (Morellet et al., 2007). For true rewilding of areas in Europe and North America to take place, ungulate populations would need to be allowed to grow without human intervention, restoring their role as a source of natural disturbance and nutrient redistribution within a complete ecosystem (Fløjgaard et al., 2021). However, this kind of approach is not feasible in human-transformed landscapes with degraded ecosystems. Rapid population expansion in landscapes lacking sufficient forage material to sustain this growth can generate fierce competition for food and result in ecological damage (O'Connor & Page, 2014). For example, Perea et al., (2015) studied the effects of a population of Iberian ibex (Capra pyrenaica) 25 years after their reintroduction to a mountain range in Spain with no natural predators. They found that the species had reached its highest population density on record. The

ibex was browsing a quarter of all woody species at unsustainable levels and preventing the regeneration of 50% of threatened species (Perea et al., 2015). Without population monitoring, understanding if a species has become "overabundant" is difficult to achieve; a population may be well below its historic "natural" size but still conflict with human land use. In the case where ungulate populations are to be culled to manage the intensity of herbivory in a landscape, monitoring the abundance or spatial distribution of individuals can be important to understand effects on the environment before and after culling (Husheer & Robertson, 2005; Enoki et al., 2016), and to maintain the viability and health of the population under culling pressure (Barton et al., 2022).

Deer (Cervidae) ecology and population expansion

Deer are an important component of temperate woodland ecosystems and mediate ecological processes such as nutrient cycling (Ramirez et al., 2018; Ramirez et al., 2021a) plant competitive interactions (Faison et al., 2016; Laurent et al., 2017; Newman et al., 2014; Stephan et al., 2017) and habitat succession (Kienast et al., 1999; Ramirez et al., 2019). Deer are also important prey species for predators and scavengers (Inagaki et al., 2022; Walton et al., 2017). With reductions in natural predators, stricter hunting laws, milder winters, and the transformation of landscapes into farmland-woodland mosaics, growing populations of deer species are expanding their range across many global regions (Côté et al., 2004; Ramirez et al., 2018; Ward, 2005). Australia and New Zealand have seen growth of significant invasive populations of fallow deer (Dama dama) and red deer in recent years due to introductions for game hunting (Davis et al., 2016; Veblen & Stewart, 1982). In Europe and North America, native or naturalised populations have taken advantage of human modification of landscapes (Côté et al., 2004; Ramirez et al., 2019; Ward, 2005). For example, the impacts of expanding North American elk (Cervus elaphus canadensis) populations have been extensively studied in the US National Parks, with the absence of wolves (*Canis lupus*) as a driving factor in their increased numbers (Beschta & Ripple, 2016; Kimble et al., 2011; Ripple & Beschta, 2012).

Deer population growth has led to unprecedented herbivory pressure on temperate woodlands and forests with considerable implications for ecosystem health (Côté et al., 2004; Gass & Binkley, 2011; Putman et al., 2011; Reimoser & Putman, 2011). For example, an overall reduction in low vegetation cover in woodlands of south and east England has been attributed to increased browsing

pressure (Amar et al., 2010). Furthermore, a study in the British lowlands showed that woodlands with higher deer numbers had reduced understory structural complexity compared to woodlands with low deer numbers (Eichhorn et al., 2017). This absence of understory vegetation can have consequences for woodland biodiversity (Bush et al., 2012; Chollet et al., 2016; Putman et al., 1989). Studies have found negative impacts of deer over-browsing on woodland animals that rely on understory vegetation habitat, such as breeding birds (Gill and Fuller, 2007; Holt et al., 2010; Newson et al., 2012; Chollet and Martin, 2013), invertebrates (Sakata and Yamasaki, 2015; Roberson et al., 2016; Bernes et al., 2018; Mahon et al., 2019) and small mammals (Flowerdew and Ellwood, 2001; Bush et al., 2012). There is a necessity to sustainably manage deer populations to mitigate ecological and economic impacts of over-browsing, especially in environments lacking large predators, while conserving their functional role in ecosystems.

Managing impacts of growing deer populations and the importance of deer behaviour

Solutions are required to mediate the herbivory pressure from growing deer populations experienced by ecological communities (Redick & Jacobs, 2020) and increasing human-deer conflict such as damage to forestry and crops and increasing road-traffic collisions (Putman et al., 2011; Valente et al., 2020). At present, culling is the main strategy for reducing deer populations or deterring them from certain areas (Barton et al., 2022; Kuijper, 2011). There is often a lack of landscape-scale organised culling efforts, therefore localised culling may lead to displacement of browsing pressure rather than an overall reduction (Hagen et al., 2018; Putman et al., 2011; Simard et al., 2013). For example, Takeshita et al., (2017) found that the density of some sika deer (Cervus *nippon*) populations in Japan resisted localised culling pressure, probably due to deer moving outside of the managed areas. Deer behaviours such as habitat selection and foraging are highly context and scale dependent (Spake et al., 2020), and are affected by season (Borkowski & Obidziński, 2003; Wam & Hjeljord, 2010), disturbance levels (Jayakody et al., 2011) habitat and food availability (Abbas et al., 2013; Gordon et al., 2004; Putman et al., 2011; Reimoser, 2003; Royo et al., 2017) and intraspecific variation among individuals (Bergvall et al., 2011; Gill, 1992; Putman & Flueck, 2011). Consequently, it can be difficult to find a clear relationship between deer density and browsing pressure (Heinze et al., 2011; Koda & Fujita, 2011).

Field studies have highlighted benefits of deer exclusion for tree growth rates and native vegetation density (Kalisz et al., 2014; Sabo et al., 2019; Shelton et al., 2014). However, these studies represent a scenario where deer are totally absent from a system, and there is considerable evidence that long-term exclusion of native deer species can have detrimental consequences for forest biodiversity (Laurent et al., 2017; Newman et al., 2014; Perrin et al., 2011). Furthermore, the cost and labour required for establishment and maintenance of deer fencing can rule out exclusion as an option for many woodland managers. Deer are a natural resource with considerable economic value for tourism, sport hunting and potential for sustainable meat production (Macmillan & Phillip, 2008; Phillip et al., 2009; Veblen et al., 2010). Total exclusion or extirpation is therefore unlikely to be a viable long-term solution in many cases. With the complex societal issues (Green & Stowe, 2000; Prager et al., 2018) and variable success rates (Hagen et al., 2018; Ramsey et al., 2018) that come with controlling deer densities, a focus on other aspects of deer biology, such as their behaviour, may provide alternative options for deer management (Apollonio et al., 2017). There is potential to reduce deer activity by modifying perceived habitat quality and disturbance levels, which could promote woodland regeneration without the need for deer exclusion (Schippers et al., 2014). Studying the behavioural ecology of deer alongside their impacts on the environment is an important step towards a clearer understanding of the complex relationships between ungulate species and vegetation communities in a world dominated by anthropogenic change (Duncan & Gordon, 1999).

Overview of the UK deer species

There are six deer species in the UK, all of which are expanding their range (Ward, 2005), with great potential for further expansion if no interventions take place (Croft et al., 2019) This has raised concerns for the health of woodland and forest environments and the species that rely on them:

The **Reeve's muntjac** (*Muntiacus reevesi*) was introduced to the UK from China in the 20th century as an escapee from multiple captive collections and is now present throughout south and east England and the midlands (Croft et al., 2019). This species is native to China and feeds as a concentrate selector, browsing on new leaves of saplings and brambles and grazing on nutritious forbs. They predominantly inhabit a mixed habitat of forest, shrubland and grassland and live alone or in pairs. This species breeds all year round and has formed a rapidly growing population in

England (Croft et al., 2019; Ward, 2005; Ward et al., 2021) resulting in considerable damage to ground flora and trees in important woodland habitats (Cooke & Farrell, 2001; Morecroft et al., 2001). The Reeve's muntjac is now considered an invasive species in the UK due to its rapidly expanding population and the damage it is causing to native woodland environments.

The water deer (*Hydropotes inermis*) is another introduced species as an escapee from Whipsnade Zoo in 1929. The subspecies introduced to the UK is the Chinese water deer *Hydropotes inermis inermis inermis* which is native to the east of China. A second subspecies *Hydropotes inermis argyropus* occurs in North Korea and South Korea. Like the Reeve's muntjac, this species has established in the east of England. The population has mostly remained relatively localised to East Anglia, with the greatest range expansion occurring on the Norfolk Broads and some westward progression into fenland areas (Cooke, 1998; Croft et al., 2019; Ward, 2005). The species is classified as Vulnerable on the IUCN red list as populations in the native range are declining (Harris & Duckworth, 2015). Therefore, the UK now contains a considerable proportion of the global population. The water deer is well adapted to wetland areas and occupies intertidal and freshwater aquatic environments as well as surrounding forests and shrublands (Xu et al., 1998; E. Zhang et al., 2006).

The **red deer** (*Cervus elaphus*) is native to the UK and has been present since the land bridge with the European continent during the last glacial maximum. This species is widespread but is particularly abundant in the north of the UK (Croft et al., 2019), thriving in the heather moorlands and pine plantations of the Scottish landscape. The red deer is a large bulk grazer and primarily feeds on graminoids and other roughage (Kerridge & Bullock, 1991) but also browses on tree shoots and dwarf shrubs such as heather and bilberry (Hester et al., 1999). Males and females mainly live in segregated herds, coming together for the rut from late September to November (Mitchell et al., 1977). The impacts of growing red deer populations on European forests are well studied (Klopcic et al., 2010; Kuiters & Slim, 2002; Welch & Scott, 2017) The close relative of the red deer, the North American elk (*Cervus canadensis*) has also been extensively studied in relation to its effects on native aspen (*Populus tremuloides*) and cottonwood (*Populus deltoides*) forests in the US and Canada. The red deer has also been introduced to areas of New Zealand (Husheer, 2007), Australia (Davis et al., 2016) and Patagonia (Barrios-Garcia et al., 2012; Veblen et al., 2006), where it is having detrimental impacts on native vegetation.

The **sika deer** (*Cervus nippon*) originates from Asia and was introduced to the UK in 1860 as an escapee from deer parks. Sika deer are particularly abundant in the north of Scotland, with some isolated populations on the south coast of England (Croft et al., 2019; Ward, 2005). This species shows similar ecology to the native red deer, feeding as a bulk grazer with opportunistic browsing on nutritious leading shoots of tree saplings (Hofmann, 1989; Sakata et al., 2021). The two species also have similar social behaviour, with the sika deer rut taking place from late September to November. This similarity has resulted in many cases of hybridisation between red and sika deer, raising concern for the genetic integrity of British red deer populations (Iacolina et al., 2019; Smith et al., 2018). The ecological effects of sika deer in their native forests of Japan have been well studied, including the effects of browsing on tree regeneration (Nomiya et al., 2003; Shimoda et al., 1994), invertebrate diversity (Sakai et al., 2013; Takada et al., 2008), soil characteristics (Harada et al., 2020; Niwa et al., 2011) small mammals (Shibata et al., 2008) and birds (Seki et al., 2014). In contrast, the effects of sika deer on European forests have received less attention, except for the widespread population in the Republic of Ireland (Kelly, 2002; Perrin et al., 2011).

Like the red deer, the **roe deer** (*Caproelus capreolus*) is an ice age native to the UK. It has a widespread distribution, occurring throughout England and Scotland with recent westward expansion into their historic range in Wales (Croft et al., 2019; Ward, 2005). This species is a medium-sized deer with a similar feeding habit to the Reeve's muntjac, primarily feeding on nutritious browse and herbaceous material with some graminoids and fungi (Jackson, 1980). Roe deer are variable in their social behaviour, often seen alone in dense woodland environments but may form herds in more open habitats (Barja & Rosellini, 2008; Pays et al., 2007). As the most widespread and numerous deer species in Europe, the effects of roe deer on woodlands and forests have been extensively studied in European forests, mostly in the context of ungulate communities (Gill & Morgan, 2010; Leonardsson et al., 2015; Nopp-Mayr et al., 2020; Ramirez et al., 2021a; Riesch et al., 2020).

The **fallow deer** (*Dama dama*), the focal species of this thesis, is thought to have been introduced to the UK several times throughout history, first with the Romans and then the Norman invasion. The species originates from areas of southern Europe such as northern Italy, Bulgaria and Macedonia, but has been translocated around the world and is now present in at least 35 countries (Chapman & Chapman, 1975; Esattore et al., 2022). It is considered "naturalised" in the UK, having been resident for nearly a millennium. Like the red deer, the fallow deer is also a

problematic introduced species in New Zealand (Husheer & Frampton, 2005), Australia (Claridge et al., 2016; Potts et al., 2015) and Patagonia (Barrios-Garcia et al., 2012; Veblen et al., 2006). Fallow deer are typically considered intermediate bulk feeders; predominantly grazers but woody browse forms a significant contribution to their diet (Borkowski & Obidziński, 2003; Caldwell et al., 1983; Hofmann, 1989). A recent review by Esattore et al., (2022) highlighted the significant flexibility of the fallow deer diet, with the ability to adapt to significant variation in resource availability. This species thrives in mixed landscapes of forests, shrublands and grasslands, utilising open fields for grazing and sheltering in adjacent forest blocks which provide important forage, especially in winter (Borkowski & Obidziński, 2003; Caldwell et al., 1983; Obidziński et al., 2013). Fallow deer social groups typically consist of single sex herds, coming together for the rutting season which takes place late September to early November (Langbein & Thirgood, 1989). Fallow deer social group sizes are highly variable across seasons and habitat types, from less than ten individuals to over a hundred (Apollonio et al., 1998; Thirgood, 1996). At high densities, fallow deer can cause significant damage to woodlands and crops (Putman & Moore, 1998). Despite this, the impact of fallow deer populations has been less extensively studied than roe deer and red deer, although several studies have identified impacts in multi-species systems (Gill & Morgan, 2010; Perea et al., 2014; Petersson et al., 2019). A few studies have examined their effects in captive settings, allowing discrimination of the effects of fallow deer alone (Marozas et al., 2009, 2011), but single-species studies in natural systems are rare.

Thesis structure

This thesis uses multiple novel methods to study interactions between fallow deer and their environment and demonstrates how these can be applied to other study systems. The thesis objectives were 1) to review the existing literature of studies addressing the impacts of the UK deer species on woodland and forest vegetation, 2) to map physical habitat structure and relate this to woodland use by fallow deer and deer management in the Elwy Valley, and 3) characterise important seasonal components and diversity of the fallow deer diet to identify which woodland types may be most at risk from browsing in the Elwy Valley.

Chapter 2 presents the results of a systematic map collating evidence for the effects of the six UK deer species and the North American elk (*Cervus canadensis*) on woodland and forest vegetation. The review reports methodologies used to measure deer numbers or activity, whether studies

accounted for other herbivores in the study system, the geographic extent of studies, and the different effects on vegetation that have been researched across the deer species.

Chapter 3 introduces the ten woodland study sites in the Elwy Valley area of North Wales, where data were collected for the proceeding chapters.

Chapter 4 reports a study investigating the use of mobile Terrestrial Laser Scanning (TLS) to quantify visibility for fallow deer in woodlands in the form of horizontal viewsheds, and how viewsheds vary with tree stem density.

Chapter 5 uses the viewshed data from chapter 4, alongside other covariates, to investigate how habitat structure and human disturbance levels influence woodland occupancy by fallow deer in the Elwy Valley over the 24-hour cycle. This chapter uses deer occupancy data collected using motion-activated cameras as part of a larger-scale study of the Elwy Valley fallow deer population (Barton, 2023).

Chapter 6 presents the results of a diet study which uses DNA metabarcoding to characterise the diet of the fallow deer in three of the ten woodland study sites and relates seasonal variation in the diet contents to resource availability at the landscape scale.

Chapter 7 discusses the main results from the preceding chapters in the wider context of deer management and woodland conservation and highlights the urgent need for a landscape-scale deer management plan for the UK.

Chapter 2

A systematic map of the effects of seven deer species on the vegetation of wooded habitats

Introduction

Deer (*Cervidae*) populations are expanding across the temperate zone, contrary to the downward trend of many wildlife population trajectories in the Anthropocene (Fløjgaard et al., 2021). Reductions in natural predators, a warmer climate, agricultural intensification, reforestation, stricter hunting laws and non-native species' introductions have contributed deer population growth (Côté et al., 2004; Martin et al., 2020). Where native populations are expanding, this may be viewed as a conservation success story, as opposed to many other large herbivores which are declining as a result of habitat destruction and hunting pressure, with consequences for ecosystem function (Ripple et al., 2015). Increasing deer populations provide opportunities for social and economic growth, such as wildlife tourism, trophy hunting and enhanced cultural value of landscapes (Linnell et al., 2020). However, they can also present environmental challenges. In the UK and internationally, there is a motivation to plant more trees in the temperate zone to enhance commercial forestry, promote carbon sequestration and conserve woodland wildlife (Putman, 1996; Reimoser, 2003). Increased herbivory pressure from growing deer populations can interfere with these aims (Bernes et al., 2018).

Large ungulates such as deer interact with woody vegetation in multiple ways: browsing and grazing of woody and herbaceous foliage; stripping, fraying and rubbing the bark of trees; and also physically trampling vegetation and soils (Gill, 1992). These behaviours contribute to a number of ecological processes. Deer can mediate competitive interactions between plant species through herbivory (Bernard et al., 2017; Newman et al., 2014) and generate changes to soil nutrient content (Niwa et al., 2008, Stephan et al., 2017). Deer can also contribute to seed dispersal through ingestion and defecation (Eycott et al., 2007). They can maintain open habitats such as forest clearings, shrubland or grassland, delaying succession towards high forest (Carranza & Mateos-Quesada, 2001). These effects of disturbance from deer can improve ecosystem resilience through

increased habitat heterogeneity, supporting greater biodiversity (Faison et al., 2016; Lilleeng et al., 2016). The total exclusion of deer can have unwanted effects, such as reduced plant species diversity (Laurent et al., 2017). However, if deer densities increase too far, this can lead to excessive browsing and grazing of vegetation, with negative consequences for the structure and function of ecosystems which are already under mounting pressure from human activity (MacSween et al., 2018; Newton et al., 2014; Reimoser & Putman, 2011).

Intensive deer herbivory has been shown to reduce regeneration and recruitment of trees and shrubs in forests where deer are highly abundant (Ramirez et al., 2018; Vila et al., 2003). For example, MacDougall (2008) found that the majority of trees in oak (*Quercus* spp.) woodlands on Vancouver Island were established when cervids were nearly extirpated by hunters in the 19th century. Almost no regeneration occurred since the recovery of the deer population due to a cessation of hunting (MacDougall, 2008). The effects of deer on tree growth and mortality also represent a concern for the forestry industry. Deer browsing in commercial plantations can stunt tree growth (Brousseau et al., 2017) and cause multi-trunking (Welch et al., 1992). These reduce timber quality and may make trees more vulnerable to mortality from light competition (Welch et al., 2013).

Browsing and grazing of growing deer populations can also impact woodland biodiversity across taxonomic groups (Putman et al., 1989). Selective, intense deer herbivory can reduce the diversity of the canopy, understory and ground flora by favouring herbivory-tolerant or unpalatable plant species (Bernes et al., 2018; Boulanger et al., 2015; Nuttle et al., 2013), which can lead to homogenisation of plant communities and forest structure (Eichhorn et al., 2017; Martin et al., 2010; Vild et al., 2017). Simplification of forest structure can have detrimental consequences for animal species that rely on dense, complex vegetation, such as small mammals (Buesching et al., 2011; Bush et al., 2012), invertebrates (Mahon et al., 2019; Roberson et al., 2016; Sakata & Yamasaki, 2015) and birds (Chollet & Martin, 2013; Gill & Fuller, 2007). Holt et al. (2010) found that male common nightingales (*Luscinia megarhynchos*) in the east of England preferentially selected deer exclosures for their home ranges, indicating that browsed control plots offered unsuitable habitat. Evidence suggests that habitat changes due to deer herbivory are contributing to the decline of the nightingale and other woodland birds in the UK (Newson et al., 2012; Palmer et al., 2015).

Deer also interact with vegetation through the removal of tree bark. This can be in the form of fraying or rubbing as a territorial marking strategy by males during the rut (Massei & Bowyer, 1999). Deer may also bark-strip as a source of supplementary food when more nutritious vegetation is scarce (Kiffner et al., 2008; Ueda et al., 2002). Fraying and rubbing can result in mortality of small saplings and sometimes larger trees, reducing capacity for forest regeneration (Yokoyama et al., 2001). Bark removal can also increase the vulnerability of trees to fungal infection (Cukor, Vacek, Linda, Vacek, et al., 2019), which can reduce timber quality (Welch & Scott, 2008).

In addition to foraging, deer can also affect their environment through general activity (Ramirez, et al., 2021a). Physical disturbance from sika deer (*Cervus nippon*) trampling was shown to increase seedling emergence of tree species benefiting from soil disturbances (Nomiya et al., 2003), but can be a major source of mortality for more disturbance-sensitive tree species (Tsujino & Yumoto, 2004). Studies have also found effects of red deer (*Cervus elaphus*) trampling on soil nutrients and soil mesofauna (Mohr et al., 2005; Mohr & Topp, 2005), while deposition of faeces and urine can alter soil chemistry (Singer & Schoenecker, 2003) and promote endozoochorous seed dispersal (Malo et al., 2000). It is important to consider the multitude of effects that deer can have on the environment and how these effects are likely to change as deer populations continue to grow.

The impacts of deer are often studied without considering the biology of the species in question (Palmer & Trustcott, 2003; Scott et al., 2009). In systems where multiple deer species coexist, it is often unclear how each species is affecting the environment, making it difficult to prioritise management. In a study of grazing in the New Forest in England, Putman (1986b) stated that simply observing the number or density of ungulate herbivores would only be useful up to a point. Instead, studying how the different ungulate species used certain habitat types would provide a measure of usage intensity for different vegetation communities within the forest (Putman, 1986b). Deer species exhibit marked differences in their body morphology, mode of foraging, home range size, sociality and reproductive strategies (Mysterud et al., 2001; Putman & Flueck, 2011; Putman, 1989). This variation inevitably leads to differences in resource selection, which is likely to influence their relative impacts on vegetation (Gill & Morgan, 2010; Gordon et al., 2004). By understanding how differences among deer species drive resource use and environmental effects in addition to deer densities, ecologists can begin to identify how ecological effects may vary among co-existing deer species and design management plans accordingly (Fattorini et al., 2020).
The causes and consequences of deer impacts on woodlands and forests have been broadly reviewed (Gill, 1992; Côté et al., 2004; Reimoser and Putman, 2011), however differences in impacts among deer species have rarely been addressed. For example, Gerhardt et al., (2013) reviewed what factors determine the effects of deer in European forests. They showed the importance of forest management and disturbance levels, however deer species identity was not explored in depth as a key factor. Spake et al. (2020) performed a meta-analysis of variables influencing the probability of deer damage across the UK, including landscape-scale variables such as land cover type and regional deer density, and local variables such as tree density and distance to forest edge. The authors concluded that the effects of deer density were context-dependent and identified key environmental drivers but did not directly address differences among the deer species. A recent review highlighted that competition with fallow deer (Dama dama) has the potential to mask the impacts of Reeves' muntjac (Muntiacus reevesi) due to their overlapping feeding height, making it more difficult to assess the impacts of individual species (Cooke, 2021). Ramirez et al. (2018) reviewed ungulate impacts on regeneration in temperate forests and identified a tipping point based on metabolic weight density, which is useful for examining the combined effects of multiple ungulate species. In a systematic review, Bernes et al., (2018) found that responses of understory vegetation abundance differed between livestock and introduced ungulates compared to native species. When exploring the temporal and spatial scales of deer-forest interactions, Ramirez (2021) highlighted that small- and large-bodied deer species differed in their foraging strategies, and that the strongest ecological effects occurred either when deer densities were very high or low, or where small- and large-bodied species co-existed.

The aim of this review was to collate current evidence on the effects of deer species present in the UK on woodlands and forests across their global range. These species are the native red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), the naturalised fallow deer (*Dama dama*) and the more recently introduced sika deer (*Cervus nippon*), Reeves' muntjac (*Muntiacus reevesi*) and Chinese water deer (*Hydropotes inermis*). Aside from the UK, the only other country where all six species are present is France, where introduced Reeves' muntjac (Ward et al., 2021) and Chinese water deer (Dubost et al., 2011) have established wild populations. The North American elk (*Cervus canadensis*) was also included due to close taxonomic association with the red deer and interchangeable use of the name *Cervus elaphus* in the literature. Table 2.1 details characteristics of each species.

The UK is a good case study for assessing the ecological effects of multiple deer species. It provides a situation where a relatively small geographical area is shared by six species, with considerable variation in their morphology, ecology, behaviour and origins of introduction. By collating the current evidence available for the impacts of each species, this systematic map may help to inform targeted, species-specific deer management in the UK and internationally. In addition, contrast with the North American elk will highlight different approaches to studying deer impacts across continents. The review will also indicate where further research is needed to understand how these deer species are influencing woodland and forest vegetation in the UK and worldwide.

The review questions are as follows:

- 1) What is the extent of the literature about impacts on woodland and forest vegetation by the focal species, and to what extent do the species overlap across studies?
- 2) What is the geographic extent of studies?
- 3) What are the impact mechanisms studied?
- 4) How do studies measure variation in deer activity or numbers?
- 5) What impacts on vegetation are assessed? What is the coverage of these effects across the focal deer species?

Table 2.1. Characteristics of the six UK deer species and North American Elk (British Deer Society, 2022; Yellowstone National Park Service (US), 2022)

Deer species	UK origin	Body size	Mode of foraging	Sociality	Reproduction	Habitat
Chinese water deer (<i>Hydropotes inermis</i>)	Introduced in 1929 as an escapee from Whipsnade Zoo. Native to eastern China and South Korea.	Fully grown adult 11- 18 kilograms, males and females similar size and weight.	Small concentrate selector for browse, forbs and herbs.	Solitary or in pairs.	Breeding pairs defend territories November- April, fawns born May – July.	Woodland, shrubland, grassland, freshwater and intertidal wetlands.
Reeve's muntjac (<i>Muntiacus reevesi</i>)	Introduced as an escapee from multiple wildlife parks in 20 th century. Native to China.	Fully grown males 10- 18 kilograms, females 9-16 kilograms.	Small concentrate selector for browse, forbs and herbs.	Solitary or in pairs.	No rutting season, reproduce year round, can form high densities very quickly.	Woodland, shrubland, grassland.
Fallow deer (Dama dama)	Naturalised, thought to have been introduced by the Romans then the Norman invasion. Native to southern Europe.	Fully grown females 35-56 kilograms.	Intermediate grazer. Grazes on high cellulose-content graminoids with some opportunistic browsing.	Single-sex social groups in woodland environments, large mixed-sex herds in open environments. Group size can be <10 individuals in woodland habitat and >50 individuals in open habitat.	Annual rut late September-early November, fawns born June-July.	Woodland, shrubland, grassland.
Sika deer (Cervus nippon)	Introduced around 1860 as an escapee from deer parks. Native to Japan.	Fully grown males 40- 70 kilograms, females 30-45 kilograms.	Large bulk-roughage grazer. Grazes on high cellulose-content graminoids with some opportunistic browsing	Solitary, small social groups in winter. Sexes strongly segregated outside of the rut.	Annual rut late September-early November, calves born early May-late June.	Woodland, shrubland, grassland.
Roe deer (<i>Capreolus capreolus</i>)	Native (since last glacial maximum).	Fully grown adult 10- 25 kilograms.	Medium sized concentrate selector for browse, forbs and herbs	Solitary, small social groups in winter. Can form larger social groups in open habitats.	Annual rut mid July- mid August, 2-3 kids born May-June. Capable of delayed fertilisation.	Woodland, shrubland, grassland, freshwater wetlands.
Red deer (Cervus elaphus)	Native (since last glacial maximum).	Fully grown females 63-120 kilograms.	Large bulk-roughage grazer. Grazes on high cellulose-content graminoids with some opportunistic browsing	Solitary or mother and calf groups in woodland environments. Large single- sex social groups persist in open habitats.	Annual rut late September-early November, calves born mid May-mid July.	Woodland, shrubland, grassland, heather moorlands, mountains.
North American elk (<i>Cervus canadensis</i>)	Close relative of the red deer, resident in North America (<u>not</u> present in UK)	Fully grown females average 159 kilograms.	Large bulk-roughage grazer but may browse on woody vegetation in winter	Herding animals, older bulls solitary.	Annual rut mid- September to mid- October. Calves born May – June.	Meadows, prairies, forest, aspen parkland, sagebrush.

Methods

Search strategy design

A systematic literature search was undertaken to ensure the review approach was repeatable and to reduce bias in the information collected (Berger-Tal et al., 2019). Peer-reviewed journal articles were obtained from searching the Web of Science (WoS) Core Collection. The searches were restricted to the UK deer species and the North American elk or wapiti *Cervus canadensis*, including any subspecies. The North American elk was added into the population terms during the scoping searches due to some interchange between *Cervus elaphus* and *Cervus canadensis* with reference to elk in the literature. No geographical limits were used in order to capture studies from the full global ranges of the species. The time period for the Web of Science search was 1970 – 2021. In addition, the online thesis database Opengrey was searched for the UK deer species and all relevant theses were downloaded when available. The UK government website Gov.UK was also searched for government literature reporting the effects of UK deer species, encompassing literature from Natural England, the Department for Environmental and Rural Affairs and the Forestry Commission. No temporal or geographical restrictions were applied to the Opengrey and Gov.UK search.

When selecting Outcome search terms (Table 2.2), each potential term was first entered into the WoS Core Collection along with the Population terms. Each Outcome search term was recorded with the date, the total number of hits, whether there were relevant hits and whether the term would be included in the final search. Outcome search terms were selected when they gave relevant results that were not already being generated by other terms. Search terms were put together in one additive search. Search terms were discussed among the authors to ensure the search encompassed everything the review aimed to address. Some terms which brought up many irrelevant sources were excluded (Table 2.2). Scoping searches were conducted to assess the quantity and relevance of articles obtained. Following the final search, a WoS weekly search alert was used to monitor new publications until the end of 2021. Linguistic limitations meant that any articles not entirely published in English were excluded.

To identify whether any key articles were missed by the search terms, reviews identified by the WoS search that were published from 2010 onwards were screened for relevant articles by back-searching through the bibliography.

Table 2.2. Structure of the final systematic search entered into the Web of Science Core Collection including the different components of the main research question, detail on each component and the search terms used to satisfy each component. The excluded terms were dealt with by specifying "NOT" in the Boolean search string.

QUESTION COMPONENT	DETAIL	SEARCH TERMS
POPULATION	The six UK deer species and <i>Cervus</i> canadensis	"Muntiacus reevesi" OR "Hydropotes inermis" OR "Cervus elaphus" OR "Cervus canadensis" OR "Capreolus capreolus" OR "Dama dama" OR "Cervus nippon" OR "muntjac" OR "chinese water deer" OR "water deer" OR "roe deer" OR "red deer" OR "elk" OR "wapiti" OR "sika deer" OR "fallow deer"
OUTCOME	Effects of deer species on woodland and forest vegetation	(("wood*" OR "forest*" OR "regen*" OR "recruitment" OR "succession" OR "vegetation") AND ("impact*" OR "damage" OR "pressure" OR "brows*" OR "graz*" OR "bark-stripping" OR "debarking" OR "trampling" OR "fraying" OR "rubbing" OR "herbivory"))
EXCLUDED TERMS	Nuisance terms producing irrelevant results	("meat" OR "archaeo*" OR "paleontolo*" OR "cancer" OR "gene" OR "Elk-1")

Article screening

The relevance of sources was first assessed based on their title, abstract and keywords. The second stage of screening involved reading the full text. Box 1 details the selection criteria used to select relevant sources and common reasons for exclusion of articles. Articles were added in at several stages of the screening process from WoS search alerts (Figure 2.1).

Box 2.1 inclusion criteria

- Primary research papers only; secondary analyses such as meta-analyses and reviews are excluded.
- 2. Study should specify the deer species in the study area, or the species should be inferable from the text.
- 3. The source must present primary research data concerning the ecological effects of any of the selected deer species on woodland or forest environments OR open woody vegetation mosaic habitats such as shrub-steppe or riparian willow communities. Data on the effects on herbaceous vegetation are only included if representing woodland or forest ground flora.
- 4. Data must address the effects of herbivory, browsing, grazing, bark-stripping, fraying or otherwise specified activity of the deer species in question.
- 5. The full text must be available in English.
- 6. Reported effect(s) must not be a result of artificial browsing, debarking etc. caused by humans to simulate deer activity.
- 7. Data must be presented from a real ecological system, not a computer simulation.
- 8. The study must demonstrate an effect and not just the intensity of herbivory. Examples include changes in plant density, growth rate, recruitment rate, mortality and reproduction, or changes in species composition and not, for example, amount of biomass removed or browsing incidence.
- 9. Studies may also report indirect effects of deer activity such as changes in soil composition, nutrient cycling, plant dispersal, or the diversity or abundance of other animals utilising habitats such as birds, invertebrates or small mammals. However, these studies must feature a primary measure of effect(s) on vegetation.
- 10. The article must report either direct comparator control data or before/after data.

Data were extracted from all selected articles into an Excel spreadsheet, including the citation, title, publication date, country and study location, deer species reported, additional herbivores reported, whether the study used captive or wild deer, use of exclosures, study duration, effects studied (browsing, grazing, bark-stripping, trampling), and outcome(s) of deer activity for forest, woodland or woody vegetation and any additional effects reported such as changes in animal populations or soil properties. Study duration was documented as the period of field investigation: for example, from when monitoring plots were established to the final year of observations, or the time period covered by historical records.



Figure 2.1. Flow diagram for acquisition and filtering of articles for the systematic map. Exclusion of articles was based on reasons such as a focus on other species not considered in this review (Population), recording frequency or intensity of herbivory without measuring the effect of that herbivory (Outcome), using simulation data rather than real field data (Simulation model), studying the effects of experimental foliage removal rather than true herbivory (Artificial defoliation) or presenting secondary data as opposed to primary data (Review or meta-analysis). Adapted from ROSES flow diagram for systematic reviews Version 1.0 (Haddaway et al., 2017).

Results & Discussion

Systematic search results

A total of 404 articles were selected for inclusion in the review (Supplementary S2.1). The multiple screening stages and the number of articles excluded at each stage are shown in Figure 2.1, adapted from the ROSES systematic review flow chart version 1.0 (Haddaway et al., 2017). The Opengrey searches identified three relevant PhD theses (Supplementary S2.2). The searches on the Gov.UK website did not identify any relevant literature.

What is the extent of the literature on impacts to woodland and forest vegetation by the focal species, and to what extent do the species overlap across studies?

Out of the 404 included sources, 150 explored the effects of North American elk, while 139 investigated effects of red deer (Figure 2.2). Roe deer and sika deer received similar coverage with 103 and 89 studies respectively. The effects of fallow deer were investigated in 53 studies, while 18 studies took place in systems with Reeves' muntjac. Chinese water deer received the least coverage with four studies identified. It is important to note that while a species may have been reported as present in a study, they were not always the species of interest. Several studies reported one or more of these species as being present, but the study primarily focused on the effects of other wild or domestic herbivores or found that the focal deer species did not contribute to effects observed e.g., Zamora et al., (2001).

Sika deer had the highest relative single-species representation, with 70 studies in the absence of the five other study species (Figure 2.2). This was due to the majority of research being conducted in their native range of Japan, where the other deer species are absent. In contrast, red and roe deer were mostly studied in the context of a deer species community, with 43 and 22 studies investigating the effects of red and roe deer in the absence of other focal species, respectively. Similarly, with a broad distribution across Europe, only eight fallow deer studies were in the absence of other focal species. The Chinese water deer was never studied in isolation of other focal species within this dataset. The most common species combination was red and roe deer (Figure

2.2, n = 49), all of which were in Europe. Red and roe deer have the strongest overlap in their global ranges, as both species are widespread across Europe (Linnell et al., 2020).

A large proportion of studies took place in systems with other ungulate herbivores (Figure 2.3). The most common species in Europe were wild boar (*Sus scrofa*) (n = 45) and moose *Alces alces* (n = 36). Fifty-three studies reported the occurrence of cattle (*Bos taurus*); most of these were in North American studies of elk (n = 39). Seventeen studies reported the presence of domestic sheep (*Ovis aries*). In North American studies, mule deer (*Odocoileus hemionus*) was the most commonly reported wild ungulate (n = 65), with others including bison (*Bison bison*) (n = 26) and white-tailed deer (*Odocoileus virginialus*) (n = 16). A total of 80 studies reported smaller herbivore taxa in addition to ungulates, such as rabbits (*Oryctolagus cuniculus*), hare (*Lepus* spp) and mice (*Apodemus spp*) (Figure 2.3).

Fourty-four percent of studies did not explicitly state whether other ungulate species were present in the area (n = 176), while only seven percent actively stated that no additional ungulate herbivores were present (n = 29) (Figure 2.3). One study reported only Reeves' muntjac present in Monk's Wood in Cambridgeshire, England (Pollard & Cooke, 1994). However, three other studies in Monk's Wood reported additional focal deer species in the community (Cooke, 2006; Cooke & Lakhani, 1996; Tanentzap et al., 2012). The deer community may change in study sites as individual species may move into or out of the area. For example, the range of the Chinese water deer is expanding following introduction to the UK in 1929, albeit at a slow pace (Croft et al., 2019; Ward, 2005), therefore this species now occupies sites where it was previously absent. This illustrates how studies may fail to account for the wider ungulate herbivore community, which could lead to an incomplete understanding of how the different ungulate species are affecting an ecosystem.

Study duration was variable across the focal species (Figure 2.4). On average, studies including sika deer and Reeve's muntjac were the shortest, with a mean of 9.1 ± 1.0 and 9.8 ± 2.0 years, respectively. Probably owing to their frequent coexistence, studies including red (15.7 ± 2.3), roe (12.3 ± 2.5) and fallow deer (11.7 ± 2.0) were similar in duration, with Chinese water deer studies having the longest average duration of the UK species (but the lowest sample size) (17.3 ± 7.8). These results indicate that most of the current evidence on the impacts of these species is based on medium- to long-term studies, rather than snapshot studies from only one or two field seasons.

Studies of the North American elk had the longest average study duration (23.0 ± 3.8), reflecting the frequent use of long-term vegetation monitoring plots or historical records.



Figure 2.2. Upset plot showing the frequency of studies where each focal species was present (horizontal bars) and the frequency of co-occurrence or single occurence of each focal species (vertical bars). Single dots show single occurrence of a species, while two or more joined dots indicate co-occurrence of deer species.



Figure 2.3. Number of studies reporting presence of other herbivores, split by whether each of the seven focal species was present.



Figure 2.4. Average duration in years of studies with each of the seven focal species present. Dots show the mean and error bars show the standard error. The numbered boxes show the sample sizes (number of studies). Note the sample sizes do not match the total number of studies per species, as some studies did not report their duration clearly so were not included in this figure.

What is the geographic extent of studies?

The global extent of studies identified in the search was heavily skewed towards North America (Figure 2.5), with 139 studies located in the United States and 11 in Canada. These all focused on the effects of North American elk. Thirty-eight US studies took place within or close to Yellowstone National Park. Many of these were in the context of the wolf reintroduction in the 1990s, observing long-term landscape-scale trends in tree growth rates or abundance (Beschta & Ripple, 2016; Kimble et al., 2011; Ripple & Beschta, 2006). Some US studies used historical data across several centuries (Beschta & Ripple, 2015; Larsen & Ripple, 2003, 2011). Other recurring study locations in the US included the Starkey Experimental Forest and Range, Oregon (n = 12) and

Coconino National Forest, Flagstaff, Arizona (n = 7). Of the 11 studies in Canada, four took place in Elk Island National Park, Alberta. Of the 150 studies in North America, 67 focused on the impacts of elk on quaking aspen (*Populus tremuloides*), probably because this species has the widest distribution of any tree on the continent (E. L. Little, 1971). Quaking aspen has been a subject of concern for several decades as recruitment largely ceased in many areas due to elk browsing (Pelz & Smith, 2018; Rhodes, Anderson, et al., 2017; Rhodes et al., 2019) and climate change (Worrall et al., 2013).

Seventy-four studies were conducted in Japan, all of which investigated the effects of sika deer on their environment. Common study sites in Japan included Mount Odaigahara on the Kii Peninsula (n = 12) and Yakushima Island (n = 4). Studies where sika deer co-occurred with other focal species took place in New Zealand (n = 5), United Kingdom (n = 4), Czech Republic (n = 4) and Republic of Ireland (n = 3). Three studies in the University of Tokyo Chiba Forest reported introduced Reeves' muntjac in the area but deemed the species unimportant (Harada et al., 2020; Suzuki et al., 2021; Suzuki & Ito, 2014). After observing negligible impacts of Reeves' muntjac compared to sika deer, Harada et al (2020) ignored the effects of Reeves' muntjac on ground vegetation and soil properties. The systematic search did not identify any studies investigating the impacts of Reeves' muntjac or Chinese water deer in their native range, probably due to their relatively low densities. Chinese water deer populations are decreasing overall across their native range (Harris & Duckworth, 2015), while Reeves' muntjac is listed as Vulnerable on the IUCN China red list (Jiang et al., 2015). The lack of understanding on the ecological roles of declining Chinese water deer and Reeves' muntjac is concerning for the conservation of the species and their native ecosystems.

The remaining studies in systems containing Reeves' muntjac all took place in south and east England, where muntjac damage to woodland vegetation is well documented (Chapman, 2021). Recurring sites were Monk's Wood in Cambridgeshire (n = 4), Wytham Woods in Oxfordshire, (n = 2) and Bradfield Woods in Suffolk (n = 4). The four studies including Chinese water deer were also in the south of England, including three of the Monks Wood studies. The remaining study was a large-scale assessment of 15 sites throughout lowland England and was the only study in the dataset containing all six UK deer species (Gill & Morgan, 2010), perhaps because this cooccurrence is relatively rare and more likely to be captured by landscape-scale studies (Chapman, 2021). Of the 103 studies that took place in systems containing roe deer, 102 were in European countries, with one study investigating plant dispersal by red and roe deer in Iran (Karimi et al., 2018). Some of the 139 studies including red deer were outside their native range, of which 16 were in New Zealand and six were in Argentina. Similarly, of the 53 studies including fallow deer, five studies were based in New Zealand, five in Argentina, and one in Australia (Ward-Jones et al., 2019). Red and fallow deer have been introduced to these countries and present a concern for the health of native vegetation communities (Tanentzap, Burrows, et al., 2009; Veblen et al., 2010). Of the studies where fallow and red deer co-occured (n = 37) four were on Isla Victoria in Argentina and two in New Zealand, while the rest took place in European countries. Studies with the combination of fallow, roe and red deer (n = 14) were all in European countries.



Figure 2.5. Global distribution of the 404 articles included in the review at the country scale. Darker red indicates a higher quantity of studies. Note that although Alaska is coloured as part of the United States, no studies were conducted there.

What are the mechanisms of impact studied?

Browsing and grazing were the most commonly studied modes of interaction with vegetation (n = 381, 94% of all studies). Herbivory of foliage influences the more frequently studied aspects of plant biology, such as growth (Scott et al., 2009; Zerbe & Kreyer, 2007), productivity (Menezes et al., 2001; Rose and Cooper, 2017) and community diversity (Boulanger et al., 2018; Kay & Bartos,

2000). Thirty-three studies (8%) investigated the effects of debarking, including fraying, rubbing or bark-stripping. These effects included mortality rates (Cukor, Vacek, Linda, Vacek, et al., 2019), growth rates (Cukor, Vacek, Linda, Sharma, et al., 2019), regeneration (Barnett & Stohlgren, 2001) and incidence of fungal infection (Vasiliauskas & Stenlid, 1998). Of these 33 studies, 12 were in systems with red deer, seven with elk and 13 with sika deer. Two studies were in systems with fallow deer (Cukor, Vacek, Linda, Vacek, et al., 2019; Valdés-Correcher et al., 2018), although one of these was focusing on the foraging habits of bison and cattle (Valdés-Correcher et al., 2018). Eight studies took place in systems with roe deer, although three acknowledged that roe deer were not the species responsible for the bark stripping damage (Cukor, Vacek, Linda, Sharma, et al., 2019; Cukor, Vacek, Linda, Vacek, et al., 2019; Welch & Scott, 2017). The search did not identify studies investigating the effects of debarking in systems with Reeves'muntjac or Chinese water deer. The larger-bodied focal species (red, elk, sika and fallow deer) are known to bark strip for food (Szukiel, 1981; Takatsuki, 2009), as they are generally more able to digest low quality plant material compared to the smaller-bodied species (Hofmann, 1989).

Six studies investigated the effects of rubbing or fraying, which are a result of territorial marking behaviour from reproductively active males during the rutting season. These focused on red deer rubbing behaviour (Charco et al., 2016; Maas-Hebner et al., 2005; Żywiec et al., 2019), elk bark scraping (Kurzel et al., 2007), red and roe deer rubbing impacts (Motta, 1996), and the effects of roe deer buck scent marking on shrub cover (Carranza & Mateos-Quesada, 2001). Scent marking behaviours of this nature are largely seasonal and specific to the rut (Motta, 1996) – see Table 2.1 for rutting seasons of each species. These behaviours are localised but can cause considerable damage to vegetation in areas of high activity (Carranza & Mateos-Quesada, 2001).

Five studies investigated the effects of trampling, one of which was the only identified study to take place in Australia (Ward-Jones et al., 2019). These studies all included at least one of the largerbodied herding species – red (Kingery & Graham, 1991), sika (Iida et al., 2018) or fallow deer (Ramirez et al., 2021a) – which generally occur in high density herds, in contrast to the smallerbodied species (Table 2.1) and are therefore more likely to generate ecological effects through trampling. Four of the studies examined effects on soil properties in addition to effects on vegetation. Soil compaction by deer can influence soil invertebrate diversity and biomass, leaf litter decomposition, and soil properties such as porosity and nutrient content (Harada et al., 2020; Ramirez et al., 2021a). Nine studies investigated the effects of defecation, namely seed dispersal (Eycott et al., 2007; Karimi et al., 2018; Malo et al., 2000), nutrient cycling in soil or vegetation (Menezes et al., 2001; Schoenecker et al., 2004; Furusawa et al., 2016) and invertebrate diversity (Iida et al., 2016; Koike et al., 2014; Ramirez et al., 2021a).

How do studies measure variation in deer activity or numbers?

Fifty-five percent of studies (n = 222) used exclosures to study the effects of deer on vegetation. The vast majority of these investigated the effects of foliage herbivory, although some studied barkstripping (Baker et al., 1997; Valdés-Correcher et al., 2018), defecation (Iida et al., 2016; Ramirez et al., 2021a; Schoenecker et al., 2004) and trampling (Kingery & Graham, 1991; Ward-Jones et al., 2019). One study used exclosures to study the influence of bark-stripping on epiphytes, using mesh around tree stems to prevent damage (Oishi & Doei, 2019). A number of studies examined release from browsing on saplings or seedlings within natural exclosure structures, where fallen trees (de Chantal and Granström, 2007; Smit et al., 2012; Kuijper et al., 2013; Hall Defrees et al., 2021), unpalatable or thorny vegetation (Schreiner et al., 1996; Forester et al., 2007; Salek et al., 2019), or steep topography (Larsen & Ripple, 2003; Moore & Crawley, 2014) may provide protection from browsing due to reduced accessibility. Deer exclusion studies are also helpful to show the effects of deer absence on vegetation recovery, while simultaneously tracking the effects of herbivory in open control areas. This can be especially important when studying the effects of invasive deer species, such as the Reeves' muntjac in east England (Cooke, 2006) or red deer in New Zealand (Forsyth et al., 2015). They can also be useful for separating the effects of deer and other herbivores, such as livestock, in multifactorial fencing experiments (Durham, 2010; Endress et al., 2016; Kilpatrick et al., 2003). The effects of smaller herbivores can be separated from the effects of deer if suitable fencing is used (Lyly et al., 2014). For example, three studies examined effects of sika deer and mice on tree seedling survival using exclosure plots on Mount Odaigahara in Japan (Itô & Hino, 2004, 2005, 2008).

Many studies used deer density or activity metrics to quantify deer pressure on vegetation. Figure 2.6 shows the use of these methods across studies that included the different deer species and Table 2.3 gives example papers for each method of quantifying deer numbers or activity. Most of these studies focused on wild deer populations, however 21 studies utilised deer farms (Lilleeng et al., 2018; Moe et al., 2018) or game enclosures (Ambroz et al., 2015), which are particularly useful for documenting the effects of deer activity at known densities (Niwa et al., 2011; Pépin et al., 2006)

and can be studied on a deer density "gradient" with wild deer populations (Hegland & Rydgren, 2016; Synnøve Lilleeng et al., 2021).

Studies identified in the search used a number of methods for estimating deer population size or density, such as bag counts from culling efforts, aerial census, terrestrial count census, camera traps and trackway counts (see Table 2.3 for example studies). Some studies sourced landscape-scale, long-term data from aerial surveys or game management records from national park authorities (Rose & Cooper, 2017; Valdés-Correcher et al., 2018), game management bodies (Heuze et al., 2005) or previously published literature (Lilleeng et al., 2016; Suzuki et al., 2021). These data can provide a fairly reliable population size or density estimate for the area surveyed. However, field studies often corroborated such estimates for their study areas using their own survey methodology (Melis et al., 2006; White et al., 2003).

Table 2.3. Methodologies used to assess or manipulate deer numbers, with example papers from the systematic search. Note that many studies used data from external sources in addition to, or instead of, primary data. Therefore, many studies used a combination of these methods.

Method		Uses	Example papers
Exclosures		Exclude deer from an area using fencing to examine presence / absence effects. Additional data were used to quantify deer numbers outside the fence, often from external sources or faecal counts.	Exclosures: (Allen et al., 1984; González Hernández and Silva-Pando, 1996; Wilson et al., 2006; Rhodes, Wan et al., 2017); With additional methods to assess deer numbers: (Beschta & Ripple, 2010; Husheer & Robertson, 2005; Ward-Jones et al., 2019)
Captive deer		Control species present and density of animals in experimental setting or game enclosure.	Single species: (Pépin et al., 2006; Brazaitis, 2011); Multiple species (Ambroz et al., 2015)
Faecal pile counts	ૡૢૢૢૢૢૢૢૢૢૢૢ	Deer density estimates, space use. Difficult to differentiate faeces between ungulate species. Often done on transects.	Density: (Barrere et al., 2021; Husheer & Frampton, 2005; Koda & Fujita, 2011); Space use: (Palmer & Truscott, 2003; Relva et al., 2009; Takada et al., 2002)
Hunting statistics: bag counts, sightings per unit effort (SUE)	\bigcirc	Estimating population density based on number of deer shot and/or sighted during regular culling efforts. Most often from external sources, sometimes contribute to long-term datasets. Reliable species identification.	Bag counts: (Tanentzap et al., 2009; Pápay et al., 2020); SUE (Akashi et al., 2011; Fujiki et al., 2010)
Count census: drive counts, thermal imaging, pedestrian counts, spotlight counts		Estimate population density or simply obtain a count. May use distance sampling or pedestrian kilometric index. Reliable species identification, although obstruction of view may hinder species ID.	Spotlight count: (Laurent et al., 2017; Pellerin et al., 2010; Schulze et al., 2014); Thermal imaging: (Gill & Morgan, 2010; Harmer et al., 2010; Hemami, 2003); Drive counts: (Cutini et al., 2011; Sage et al., 2004); Pedestrian counts: (Barrere et al., 2019)
Telemetry: tracking collared individuals		Estimate deer density by counting observations of tracked and untracked individuals. Can also be used to quantify deer habitat use or deer pressure.	Habitat use: (Riesch et al., 2020; Rowland et al., 2017); Deer density: (Beschta & Ripple, 2013; Cooke, 2006; Stewart et al., 2006)
Trail cameras		Confirming species presence and quantifying habitat use. Reliable species identification and temporal data.	Species presence: (Katagiri & Hijii, 2015; Stephan et al., 2017); Habitat use ; (Brodie et al., 2012; Ramirez et al., 2021b; Rhodes et al., 2018)
Sign surveys: trackway counts, browsing, faecal pellets, scrapes, roaring stag counts.	11	Quantifying space use or deer density. May survey some or all sign types. Sign can be difficult to differentiate between species. Browsing intensity is sometimes recorded as a metric of deer numbers or activity, as well as an impact mechanism.	Trackway counts: (Bergquist et al., 2009; Holt et al., 2011); Browsing sign surveys: (Heinen and Currey, 2000; Anderson, 2007); Multiple sign surveys: (Joys et al., 2004; Relva et al., 2009); Roaring stag count: (Lovari et al., 2007)
Aerial census	<u>, </u>	Landscape-scale population census. Most often reported from long-term datasets from external sources. Most suitable for open landscapes as tree cover can obscure view.	Density (Hebblewhite et al., 2005); Population size (Irby et al., 2002); Concentration (Barnett & Stohlgren, 2001)



Figure 2.6. Structural matrix showing the number of studies identified by the systematic search that reported the presence of each deer species, and the methods used to quantify deer numbers or activity across studies. Note that the total values in the matrix will not add up to the total number of studies (n = 404), as some studies included more than one deer species and/or more than one method or did not report a measure of deer numbers. Some studies included in this matrix did not use these methodologies directly but reported their use in external surveys from which data were obtained.

Many studies did not report deer numbers, as achieving a reliable estimate can be difficult (Boulanger et al., 2015). Instead, some studies used faecal counts (Heinen & Castillo, 2019; Palmer et al., 2004), camera data (Brodie et al., 2012; Iijima & Iijima, 2018) or browsing intensity (Anderson, 2007; Kay, 1997) as a measure of deer habitat use. Out of the 404 identified studies, 101 did not give any information on deer numbers or activity. Fifty-three of these used fenced exclosures, while 48 did not. Of these 48 studies, some reported effects as a consequence of barkstripping incidence, so did not require an additional "intensity" or "activity" metric (Vasiliauskas & Stenlid, 1998; Welch & Scott, 1998). In addition, several of these studies were examining long-term changes in forest dynamics, such as plant species composition (Boulanger et al., 2015; Šebková et al., 2011) or tree cover (Rogers & Leathwick, 1997). These studies were often in the context of a significant timepoint in the landscape ecology of deer species present, such as the introduction of non-native deer species (Husheer et al., 2003; Husheer & Frampton, 2005; Peltzer et al., 2014). Furthermore, some studies focused on the reintroduction of wolves to Yellowstone in the mid-1990s as a potential turning point in elk browsing behaviour for the regeneration of aspen, rather than specifically changes to elk numbers (Kay, 2001; Larsen & Ripple, 2003; Ripple & Larsen, 2000). Long term data sources such as landscape photographs or vegetation surveys can be used to assess changes to vegetation communities at the landscape scale, but without reliable data on deer numbers or activity, studies can only speculate on whether any changes detected were driven by deer herbivory (Peinetti et al., 2002; Ripple & Beschta, 2003). Shifts in forest dynamics can take many decades to detect (D'Aprile et al., 2020; Petersson et al., 2019), therefore long-term monitoring of the resident deer populations is necessary to truly understand how they are contributing to these changes.

Studies which used both exclosures and a measure of browsing pressure or deer numbers had an advantage of both controlling for deer presence and exploring the effects of different levels of deer pressure (Ramirez et al., 2021a). For example, changes in competitive interactions between plants have been documented at different deer densities (Millett et al., 2006), with high deer densities often generating lower plant species diversity (Charro et al., 2018; Suzuki et al., 2008, 2013). Exclosure studies that do not account for differences in browsing pressure across non-fenced sites have the inherent weakness that they can only report gross effects of the presence or absence of deer. Deer are important for the ecology of many terrestrial ecosystems and are a valuable cultural and economic resource (Linnell et al., 2020), therefore total exclusion or eradication is often not a suitable management option.

In study systems containing an ungulate community, distinguishing browsing effects of individual species can be difficult. The main indication of differences in relative impacts were species density estimates from count census data, camera traps or bag counts, where species can be reliably identified (Table 2.3). Studies of browsing in planted experimental plots may use camera traps to quantify direct visitation rates of different species (Kupferschmid et al., 2015). Perea & Gil (2014) were able to distinguish seedling mortality caused by deer and wild boar, as deer browsed the seedlings while wild boar uprooted them by turning over the soil during foraging, presenting very different mechanisms of impact (Perea and Gil, 2014). Ungulate browsing leaves characteristic

rough cuts on browsed twigs, which can give some indication of levels of ungulate herbivory relative to other herbivores, such as lagomorphs (Chauchard et al., 2018). Browsing height can give an indication of the most likely species responsible for a browsing mark (Chauchard et al., 2018), but this usually remains speculative, especially if species are browsing at similar heights (Holloway, 1967). Furthermore, faecal counts are often unable to distinguish between deer species of a similar size (Hegland et al., 2005; Vuorinen et al., 2020). Valdés-Correcher et al (2018) compared the impacts of bison and cattle with wild herbivores, namely roe deer, fallow deer and rabbits, however the impacts of the individual wild herbivore species were not separated as herbivore densities were too variable across the grazing areas (Valdés-Correcher et al., 2018).

Uncertainty can lead researchers to adopt the precautionary approach of attributing ecological effects to whole herbivore communities or groups. This gives no clear information on how individual deer species are influencing the environment or how they should be managed. Single-species study systems in the wild provide a rare opportunity to study the effects of single species on woodland environments. This is most commonly achieved by studying deer in captive experimental setups (Marozas et al., 2009; Bideau et al., 2016). Captive deer studies not only allow control over herbivore species present, but also the density of each species. Any effects documented in single-species captive systems are not likely to be directly comparable to unenclosed woodlands and forests owing to effects of interspecific competition on deer foraging behaviour and the influence of varying deer densities on vegetation. However, improving understanding of the effects of individual species is likely to enhance overall knowledge of multi-species systems. For example, a study used camera trap data to quantify habitat utilization of red and fallow deer (Ramirez et al., 2021b). They found different effects of utilization rates on sapling diversity and density depending on whether deer species were considered individually or as a single guild. Cameras allow easy species identification in most cases, compared to more cryptic techniques such as sign surveys.

The systematic search highlighted many studies that investigated additional contributing factors to changes in vegetation, stressing that it is important to be mindful of the wider ecosystem when assessing deer impacts. For example, some studies assessed interacting effects of deer browsing and wild or prescribed fire treatments in the United States (Bailey & Whitham, 2002; Fairweather et al., 2014; Hessl & Graumlich, 2002; Walker et al., 2015). The US Department of Agriculture has controlled burning programmes in place to improve habitat quality for native species and reduce fuel loads that lead to uncontrolled wildfires (Hall Defrees et al., 2020). In Europe, wildfire was

studied alongside deer herbivory in Portugal (Lecomte et al., 2019; Silva et al., 2014, 2015) and Sweden (de Chantal & Granström, 2007). Other forest management strategies were also studied with the effects of deer herbivory on vegetation (Hannah et al., 2007; Pekin et al., 2015; Schulze et al., 2014). For example, vegetation succession driven by deer has been studied in clear-cut forest stands (Heinen & Castillo, 2019; A. Sakai et al., 2006). In addition, mixed stands have been used to assess the relative vulnerability of different tree species to browsing pressure, such as oaks planted with less palatable nurse conifers (Dobrowolska et al., 2020; Maltoni et al., 2019).

What impacts on vegetation are assessed? What is the coverage of these effects across the focal deer species?

The systematic search identified a wide range of impacts on woody and herbaceous vegetation resulting from deer activity or herbivory. Common metrics included tree recruitment rate, tree regeneration, annual growth rate, height growth, vegetation cover, diversity, diameter growth, stem density, dispersal success, structural complexity and mortality (Table 2.4). There was also some focus on plant traits or resource allocation, such as changes in leaf C:N ratio, production of defensive compounds and reproductive rates. Some inconsistencies across studies often made direct comparisons across study systems difficult. For example, the terms "regeneration" and "recruitment" were used interchangeably. Recruitment was defined by tree height in some studies e.g., (Painter et al., 2014; Smit et al., 2012) and by stem diameter e.g., (Ambroz et al., 2015; Kimble et al., 2011) in others. In addition, height and stem diameter thresholds that defined a "recruit", "sapling" or "seedling" were highly variable across studies and tree species. To investigate the spread in the literature of this wide range of effects and diverse terminology across the focal deer species, impacts were classified into broad categories similar to those previously used to describe canopy structure (Atkins et al., 2018). Table 2.4 shows the resulting vegetation effect categories and the metrics that were included within each category, with example papers identified in the search. Studies were then grouped by whether they included each focal deer species and effects measured and plotted in a matrix (Figure 2.7).

Table 2.4. The nine categories of effects on vegetation used to classify the 404 studies identified in the systematic search, with examples of metrics and sources included in each category.

Effect category	Included metrics	Example papers
Area, density & population structure	Stem diameter or volume, density, age structure	Density: (Akashi et al., 2011; Allen et al., 1984; Barnett & Stohlgren, 2001; Gill & Morgan, 2010; Koda et al., 2008); Tree diameter or volume: (Beschta & Ripple, 2007; Cukor, Vacek, Linda, Sharma, et al., 2019; Forester et al., 2007; Kupferschmid et al., 2015; Petersson et al., 2019); Age structure: (Larsen & Ripple, 2003; Veblen et al., 2006)
Height	Long-term annual height growth, one-off height measurements, leader shoot length	Leader shoot length: (Herrera, 1995; Cooke and Lakhani, 1996; Palmer and Truscott, 2003); Annual height growth: (Best et al., 2003; Huffman and Moore, 2004; Endress et al., 2016); One-off height measurements: (Iijima and Nagaike, 2015; Hegland et al., 2016)
Plant form	Tree morphology and architecture, multi- trunking/stemming, branching, shoot or twig number, vertical and horizontal spatial variability in vegetation structure	Multi-stemming: (Bergquist et al., 2003; Scott et al., 2009; Welch et al., 2013); Architecture and branching: (Drexhage & Colin, 2003; Johnston et al., 2007); Structural diversity: (Baril et al., 2011; Takada et al., 2008)
Cover & openness	Tree canopy cover, shrub and sapling cover, understory vegetation cover, tree cover, forest cover. Most often expressed as percentage cover.	Ground flora cover: (Cooke, 2006; Marozas et al., 2009); Understory cover: (Takarabe & lijima, 2020; Tsuboike et al., 2021); Shrub and sapling cover: (Pekin et al., 2014; Rowland et al., 2017); Tree cover: (Peinetti et al., 2002; Zeigenfuss et al., 2011)
Diversity & composition	Biodiversity metrics, e.g. Shannon's diversity, species composition or assemblage, relative species abundance or dominance, exotic vs native species, specialists vs generalists, palatable vs unpalatable species	Specialist vs generalist: (Boulanger et al., 2018; Naaf & Wulf, 2007); Native vs non-native (Pekin et al., 2016; Relva et al., 2010; Veblen et al., 2010); Palatable vs unpalatable (Koda & Fujita, 2011; Relva et al., 2009; Suzuki et al., 2021); Grazing tolerant vs susceptible (Tamura & Yamane, 2017); Ground flora & understory vegetation (Boulanger et al., 2015; Morecroft et al., 2001); Tree species composition (D'Aprile et al., 2020; Klopcic et al., 2010); Tree species richness (Kumar et al., 2006; Perea et al., 2014)
Productivity	Biomass, reproductive output, nutrient content (C, N), NDVI, leaf area, resource allocation	Biomass: (Melis et al., 2006; Morimoto et al., 2021); Resource allocation: (Drexhage & Colin, 2003; Peinetti et al., 2001); Nutrient content: (Alstad et al., 1999; Carline et al., 2005)
Mortality	Mortality, survival, proportions of dead and live stems	Trees: (Tanentzap et al., 2012; Welch & Scott, 1998); Saplings: (Forsyth et al., 2015; Żywiec et al., 2019); Seedlings: (Itô & Hino, 2008; Kingery & Graham, 1991; Perea & Gil, 2014b)
Condition	Disease e.g., fungal infection, degradation index, wound healing	Fungal infection: (Shibata & Torazawa, 2008; Vasiliauskas & Stenlid, 1998; Welch & Scott, 2008); Vegetation degradation index: (Fujiki et al., 2010; Seki et al., 2014; Taniwaki et al., 2020); Wound healing rate: (Welch et al., 1997)
Dispersal	Seed germination propensity following ingestion, species of seeds in faecal pellets	Seed deposition and diversity in dung: (Eycott et al., 2007; Malo et al., 2000); Abundance of zoochorous plant species in environment: (Karimi et al., 2018; Naaf & Wulf, 2007)



Figure 2.7 Structural matrix showing the number of studies identified by the systematic search that reported the presence of each deer species, and the effects investigated in the identified studies. Note that the total values in this matrix add up to more than the total number of studies (n = 404), as many studies reported more than one deer species present and more than one effect category.

Area, density & population structure was the most researched category for all seven deer species (Figure 2.7). Within this category, the most frequently used metric was stem density. Stem diameter or volume was also commonly reported (Table 2.4). In addition, effects on the *Height* of vegetation were commonly researched (Figure 2.7). Many studies in elk systems focused on recruitment or regeneration of dominant tree species, such as aspen or cottonwood, often measured as patch size or stem density (Beschta, 2005; Biggs et al., 2016; White et al., 2003). Similarly, aspen sapling and sucker height was commonly studied in North American systems (Durham, 2010; Painter et al., 2014; VerCauteren et al., 2010). Studies of the other focal deer species' effects on *Area, density & population structure* and *Height* covered a greater variety of forest types and tree species compared to studies on elk, including oak (Dobrowolska et al., 2020; Leonardsson et al., 2015; Maltoni et al., 2019), pine (*Pinus* spp) (Herrero et al., 2016), birch (*Betula* spp.) (Harmer et al., 2010), mountain beech (*Fuscospora cliffortioides*) (Bellingham et al., 2016), spruce (*Picea* spp.) and rowan (*Sorbus aucuparia*) (D'Aprile et al., 2020; Kamler et al., 2010).

While studies of Area, density & population structure took place across a range of systems, it was clear that deer numbers were important in determining the magnitude of the effects observed. In general, higher deer densities or browsing intensity were shown to have a negative effect on woody plant size and density, while moderate or low deer densities generated smaller effects or no significant effect. This was evident across the more commonly studied deer species: elk (Rhodes, Wan, et al., 2017; Strand et al., 2009), sika (Akashi et al., 2011) red, roe, and fallow (Gill & Morgan, 2010; Petersson et al., 2019; Relva et al., 2009). The effects of very high deer densities on the environment were particularly obvious in studies utilising deer farms, but even under these conditions, some plant species benefitted from heavy browsing (Hegland & Rydgren, 2016). In addition, some studies found a positive effect of deer browsing on tree regeneration. For example, Stokely et al., (2018) found that herbivory by elk and black-tailed deer (Odocoileus hemionus columbianus) suppressed competing vegetation and improved crop-tree survival of newly planted Douglas fir (Pseudotsuga menziesii). However, a later study found that herbivory became detrimental if herbicides were not used in tandem to suppress competition from broadleaf trees (Stokely & Betts, 2020). While the suppression of the size, density or frequency of valuable species of woody plant might seem detrimental to forest managers looking to regenerate and grow timber stocks (Ando et al., 2006), suppression of tree establishment may prove beneficial for conserving open habitats degraded by tree encroachment (Widenmaier & Strong, 2010).

The *Diversity & composition* category received moderate coverage across elk, red, sika, roe and fallow deer studies, but was more common for red deer (Figure 2.7). Studies frequently measured aspects of *Diversity & composition* and *Cover & openness* together, as cover is a useful metric to compare the relative abundance of different plant species under herbivory pressure (Meier et al., 2017). The comparison of exclosures with open plots was a common method to assess effects on diversity, as shifts in community structure are typically medium- to long-term processes (Klopcic et al., 2010; Morecroft et al., 2001; Stohlgren et al., 1997). Studies observed shifts in vegetation under deer browsing from palatable, browse-intolerant, or native plants towards unpalatable species (D'Aprile et al., 2020), browse-resistant species such as grasses (Gerber & Schmidt, 1996; Meier et al., 2017) or exotic species (Relva et al., 2010). While this may be a concern for biotic homogenisation of forest habitats (Boulanger et al., 2018; Ohashi & Hoshino, 2014), deer exclusion can also result in biodiversity loss. For example, on Svanøy Island in Norway, Lilleeng et al., (2016) found that total exclusion of red deer resulted in reduced understory species diversity and greater dominance by a few plant species in boreal forest. Also, on Svanøy Island, Hegland and Rydgren, (2016) utilised a red deer farm to compare high and low deer density areas by using

exclosures. They found that while woody species such as trees and shrubs were supressed by browsing, the majority of understory plant species benefitted from some browsing pressure, with some thriving under even the heaviest herbivory. In temperate hardwood forests in France, Laurent et al. (2017) also found a detrimental impact of total roe and red deer exclusion on understory plant diversity. Similarly, intermediate browsing by sika deer was also found to be beneficial to understory plant diversity in their native range in Japan (Suzuki et al., 2013). For sika deer in their invasive range in the Republic of Ireland, where they have successfully expanded and introgressed into the native red deer populations, their exclusion was shown to be detrimental to woodland specialist species (Perrin et al., 2011). It is notable, however, that some studies of invasive red deer populations in New Zealand and Argentina (where native ungulates tend to occur at comparatively lower densities) found negative effects on the native vegetation even at low deer densities (Veblen et al., 2006) despite intensive culling efforts (Husheer, 2007) with total extirpation recommended as the only hope of restoring ecosystems (Mark et al., 1991).

The Productivity category received moderate coverage across the focal species, most commonly for elk (Figure 2.7; Riggs et al., 2000; Smith et al., 2015). The most frequently assessed metric was biomass, which generally declined with greater deer browsing pressure (Bergquist et al., 1999; Bergström & Bergqvist, 1997; Morimoto et al., 2021). This was especially apparent when comparing enclosed and browsed areas (Maschinski, 2001; Menezes et al., 2001; Riggs et al., 2000). Notably, some studies found mixed effects on biomass among plant species due to factors such as the propensity for compensatory growth (Case & Kauffman, 1997; Jobe & Gedan, 2021) or palatability (Geary et al., 2017), with the potential to alter plant community diversity. For example, on Mount. Ôdaigahara in Japan, Itô and Hino, (2005) found that sika deer browsing reduced the aboveground biomass of dwarf bamboo (Sasa nipponica) which benefitted some cohorts of tree seedlings, however browsing of other cohorts masked this positive effect. Other Productivity metrics included reproductive outputs such as cone masting (Shibata, 2007), fruit production (Becklin & Kirkpatrick, 2006; Endress & Averett, 2020; Hegland et al., 2005) and flowering success (Huffman & Moore, 2003) as well as resource allocation metrics such as nutrient content of foliage (Alstad et al., 1999; Carline et al., 2005; Furusawa et al., 2016) and primary productivity (Bork et al., 1997; Giralt-Rueda & Santamaria, 2021). These metrics provide useful indications of how deer activity might influence plant fitness, bridging the gap in understanding how effects on plant Area, density & population structure may lead to changes in community Diversity & *composition* through differential impacts on the competitive ability of individual plant species.

Mortality received comparable coverage to Productivity across the focal deer species, especially elk, red, roe and sika deer (Figure 2.7). Most studies focused on browsing-induced increases in mortality rate of seedlings or saplings (Maltoni et al., 2019; Rowland et al., 2017). A few studies investigated mortality effects of browsing on larger trees and shrubs, but mostly found negligible effects (Lovari et al., 2007; Zegler et al., 2012). Elk studies mostly focused on mortality of aspen, (Bork et al., 2013; Kurzel et al., 2007) while roe and red deer studies focused more on oak (Barrere et al., 2021; Jensen et al., 2012) and conifer seedlings (Ameztegui & Coll, 2015; Bergquist et al., 2003; O'Reilly-Wapstra et al., 2014). Studies of mortality involving sika deer mainly focused on both coniferous (Shibata & Torazawa, 2008; Yokoyama et al., 2001) and mixed forests (Akashi & Nakashizuka, 1999; Itô & Hino, 2005) in Japan. Fallow deer received relatively lower coverage in the Mortality category, with just six studies (Figure 2.7). Confirming the cause of tree death can be difficult, especially when multiple factors are at play in addition to herbivory, such as disease or windthrow (Das et al., 2016). Accounting for background mortality rates is important when assessing effects of foliage herbivory or bark stripping (Welch & Scott, 2017). Herbivory alone is unlikely to be a major driver of mortality unless deer densities are high and browsing or barkstripping intensity is severe and repeated on the same plants (Nagaike, 2020). Bellingham et al., (2016) found that browsing from red deer at low densities did not significantly inhibit growth or survival of mountain beech seedlings. Furthermore, Motta (1996) found that while lethality from browsing at low deer densities was negligible, bark removal had an influential impact on tree mortality. Motta (1996) was able to separate whether the damage was caused by red or roe deer, as red deer fray bark in September-October during the rut, while roe deer mark their territories through bark fraying during March-August. This illustrates the importance of accounting for the ecology of co-existing deer species when studying their effects on vegetation. Habitat structure seems to be an influential determinant of browsing-induced mortality, such as the protective effect of shrub cover (Jensen et al., 2012; Perea & Gil, 2014a). Żywiec et al. (2019) demonstrated a positive density dependence of Norway spruce (Picea abies) survival, with isolated saplings more vulnerable to bark rubbing from red deer. In addition, Ameztegui and Coll (2015) found that browsing-induced mortality of conifer seedlings was dependent on distance to protective shrubs, site elevation and forest cover.

Across all deer species, there were very few studies addressing effects on *Plant form, Condition* or *Dispersal* (Figure 2.7). These categories cover the wider ecological effects of deer on vegetation beyond the number, size or cover of plants. *Plant form* concerns structural heterogeneity of vegetation, such as multi-trunking (Bergquist et al., 2003; Scott et al., 2009; Welch et al., 2013),

number of branch junctions (Millett et al., 2006; Lyly et al., 2014), stand height distribution (Tamura & Nakajima, 2017) and structural diversity (Kurzel et al., 2007; Putman et al., 1989; Tinsley-Marshall, 2010). These factors are important for the wider ecological community. Indeed, the systematic search highlighted a number of studies investigating the effects of deer on vegetation structure and consequences for other taxa, such as arthropods (Bailey & Whitham, 2002; Miyashita et al., 2004; Tinsley-Marshall, 2010) and birds (Baril et al., 2011).

A total of 52 studies addressed effects on other animals, although this was not the main focus of this review. Several studies addressed the potential effects of understory vegetation browsing on bird diversity and abundance in Europe (Baltzinger et al., 2016; Holt et al., 2011; Machar et al., 2018) and North America (Anderson, 2007; Hebblewhite et al., 2005; Martin, 2015; Martin & Maron, 2012). Others looked at the effects of deer browsing on soil erosion around waterways (Beschta & Ripple, 2019), and consequences for aquatic invertebrate communities (Sakai et al., 2012, 2013). In addition, the search identified studies providing evidence of competition with other taxa, including invertebrates experiencing deer browsing of their obligate host plants (Moe et al., 2018; Takagi & Miyashita, 2012). One study found a negative relationship between the level of elk browsing pressure and the proportion of serviceberry in the diet of grizzly bears (*Ursus arctos horribilis*) in Yellowstone National Park (Ripple et al., 2014). Some studies investigated effects on invertebrate diversity (Katagiri & Hijii, 2015), such as carabid beetles (Melis et al., 2006) and other soil mesofauna (Katagiri & Hijii, 2017).

Limitations of the review

Due to linguistic limitations of the authors, any sources not published in English were rejected from the final list. In addition, the searches were limited to Web of Science, Opengrey and the UK Government website. Additional databases such as Scopus, Google Scholar, or government resources from Scotland and Wales were not consulted. These limitations may have resulted in key resources being missed. In addition, the dominance of studies on North American elk identified by the systematic search illustrates the significant bias in the literature towards certain study regions and topics, particularly the effects of "trophic cascades" on vegetation in and around Yellowstone National Park. The timing of extirpation and reintroduction of wolves to Yellowstone provided opportunity for highly productive research groups to generate numerous publications on the subject, such as Beschta & Ripple (2005, 2007, 2010, 2013, 2015, 2016, 2019) and Ripple & Beschta (2003,

2006, 2012). Therefore, the inclusion of elk in the systematic map resulted in inherent bias in the search towards North American studies on elk by a relatively low diversity of authors.

Recommendations for future research

Novel approaches are available to study the fine-scale complexities of ungulate community foraging, which may shed light on differences among sympatric deer species regarding their ecological impacts. For example, Nichols and Spong (2014) analysed environmental DNA in saliva left on browsed twigs in Swedish conifer plantations. They were able to identify the deer species that had browsed individual twigs in this multi-ungulate system and showed that moose were primarily responsible for the browsing damage observed, despite a recent increase in red deer abundance in the area (Nichols & Spong, 2014). (Nichols et al., 2015) also used this technique to study similarities and differences in browsing heights and diet components of sympatric moose, red and roe deer. Deer foraging habits can also be studied through the analysis of faeces or rumen contents; multiple studies have identified diet components through microscopy of partially digested plant material (Borkowski & Obidziński, 2003; Ismaili et al., 2018). In addition, molecular approaches can identify plants present in herbivore faeces through DNA barcoding (Gebremedhin et al., 2016; Nakahama et al., 2021; Nichols et al., 2016). Faecal analysis can indicate the dominant components of the diet and how the diet changes with season (McShea et al., 2019; Minder, 2012). Similar methods can also use deer DNA in faeces to identify the deer species which left the faecal material, which would improve the accuracy of species density estimates using faecal counts by allowing reliable, simultaneous monitoring of multiple species (Ushio et al., 2017). These techniques could give a clearer picture of how different deer species are influencing the vegetation and wider ecosystem in multi-herbivore communities.

Red and sika deer are known to successfully hybridise, owing to their similar body size and rutting behaviour. This has led to extensive introgression of non-native sika deer into native red deer populations in Great Britain (Smith et al., 2018). A recent camera trapping study in Ireland found that sika deer and sika-red hybrids were far more numerous than the native red deer (Smith et al., 2022). Although 15 studies identified in the search reported coexistence of red and sika deer in their study area (Figure 2.2), there was little mention of hybridisation. Hybridisation of red and sika may exacerbate the rapid expansion and resulting ecological impacts of growing deer populations, but this has not been explicitly studied.

The findings of this review have highlighted the necessity of accounting for deer population density. If deer density is sufficiently low, studies may not observe a difference between exclosed and open areas (Bellingham et al., 2016). This does not mean that an effect would not be observed at higher deer densities. Ultimately, the studies that provide the clearest picture of how deer influence habitats at the landscape scale generally include a clear measure of population sizes, local densities and/or activity metrics. While exclosures provide an indication of how the presence of deer is influencing a site, lack of data on deer numbers or activity means that deer managers won't know whether shooting is required, what their culling targets should be, or whether species-specific targets are required where a multi-species deer community is present.

The development of high-resolution GPS tracking technology has facilitated the study of fine-scale deer movement in forest environments (Dupke et al., 2017; Ewald et al., 2014). While a few studies highlighted in this review utilised GPS to understand spatial and temporal variation in deer browsing pressure (Beschta & Ripple, 2013; Lovari et al., 2007; Riesch et al., 2020), there is great potential for GPS tracking to improve understanding of how different deer species use forest environments and implications for forest management. GPS tracking of multiple species in the same landscape may highlight how competition among species influences browsing pressure and identify which species may be responsible for the majority of unwanted damage. Trail cameras can also provide large amounts of temporal and spatial data, with reliable species identification (Ramirez et al., 2021b), but have been used surprisingly infrequently when studying deer impacts (Figure 2.6). It is important to consider that short-term assessment of deer numbers may not truly represent the herbivory pressure experienced by an area in the medium- to long-term, potentially leading to illinformed conclusions concerning deer impacts and management plans. While fine-scale deer habitat use and activity has been extensively studied using faecal counts (Bergquist et al., 2009; Forester et al., 2007; Palmer & Trustcott, 2003), there can be substantial error rates in species identification (Pfeffer et al., 2018; Spitzer et al., 2019). Utilising advancing camera and GPS technologies, longterm monitoring may allow more accurate quantification of temporal changes in habitat use (Licoppe, 2006; Niwa, 2021) or trends in deer numbers (Smith et al., 2022) in conjunction with changes to the vegetation. This would increase our understanding of how long-term processes in deer populations influence their ecological role as large herbivores.

While studying differences among species should shed light on knowledge gaps and management needs, it is important to remember that intra-specific variability can be considerable. Foraging and anti-predator behaviours such as vigilance and herding can vary with environmental conditions,

especially across large geographic areas (Putman and Flueck, 2011). Deer respond to perceived risk from anthropogenic disturbance or natural predators through changes in habitat selection and feeding rates (Kuijper et al., 2013; Lovari et al., 2007; Mols et al., 2022). They also react to adverse weather conditions (Conradt et al., 2000) and competition when deer densities are high (Bartos et al., 2002). Behaviour also varies according to reproductive status, age and sex (Bartolomé et al., 2012; Pecorella et al., 2019). When assessing which individuals are generating effects on a habitat, the most important comparisons may not all be among species, but also within species. Context-dependency should always be considered when assessing deer populations for management (Spake et al., 2020).

Synthesis & conclusions

This review summarised the coverage of the literature investigating the effects of the seven focal deer species on woodland and forest vegetation. Elk and red deer were the most commonly studied species overall, followed by roe deer, sika deer and fallow deer. Only a few studies investigated the impacts of Reeves' muntiac and Chinese water deer, none of which were in their native range. Owing to the frequency of studies on elk, the global distribution was skewed towards North America. Most other studies either investigated sika deer impacts in Japan, or mixed ungulate communities in eastern Europe. The vast majority of studies investigated the effects of foliage herbivory, with bark removal the second most commonly studied, and just a few studies covering trampling and defecation. Methodologies for investigating deer impacts typically involved either monitoring of exclosures and control plots or assessing changes to vegetation with variation in browsing pressure or deer numbers. The identified studies included a range of methods to assess deer numbers or activity levels, such as faecal counts, sign surveys, bag counts from hunting efforts and count census. It is recommended that exclosures should be used in combination with one or more species-specific monitoring methods - this will ensure a better understanding of how variation in deer density, in addition to the binary variable of deer presence/absence, influences the vegetation in a study system. In terms of effects on vegetation, Area, density & population structure received the greatest coverage across all species. The methods used to measure plant size and density are often straightforward to implement and can be used for both short-term snapshot studies and long-term monitoring of vegetation responses to deer activity. Height, Diversity & composition,

Cover & openness, Productivity and *Mortality* received moderate coverage, while *Plant form, Dispersal* and *Condition* categories received lower coverage.

Negative effects were usually observed where deer densities were high, or where damage was repeated on the same trees or saplings. Whether a given effect is deemed "positive" or "negative" should be determined by the wider management objectives in the study area. While most studies focused on the negative effects of deer on tree regeneration, some treated those effects as positive, such as when discouraging scrub encroachment on to grassland habitats. Some studies observed positive effects of deer herbivory at low to moderate deer densities, mostly mediating competition between plant species which promoted community diversity. Many studies did not find a significant effect, again most commonly where deer densities were low. In systems where invasive deer species were present, some studies found negative effects even at low densities.

Deer populations are expanding rapidly in the temperate zone, in contrast to trends in many wildlife populations (including wild ungulates in many tropical areas). This review has highlighted that whilst there is extensive knowledge of the ecological effects of well-studied ungulate communities on woodlands and forests, individual species often receive much less attention. There is an urgent need to monitor deer population growth and how their environment responds to changes in density and activity. It is vital that the ecological role of different deer species is well understood as we strive to reforest the temperate zone. Management strategies should be informed by species-specific ecological knowledge as herbivore communities develop with non-native species introductions and expanding global ranges. The combined effects of anthropogenic transformations of our landscapes, climate change and expanding deer populations should not be underestimated.

Chapter 3

Woodland study sites in the Elwy Valley

Introduction

The source of the Elwy River is located in Llangernyw in North Wales, where the channels of the rivers Collen, Cledwen and Gallen merge into a single channel. The river flows east, then north towards St Asaph and finally joins the river Clwyd before the estuary at Rhyl on the north coast of Wales. The east-west stretch of the Elwy Valley spans around 24 kilometres and flows directly through the study area (Figure 3.1). The ten woodland sites considered in this study are situated in the river valleys associated with the this stretch of the River Elwy and associated tributaries. The area encompasses a diverse range of land uses: 1) commercial and small-scale forestry, including monospecific conifer, mixed broadleaf / conifer, and mixed broadleaf plantations; 2) pastoral and arable agriculture, and 3) nature reserves or unmanaged woodlands, typically semi-natural mixed broadleaf. Figure 3.2 shows the percentage of tree stems in the different size classes (Table 3.2) and genera recorded during the woody plant surveys described in chapters 4 and 5. Figure 3.3 shows the cumulative percentage cover of frequently occurring ground flora from the ground flora surveys described in Chapter 6. The woodland site names are given as three-letter acronyms to protect the anonymity of landowners to satisfy GPDR obligations.

The connectivity of the woodlands on the slopes of the river valleys is believed to have facilitated dispersal of the local fallow deer (*Dama dama*) population from their point of origin near Bodelwyddan. From a large-scale study of the Elwy Valley fallow deer using motion-activated cameras, (Barton, 2023) it was confirmed that the range of this deer population included the ten woodland sites in this study (Figure 3.1). The southern-most site, EWD, was situated on the slopes of the river Aled, which provides a direct connection to the Elwy further north. This site had consistent deer detections, despite being the furthest site from the population's origin. Sites east of the Clwyd River (not included in this study) have much lower rates of detection of fallow deer,

probably due to the river acting as a barrier to dispersal (Barton, 2023). Deer management was intermittent across the Elwy Valley and took place in four of the six study sites (Table 3.1). Some woodland owners hired a hunter a few times a year, while others permit access for sport shooting, or conducted shooting themselves As a Site of Special Scientific Interest (SSS), site PCG were systematically managed and high seats were in place, with hunters present several times a month throughout the open season.

In the following sections, all maps were generated using ArcGIS Desktop © 1999-2020, Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.



Figure 3.1: Map of the Elwy Valley study region in North Wales. The yellow dots show the position of the ten woodlands containing the 71 circular sampling plots surveyed for this study.

Study Site	Number of survey	Area (ba)	Hunting	Recreation (Low/High)	
	plots	Aled (IId)	(Present/Absent)		
BHL	6	5	Р	Н	
BWN	8	11	А	Н	
EWD	6	12	А	L	
EWW	10	20	Р	Н	
HFD	10	64	А	Н	
LNH	8	10	Р	L	
MRN	5	6	Р	L	
PCG	7	12	Р	Н	
TCL	4	2	А	L	
WFR	7	11	Р	L	

Table 3.1. Details of the ten woodland study sites in the Elwy Valley

Table 3.2. Woody plant stem size class categories recorded in the woody plant surveys. DBH = diameter at breast height.

Category name	Stem size category		
Sapling	> 0.3 m, < 1.3 m height		
Small	>= 1.3 m height, < 10 cm DBH		
Medium	10 – 20 cm DBH		
Large	21 – 30 cm DBH		
Very large	>= 31 cm DBH		


Figure 3.2. Percentage of woody plant stems belonging to different genera across the ten sampling sites, split by stem size. Each bar plot contains data for a different stem size category, and the columns represent data from the ten sites. Dominant genera include ash (*Fraxinus*), birch (*Betula*), hazel (*Corylus*) and oak (*Quercus*).



Figure 3.3. Families that represented ten percent or more of the ground flora cover for each woodland survey. Each plot represents data from a site, and the columns represent data from the four seasons. The dominant components are *Araliaceae* (ivy *Hedera* sp.), *Rosaceae* (mostly

bramble *Rubus fruticosus agg.*), *Bryophyta* (mosses) and *Euphorbiceae* (dog's mercury *Mercurialis perennis*).

Site BHL

BHL was a professionally managed small-scale broadleaf forestry site surrounded by livestock pasture, with a single-track road on the eastern edge (Figure 3.5). It was planted around 20 years ago by the owners and comprised high pruned sweet chestnut (*Castanea sativa*), cherry (*Prunus avium*), birch (*Betula pendula*), ash (*Fraxinus excelsior*) with some coppiced hazel (*Corylus avellana*) and a stand of red alder (*Alnus rubra*) and beech (*Fagus sylvatica*) (Figure 3.4). The single stem trees were uniform in size as they were all planted around the same time, either 10-20 or 21-30 centimetres DBH (Figure 3.2). The understory was largely dominated by hazel coppice (Figure 3.4) and bramble (*Rubus fruticosus L. agg.*), with some open patches where the canopy presented dense shade. The site is used intermittently by walkers, and shooting is carried out several times a year.





Figure 3.4. Photographs from site BHL showing one of the coppiced hazel trees (top) - note the bramble cover - and a mixed stand of red alder and beech (bottom). Photos taken August 2020.



Figure 3.5. Map of site BHL. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Plot ID numbers are shown.

Site **BWN**

The Bodelwyddan Castle estate is thought to be the earliest site occupied by the fallow deer when they were released from a nearby estate. The site consisted of a woodland to the south of the hotel (Figure 3.7). The woodland comprised a mix of planted ornamental evergreens and naturally regenerated broadleaf species (Figure 3.2). Overall, the canopy was dominated by ash (Figure 3.6), birch, sycamore maple (Acer pseudoplatanus) and wych elm (Ulmus glabra) with some localised patches of mature cedar (Thuja sp.) and beech. There were pockets of cherry laurel (Prunus laurocerasus) (Figure 3.6) and Cotoneaster sp. which the deer used as shelter. The understory was generally very open; dense patches of nettles dominated in summer but died back in the winter. Consequently, visibility was high with a notable browse line throughout, especially on the ivy Hedera helix growing up the tree stems. As the woodland formed part of the grounds of the hotel, there were public footpaths which were frequently used by hotel guests, and a bird hide (near Plot 5). The deer were frequently spotted in large groups while on survey in this woodland and tended to flee when disturbed. They either left the woodland and ran across the neighbouring fields or took shelter in the dense clumps of shrubs. Despite this fleeing response when disturbed in the woodland, the deer seemed more habituated to human presence nearer the hotel and were seen grazing next to the car park on occasion. No shooting was carried out at this site.





Figure 3.6. Photographs of site BWN. The first photo shows the typically open understory of the woodland in a mixed stand of ash and sycamore with some hawthorn. The second photograph shows one of the cherry laurel thickets that provided pockets of dense shelter for the deer.



Figure 3.7. Map of site BWN. The Bodelwyddan Castle Hotel is visible to the north, with an amenity grassland to the northeast and sheep pasture encompassing the rest of the boundary. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Plot ID numbers are shown.

Site EWD

EWD was planted around 15 years ago. It was situated on a steep hillside of the Aled River Valley sloping east to west (Figure 3.9) and mainly consisted of birch (Figure 3.8) and some rare oak in the smaller stem size classes (Figure 3.2). Larger stem size classes were rare at this site, mostly consisting of a few willow (*Salix* sp.) trees in the lower areas where the soil is moister (Plot 6 in Figure 3.9). The understory was heavily dominated by dense bramble with some localised blackthorn (*Prunus spinosa*) and elder (*Sambucus nigra*), again in the lower wetter areas. While the site was initially created through a substantial planting effort, considerable natural regeneration of birch had occurred since initial establishment. This site was not authorised for public access or shooting, although trespassers were seen on the camera on occasion.



Figure 3.8. Photographs of site EWD. The first photograph shows a mixed stand of birch, oak and hazel, all in the small stem size class. The second photo illustrates dominance of birch throughout the site. Photographs taken in August 2020.



Figure 3.9. Map of site EWD. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Numbers are the plot ID numbers.

Site EWW

At the time of writing, EWW is the home of Elwy Working Woods, a co-operative dedicated to managing local woodlands of the Elwy and producing sustainable building materials with harvested timber. The woodland was comprised of distinct blocks: hazel coppice (Figure 3.10), a larch (*Larix decidua*) plantation, a mixed area of ash, larch and birch, patches of pine (*Pinus sp*) and a few fruit trees (apple *Malus* sp. and pear *Pyrus* sp.). The site was situated on a higher slope of the Elwy Valley and the terrain was steep, sloping north-south. The understory was generally very open, with some patches of bramble. This was perhaps the most intensely managed woodland in this study with frequent human disturbance, including a sawmill and large workshop (Figure 3.11). In addition, the site was used by dog walkers most days. Occasional shooting was permitted at this site.



Figure 3.10. Photographs of site EWW. The top photograph shows one of the hazel coppice compartments; note the bare ground. The bottom photograph shows part of the planted ash stand and some low bramble cover. Pictures taken in July 2020.



Figure 3.11. Map of site EWW. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Plot ID numbers are shown. Note the large workshop outside the survey area in the east section of the woodland, and the sawmill on the most westerly corner.

Site HFD

Site HFD was the largest of the ten sites (Table 3.1). This woodland was on the site of an ancient oak woodland which was felled during the second World War and replaced with a Douglas fir (Pseudotsuga menziesii) plantation. Therefore, Douglas fir dominated the larger stem size classes (Figure 3.2). Oak was still present on the site, mostly more than 20 centimetres in diameter (Figure 3.12). In addition to oak, naturally regenerated windblown broadleaf trees were interspersed with the Douglas fir, mainly sycamore and ash. There were also sizeable patches of naturally regenerated birch where Douglas fir was less prominent (e.g., Plot 12 in Figure 3.13). Woodland management was largely absent for the duration of the study. However, in 2021 a site management plan was agreed to gradually transition the site back to an oak woodland and extract the mature Douglas fir for timber. The site was in daily use by dog walkers and occasionally as a campsite, with a public footpath running through the southern third of the woodland. Heavy deer activity was very apparent, with little ground vegetation in large parts of the woodland, even in summer, and strong visibility throughout the understory (Figure 3.12). Patches of bramble dominated the centre of the wood where there were large canopy gaps. At the time of writing, shooting was not taking place in this woodland. Like site BWN, this site was considered a "resident" woodland as deer were consistently present throughout the year, including large groups of females during the rut, and mothers with their dependent fawns. There was also evidence of deer hollows in the bramble banks, suggesting that the deer frequently rested in the denser areas of this site. In addition, there was significant browsing damage noted on much of the bramble across the site, indicating it was frequently used as a source of food.





Figure 3.12. Photographs of site HFD. The first photo typifies most of the woodland – planted Douglas fir interspersed with naturally regenerated sycamore, ash, oak, and birch with little to no understory vegetation. The second photo shows the stand of small diameter oak trees in the centre of the woodland (Plot 3). The third photo shows one of the canopy gaps that has been taken over by bramble (Plot 4). Photos taken in August 2020.



Figure 3.13. Map of site HFD. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Plot ID numbers are shown.

Site LNH

Site LNH was located near the Llannerch Park Golf Club in St Asaph. This woodland contained distinct blocks; the canopy of the northwest square block (Figure 3.15) comprised a Sitka spruce (*Picea sitchensis*) plantation, while the canopy in the southwest was dominated by several mature oak trees exceeding 50 centimetres in diameter (Figure 3.14). The understory of the spruce plantation was dominated by bramble and ivy, with dense bramble banks limiting visibility and movement in the summer months. The southwest plots had less bramble cover, and the understory was dominated by dense, naturally regenerated ash saplings. The spruce block contained a disused pheasant pen with derelict fencing. No woodland management took place in any of the compartments, however there was some ad hoc deer shooting by a local hunter. On several occasions in the summer, a fallow deer fawn was spotted in the north section of the Sitka spruce plantation. This indicated that the woodland was being used as a fawn bedding site, where the mother would leave the fawn in shelter as an anti-predation strategy.





Figure 3.14. Photographs of site LNH. The first photo shows the south section of the woodland which was characterised by mature oak trees in the canopy with abundant ash regeneration in the understory. The second photo shows the Sitka spruce plantation with abundant bramble and ivy in the understory. Pictures taken July 2020.



Figure 3.15. Map of site LNH. Note the developed area to the south which comprises a residential area and stables. The surrounding fields were pasture for livestock. The golf course is out of view to the southwest. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Numbers are the plot ID numbers.

Site MRN

This woodland bordered livestock pasture on the steep north-south slope of a small river valley. The canopy of this site was dominated by beech, hornbeam (*Carpinus betulus*) and ash with the occasional oak tree. Overall, the understory was open, the ground vegetation mostly composed of ferns (*Pteridium* sp.), wood false brome grass (*Brachypodium sylvaticum*) and dense patches of wild garlic (*Allium ursinum*) and dog's mercury in the spring. Midstory trees were mostly coppiced hazel and holly (Figure 3.16). A dense patch of naturally regenerated hornbeam saplings was noted on the riverbank (Plot 4 in Figure 3.17). There was a disused pheasant pen adjacent to the camera (Figure 3.17). Public access of the site was not authorised, however occasional shooting took place. Numerous deer pathways were evident from intense deer activity, notably along the north edge of the valley. It is highly likely that site MRN served as a "transit" woodland for the deer, as this site formed part of the woodland corridor leading to the Elwy Valley (Figure 3.1).





Figure 3.16. Photographs of site MRN. The first photo shows the top of the north slope where a deer pathway traversed the top section of the woodland east-west. The second photo is looking south into the small river valley. The understory was very open throughout. Photographs taken August 2020.



Figure 3.17. Map of site MRN. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Numbers are the plot ID numbers.

Site PCG

PCG was connected to the main woodland corridor on the south side of the Elwy valley, directly opposite site WFR (Figure 3.1). The ground flora was dominated by dog's mercury in summer (Figure 3.18). The canopy was mainly composed of mature ash trees, with some oak and wych elm (Figure 3.2). There was a small beech stand on the western side (Plot 5 in Figure 3.19). The midstory and understory were largely open, although there were some dense patches of blackthorn and bramble on the southeast edge of the woodland (Figure 3.18). There were at least three high seats in this woodland and deer shooting took place on a regular basis, sometimes multiple occasions per week. The woodland was closely managed as a Site of Special Scientific Interest (SSSI). There was a store for drying logs when trees were removed. In addition, the site was frequently used by dog walkers.





Figure 3.18. Photographs of site PCG. The first photo typifies the structure of the woodland: open understory with ash trees dominating the canopy and herbaceous ground vegetation (dog's mercury and ferns). The second photo shows the blackthorn thicket on the southeast edge of the woodland (Plot 3). Photographs taken August 2020.



Figure 3.19. Map of site PCG. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Plot ID numbers are shown.

Site TCL

This linear section of woodland was adjacent to a track leading to a farm on the side of a very steep valley (Figure 3.21). There were some mature holly trees which had grown past browsing height, and some which had been browsed down to stunted shrubs. The canopy was made up of sycamore, ash, birch and oak, with some hazel coppice in the midstory. Birch and oak trees dominated the larger stem size classes (Figure 3.2). The understory was largely dominated by bramble and hazel foliage in the summer (Figure 3.20). The woodland was not under management and no deer shooting took place.



Figure 3.20. Photographs of site TCL. The first photo shows the dominance of bramble in the understory, with ash, sycamore hazel and mature birch stems (Plot 3). The second photo shows Plot 4, which was directly next to the farm track and had a dense understory of hazel foliage and bramble. Photographs taken August 2020.



Figure 3.21. Map of site TCL. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Numbers are the plot ID numbers.

Site WFR

WFR formed part of the woodland corridor on the north side of the Elwy River, sloping northsouth, directly opposite site PCG (Figure 3.1). The topography was generally very steep with frequent rocky outcrops. The canopy was made up of ash, oak, and sycamore, with some mature hornbeam (Figure 3.2), which was historically used to build a nearby mill. There was a patch of midstory holly trees on the western side (Plot 6 in Figure 3.23) which displayed a clear browse line. Holly was the densest component of the understory and occurred in patches throughout the site (Figure 3.22). Aside from the holly, the understory was very open with almost no ground vegetation in winter, although dog's mercury and wood false brome grass were abundant in summer and rare early purple orchid occurred in the spring. There was some tree extraction during the study period, although this was outside of the core sampling area to the east along a farm track. Dog walkers used the core sampling area on an infrequent basis. There was a high seat near Plot 6 where shooting took place several times a year. This site was considered to be a "transit" woodland, with numerous deer paths running east-west through the site, indicating the woodland was an important component of the Elwy Valley corridor. The lack of dense cover meant there were few areas that likely would be suitable resting places for the deer.





Figure 3.22. Photographs of site WFR. In the first and second photographs, note the dense holly in the background. In the foreground of the first photograph, there are some knee-high holly bushes that have been stunted from repeated browsing. The second photograph shows a mixed stand with wild cherry, oak, ash and hazel. The third photograph characterises the southeast portion of the site (Plots 2 and 3) which was mostly dominated by ash and sycamore. Photographs taken August 2020.



Figure 3.23. Map of site WFR. The yellow line denotes the boundary of the survey area for this study. The blue dot indicates the location of the camera. The yellow dots indicate the centre of the survey plots, and the red buffer zones show the extent of the plots (15-metre radius). Numbers are the plot ID numbers. Steep topography south of the camera prevented survey of that area. The south boundary of the sampling area is adjacent to the Elwy River running east-west.

Chapter 4

Horizontal viewsheds of large herbivores as a function of woodland structure

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AG was the lead author of this work and lead conceptualization, method development, data curation, investigation, data analysis and visualisation, and writing the original draft and subsequent edits. GS, JRH and MPE supervised this work and supported AG with conceptualization, method development, project resources, administration, data analysis and reviewed and edited drafts of this work. OB supported method development and data visualization. Post-viva, AS provided feedback on the manuscript and worked with AG to refine some aspects of the analysis.

Introduction

Remote sensing methods have extensive applications in wildlife ecology research (Kays et al., 2015; Neumann et al., 2015). For example, trail cameras have revolutionised our understanding of animal habitat use and activity patterns at the population level (Green et al., 2020), while GPS tracking technology has allowed the study of these processes in individual animals (Hebblewhite & Haydon, 2010). Over the past decade, Light Detection and Ranging (LiDAR) methods such as Airborne Laser Scanning (ALS) has been increasingly used to assess how physical habitat structure influences animal ecology and behaviour across a range of taxa in terrestrial and aquatic

environments (Acebes et al., 2021; Davies & Asner, 2014a; Goetz et al., 2014; Rauchenstein et al., 2022; Wedding et al., 2019). However, when measuring structural characteristics of more closed habitats such as forest understory vegetation, the density and height of the overstory can limit the accuracy of ALS (Campbell et al., 2018; Hull & Shipley, 2019). Recent reviews have highlighted opportunities for the application of Terrestrial Laser Scanning (TLS) to study habitat structure on a fine scale in forest environments (Aben et al., 2018; Olsoy et al., 2015). For example, studies using static TLS have shown reduced understory vegetation density in forests with high-density deer populations (Eichhorn et al., 2017; Li et al., 2022), which can lead to degraded habitat quality for birds, particularly woodland specialists (Allombert et al., 2005; Chollet & Martin, 2013; Gill & Fuller, 2007) and small mammals (Buesching et al., 2011; Flowerdew & Ellwood, 2001). Mobile TLS methods differ from static TLS in that the surveyor carries the scanning device and moves through the survey area, which often requires only a single survey as opposed to multiple static surveys. Mobile terrestrial laser scanners may have higher error rates compared to static terrestrial scanners, as the walking speed and pattern of the surveyor influences scan quality (Ryding et al., 2015). However, mobile scanners sample surfaces from multiple angles, which reduces occlusion (Wei et al., 2020) and survey time (Ryding, 2016) compared to static scanners. With recent technological advances and greater affordability, mobile laser scanners are now capable of providing detailed habitat structure data for the study of animal behaviour (Malhi et al., 2018).

Viewsheds (the area visible from a given location) are affected by the physical structure and density of features such as vegetation and topography (Kuijper et al., 2014; Ndaimani et al., 2013; Parsons et al., 2021), which can influence factors such as predation risk or hunting success (Bellamy et al., 2018; Brown, 1988). In a "landscape of fear" (Gaynor et al., 2019; Laundré et al., 2011; Palmer et al., 2022), behavioural responses to risk induce trade-offs between concealment, thermoregulation, vigilance, and foraging efficiency (Acebes et al., 2013; Glass et al., 2021; Panzacchi et al., 2010; Ratikainen et al., 2007; Wiemers et al., 2014). In dense forest habitats, viewsheds are often restricted to short distances, therefore animal behavioural responses can be shaped by fine-scale habitat characteristics. For example, fallen trees and other structural impediments have been shown to reduce ungulate visitation and browsing of vegetation (Hall Defrees et al., 2021; Milne-Rostkowska et al., 2020; Smit et al., 2012; van Ginkel et al., 2021). This effect has been attributed to physical barriers impeding escape routes and detection of predators in forest environments (Kuijper et al., 2013). In addition to risk from natural predators, perceived risk from human recreational activity (Coppes et al., 2017; van Beeck Calkoen et al., 2022; Wisdom et al., 2018),

hunting (Lone et al., 2015; Pecorella et al., 2016), and roads (Eldegard et al., 2012; Mathisen et al., 2018; Montgomery et al., 2012) influences animal space use and vigilance. This perceived risk is likely to vary with visibility in the environment (Mols et al., 2022; Parsons et al., 2021). For example, a study of red deer (*Cervus elaphus*) stress responses in Lyme Park (UK), found that woodland and scrub landscape features decreased the probability of human-deer encounters, which could help buffer stress associated with high human activity (Dixon et al., 2021). Furthermore, a recent study used TLS to assess viewsheds at multiple heights in the vegetation canopy in forest, shrub-steppe, prairie and desert habitats, and showed that the density, variability and distribution of vegetation is influential for viewshed occlusion (Stein et al., 2022).

There is great potential for TLS studies to quantify viewsheds in forest environments and further our understanding of how physical habitat structure may influence fine-scale animal space use, foraging behaviour and predation risk (Aben et al., 2018; Lecigne et al., 2020). This has been previously studied at the landscape scale using ALS technology. For example, an ALS study found that grizzly bears (*Ursus arctos horribilis*) were less likely to select habitats more visible from roads when resting, but selected more visible areas when travelling, indicating selection for perceived safety when resting and easier passage when travelling (Parsons et al., 2021). Another ALS study found that predation risk from human hunters on roe deer (*Capreolus capreolus*) decreased with understory cover density, probably due to reduced sightline length, while predation risk from an ambush predator, the Eurasian lynx (*Lynx lynx*), increased (Lone et al., 2014). Most recently, a study in the Bavarian Forest National Park (Germany) combined ALS and static TLS to study how visibility influenced movement rates of red deer (Zong et al., 2022).

This study aimed to evaluate the extent to which woodland structure influences horizontal visibility at a height relevant to large herbivores, through the novel application of a technology. I used mobile TLS to quantify horizontal viewsheds, summarized as Viewshed Coefficients (VC) one metre above the ground. Woodland structure was assessed by surveying the stem size-class structure, density, and species composition of woody vegetation (trees and shrubs) and cover of the scrambling shrub bramble (*Rubus fruticosus* agg.). The expectation was that higher densities of tree stems of all size classes and higher bramble cover would result in a reduction in horizontal visibility as a function of distance from a given point. Leaf Area Index (LAI) of the understory was also calculated from the TLS data to assess the extent to which leafy foliage influenced the horizontal viewsheds. I predicted that higher LAI values would correspond to lower horizontal visibility as a function of distance from a given point. In addition, a subset of plots was scanned in both summer and winter to compare horizontal viewsheds in different seasons. Horizontal visibility may be reduced in leaf-on compared with leaf-off conditions of deciduous vegetation due to greater foliage density. Each winter scan was also repeated to check the consistency of the mobile scanning method. Through this work, I demonstrate how potential sightlines of large herbivores are altered by properties of forest understory structure.

Methods

Ten woodland study sites were established in the Elwy Valley area of North Wales (see Chapter 3). The Elwy Valley is a landscape mosaic of farmland (predominantly livestock pasture and forage crops) and patches of woodland under different ownership and management objectives. These woodlands vary in composition and maturity and included conifer plantations, mixed broadleaf-conifer woodland and semi-natural broadleaf woodlands (see Chapter 3 for details). There is a population of approximately 1500 fallow deer (*Dama dama*) occupying this area.

A total of 71 circular plots (15 metre-radius) were located to capture as much variation as possible in density, structure, size and diversity of the tree and shrub communities within each of the ten woodland sites (Table 3.1, Figure 4.1). Sample plots were positioned to avoid human constructed paths or roads, although these features were sometimes close to plot edges. Plot edges were marked using red biodegradable flagging tape tied to tree branches. Sites WFR, TCL and MRN had some very steep slopes which could not be surveyed due to safety constraints. Woodland edges were not avoided.



Figure 4.1. a) Site HFD in summer 2019. There is a notable browse line from deer herbivory and lack of dense understory vegetation, with most trees belonging to larger size classes. b) Site EWD in summer 2020. The understory is relatively dense with many smaller trees and dense bramble cover.

LiDAR scans were taken with a GeoSLAM (Nottingham, UK) ZEB Revo TLS to determine the horizontal visibility and Leaf Area Index in each plot. Previous studies have validated GeoSLAM ZEB devices for use in forest surveys (Bauwens et al., 2016; Camarretta et al., 2021; Ryding, 2016). Each of the 71 plots was scanned once in August 2020. The conditions required for these surveys were a) no rain and b) wind speeds of < 16 kilometres per hour. This reduced the risk that rain or moving foliage would artificially elevate point density. The laser scanner was placed on the ground at the centre of the plot during setup to mark the start and finish point. The scanning procedure involved the same surveyor walking around and through each 15-metre radius circular plot multiple times for 15 - 20 minutes, with the scanner held at breast height. During the scan, care was taken to present the scanner to habitat features from several angles to minimize occlusion effects. The walking pattern consisted of walking to the edge of the plot, walking around the edge in both

directions, then crossing the plot from different angles in a closed loop, starting and finishing in the plot centre (Bauwens et al., 2016; Ryding, 2016). Areas with thick cover of shrubs or scrambling plants, for example, bramble and blackthorn (*Prunus spinosa*), were surveyed as thoroughly as possible.

Scans were also conducted in a subset of eight plots in winter (January 2021) to compare the horizontal visibility in leaf-off vs leaf-on seasons for deciduous species. This January sampling period was also used to assess the consistency of both the scanner and the data collection methodology by repeating all the scans in the eight sample plots, one directly after the other. The two scans per plot were then compared for significant differences in horizontal visibility.

In addition to the mobile TLS surveys, all trees, saplings and shrubs (hereafter referred to as "woody plants") greater than 0.3 m in height were surveyed in each plot. For each woody plant, the taxon was identified as precisely as possible (usually species, otherwise genus). For woody stems taller than or equal to breast height (1.3 m), the size class of diameter at breast height (DBH) was determined using a diameter tape and classified into size classes (Table 3.2). For multi-stemmed woody plants, the DBH of the largest stem was measured and the total number of stems was counted. For saplings shorter than breast height, the height was measured using a metre ruler. Woody plants less than 0.3 m in height were not recorded. Both dead and living woody plants were included in the inventory. In two plots at site LNH, there was very dense growth of saplings and small trees, particularly ash (*Fraxinus excelsior*). To enable measurement of these saplings within a practical timeframe, all ash stems within the "Sapling" and "Small" categories (Table 3.2) within plot LNH4 were converted to estimate the number of ash saplings in the whole 15-metre radius plot area (Equation 4.1 where X = Stem density in 4.5 m radius circle and Y = Converted stem density). The same approach was used for "Saplings" and "Small" stems of all tree species in plot LNH8.

$$Y = \left(\frac{X}{63.62}\right) \times 706.86$$

In addition to the woody plant survey, summer bramble cover of each plot was measured using a 0.25 m^2 quadrat sub-divided into 25 x 0.01 m² squares. Each plot was surveyed either two or three times across the summers of 2019 - 2021. For each survey, eight quadrats were randomly placed inside the plot using cardinal directions and distance from the plot centre (1–15 metres). At each of

these eight locations, a quadrat was placed on the ground and the number of squares containing bramble foliage and stems was counted from above. These eight counts were averaged to obtain a bramble count value for each plot survey (Equation 4.2). These two or three values from across the survey years were then averaged to obtain mean percentage bramble cover for each plot.

$$B = \left(\frac{T1 + T2 + T3}{N}\right) \times 100$$

Equation 4.1. B = mean percentage bramble cover, T = total number of 0.01 m² squares containing bramble per sampling occasion and N = total number of 0.01 m² squares surveyed per plot across sampling occasions. For plots surveyed twice, N = 400, for plots surveyed three times, N = 600.

Point clouds were processed in R version 4.0.3 (R Core Team, 2021) using the *viewshed3d* (Lecigne et al., 2020; Lecigne & Eitel, 2022) and *lidR* (Roussel et al., 2020) packages. Due to the memory constraints of a standard computer, the analysis was run on the Super Computing Wales platform. The processing broadly followed example workflows in the viewshed3d handbook. The cloud was first cropped to a 15-metre radius using the *sample_scene* function from the *viewshed3d* package. Duplicate points were removed using the *filter_duplicates* function from the *lidR* package, then isolated points were removed using the *classify_ground* function (*lidR*). The topographical slope was removed using the *remove_slope* function (*viewshed3d*) to make sure that the effect of vegetation in each plot could be examined independently of slope, then the ground was reconstructed with the optimal resolution to ensure that sightlines did not pass through the ground using the *reconstruct_ground* function (*viewshed3d*).

The Viewshed Coefficient (VC) was calculated using the $h_visibility$ function within the *viewshed3d* R package. The VC is defined as "the area under the curve of visibility as a function of distance from the animal's location" (Figure 4.2, Lecigne and Eitel, 2022).



Figure 4.2. An example curve of percentage horizontal visibility for plot EWW1 one metre above the ground surface. Percentage horizontal visibility (unobscured sightlines) declines with distance from the origin (plot centre) as objects obstruct the view. In this example, the visibility declines sharply between one and three metres from the plot centre. The Viewshed Coefficient (VC) represents the total area under the curve of percentage visibility for each circular sampling plot.

The location of the deer in each plot was defined using XYZ coordinates 0,0,1. This placed the animal at the centre of each plot and one metre above the ground surface. Fully grown fallow deer females stand at 0.7 - 0.8 m at the shoulder, while fully grown males stand at 0.7 - 0.9 m (Putman, 1989). Therefore, the VC was a representation of visibility at the eye height of fallow deer standing in the centre of the plot over a 360 degree viewshed as a horizontal disc of 0.1 m thickness, one metre from the ground (Figure 4.3).

In addition, Leaf Area Index (LAI) values were calculated for each point cloud within the bounds of 0.75 - 1.5 metres in height. Pointcloud processing used the same functions as for the Visibility Coefficient estimates, except for the *reconstruct_ground* function. In addition, the *filter_poi* and *clip_poi* functions (*lidR*) were used to crop the point cloud to two metres in height and 15 metre
radius, respectively. The data were then filtered to include the z coordinates only, then a Leaf Area Density (LAD) profile was generated for each point cloud at height bands of 0.75, 1.25 and 1.75 metres using the *LAD* function from the *lidR* package. The LAI for each point cloud was calculated from the LAD profiles for the height range of 0.75 - 1.5 metres using the *lai* function in the *leafR* package (de Almedia et al., 2021).



Figure 4.3. Illustration of the viewshed concept in a 15-metre radius circular sampling plot in a study woodland. The solid and dotted red lines represent a subset of individual viewsheds. The solid red line illustrates the thickness of each measured viewshed. Where the viewshed hits the tree trunk, the view is obstructed. The Viewshed Coefficient (VC) calculation assumes the deer is at the centre of the plot with a horizontal sightline one metre above the ground surface. The VC encompasses a 360-degree view at this height in one-degree increments.

The large number of woody plant species across the ten sites (n = 44), combined with the high level of variability among plots in species composition, meant that there were no clear relationships between species and VC that could be demonstrated statistically. While certain species provided a notably strong obstruction of view, such as patches of large *Cotoneaster* spp. and cherry laurel (*Prunus laurocerasus*) evergreen shrubs at site BWN, they occupied an insufficient number of plots to test the individual effects of these species. Our analysis therefore focused primarily on the effects of woody plant size, understory LAI and bramble cover on VC. The densities of saplings, small, medium, large and very large woody plants (Table 2) was calculated for each plot using the formula in Equation 4.4.

$$Y = \left(\frac{X}{706.86}\right) \times 10,000$$

Equation 4.2. Y = stem density per hectare, X = total number of stems per plot, 706.86 m^2 = area of 15-metre radius sample plot and 10,000 = square metres per hectare.

Effects of stem density, LAI and mean percentage bramble cover on VC were tested using linear mixed effects models in the R package *lme4* (Bates et al., 2015). Prior to analysis, collinearity between fixed effects was examined in a correlation matrix. Sapling density and small stem density were found to be significantly correlated (r = 0.74). In addition, data exploration using dot plots, histograms and box plots was conducted for each of the fixed effects and the dependent variable (VC) to check whether a normal error structure was appropriate. Based on this data exploration, a log transformation was applied to correct zero-skewness in the following variables: Very large stem density, small stem density, sapling density and mean percentage bramble cover. In addition, all explanatory variables were scaled through z-scoring to bring them on to comparable scales for analysis. A global linear mixed model including every explanatory variable was then analysed using the *dredge* function from the *MuMIN* package (Bartoń, 2022), with the condition that small tree density and sapling density did not co-occur in any models due to their strong collinearity. The significance of the beta estimates was assessed by whether the 95% CI overlapped zero.

To gain an understanding of how the shading effect of larger trees may have influenced understory density and resulting viewsheds, I classified the species of all medium, large and very large woody plants (mature stems) by their propensity to cast shade using values reported by Ellenberg (Ellenberg, 1988) (p. 50) (Supplementary S4.1). These values were on a scale of increasingly strong shade from one to six: extremely low, very low, low, medium, high and very high. Where species from the study plots were not included in the original classification table, a category was assigned based on a close relative in the table, or by JRH. The average shade value of each survey plot was then calculated using the formula in Equation 5. Ellenberg values have previously been used to obtain average estimates for abiotic conditions in forests (Boulanger et al., 2015). A linear mixed model was used to examine the relationship between average Ellenberg value and log small stem density, with site as a random effect.

$$A=\frac{(S\times E)}{T}$$

Equation 4.3. A = average shade value, S = total number of stems in an Ellenberg shade category, E = Corresponding Ellenberg category value and T = total number of mature stems per plot.

The following statistical tests were conducted using the scaled VC data: 1) The point cloud processing was repeated without the slope removal step to assess whether the slope of the ground influenced the viewshed coefficient in each plot. I compared VC values of point clouds from the same plots with and without ground slope removed using a Wilcoxon signed-rank test. 2) I used a paired t test to compare summer and winter scans to determine whether there was any significant difference between the VCs of plots between seasons. A mean value of VC from each of the eight pairs of winter scans was taken, and these were then compared with the eight summer scans. 3) I used a paired t test to compare same day repeat winter scans to assess whether error in the methodology generated differences in VC between scans. Scan pairs were randomised into two groups (A, n = 8 and B, n = 8) prior to this paired test to remove the influence of any order effects.

Results

A total of 71 Viewshed Coefficient (VC) values from summer scans of individual sample plots across ten woodland sites were used in the analysis. 20,555 woody plant stems were recorded across the 71 plots, which included the amended counts for plots LNH8 and LNH4. Of these, 601 were dead. Calculated stem densities per size class are shown in Supplementary S4.2.

The global model containing small tree density (not sapling density) had a Δ AIC of 0, while the next top ranked model had a Δ AIC of 5.20. In addition, the top model had an AIC weight of 80 %. Given the importance of the top model, the model estimates and 95 % confidence intervals from the top model were examined for each explanatory variable. VC significantly decreased with increasing density of small stems (> = 1.3 m in height, < 10 cm DBH), which presented the strongest overall effect (β = -103.84, 95% CI = -149.67, -58.00, Figure 4.4, Table 4.1). The density of the remaining stem size categories did not have a significant effect on VC (Table 4.1). Understory Leaf Area Index did not have a significant effect on VC (Table 4.1). Despite there being notable bramble cover in most of the study sites (Supplementary S4.3), average percentage bramble cover did not significantly affect VC. A linear model showed that logged density of small stems was significantly

negatively related to average strength of shade from mature trees ($\beta = -0.45$, 95% CI = -0.80, -0.09, Figure 4.5).

Table 4.1. Model estimates and 95 % confidence intervals for each of the variables that featured in the top model ($\Delta AIC = 0$).

Fixed effect	Lower 95% Cl	Estimate	Upper 95 % Cl
Log small stem density	-149.67	-103.84	-58.00
Medium stem density	-49.99	-3.57	42.86
Large stem density	-70.04	-27.04	15.97
Log very large stem density	-16.15	33.40	82.95
Log average bramble percentage cover	-70.01	-25.05	19.91
Leaf Area Index (0.75 – 1.5 metres)	-38.04	1.93	41.90



Figure 4.4. Predicted values from the top model for predicting Viewshed Coefficient (y) as a function of log small stem density (x). The error around the line represents the 95% confidence intervals.



Figure 4.5. Predicted values from a single factor linear mixed model showing that logged density of small stems (y) was significantly negatively related to the average shade intensity from mature trees (x). The error around the line represents the 95% confidence intervals from the model.

Topographical slope

The mean VC was marginally higher when the ground slope was removed (mean = 347.80, SE= 23.72, n = 71) compared with when the ground slope was included (mean = 334.36, SE = 24.15, n = 71) during point cloud processing. However, the difference was not significant (mean difference = -13.44, SE = 9.27) between point clouds with and without slope included (V = 1184, p-value = 0.59, Figure 4.6.a).

Season

The mean VC was higher in winter scans (mean = 366.87, SE = 59.49, n = 8) than summer scans (mean = 280.91, SE = 52.51, n = 8), but the difference was no significant (mean difference = - 85.96, SE = 31.54) between the VCs of winter and summer scans (t = 0.09, df = 7, p-value = 0.93, Figure 4.6.b).

Scan consistency

The mean VC for scans in group A (mean = 367.78, SE = 56.19, n = 8) and group B (mean = 365.96, SD = 64.05, n = 8) sets of winter scans were very similar. There was no significant mean difference (mean difference = 1.82, SE = 19.21) between the VCs of scans in groups A and B (t = 0.09, df = 7, p-value = 0.93, Figure 4.6.c). This indicates that the walking pattern of the surveyor was not sufficiently variable to influence the outcome of the viewshed analysis.





Figure 4.6. a) Viewshed Coefficients calculated with ground slope included (orange box) and with ground slope removed (blue box). b) Viewshed Coefficients from eight study plots scanned in summer (orange box) and again in winter (blue box). Ground slope was removed. c) Viewshed Coefficients from scans of eight plots taken twice on the same day. Each pair of scans was randomised into group A (orange box) or group B (blue box). Ground slope was removed. The central black lines show the median, the boxes show the upper (75 %) and lower (25 %) quartiles and the tails show the minimum and maximum values.

Discussion

Woodland plots with a higher density of small woody plant stems had lower horizontal visibility, quantified through a Viewshed Coefficient (VC), one metre from the ground. This result is intuitive, as small woody plant stems occurred at high density compared to other woody plant size categories. This fits with the gap-phase paradigm in forest ecology: openings in the canopy due to windthrow or disease allow light to reach the forest floor, which stimulates seed germination and release of the growth of previously shaded seedlings, which generally results in the formation of a patch with a high density of small woody stems (Attiwill, 1994). This was evident for the pioneer species birch (*Betula* spp) and light-demanding species ash (*Fraxinus excelsior*) in several study plots at sites LNH, HFD and EWD (Figure 3.2). In addition, the common practice of coppicing hazel (*Corylus avellana*) leads to the dense growth of small stems from the same rootstock (Buckley, 1992; Joys et al., 2004) which probably contributed to reduced VC, particularly at EWW where coppiced hazel was widespread.

Larger stem size classes (medium, large, and very large) had negligible independent effects on VC. The density of larger trees in woodlands is restricted by their greater resource requirements. In addition, due to self-shading the foliage of larger trees is generally concentrated in the main canopy, above the eye height of large herbivores. Therefore, they are less likely to significantly hinder viewsheds at one-metre height across a study plot. Canopy trees can also influence the understory themselves through shading from dense foliage, which reduces the density of light-demanding understory vegetation (Coomes et al., 2005; Ellenberg, 1988). In our study sites, this was especially true of plots that contained beech (*Fagus sylvatica*) or hornbeam (*Carpinus betulus*), which cast especially heavy shade (Ellenberg, 1988). This is supported by our post hoc examination of the density of small stems using Ellenberg's species' shade values (Ellenberg, 1988), which indicated that plots with a canopy dominated by trees casting a heavier shade had lower densities of small stems.

Mean percentage bramble cover had no significant effect on VC. Bramble cover can become depleted in woodlands with heavy deer browsing (Cooke & Farrell, 2001; Gill & Fuller, 2007), but was nonetheless present in most of our study plots and was particularly dominant at sites EWD and TCL (Supplementary S4.3). The lack of an effect on visibility may be because bramble cover was

concentrated in the field layer, which was rarely above one metre in height (Supplementary S4.4). It was apparent at several sites that the fallow deer were using bramble patches as refugia, with deersized hollows inside some of the thickets with lots of deer faecal droppings in the vicinity (AG pers. observ.). Whilst the results did not show a significant effect of bramble cover on horizontal viewsheds at one metre height, it may be that localized thickets serve as an important component of habitat structure for animals seeking cover.

Understory LAI was not a significant predictor of VC in the summer scans. This may be because there was very little variation in understory LAI in this dataset (Supplementary S4.5). These uniform LAI values could be symptomatic of widespread browsing by the abundant deer population reducing structural complexity of the understory or dense canopy foliage restricting light availability to lower layers. Both mechanisms could lead to the low density of saplings relative to larger stems found in the woody plant surveys at most sites (Supplementary S4.2). Sapling stem density did not feature in the top model, supporting the notion that saplings and associated foliage have very little influence on horizontal visibility, particularly given their small size (<1.3m) and sparse occurrence across the study plots. The lack of variation in LAI may also be due to limitations of the data collection methods using TLS (Wang & Fang, 2020) or the methodology used to generate the LAI values using the *leafR* package (de Almeida et al., 2021). Leaf Area Density (LAD) may have provided a better measure of how foliage influenced visibility within such a specific height band.

Horizontal visibility was greater in the winter scans than in summer scans of the same plots, but the difference was not significant. Although the direction of the effect was as expected, this finding goes against our expectation that visibility would be much greater in winter due to loss of deciduous leaves. The lack of seasonal difference may be linked to the small variation in summer foliage density within the understory, indicated by the LAI data (Supplementary S4.5). Interpretation is also limited by a low sample size of eight plots with scans from both seasons. Nonetheless, the repeated winter scans showed that the scanning methodology produced consistent VC values, indicating that the technology used is a reliable method for measuring and comparing horizontal viewsheds.

Exclusion of topographical slope during point cloud processing did not significantly alter VC. This does not, however, confirm whether slope is an important factor for deer refuge in the study area. Topographical slope has been shown to affect viewsheds and ungulate browsing behaviour at the

landscape scale using Digital Elevation Models (DEM) (Ndaimani et al., 2013; Roženbergar et al., 2019) but this is outside the scope of the present study. It is important to consider the perceptual range of animals when assessing potential effects of disturbance and habitat structure (Aben et al., 2021; Parsons et al., 2020). Studies have found that when exposed to increased disturbance, ungulates select more rugged terrain where there is reduced hunter access and increased vegetation cover (Buchanan et al., 2014; Sergeyev et al., 2020). In landscapes like the Elwy Valley with steep topography and frequent human disturbance from culling and recreation, it would be interesting to examine the effects of slope on viewsheds at a larger scale.

Hunting takes place in the Elwy Valley, both for recreation and management of the fallow deer population. It is good practice for hunters to ensure a clear line of sight before making a shot; this reduces the risk of deer being disturbed and escaping the cull or an unclean shot leading to wounding and distress of the animal (Aebischer et al., 2014). Therefore, where humans are the only predator and adopt a "sit and wait" shooting strategy – the main method of hunting in the study area – open areas present the greatest risk (Lone et al., 2015; Norum et al., 2015). In the present study, plots with higher densities of small stems had shorter average viewsheds, which may reduce both the perceived and actual threat from human hunters compared with plots that had lower densities of small stems.

This study has demonstrated a novel application of mobile terrestrial laser scanning to studying habitat-scale structure with specificity to large herbivores. The functionality of advancing R packages and rapid quantification of habitat structure using TLS provides a user-friendly opportunity to study the same viewshed metrics for multiple animals in the same system (Lecigne & Eitel, 2022). For example, Lecigne et al. (2020) used TLS data to compare how forest structure influenced the viewsheds for an airborne predator, a terrestrial predator, and a terrestrial prey species. This could also be applied to studying how habitat structure influences viewsheds at different heights for the same animal. For example, when prey animals bed down in vegetation, their viewshed is likely to be significantly reduced compared to when they are standing. Zong et al., (2022) combined ALS and static TLS to quantify red deer habitat selection in relation to visibility using averaged three-dimensional cumulative viewsheds for eye-lines of bedded deer (30 cm) or standing deer (140 cm). While dense cover conceals animals from potential predators, it may also reduce ability to perceive and avoid ambush predation attempts (Lone et al., 2014; Norum et al., 2015). In addition, other metrics such as leaf area or density could be used to study, for example,

the shelter quality of vegetation for thermoregulation or seasonal availability of forage material (Hill & Broughton, 2009; Z. Li et al., 2018). For example, Ewald et al. (2014) used ALS to study how canopy and understory cover influenced roe deer habitat selection according to wind speed and snow depth (Ewald et al., 2014). These concepts may be of interest for future research using TLS to address behavioural trade-offs relating to fine-scale habitat structure in animal populations (Davies & Asner, 2014a; Olsoy et al., 2015; Vierling et al., 2008).

Conclusions

Using a novel 3D mobile Terrestrial Laser Scanning approach, I demonstrate that higher densities of small woody stems reduced horizontal visibility at one metre height from the ground, while foliage quantities as measured by LAI and average bramble cover had no significant effect. Higher densities of small stems occurred in plots with a lighter shade from canopy trees. High densities of small woody stems may break up sightlines in the understory and reduce perceived threat levels for large herbivores – particularly the risk associated with humans. Behavioural responses to perceived risk may be related to understory structure in such temperate forests. The study of viewsheds using terrestrial LiDAR has great potential for improving our understanding of how habitat structure influences animal behaviour.

Chapter 5

Woodland habitat use by fallow deer is shaped by human activity and understory structure

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Author contributions

AG was the lead author of this work and led the conceptualization, writing and data analysis. OB collected and curated the camera data and landowner survey data used for the occupancy analysis. GS, JRH and MPE supervised this work and supported AG with conceptualization, method development, project resources, administration, data analysis and reviewed and edited drafts of this work. OB assisted with study conceptualization, designing the stacked occupancy modelling and model averaging methodology and writing R code for the analyses.

Introduction

In a "landscape of fear" (Laundré et al., 2001; Palmer et al., 2022) animals respond to risk through changes in their habitat use, influenced by trade-offs between concealment and thermoregulation (Glass et al., 2021; Mysterud & Ostbye, 1999; Ratikainen et al., 2007) or foraging (Dupke et al., 2017; Mathisen et al., 2018). Perception of risk is shaped by the physical structure and density of habitat features, such as vegetation and topography (Kuijper et al., 2014; Ndaimani et al., 2013; Parsons et al., 2021). Vegetation structure has been shown to affect habitat use of large mammals in wooded environments, as dense cover can affect their ability to escape from predators (Kuijper et al., 2013; van Ginkel et al., 2021) and facilitates ambush predation (Belotti et al., 2013; Loarie et al., 2013) but sparse cover can provide insufficient concealment (Borkowski & Ukalska, 2008;

Olsoy et al., 2015). For example, a study quantifying the landscape of risk for roe deer (*Capreolus capreolus*) exposed to predation by humans and Eurasian lynx (*Lynx lynx*), an ambush predator, found that deer were killed by lynx most often in more closed habitats, whereas kills by humans were most common in open habitats, which provided longer sightlines for hunters with rifles (Norum et al., 2015). A study of a hunted red deer population in Poland found that the availability of cover encouraged habitat use in forests, indicating that security cover can be a key factor driving space use by deer experiencing hunting pressure (Borkowski et al., 2016). In addition to hunting pressure, non-lethal disturbance from human recreation (Hagen et al., 2017; Wisdom et al., 2018; van Beeck Calkoen et al., 2022), roads (Eldegard et al., 2012; Mathisen et al., 2018; Montgomery et al., 2012) and infrastructure development (Stankowich, 2008) contributes to perceived risk in forested landscapes and can alter deer habitat use. For example, in a national park in the Netherlands, deer space use was highest in the zone without hunting or recreation, which led to reduced sapling browsing on open heathlands where deer were most exposed (Mols et al., 2022).

Variation in predation risk can influence changes in deer woodland use over time. For example, a study found that male red deer shifted their habitat use with the onset of the hunting season to more concealing cover, although males that were later shot did not make this shift (Lone et al., 2015). Perceived predation risk from humans also varies through the 24-hour period (Gaynor et al., 2018; Sullivan et al., 2018). Gaynor et al. (2022) showed that Columbian black-tailed deer (*Odocoileus hemionus columbianus*) adjusted their diel activity patterns in response to higher risk from human hunters near roads and in open grasslands, which provide clear sightlines for shooting. The deer avoided open areas during daylight hours, as the hunters were most active from sunrise to sunset. (Gaynor et al., 2022). This shift in diel activity can also occur in response to non-lethal human disturbance (Coppes et al., 2017; Lewis et al., 2021; Marion et al., 2021). For example, a study near a military training site in Germany found that red deer inhabiting the most disturbed site selected locations providing cover during the day (Richter et al., 2020). If deer spatially and temporally separate themselves from humans, this can reduce the efficacy of management strategies to mitigate against overbrowsing (Ikeda et al., 2019; Yamaguchi et al., 2020).

In addition to human activity, temporal variation in environmental conditions may influence deer habitat use. For example, harsh winter conditions may drive deer to spend more time in the shelter of woodland environments (Mysterud and Ostbye, 1999; Szemethy et al., 2003; Ratikainen et al., 2007; Borkowski and Ukalska, 2008), or conversely in areas with higher solar radiation (Allen et al., 2015). Tolerance of seasonal environmental conditions can also differ between the sexes (Conradt et al., 2000). Rutting males may prioritise habitats with abundant mating opportunities (Latham et al., 2015) while mothers and dependent calves may choose to spend more time within or close to woodland shelter (Long et al., 2016; Panzacchi et al., 2010) or in areas with nutritious forage to support lactation (Clutton-Brock et al., 1982). The understory layer of woodlands offers important forage resources for deer such as nutritious ground flora, woody browse and large tree seeds such as those of oaks (*Quercus* spp.) (Azorit et al., 2012; Esattore et al., 2022; Perrin et al., 2011). In winter, deer may become more reliant on woodland forage resources such as evergreen trees, ivy (*Hedera helix*) and bramble (*Rubus fruticosus* agg.) due to reduced productivity of herbaceous vegetation (Borkowski & Obidziński, 2003; Jackson, 1977).

The aim of this study is to assess how woodland understory structure and human disturbance influence woodland occupancy by a deer species (fallow deer, Dama dama) over the 24-hour cycle in the landscape of the Elwy Valley, North Wales. The fallow deer is a highly generalist ungulate herbivore and is one of the most widespread deer species in the world (Esattore et al., 2022; Hofmann, 1989). Fallow deer thrive in landscape mosaics of crop fields, pasture and woodlands, such as those in North Wales and throughout the UK and Europe (Esattore et al., 2022; Fuller & Gill, 2001; Putman et al., 2011). Aside from this Elwy Valley population, woodland occupancy by fallow deer has not previously been explored in relation to disturbance and habitat structure (Barton, 2023). Woodland occupancy may be related to the reproductive cycle, as fallow deer may use woodlands as lekking sites during the rut from September - November (Apollonio et al., 1992; Thirgood, 1990), as a source of forage from January – March during the post-rut recovery period (Borkowski & Obidziński, 2003; Caldwell et al., 1983) and as shelter for dependent fawns from May - July during the birthing period (Kjellander et al., 2012). While there are no natural predators in the Elwy Valley, the deer exhibit characteristic avoidance behaviours, reacting to disturbance from humans and dogs (AG and OB pers. obs.). Human hunters are present in the area and primarily harvest deer for the purpose of woodland management. For fallow deer in England and Wales, the shooting season is open during August-April for males, and November-March for females, therefore the deer experience the threat of being hunted for most of the year. Notably, however, the open seasons do not overlap with the birthing period. In addition, shooting only takes place during daylight hours unless a night license is obtained. To the best of our knowledge, no night hunting took place in the woodlands under study. Therefore, woodlands that may be safe to occupy at night may become dangerous places for the deer to visit during the day, shifting deer

habitat preferences and activity patterns over the 24-hour period. Conversely, the presence of dense cover may allow tolerance of human disturbance, allowing the deer to occupy disturbed sites even during periods of peak human activity.

Methods

Study site

Ten woodlands were selected for study throughout the Elwy Valley landscape (Figure 3.1). Fallow deer have been present in the Elwy Valley for just over 100 years. The population is now estimated at around 1500 individuals (Lee Oliver pers. comm.). To our knowledge, no other deer species were present, though there have been reports of some isolated Reeves' muntjac (*Muntiacus reevesi*) to the east of the river Clwyd outside of the main study area.

The woodland sites were selected where fallow deer presence had been previously recorded to ensure that deer activity levels could be quantified and compared across sites. The woodlands comprised a range of tree communities, ground vegetation and topography. Most sites contained broadleaved trees mixed with some conifers such as larch (*Larix decidua*), sitka spruce (*Picea sitchensis*), Scots' pine (*Pinus sylvestris*), western red cedar (*Thuja plicata*) and Douglas fir (*Pseudotsuga menziesii*). The most common broadleaved trees included oak (*Quercus* spp.), ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*), beech (*Fagus sylvatica*), birch (*Betula pendula*), hazel (*Corylus avellana*, usually coppiced), holly (*Ilex aquifolium*), elm (*Ulmus glabra*) and locally dominant hornbeam (*Carpinus betulus*) and wild cherry (*Prunus avium*). Less common species included sweet chestnut (*Castanea sativa*), willow (*Salix* spp.) and hawthorn (*Crataegus spp.*). Some monospecific conifer stands were also present. The woodlands varied considerably in their age and management intensity (see Chapter 3). Some were completely unmanaged, others were rotationally felled or coppiced for timber production. Some were designated sites managed for conservation purposes, such as Sites of Special Scientific Interest (SSSIs) (e.g., Figure 5.1).

Site-level human disturbance variables were included as covariates in the analysis. These data were collected during a larger-scale study of the Elwy Valley fallow deer population (Barton, 2023), in which landowners were asked to report the presence or absence of hunting and the levels of recreational activity in their woodlands. The present study used the results of these surveys to

categorise the woodlands as "not hunted or "hunted" and "low recreation or "high recreation" (Table 3.1).



Figure 5.1. View of the understory in one study woodland (PCG) in summer 2020. This site contains SSSI areas and is actively managed, including the culling of fallow deer - note the high seat to the left of the photograph.

Motion-activated cameras

Deer detections were recorded using one motion-activated camera in each of the ten woodlands as part of the landscape-scale study of this deer population (Barton, 2023). Each camera was placed on deer trails following expert advice to maximise detection rate. Placing cameras on wildlife trails has been shown to increase detection probability in some large mammals (Cusack et al., 2015; Hofmeester et al., 2021). The cameras were locked to a tree approximately 80 cm above the ground. Cameras were operational across a period of two years (January 2019 – December 2020) over three seasons per year that were deemed biologically relevant to deer behaviour: January-March (Postrut), May-July (Birthing) and September-November (Rut).

Images were processed during the landscape-scale Elwy Valley study (Barton, 2023). When triggered by movement, the cameras were set to take a burst of three photographs. Images were manually tagged using the open-source software *digiKam* (www.digikam.org) as "deer present" or "deer absent". The metadata were then extracted and converted into a spreadsheet in R version 4.1.1 (R Core Team, 2021) using the *camtrapR* package (Niedballa et al., 2016). Images that were taken within ten minutes of each other were considered non-independent (Barton, 2023). Therefore, for each detection, the first image of the three-image burst was used for analysis and only detections at least ten minutes apart were included.

Surveying for environmental covariates

In each woodland, a series of 15-metre radius sample plots were established (see Chapter 3). The location of the plots was stratified to capture as much variation as possible in density, size structure, and species diversity of the tree and shrub communities within each of the ten woodland sites. Sample plots were positioned to avoid human constructed paths or roads, although these features were sometimes close to plot edges. Sites WFR, TCL and MRN contained steep slopes, which could not be surveyed due to safety constraints. Woodland edges were not avoided. The woodland unit was primarily defined as the area within 300 metres of the camera but was also constrained by a) access permission and b) woodland cover directly contiguous with the location of the camera.

The position of plots was recorded using a Garmin handheld GPS unit which was then used to locate plots for later sampling. On the first visit to a plot, a wooden stake was hammered into the ground to mark the plot centre. A tape measure was used to measure the 15-metre radius from the centre point to identify the limits of the sampling plot, which were marked with flagging tape.

Horizontal visibility at deer eye-height

The use of new remote sensing technology such as terrestrial Light Detection and Ranging (LiDAR) provides an opportunity to accurately quantify metrics such as cover and understory openness as potential influencers of animal vigilance and risk perception (Lecigne et al., 2020). Surveys were carried out using a mobile GeoSLAM ZEB-REVO laser scanner in August 2020. Previous studies have validated GeoSLAM ZEB devices for use in forest vegetation surveys (Bauwens et al., 2016; Camarretta et al., 2021; Ryding, 2016). The conditions required for these surveys were a) no rain and b) wind speeds below 16 kilometres per hour. This reduced the risk that rain or moving leaves

and branches would artificially elevate point density. The GeoSLAM ZEB device was placed on a clipboard at the centre of the plot during setup to mark the start and finish point. The walking pattern consisted of walking to the edge of the plot and around the edge in both directions, then crossing the plot from different angles in a closed loop, starting and finishing in the plot centre (Bauwens et al., 2016; Ryding, 2016). Areas with thick scrub (e.g., bramble or blackthorn *Prunus spinosa*) were surveyed as thoroughly as possible.

Point clouds were processed in R version 4.0.3 (R Core Team, 2021) using the *viewshed3d* (Lecigne et al., 2020; Lecigne & Eitel, 2022) and *lidR* (Roussel et al., 2020) packages. Due to the memory constraints of a standard computer, the analysis was run on the Supercomputing Wales platform. The processing broadly followed example workflows in the *viewshed3d* handbook. Each point cloud was cropped to a 15 metre-radius circle. Duplicated points were deleted and any "noise" in the form of isolated points was also removed. Remaining points were then classified as "ground" or "not ground", then the topographical slope of the ground points was removed. This was to make sure that the effect of vegetation in each plot could be examined independently of slope. The ground points were then reconstructed following slope removal.

The Viewshed Coefficient (VC) was calculated using the $h_visibility$ function within the R package *viewshed3D* (Lecigne et al., 2020). The VC is defined as "the area under the curve of visibility as a function of distance from the animal's location" (Lecigne & Eitel, 2022). The average VC for each site was then calculated. See Supplementary S5.1 for average VC values per site.

The standardised location of a deer in each plot was defined using XYZ coordinates 0,0,1. This placed the animal at the centre of each plot and one metre above the ground surface. Fully grown fallow deer females stand at 0.7 - 0.8 m at the shoulder, while fully grown males stand at 0.7 - 0.9 m (Putman, 1989). Therefore, the VC at one metre was a representation of visibility at the eye height of fallow deer standing in the centre of the plot over a 360 degree viewshed as a horizontal disc of 0.1 m thickness, one metre from the ground.

Bramble surveys

Percentage cover of bramble was surveyed in the ten woodland sites. Bramble is potentially an important resource for the deer in this area. It is an abundant scrambling shrub with evergreen foliage, providing potential foraging material during the winter (Caldwell et al., 1983). In addition,

the growth form of bramble forms dense thorny "banks" which may provide important shelter from human hunters, who require long sightlines to make a kill using rifles (Aebischer et al., 2014; Norum et al., 2015).

Bramble cover of each plot was measured using a 0.25 m^2 quadrat sub-divided into $25 \times 0.01 \text{ m}^2$ squares. Each plot was surveyed either two or three times across the summers (June – August) of 2019 - 2021. For each survey, eight quadrats were placed inside the plot using randomly generated cardinal directions and distances from the plot centre (1–15 m). At each of these eight locations, a quadrat was placed on the ground and the number of squares with any cover of bramble foliage and stems was counted from above. These eight counts were averaged to obtain a bramble count value for each plot survey. These two or three values from across the survey years were then averaged to obtain the mean percentage bramble cover for each plot. These values were then used to calculate an average percentage bramble cover value per site. See Supplementary S4.3 for average percentage bramble cover per site.

Data analysis

Diel occupancy modelling

An occupancy modelling approach was used to quantify deer woodland use. Occupancy modelling provides two metrics. The first is occupancy probability (Ψ): the probability that a species is present within a survey site over a given time period. The second is detection probability (*p*): the probability that a species will be detected at a given survey site if that site is occupied (MacKenzie et al., 2002). While detection probability is often viewed as a nuisance parameter in occupancy modelling, which is necessary to estimate the false absence rate in detection methodology, it can be used as a relative measure of habitat use (Lewis et al., 2015). If a species uses a habitat frequently and in high numbers, it is more likely to be detected than if it used a habitat rarely and in low numbers (Lewis et al., 2015). This is especially useful where occupancy is expected to be high throughout a landscape, as occupancy probability may not pick out more fine-scale variation in habitat use. Therefore, occupancy was used as a measure of deer presence and detection probability as a relative measure of variation in woodland use over the 24-hour period.

A detection history contains presence-absence data of detections and non-detections for a species within a given sampling unit and occasion (MacKenzie et al., 2017). Single-season occupancy studies typically define a closed sampling occasion as a full day, or multiple consecutive days (Li et al., 2020; Oberosler et al., 2017). While this is useful for examining long-term trends in occupancy, these models only account for "average daily conditions", when in fact conditions are likely to change over the 24-hour cycle (Gaston, 2019; Rivera et al., 2022). Instead, this study used a novel approach with three separate detection histories, one for each period within the 24-hour cycle: diurnal, crepuscular and nocturnal. This allowed examination of finer-scale temporal variation in the influence of risk factors and habitat characteristics on site occupancy and detection probability (Rivera et al., 2022). The crepuscular period consisted of two hours either side of dawn and dusk, so four hours per 24 hours across the survey seasons. In contrast, the length of the diurnal and nocturnal periods varied with the number of daylight hours per day, therefore detections were classified into the three diel periods accounting for variation in sunrise and sunset. The detection histories spanned six survey seasons over two years (January 2019 – November 2020). The survey seasons corresponded to the biological survey seasons (Post-rut = January-March, Birthing = May-July, Rut = September-November) and were 90 days each in length. The covariates under investigation were as follows:

- Visibility (Vis, numeric) average Horizontal Visibility Coefficient across woodland. Visibility influences how far deer can see in a woodland so may influence their threat perception, although low visibility habitat may provide better hiding cover.
- Mean summer bramble cover (Bramble, numeric) average summer bramble cover taken from ground vegetation surveys of the ten woodland sites. Bramble provides a source of cover and food.
- Biological season (Bioseason, categorical) corresponding to the six survey seasons. Seasons 1 & 4 = Post rut, seasons 2 & 5 = Birthing, seasons 3 & 6 = Rut.
- **4) Hunting** (Hunt, categorical) presence / absence of stalking during the sampling period, obtained from landowner surveys (Barton, 2023).
- 5) **Recreation** (Rec, categorical) low / high levels of recreation (e.g., dog walking) during the sampling period, obtained from landowner surveys (Barton, 2023).

The following occupancy modelling methodology was based on a protocol developed by Barton (2023) using the *RPresence* package (MacKenzie & Hines, 2023). A single-season occupancy

modelling approach was used, whereby sites were grouped by survey season to produce a total of 60 "site-seasons" (e.g., site1-Rut, site2-Rut etc.). The biological seasons can be considered temporally independent from one another, as they were separated by a one-month gap. By using this site-season categorisation, I was able to maximise available degrees of freedom for the occupancy models with a small number of sites (n = 10) while still measuring relative differences in occupancy and detection probability across sites.

The following methodology was repeated for each diel period using the three detection histories. Firstly, occupancy (Ψ) was modelled in a series of candidate models using each of the covariates. Within these models, Ψ was allowed to either remain constant, vary by a single covariate, or vary by two covariates in a series of single-factor and two-factor combinations of all covariates. Initial trials of the modelling approach flagged convergence issues when more than one variable was included for detection probability (p). Therefore, for these models investigating the influence of covariates on Ψ , p was modelled using single covariates, which included each of the environmental variables and Bioseason (see Supplementary S5.2 for full model list).

The opposite was then conducted for occupancy models that were used to investigate effects of the covariates on detection probability (p), which was allowed to either remain constant, vary by a single covariate, or vary by two covariates in a series of single- and two-factor occupancy models. As the additional parameter in the models, Ψ was modelled using a single environmental covariate in each candidate model (see Supplementary S5.3 for full model list).

Using the top models from these two sets (model weight > 0.05), beta estimates and 95 % confidence intervals were then obtained for Ψ and p. For covariates which had significant beta estimates (confidence intervals did not overlap zero), model averaging of the top models was used to produce predictive values for Ψ and p using the *MuMIn* package (Bartoń, 2022). This involved testing each covariate individually using a dummy dataset, where all other covariates that featured in the top models were held constant. Numeric variables were held at their median value, while factors were held at one reference level. Predicted estimates for Ψ and p were then plotted against each covariate of interest.

Results

The motion-activated camera survey took place across 10 woodland sites for 6 three-month survey seasons, each 90 days in duration, with a potential total of 5400 active "camera days". A total of 556 active camera days were lost due to asynchronous deployment and incidents of camera malfunction. The 4844 active camera days were distributed across all six survey seasons and all 10 sites (Figure 5.2) and resulted in a total of 2760 fallow deer detections. For eight sites, most detections occurred in the post-rut seasons, while the rut seasons had the fewest detections in nine of the sites (Table 5.1). Prior to modelling, the raw occupancy data indicated lower diurnal and crepuscular occupancy in the hunted woodlands compared to the woodlands where hunting was absent, with the opposite effect in the nocturnal period (Figure 5.3). In addition, the raw data indicated that diurnal, crepuscular and nocturnal occupancy were higher in sites with high recreation compared to sites with low recreation (Figure 5.4).



Figure 5.2 Number of active camera days across sites, coloured by season. The six survey seasons correspond to the biological seasons as follows: Post-rut = seasons 1 & 4, Birthing = seasons 2 & 5, Rut = seasons 3 & 6.

Table 5.1 Number of fallow deer detections across each site and survey season. The six surveyseasons correspond to the biological seasons as follows: Post-rut = sum of seasons 1 & 4, Birthing =sum of seasons 2 & 5, Rut = sum of seasons 3 & 6.

Site	Season1	Season2	Season3	Season4	Season5	Season6	Post-rut	Birthing	Rut
BWN	36	214	181	68	292	89	104	506	270
BHL	15	87	65	21	32	19	36	119	84
EWD	14	21	14	7	35	22	21	56	36
EWW	1	2	0	0	0	0	1	2	0
HFD	74	223	64	6	118	201	80	341	265
LNH	2	27	1	0	35	158	2	62	159
MRN	16	99	0	0	0	19	16	99	19
PCG	7	79	1	15	67	26	22	146	27
TCL	7	18	12	9	8	10	16	26	22
WFR	22	18	52	18	33	79	40	51	131
Total	194	788	390	144	620	623	338	1408	1013



Figure 5.3 Mean number of days occupied in each of the three diel periods across woodlands where hunting was absent (n = 4) and woodlands where hunting was present (n = 6). The error bars represent the standard error of the means.



Figure 5.4 Mean number of days occupied in the three diel periods across woodlands where recreation levels were low (n = 5) and woodlands where recreation levels were high (n = 5). The error bars represent the standard error of the means.

Diurnal occupancy & detection probability

For diurnal occupancy, the top two candidate models contributed 98% of the AIC weight (Table 5.2). There was a significant negative effect of hunting on diurnal occupancy (Table 5.2), although confidence intervals could not be generated for the model-averaged estimate for hunted woodlands (Figure 5.5). This was probably due to the high levels of occupancy in woodlands where hunting was not present. Diurnal detection probability was also significantly reduced by the presence of hunting (Table 5.3, Figure 5.6). In addition, diurnal detection probability was lower in woodlands with higher bramble cover (Figure 5.7).

Table 5.2 The top two candidate models (model weight > 0.05) for diurnal occupancy probability (Ψ) with beta estimates and confidence intervals (CI) for each Ψ covariate. *p* = detection probability, DAIC = delta AIC. See Supplementary S5.4 for the full AIC table and Supplementary S5.5 for the summed Akaike weights for each covariate.

Model		DAIC	Model	Ψ	Data actimate and 05% Cl
ID	Ψ and p covariates		weight	covariate	Beta estimate and 95% CI
39	Ψ(Vis+Hunt) <i>p</i> (Bramble)	0	0.55	Hunt	-23.98 (-30.74/-17.22)
				Vis	0.42 (-0.4/-1.25)
40	Ψ(Bramble+Hunt) <i>p</i> (Bramble)	0.5	0.43	Hunt	-22.94 (-29.96/-15.91)
				Bramble	-0.4 (-1.44/ - 0.64)



Figure 5.5 Model-averaged beta estimates for diurnal occupancy probability (Ψ) for woodlands where hunting was absent (n = 4) and present (n = 6). Error bars represent 95% confidence intervals.

Table 5.3 The top scoring model in the AIC table (model weight > 0.05) with beta estimates and covariates for each of the covariates for diurnal detection probability (*p*) that featured in the model (Hunting and Bramble). Ψ = occupancy probability, DAIC = delta AIC. Significant results are highlighted in bold. See Supplementary 5.6 for the full AIC table of candidate models and Supplementary S5.7 for the summed Akaike weights for each covariate.

78 $\Psi(Hunt)p(Bramble+Hunt)$ 0 0.99 Hunt -1.27	(-1.45/-1.09)
Bramble - 0.75 ((-0.84/-0.66)



Figure 5.6. Model-averaged predicted beta estimates for the effect of the presence of hunting on diurnal detection probability (*p*). Error bars represent 95% confidence intervals.



Figure 5.7. Model-averaged predicted beta estimates and 95% confidence intervals (shaded area) for the effect of average summer bramble cover on diurnal detection probability (*p*).

Crepuscular occupancy and detection probability

The occupancy models did not identify any significant effects on crepuscular occupancy (Table 5.4). The null model for occupancy was the highest ranked by DAIC and accounted for the majority of model weight. From the top models, the confidence intervals of the beta estimates for each of the covariates overlapped zero (Table 5.4).

Table 5.4. Top scoring occupancy models (model weight ≥ 0.05) for investigating effects on covariates on crepuscular occupancy probability (Ψ) with beta estimates and 95% confidence intervals (CI) for each covariate for Ψ that featured in the models. p = detection probability, DAIC = delta AIC. No results were significant. See Supplementary S5.8 for the full AIC table and See Supplementary 5.9 for the summed Akaike weights for each covariate.

Model ID	Ψ and p covariates	DAIC	Model weight	Ψ covariate	Beta estimate and 95% Cl
16	Ψ(.) <i>p</i> (Bioseason)	0	0.21	-	-
19	Ψ(Bramble) <i>p</i> (Bioseason)	0.94	0.13	Bramble	-0.36 (-1.04/0.32)
18	Ψ(Vis) <i>p</i> (Bioseason)	1.01	0.13	Vis	0.35 (-0.34/1.04)
20	Ψ(Rec) <i>p</i> (Bioseason)	1.68	0.09	Rec	0.39 (-0.97/1.74)
29	Ψ(Vis+Bramble) <i>p</i> (Bioseason)	2.58	0.06	Vis	0.23 (-0.53/0.99)
				Bramble	-0.26 (-1.02/0.51)
28	Ψ(Bramble+Hunt)p(Bioseason)	2.62	0.06	Bramble	-0.47 (-1.28/0.34)
				Hunt	-0.45 (-2.07/1.16)
26	Ψ(Bramble+Rec)p(Bioseason)	2.83	0.05	Bramble	-0.33(-1.02/0.37)
				Rec	0.24 (-1.17/1.65)
25	Ψ(Vis+Rec) <i>p</i> (Bioseason)	2.83	0.05	Vis	0.32(-0.37/1.01)
				Rec	0.3(-1.09/1.69)

Crepuscular detection probability was significantly influenced by Bioseason and the presence of hunting (Table 5.5). Crepuscular detection probability was higher in the birthing season compared to the post rut and rutting seasons (Figure 5.8). In addition, the presence of hunting led to an increase in crepuscular detection probability (Figure 5.9).

Table 5.5. Top scoring occupancy models (model weight > 0.05) for investigating effects of covariates on crepuscular detection probability (*p*) with beta estimates and 95% confidence intervals (CI) for each covariate for p that featured in the models. Ψ = occupancy probability, DAIC = delta AIC. Significant results are highlighted in bold. For the Bioseason covariate, the "birthing" season was used as the reference level. See Supplementary S5.10 for the full AIC table and Supplementary S5.11 for the summed Akaike weights for each covariate.

Model ID	Model	DAIC	Model weight	p covariate	Beta estimate and 95% Cl
10	Ψ(.) <i>p</i> (Bioseason+Hunt)	0	0.34	Bioseason(Rut)	-0.48 (-0.72/-0.24)
				Bioseason(Post.rut)	-0.44 (0.12/0.66)
				Hunt	0.37 (0.16/0.58)
50	Ψ(Bramble) <i>p</i> (Bioseason+Hunt)	1.05	0.20	Bioseason(Rut)	-0.48 (-0.72/-0.24)
				Bioseason(Post.rut)	-0.44 (-0.67-0.21)
				Hunt	0.37 (0.16/0.57)
34	Ψ(VIS) <i>p</i> (Bioseason+Hunt)	1.12	0.17	Bioseason(Rut)	-0.48 (-0.72/-0.24)
				Bioseason(Post.rut)	-0.44 (-0.67/0.21)
				Hunt	0.37 (0.16/0.57)
65	Ψ(Rec) <i>p</i> (Bioseason+Hunt)	1.73	0.13	Bioseason(Rut)	-0.48 (-0.72/-0.24)
				Bioseason(Post.rut)	-0.44 (-0.67/-0.21)
				Hunt	0.36 (0.16/0.57)
22	Ψ(Bioseason) <i>p</i> (Bioseason+Hunt)	3.51	0.05	Bioseason(Rut)	-0.48 (-0.72/-0.24)
				Bioseason(Post.rut)	-0.44 (-0.67/0.21)
				Hunt	0.37 (0.16/0.57)



Figure 5.8. Model-averaged beta estimates for the effect of each Bioseason on crepuscular detection probability. The biological seasons correspond to the following time periods: Post rut = January-March, Birthing = May-July, Rut = September-November. Error bars represent 95% confidence intervals.



Figure 5.9. Model-averaged beta estimates for the effects of the absence and presence of hunting on crepuscular detection probability. Error bars represent 95% confidence intervals.

Nocturnal occupancy and detection probability

No significant effects on nocturnal occupancy were found (Table 5.6). The null model for occupancy was the highest ranked by AIC and accounted for the majority of the AIC weight. For all four covariates, the confidence intervals for the beta estimates from model averaging overlapped zero.

Table 5.6. Top scoring occupancy models (model weight > 0.05) for investigating effects of covariates on nocturnal occupancy probability (Ψ), with beta estimates and 95% confidence intervals (CI) for each covariate for *p* that featured in the models. No results were significant. See Supplementary S5.12 for the full AIC table and Supplementary S5.13 for the summed Akaike weights for each covariate.

Model ID	Model	DAIC	Model weight	Ψ covariate	Beta estimate and 95% CI
17	Ψ(.) <i>p</i> (Bioseason)	0	0.12	-	-
58	Ψ(.) <i>p</i> (Rec)	0.95	0.07	-	-
19	Ψ(Vis) <i>p</i> (Bioseason)	1.02	0.07	Vis	0.30 (-0.30/0.91)
21	Ψ(Rec)p(Bioseason)	1.09	0.07	Rec	-0.58 (-1.77/0.62)
22	Ψ(Hunt) <i>p</i> (Bioseason	1.59	0.05	Hunt	-0.40 (-1.64/0.84)

Nocturnal detection probability was significantly influenced by Bioseason in a similar way to crepuscular detection probability (Table 5.7). The birthing season had consistently higher detection probability compared to the other two seasons (Figure 5.10). Nocturnal detection probability was lower in woodlands with high levels of recreation compared to woodlands with low levels of recreation (Figure 5.11). Although two of the top models (Model ID 8 and 60) indicated a significant negative effect of bramble cover on nocturnal detection probability, the contribution of these models to AIC weight was negligible (Table 5.7), and post-hoc examination of the predicted values indicated that the effect size was minimal.

Table 5.7. Top scoring occupancy models (model weight > 0.05) for investigating effects of covariates on nocturnal detection probability (p) with beta estimates and 95% confidence intervals (CI) for each covariate for p that featured in the models. Significant results are highlighted in bold. For the Bioseason covariate, the "birthing" season was used as the reference level. See Supplementary S5.14 for the full AIC table and Supplementary S5.15 for the summed Akaike weights for each covariate.

Model ID	Ψ and p covariates	DAIC	Model weight	p covariate	Beta estimate and 95% Cl
9	$\Psi(.)p(Bioseason+Rec)$	0	0.2	Bioseason(Rut)	-0.48 (-0.77/-0.20)
				Bioseason(Post.rut)	-0.49 (-0.78/-0.19)
				Rec	-0.44 (-0.69/-0.19)
32	Ψ(VIS) <i>p</i> (Bioseason+Rec)	0.93	0.13	Bioseason(Rut)	-0.48 (-0.77/-0.19)
				Bioseason(Post.rut)	-0.49 (-0.78/-0.19)
				Rec	-0.44 (-0.69/-0.20)
61	Ψ(Rec) <i>p</i> (Bioseason+Rec)	1.25	0.11	Bioseason(Rut)	-0.48 (-0.77/-0.20)
				Bioseason(Post.rut)	-0.48 (-0.78/-0.19)
				Rec	-0.44 (-0.69/-0.19)
77	Ψ(Hunt) <i>p</i> (Bioseason+Rec)	1.63	0.09	Bioseason(Rut)	-0.48 (-0.77/-0.20)
				Bioseason(Post.rut)	-0.49 (-0.78/-0.19)
				Rec	-0.44 (-0.69/-0.19)
8	Ψ(.) <i>p</i> (Bioseason+Bramble)	1.86	0.08	Bioseason(Rut)	-0.60 (-0.89/-0.31)
				Bioseason(Post.rut)	-0.53 (-0.82/-0.23)
				Bramble	-0.21 (-0.34/-0.08)
60	Ψ(Rec) <i>p</i> (Bioseason+Bramble)	1.91	0.08	Bioseason(Rut)	-0.60 (-0.89/-0.31)
				Bioseason(Post.rut)	-0.52 (-0.82/-0.22)
				Bramble	-0.21 (-0.34/-0.08)


Figure 5.10 Model-averaged beta estimates for the effect of each Bioeason on nocturnal detection probability. The biological seasons correspond to the following time periods. Post rut = January-March, Birthing = May-July, Rut = September-November. Error bars represent 95% confidence intervals.



Figure 5.11 Model-averaged beta estimates for the effects of low and high levels of recreation on nocturnal detection probability. Error bars represent 95% confidence intervals.

Discussion

Diurnal woodland occupancy and detection probability of fallow deer were negatively affected by the presence of hunting. In contrast, crepuscular and nocturnal woodland occupancy were not affected by any of the covariates investigated. This suggests that the deer exhibited a direct, short-term response to the threat of hunters, who are generally only active during daylight hours. Therefore, the deer may continue to utilise the woodlands unincumbered outside of the diurnal period. For example, a study on Nakanoshima Island in Japan found that sika deer (*Cervus nippon*) shifted their activity patterns to become more nocturnal as culling intensity increased, temporally separating their activity peaks from those of humans (Ikeda et al., 2019). In addition, a study showed that North American elk (*Cervus canadensis*) reduced their foraging time and avoided roads and trails during the diurnal period when hunters were active, although they suffered nutritional costs as a result (Apollonio et al., 2014). In the present study, if the fallow deer can temporally separate their activity peaks from those of humans without substantial reductions in their foraging rate, hunting may be having a minimal effect on browsing pressure.

A larger-scale study across 29 woodlands in the same study area assessed the influence of lethal and non-lethal disturbance on fallow deer activity across the three diel periods, using a different set of landscape covariates (Barton, 2023). Crepuscular and nocturnal activity increased relative to diurnal activity where hunting was present, while high levels of recreation and woodland management generated a shift towards diurnal activity patterns. However, when both lethal and non-lethal human disturbance were present, hunting was the overriding driver and maintained a crepuscular / nocturnal pattern of activity (Barton, 2023). This shift towards nocturnal activity in response to diurnal hunting has been demonstrated in other deer populations as an avoidance of peak human activity (Bonnot et al., 2020; Gaynor et al., 2022). Nonetheless, while the Elwy Valley fallow deer have apparently adjusted the timing of their activity peaks in response to hunting, overall activity levels were not very different between hunted and non-hunted sites (Barton, 2023). In addition, Barton (2023) did not find a significant effect of hunting on occupancy. By conducting separate model sets for the diurnal, crepuscular and nocturnal periods, the present study identified a strong effect of hunting in the diurnal period only. Taken together, it seems that current hunting strategies are not generating significant overall reductions in woodland use by fallow deer in the Elwy Valley, as the deer are shifting the timing of their habitat use to compensate for elevated risk in the diurnal period. Strategies for species management and conservation should account for temporal variation

in human disturbance and diel activity patterns when assessing impacts on animal habitat use (Rivera et al., 2022).

Probability of diurnal detection of fallow deer declined with increasing bramble cover. The deer may use dense bramble thickets as a form of shelter during the day, when perceived risk is highest due to peaks in human activity. Dense vegetation cover can reduce deer predation risk by humans, as the use of rifles require clear sightlines over relatively long distances (Gaynor et al., 2022; Lone et al., 2014; Norum et al., 2015). Therefore, diurnal movement rates in woodlands with high bramble cover may be lower, as the deer may bed down under the bramble as a sheltering behaviour. This was particularly evident at sites PCG and HFD, where deer-sized hollows were present in the bramble thickets surrounded deer signs (tracks and droppings). Deer lay down to ruminate as they digest their food, therefore budgeting for rest in safe sites during risky periods may be an efficient use of time (Bose et al., 2018). Previous studies have demonstrated reduced movement rates in deer populations in response to predation risk by human hunters (Little et al., 2016; Picardi et al., 2019; Wiskirchen et al., 2022). A recent study of red deer in Norway showed that deer preferred more dense resting sites, especially during the hunting season (Meisingset et al., 2022). Lower movement rates due to increased sheltering behaviour could lead to a reduction in detection probability (Caravaggi et al., 2020; Neilson et al., 2018; Rogan et al., 2019; Stewart et al., 2022; Stewart et al., 2018) which may have manifested as reduced movement rates past the cameras in the present study. An alternative explanation is that dense brambles present a barrier to deer movement. For example, bramble and other dense understory vegetation can act as browsing refugia for tree saplings (Harmer et al., 2010; Ward et al., 2008). In the present study, bramble may have restricted the speed and directionality of deer movement, which could reduce probability of detection. Frequently used deer pathways were present throughout the survey sites, indicating the deer favoured paths of least resistance. Furthermore, dense bramble near the cameras may have reduced the distance over which deer triggered the cameras (Hofmeester et al., 2017), however the cameras were deliberately placed on deer trails to minimise this effect Another consideration is the possible negative effect of high deer browsing pressure on bramble cover. However, there was no effect of bramble cover on crepuscular detection probability, and the effect on nocturnal detection probability was very weak. This provides strong evidence for the first explanation – that the deer utilise bramble as a form of cover during the riskiest diel period.

Diurnal hunting often begins or ends during the crepuscular period, as the sun is rising or setting respectively. As a result, deer movement rates may increase during this transition period. When hunters move into a woodland, they may disturb the deer and cause them to flee. Conversely, when hunters leave a woodland, the deer may move more freely in open areas and reduce their use of protective shelter. Previous studies have identified increased crepuscular activity in hunted deer populations relative to the diurnal period, indicating deliberate avoidance of peaks in human activity (Agetsuma et al., 2016; Ikeda et al., 2019; Sullivan et al., 2018). In addition, studies of deer movement rates have identified peaks in velocity during the crepuscular period as they transition between secure resting sites and feeding areas (Ager et al., 2003; Ensing et al., 2014; Zong et al., 2022). This seems to be true of the present study population, as the larger-scale Elwy Valley study found that fallow deer activity peaked in the crepuscular period in woodlands where hunting was present (Barton, 2023). Therefore, if sheltering behaviour generates a reduction in detection probability (as suggested by the effect of bramble in the diurnal period), release from sheltering behaviour may generate an increase in detection probability. Nocturnal detection probability was higher in woodlands where recreation levels were low. The fact that recreation only generated a detectable effect in the nocturnal period is surprising, as recreation is supposedly more likely to affect deer behaviour during the day when humans are more active (Coppes et al., 2017; Ensing et al., 2014; Lewis et al., 2021). Although this analysis did not identify any significant effects of recreation on occupancy, the larger-scale Elwy Valley study on deer activity indicated that overall occupancy was higher in woodlands with high recreation levels across all three time periods (Barton, 2023). Previous studies have documented shifts to nocturnality in human-disturbed deer populations (Lewis et al., 2021; van Doormaal et al., 2015). Conversely, in woodlands in the Elwy Valley where hunting is absent and recreation is high, the fallow deer tend to shift towards a more diurnal pattern of activity, indicating habituation to non-lethal human disturbance (Barton, 2023). Habituation to frequent and predictable non-lethal human disturbance has previously been documented in red and fallow deer, such as reduced vigilance or fleeing responses in deer parks (Langbein & Putman, 1991; Recarte et al., 1998) and near public trails (Marion et al., 2022; Schuttler et al., 2017). In addition, prey species such as deer may instinctively shift towards a diurnal activity pattern if human disturbance may disrupt hunting success of their natural predators (Basille et al., 2009; Ordiz et al., 2021; Shannon et al., 2014). Therefore, in the present study, fallow deer nocturnal activity may have been relatively higher in woodlands with low recreation, leading to increased detection probability.

Crepuscular and nocturnal detection probability were both influenced by biological season in a very similar way, with the birthing period exhibiting higher detection probabilities than the rut or birthing periods. A greater detection probability in the birthing period agrees with the findings of the larger-scale Elwy Valley study, which showed higher detection rates in the birthing season compared to the rut and post-rut seasons (Barton, 2023). Movement rates may have been relatively higher during the birthing period. Although male fallow deer are generally more mobile within their territories during the rut (Apollonio et al., 1992; Davini et al., 2004), on a landscape-scale their movements may become restricted to a smaller area as they attempt to intercept female movements and defend a valuable mating area (Thirgood, 1990; Thirgood et al., 1999) as was shown in a study on male white-tailed deer (Odocoileus virginianus) (Foley et al., 2015). Females may cluster in defended harems, perhaps where high quality foraging resources are available, or exhibit excursion behaviour where they pass through defended territories but do not always remain near males (Apollonio et al., 2014; Clutton-Brock et al., 1988). The rut is typically associated with increased movement rates across deer species due to mate-searching behaviour, while post-rut activity is generally lower as males recover from exertion and individuals slow their movement rates to conserve energy over winter (Csányi et al., 2022; Hothorn et al., 2015; Kämmerle et al., 2017; Pépin et al., 2009; Richard et al., 2008). During the birthing period (May-July), there may be less need to conserve energy due to warmer temperatures and greater food availability, and there may be less social clustering (Thirgood, 1996), so individual movement rates may be greater. In addition, the hunting seasons for male and female fallow deer do not overlap the birthing period, therefore there may have been relatively reduced diurnal risk during the birthing period and subsequent effects on deer behaviour. For example, a study of a hunted roe deer population in the Italian Alps found that movement rates were lower in hunted areas during the open season (Picardi et al., 2019). Nonetheless, the data from the present study showed that detection rates was generally higher in both hunted and non-hunted sites during the birthing period.

It is likely that biological season influenced diurnal detection probability in the same way as during the crepuscular and nocturnal periods, but the strong effects of hunting and bramble dominated in the diurnal period. This demonstrates the uncertainty brought about by limitations of our modelling approach, with restricted numbers of covariates in each candidate model due to the limited number of sites, and lack of testing of interactions between covariates. Therefore, caution is advised when interpreting the effect of biological season on diel detection probability in the present study.

The models identified no effect of horizontal visibility at deer eye height (one metre) on occupancy or detection probability throughout the 24-hour cycle. This may indicate a mismatch in the spatial scale of the TLS surveys in multiple sampling plots and the single cameras, however an effect of bramble cover - surveyed at the same scale as visibility - was identified by the models. Averaging the horizontal visibility measurements across whole woodlands provided a very coarse representation of the variation in understory structure within each site. In addition, the visibility measurements were set to be one metre from the ground at deer eye height, when in fact visibility as perceived by humans may have been a bigger driver of perceived risk and deer movement (Gaynor et al., 2022; Norum et al., 2015; Olsoy et al., 2015). For example, several of the woodlands contained high-seats from which hunters used the sit-and-wait strategy to shoot deer. These seats are typically at least four metres above the ground, which would reduce the obscuring effect of vegetation 1 m in height, especially when deer are standing or moving. Dense bramble may provide the most efficient cover, as deer can bed down under bramble to hide. In addition, high seats are deliberately placed in areas with good visibility, therefore areas with dense bramble may be hunted less often. A more targeted survey of habitat structure in the direct vicinity of the cameras, more cameras distributed throughout the sampled area, or information on vertical vegetation structure and horizontal cover at different heights in the understory (Stein et al., 2022) may have provided a clearer picture of how woodland habitat structure influences deer habitat use. For example, a recent study in the Bavarian Forest National Park in Germany studied the habitat use of GPS-collared red deer using visibility measures averaged from the eye heights of resting deer (30 cm) and standing deer (140 cm) (Zong et al., 2022). The fine-scale behaviour data from the collars, combined with detailed TLS data, provided a clear picture of deer habitat selection according to visibility (Zong et al., 2022). The present study has demonstrated the potential for integration of mobile TLS technology into studies of interactions between habitat structure and deer risk perception and behaviour. Given the importance of cover as a factor for habitat selection in deer and other prey animals (Mysterud & Ostbye, 1999), this technology could be hugely valuable for informing wildlife management and conservation (Lecigne et al., 2020; Olsoy et al., 2015).

Conclusions

This study aimed to improve understanding of how human disturbance and woodland understory structure influenced occupancy and detection probability of fallow deer in the Elwy Valley, using a novel occupancy modelling approach split across the three diel periods and three biological seasons with visibility data from terrestrial laser scanning and summer bramble cover. Diurnal occupancy and detection probability were lower in woodlands where hunting was present, but this did not extend to the crepuscular and nocturnal periods. This indicated that behavioural responses to hunting occurred over short timescales within the 24-hour cycle, and that deer were able to make fine-scale adjustments to their habitat use in response to predation risk. This was supported by increased crepuscular detection probability in hunted woodlands, which suggested an increase in movement rate in response to changes in perceived risk in the crepuscular period. The negative effect of bramble cover on diurnal detection was likely associated with lower deer movement rates, suggesting that bramble may be an important shelter resource during the riskiest period in the 24hour cycle. This study supports the findings of the larger-scale Elwy Valley study that the fallow deer in this landscape are highly adaptable to fine-scale temporal variation in perceived predation risk. Management of growing deer populations requires careful consideration of their ability to compensate for variation in perceived risk and how this interacts with dense vegetation cover, especially where human activity peaks are generally very predictable.

Chapter 6

Woodland plants dominate fallow deer diet across seasons in a woodland-pasture mosaic landscape

Introduction

The diets of "ecosystem engineer" species such as large herbivores can shape ecosystem function and habitat structure (Apollonio et al., 2017; Forbes et al., 2019). Ungulates mediate natural processes such as nutrient cycling (Ramirez et al., 2018; Ramirez et al., 2021a), plant competitive interactions (Faison et al., 2016; Newman et al., 2014; Stephan et al., 2017) and vegetation succession (Kienast et al., 1999; Ramirez et al., 2019). These ecological mechanisms are crucial for maintaining biodiversity (Fløjgaard et al., 2021; Perrin et al., 2011). For example, foraging activity of multiple African ungulate herbivores was found to maintain species richness of savannah habitats by inhibiting encroachment of woody vegetation and mediating dominance of more competitive plant species (Burkepile et al., 2017). In northern France, deer exclusion led to dominance of beech (*Fagus sylvatica*) or bramble (*Rubus fruticosus* agg.), which reduced the diversity of the plant community (Laurent et al., 2017). Wild populations of large herbivores are in crisis across the globe, with significant declines in population sizes and ranges, which has considerable implications for ecosystem function (Forbes et al., 2019; Ripple et al., 2015). Conversely, where large herbivores are at very high densities, they can have detrimental effects on habitat structure and diversity (O'Connor, 2017; Schulze et al., 2014).

Deer (Cervidae) populations are expanding throughout the temperate zone, raising concerns for woodland conservation and management (Fuller and Gill, 2001; Côté et al., 2004; Reimoser and Putman, 2011). In human altered landscapes such as in the UK, woodlands often exist as relatively small patches in a mosaic of pasture and crop fields. Woodland-pasture mosaic landscapes are particularly suitable for deer (Bjørneraas et al., 2011; Spitzer et al., 2020; Ward, 2005). The fields offer highly fertilised, nutritious crops and grasses (Corgatelli et al., 2019; Kjøstvedt et al., 2018)

while woodland cover can provide a refuge from predation risk (Bongi et al., 2008; Bonnot et al., 2013; Theuerkauf & Rouys, 2008) and shelter from adverse weather conditions (Melin et al., 2014; van Moorter et al., 2009; Wiemers et al., 2014). Woodlands themselves also offer a variety of foraging resources including browse material from trees and shrubs and herbaceous material in the ground layer. A study in Japan found that woodlands surrounded by a high percentage of grassland had the highest sika deer (Cervus nippon) densities, leading to reduced understory vegetation cover and greater incidences of debarking compared to woodlands with lower deer numbers (Takarabe & Iijima, 2020). In addition, a study in Sweden found that bark-stripping damage by red deer (Cervus elaphus) was higher in conifer forests closer to nutrient-rich rapeseed (Brassica napus) fields (Jarnemo et al., 2022). At elevated densities, deer browsing can reduce understory structural complexity (Eichhorn et al., 2017), reducing habitat suitability for various bird, mammal and invertebrate species (Gill & Fuller, 2007). Deer can also reduce the biodiversity of the plant community by favouring grazing-tolerant (Tamura & Yamane, 2017), unpalatable (Ramirez et al., 2019) or more generalist (Boulanger et al., 2018; Perrin et al., 2011; Vild et al., 2017) plant species. Additionally, deer browse the leading shoots of tree saplings and seedlings, which can inhibit growth and alter growth form, with detriment to timber yield (Bergquist et al., 2009; Kupferschmid et al., 2015; Reimoser, 2003). Tracking deer foraging behaviour and diet can improve our understanding of how increasing deer populations are affecting woodland environments (Apollonio et al., 2017).

Resource availability data allow interpretation of deer diet selectivity, which is crucial to understanding their foraging ecology (Norbury & Sanson, 1992; Sakata et al., 2021). If there is a large proportion of a relatively rare plant in the diet, this indicates selection for a preferred food source, while absence of a frequent and widespread plant species may indicate avoidance (Forsyth et al., 2002; Jackson, 1977; Tanentzap, Bee, et al., 2009). On the other hand, dominance of a common plant may show foraging for convenience rather than active selection (Johnson et al., 2001). These factors are interesting in the context of controlling deer browsing pressure. For example, diversionary feeding with natural or human-provisioned food can protect tree saplings from browsing by providing alternative, high quality foraging resources (Arnold et al., 2018; Bobrowski et al., 2020; Borowski et al., 2019), while dense thorny shrub cover or unpalatable vegetation can discourage sapling browsing (Champagne, Dumont, et al., 2018; Maublanc et al., 2021; Smit et al., 2006). Conversely, a study of invasive red deer (*Cervus elaphus*) in New Zealand found that forest plants were more likely to be browsed if they were in a patch of high-quality forage vegetation (Bee et al., 2009). Palatable foraging resources may inadvertently attract deer into an area and increase the risk of browsing damage to neighbouring plants (Bee et al., 2009; Čermák et al., 2011; Holík et al., 2021), especially when resources are heterogenous at the landscape scale (Ohse, Seele, et al., 2017). At the foraging patch scale, however, unpalatable neighbouring plants may make palatable plants more susceptible to browsing due to their relatively high quality (Champagne, Perroud, et al., 2018). Spatial distribution of resources is an important and complex driver of deer foraging decisions (Hagen & Suchant, 2020; Morellet & Guibert, 1999).

Temporal fluctuation in resource availability is an important factor in deer diet composition. Deer can afford to be more selective during the growing season when more diverse, nutritious plants are available, but in winter may resort to bulk foraging with reduced selectivity of more fibrous material to meet their nutritional requirements (Bee et al., 2011; Dumont et al., 2005; Storms et al., 2008; Verheyden-Tixier et al., 2008). Consequently, grazing species such as fallow deer (Dama dama) and red deer (Cervus elaphus) tend to increase their reliance on low quality browse of evergreen species in winter (Borkowski & Obidziński, 2003; Caldwell et al., 1983; Kamler & Homolka, 2011; Spitzer et al., 2020). A study of red deer and roe deer (Capreolus capreolus) in France found that the winter diets of both species contained significantly greater proportions of conifers, which have low palatability and high fibre content, compared to the other seasons (Storms et al., 2008). In addition, a Europe-wide analysis found that the diets of fallow and red deer, (intermediate bulk-roughage grazers), became more similar to those of moose (Alces alces) and roe deer (selective browsers), in the winter due to reduced grass content in the diet (Spitzer et al., 2020). Deer density can also modulate resource selection, as higher densities can lead to more intense competition for preferred food (Kalb et al., 2018; Koda & Fujita, 2011; Spitzer et al., 2021). For example, a study in Roztocze National Park in Poland found that increasing red deer density promoted more consumption of unpalatable beech (Fagus sylvatica) saplings relative to more palatable sycamore (Acer pseudoplatatnus), possibly because high deer density increased browsing pressure at the wider landscape scale, where beech was the dominant tree species (Borowski et al., 2021).

Previous studies have assessed the diet of deer species through direct observation of grazing behaviour of wild or captive individuals (Bergvall, 2009; Pompanon et al., 2012; Putman, 1986a) or visual examination of diet contents from faecal material (Putman et al., 1993; Shannon et al., 2013; Zweifel-Schielly et al., 2012) and the rumen contents of culled animals (Jackson, 1977, 1980; Riganelli et al., 2010). Whilst visual examination of partially digested plant tissue is technically simple and affordable, taxonomic resolution is limited as usually only the most undigested material is identifiable (Garnick et al., 2018; Nichols et al., 2016; Tanentzap, Bee, et al., 2009). This often leads to diet contents being categorised into broad groups, such as "grass" or "woody browse" (Riganelli et al., 2010; Shannon et al., 2013; Tixier & Duncan, 1996). In contrast, DNA metabarcoding provides the opportunity for more precise identification of dietary components that are not always visible by eye.

Metabarcoding the DNA of faecal remains is a well-established technique for studying the diet of ungulate herbivores such as European bison (*Bison bonasus*) (Cellura et al., 2010; Kowalczyk et al., 2019), tapir (*Tapirus terrestris*) (Hibert et al., 2013), African elephants (*Loxodonta Africana*) (Kartzinel et al., 2015), and deer (Czernik et al., 2013; Erickson et al., 2017). Metabarcoding has also been used to reveal the foraging habits of ungulate herbivores from rumen contents (Nichols et al., 2016), and saliva from browsed branches (Nichols et al., 2012, 2015; Nichols & Spong, 2014). Universal primers are designed to bind to regions of DNA conserved within a taxonomic group that have sufficient resolution to discriminate among taxa in the diets of animals using high through-put sequencing (Deiner et al., 2017). For plants, combining the chloroplast DNA marker **rbcL** and nuclear ribosomal DNA from the internal transcribed spacer 2 (**ITS2**) regions ensures both a wide range of detection and good taxonomic discrimination, respectively (Brennan et al., 2019; Hollingsworth, 2011; Moorhouse-Gann et al., 2018). The creation of the Barcode UK database has greatly increased the reliability of these markers for taxonomic identification of UK plants (Jones et al., 2021), making them ideal for studying the diets of herbivores.

Following expansion of a fallow deer (*Dama dama*) population in the Elwy Valley (North Wales) since introduction from a deer park just over 100 years ago, there has been growing concern amongst landowners that increased herbivory pressure has had a detrimental impact on the ecological function of their woodlands and the growth rates of trees planted for timber. The Elwy Valley area is a mosaic landscape, with patches of woodland surrounded by a matrix of pastoral and arable farmland (Chapter 3). Fallow deer can be described as an intermediate grazing herbivore, as their diet primarily consists of low-quality bulk roughage grasses (Borkowski & Obidziński, 2003; Hofmann, 1989; Kerridge & Bullock, 1991). However, they also consume broadleaved and coniferous tree and shrub browse, climbing and scrambling plants such as ivy (*Hedera helix*), honeysuckle (*Lonicera* spp.) and bramble, and nutritious herbs (Bruno & Apollonio, 1991; Jackson,

1977; Nugent, 1990). In fact, a recent review of fallow deer feeding ecology and distribution found it to be one of the most widespread deer species on the planet, with very adaptable dietary habits (Esattore et al., 2022). The fallow deer has a variable home range size of 1 - 10 square kilometres, depending on sex, season and landscape configuration (Borkowski & Pudełko, 2007; Davini et al., 2004). In addition, the gut retention time of a fallow deer has been reported to be 31.4 hours (Ramanzin et al., 1997). Therefore, it is probable that deer will enter and leave woodland patches multiple times during feeding and digestion.

The aim of this study was to characterise seasonal variation in the diet of a UK fallow deer (*Dama dama*) population using DNA metabarcoding in a mosaic landscape of agricultural land and woodland pasture, in relation to resource availability. The expectation was that the faecal samples would not only reflect plants that deer consume within the study woodlands, but also in the surrounding environment. I expected that grasses would form a principal dietary component, and that the diet would be more diverse in the autumn and winter as availability of this key resource declines and thus deer are forced to be less selective. In addition, I predicted that woody browse would be mostly utilised in the winter, especially evergreen foliage. If certain plants were selected for in the diet, they should be overrepresented in the diet relative to their availability.

Methods

Study sites

Three woodlands in the Elwy Valley were surveyed once per month for two years (September 2019 – August 2021), excluding April – June 2020 due to the COVID-19 pandemic (Figure 6.1). These woodlands were selected for survey as they were shown to be actively used by deer in a landscape-scale motion-activated camera study of the Elwy Valley fallow deer population (Barton, 2023). As deer are unlikely to remain in a single woodland between feeding bouts, the three woodlands should be considered as sampling points, not exclusive foraging locations (Jayakody et al., 2011). Seven additional woodlands in the landscape were surveyed for seasonal resource availability. For full descriptions of the tree species composition and characteristics of the understory in these woodlands, see Chapter 3.

To explore how the diet of deer using woodlands might vary compared to deer restricted to grassland foraging, six faecal samples were also collected in December 2020 from the fallow deer enclosure (approx. 200 x 70 metres in size, location: 53.29565 N, -3.75060 W) by keepers at the Welsh Mountain Zoo, Colwyn Bay, North Wales. The enclosure consisted of a grass field with a hedgerow. Six samples only were collected from the zoo during a single December sampling occasion due to time constraints. This limits direct comparison with the wild samples from other time periods, however the diet of the captive deer grazing the paddock was likely to remain consistent throughout the seasons (aside from provided feed).



Figure 6.1. The Elwy Valley study area in North Wales and locations of the three study woodlands where diet samples were collected, marked with blue circles. The yellow circles indicate the remaining seven sites that were surveyed for resource availability across the study area. Map generated using ArcGIS Desktop © 1999-2020, Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

Field data collection

The following protocol was used at the three study woodland sites. Initially, a well-used deer path with deer faeces present was located within the woodland. For each survey, the surveyor walked along the track, scanning the ground for faecal material. Only distinct faecal mounds of six or more pellets were collected. Fresh samples were prioritised for collection and were identified as dark in colour and shiny from residual mucous. A 50-millilitre Falcon tube or zip-lock bag was labelled with the site name and date. The faecal pellets were placed in the labelled tube or bag using clean nitrile gloves. The surveyor aimed to collect six faecal mound samples per survey. If six mounds were not found, the surveyor continued searching for up to an hour. When insufficient samples were found along the track, the surveyor searched off-track within the bounds of the woodland in an opportunistic fashion. In total, 353 field samples were collected and analysed. For the captive deer, a keeper collected six samples from the paddock while wearing nitrile gloves. All samples were double-bagged and stored at -20 °C within eight hours of collection. The number of samples collected per woodland per month is shown in Table 6.1.

Study Site	Month	Sampling occasions	Number of samples
· · · · · · · · · · · · · · · · · · ·	January	2	11
	February	2	12
	, March	2	11
	April	1	5
	Mav	1	5
	June	1	6
	July	2	13
BWN	August	2	11
	September	2	12
	October	2	10
	November	2	10
	December	2	10
	Total	21	116
	January	2	10
	February	2	11
	March	2	12
	April	1	6
	May	1	5
	June	1	5
	July	2	10
HFD	August	2	11
	September	2	12
	October	2	15
	November	2	11
	December	2	11
	Total	21	119
	January	2	10
	February	2	11
	March	2	7
	April	1	5
	May	1	6
	June	1	6
WFR	July	2	13
	August	2	11
	September	2	11
	October	2	11
	November	2	11
	December	2	10
	Total	21	112
Zoo	December	1	6

Table 6.1. Number of surveys per site and month over two years (2019-2020) and number of samples collected per month.

An experiment was carried out at site WFR to assess the degree of contamination from pollen and other plant material that may stick to the faecal samples (Table 6.2). Small pebbles approximately 5 millimetres in diameter were sterilised with bleach and dried in a UV hood for 30 minutes. The pebbles were then coated with an adhesive mixture of 9:1 petroleum jelly and paraffin oil and sterilised again under UV light for 30 minutes. Three groups of these blank pellets were then placed on the ground at a random location between 0 and 60 steps from the starting points for the faecal surveys and covered with chicken wire to allow air to circulate to the pellets while minimising disturbance from animals. The pebbles were then left in the woodland for at least two weeks (Table 6.2). One tube of pellets was retained in the lab at room temperature as a control. The field pebbles were collected into falcon tubes following the same methods as for the faecal samples and frozen with the control tube at -20 °C for storage, along with the control sample.

Table 6.2. Timing of sampling occasions for blank pellets, including the dates samples were deployed in the woodland and later collected, and the codes assigned for each sampling occasion. Samples marked "W" were in the woodland; samples marked "C" were laboratory controls and were not taken into the woodland.

Sample codes	Sampling period	Woodland deployment date	Retrieval date
W1, W2, W3, C1	Nov – Dec 2020	19/11/2020	07/12/2020
W4, W5, W6, C4	Jan – Feb 2021	12/01/2021	16/02/2021
W7, W8, W9, C7	Feb – Mar 2021	16/02/2021	17/03/2021
W10, W11, W12, C8	Mar – Apr 2021	17/03/2021	16/04/2021
W13, W15, C9	Apr – May 2021	16/04/2021	25/05/2021

Plant resource availability surveys

Woodland ground vegetation cover was surveyed once every three months in ten woodland sites across the Elwy Valley, including the three sites surveyed for faeces (Figure 6.1). This included scrambling vines such as bramble, ivy and honeysuckle. Woody plants less than 30 cm tall (such as tree seedlings) were also included. Any woody plants taller than 30 cm were excluded from this survey, except for scrambling vine cover (ivy, bramble or honeysuckle). There was at least one

month between successive woodland surveys, and the site survey order was randomised for each season. This ensured that enough time had passed to observe seasonal change and that the survey order would not become an artefact in any temporal trends observed. Between four and ten 15-metre radius permanent sample plots were established in each woodland (Chapter 3). For each survey, eight 0.25 m² quadrats were located at randomly positioned points within each plot, with independent positions in each survey. Each 0.25 m² quadrat was sub-divided into 25 x 0.01 m² squares. The position of each quadrat was selected using polar coordinates from a randomly generated compass bearing and a random number of paces (0-15) from the plot centre. If a standing tree was obstructing the placement, the quadrat was moved a step further out from the centre (not exceeding the plot perimeter) until a position was found where the quadrat could be placed. Percentage cover of all plant taxa in each quadrat was assessed by counting the number of 0.01 m² squares that contained each plant species. For any unidentifiable plants, the number of squares containing the plant was recorded, then a sample was taken for subsequent identification. Samples were taken from outside the sample plot to avoid changing the vegetation under study. See Figure 3.3 for visualisation of the seasonal ground flora survey data.

In addition to seasonal ground vegetation surveys, to sample vegetation potentially available at browsing height for deer, surveys of trees and shrubs > 30 cm in height were made in all sample plots. The number of tree and shrub stems was recorded, the size was measured using a DBH tape (or for those shorter than 1.3 m, a metre ruler) and the species identified. See Figure 3.2 for visualisation of the tree and shrub survey data.

Laboratory protocol

Faecal samples were defrosted and crushed with a pestle and mortar, using a sterile approach (Supplementary S6.1). A portion of 0.04 - 0.08 grammes was weighed out into a 1.5-ml Eppendorf tube. DNA was then extracted using the Qiagen DNA Plant Mini kit, following a modified protocol (Supplementary S6.2). The lysis solution was added to the sample tubes, which were then put on a bead-beater for four minutes at 1800 rpm, followed by a 30-minute incubation period at 65 °C. Samples were then put through a Qiagen spin column in several washing steps with buffer and then 100% ethanol to remove any staining from the column membrane. The DNA was then eluted in 60 μ l of AE buffer. The elution step was repeated by putting the AE buffer through the column a second time to increase the yield.

For the blank pellets, each pebble was placed in a 1.5 millilitre microcentrifuge tube and the protocol was followed as for the faecal samples. For downstream processing, the DNA extracts from each of the time points at which the blanks were deployed in the woodland were combined to produce five pooled samples in total – one for each time point (Table 6.2). The laboratory controls were combined into two pools: 1) C1, C4 and C7, and 2) C8 and C9.

The target ITS2 and rbcL fragments were amplified using a two-step PCR protocol. All DNA extractions, including the blank pellets and zoo samples were randomised across four 96-well plates. The first round of PCR served to increase the concentration of the target fragments; the second round attached dual-indexed barcodes for sample identification and adaptors to facilitate Illumina sequencing.

All primer sequences included 5' universal tails to enable annealing of Illumina barcodes. The first round PCR primers for ITS2 were ITS2F ACACTCTTTCCCTACACGACGCTCTTCCGATCT-NNNNN-ATGCGATACTTGGTGTGAAT (Chen et al., 2010) and UniplantR GTGACTGGAGTTCAGACGTGTGCTCTTCCGATCT-CCCGHYTGAYYTGRGGTCDC (Moorhouse-Gann et al., 2018). The first round rbcL primers were *rbcla-F* ACACTCTTTCCCTACACGACGCTCTTCCGATCT-NNNNN-ATGTCACCACAAACAGAGACTAAAGC (Khanam et al., 2016) and rbclr506 GTGACTGGAGTTCAGACGTGTGCTCTTCCGATCT-AGGGGACGACCATACTTGTTCA (de Vere et al., 2012). This combination of rbcL primers and the ITS2F primer have been used previously for DNA metabarcoding of UK plants in pollen (Brennan et al., 2019) and honey (de Vere et al., 2017). All primers were diluted from a starting stock of 4 nmol to 10 µmol. The first round PCR amplification was carried out in 25 µl sample volumes using 12.5 µl of Qiagen Multiplex PCR Master Mix (2X), 0.5 µl of the forward primer, 0.5 µl of the reverse primer and 10.5 µl of DNA-free water. Thermocycling conditions began with a Hot start Taq activation step of 95 °C for 15 minutes, followed by 35 cycles of the following program: 94 °C for 30 seconds, 50 °C for 90 seconds, 72 °C for 1 minute. The final extension step was 10 minutes at 72 °C.

The first round PCR products were then cleaned using magnetic beads (Agencourt $\$ AMPure $\$ XP, Beckman Coulter) at a volume of 0.7 x the original PCR reaction volume (17.5 μ l of beads added to 25 μ l of PCR product) to remove unused primers and primer dimers (see Supplementary S6.3 for full bead cleaning method). The second round of PCR was also carried out in a 25 μ l

volume using 12.5 µl of Qiagen Multiplex PCR Master Mix (2X), 1 µl of the corresponding second round primer index i5-i7 (10nM) for each sample, 6.5 µl of DNA-free water and 5 µl of first round PCR product. Thermocycling conditions began with a Hot start Taq activation step of 95 °C for 15 minutes, followed by 15 cycles of the following programme: 98 °C for 10 seconds, 65 °C for 30 seconds, 72 °C for 30 seconds. The final extension step was 5 minutes at 72 °C.

Sample pooling and size selection

The second round PCR products were electrophoresed on a 96-well 1% agarose gel and categorised by DNA concentration according to brightness of each band. The second round PCR products were then combined into pools of the same concentration category at 10 µl per sample. Samples of the strongest concentration category were combined within PCR plates only; samples in the medium, weak and no band categories were combined across plates. This gave a total of 11 pools for ITS2 and 11 pools for rbcL (see Supplementary S6.4 for full pool list). The negative controls for extractions and PCRs were added into the strongest pools of each plate at 1 µl per control. The positive controls were added into their respective concentration category pool at 1 µl per control. For rbcL, ten samples were not sequenced as they did not produce a band after second round PCR and quantification using a high-sensitivity Qubit found no detectable DNA.

The fragment sizes and their relative concentrations were analysed on a 4150 TapeStation System (Agilent), following the manufacturer's instructions. The pools were combined according to the concentration of the target band to obtain a final volume of 325 μ l each for ITS2 and rbcL (see Supplementary S6.4. for target band concentrations and Supplementary S6.5. for volumes of each plate pool added into final combined pools). The two weakest pools were limited to 100 μ l within these final volumes to ensure they were represented during sequencing but did not overdilute pools with stronger concentrations. Pooling in equimolar concentrations was not possible, as this would overdilute the final pool.

The two final 325 μ l pools were isolated using a Pippin Prep (Sage Science) to remove any nontarget bands, following manufacturer's instructions. For ITS2, the size range selected was 500 – 700 bp, and for rbcL, 600 – 800 bp, terminating with an elution into 40 μ l. The libraries were sequenced on an Illumina MiSeq using a MiSeq Reagent Kit v3 (600-cycle) at 8 picoMoles, spiked with 20% Phi-X to reduce the risk of under-clustering due to the low diversity nature of ruminant faecal samples.

Processing of sequencing data

Data processing was carried out in R version 4.1.0 (R Core Team, 2021) using the Supercomputing Wales (SCW) facility. Initially, the ITS2 and rbcL primers were removed using *cutadapt* (Martin, 2011). This step also removed any sequences where the primers were not present. The fastqc quality scores were then inspected for the forward and reverse reads of each sample. A QC quality score of 30 (99.9% inferred base call accuracy) is considered the highest standard for next generation sequencing (NGS), however the vast majority of reads did not meet this threshold. Therefore, to retain sufficient reads for meaningful analysis, a QC quality score of 20 (99.0% inferred base call) was used as the threshold for downstream processing. The sequences were filtered and trimmed using the *DADA2* package (Callahan et al., 2016). For the *filterAndTrim* function, I specified a trunQ score of 20 and a max error rate of 2 for the forward reads and 5 for the reverse reads. For the *mergePairs* function, I specified a maximum mismatch of 1 and a minimum overlap of 10. Any detected chimeras were also removed. For rbcL, the *filterAndTrim* step resulted in heavy losses of reads, therefore I took the decision to only use unmerged forward reads for taxonomy assignment. In contrast, the ITS2 marker performed well during merging, therefore the merged reads were used for taxonomy assignment.

Before taxonomy assignment, the text file containing the filtered sequences was converted to a fasta file containing the number of occurrences of each Amplicon Sequence Variant (ASV) per sample. The ASVs were then blasted against a curated ITS2 and rbcL plant database from Barcode UK (Jones et al., 2021) using the *blastn* function on the SCW platform, resulting in the assignment of plant species codes for ASVs across all samples.

After taxonomy assignment, downstream processing was carried out using the *phyloseq* package (McMurdie & Holmes, 2013) in R version 4.1.1 (R Core Team, 2021). Initially, 1386 and 8195 unique ASVs were identified for ITS2 and rbcL, respectively. Rarefaction curves were inspected to identify the quality of coverage for both markers. On this basis, samples with less than 100 reads were removed prior to further analysis, reducing the sample total to 309 woodland samples, 4 zoo samples and one blank sample for ITS2. For rbcL, 319 woodland samples, 4 zoo samples and 3 blank samples were retained. None of the extraction or PCR blanks survived this step for ITS2. For rbcL, some ASVs were present in blanks in sufficient number that they survived filtering. ASV "seq_26" was present in Extraction blank 22/04/2021 and the R1 PCR control for plate D. ASVs "seq1661" and "seq1807" were also present the R1 PCR control for plate D. These ASVs were

identified as *Silene* sp., which were subject to DNA extractions during a different study conducted in the same laboratory, therefore these ASVs were likely the result of contamination. Consequently, these ASVs were removed from the final ASV table.

Data Analysis

The reads from ITS2 and rbcL were joined to give a consensus dataset whereby taxa were assigned to the highest taxonomic level reached by both markers, following methodology from Lowe et al., (2022). For each sample, the number of reads for each consensus taxon were summed for both markers. The proportion of reads per taxon per sample was then used as a measure of relative read abundance (Lowe et al., 2022). For each consensus taxon, I examined the relationship between the percentage of reads per sample for ITS2 and rbcL using a Spearman's rank test with Holm correction for multiple testing (Lowe et al., 2022). Following the methodologies of previous metabarcoding studies using similar plant primers, I treated the metabarcoding data as "semi-quantitative" due to the inherent biases in species detection and DNA extraction, PCR and sequencing (Jones et al., 2022; Lowe et al., 2022). Accordingly, I used presence / absence data or proportional read abundance data for all analyses. I took a post hoc decision to remove sample S295 from the dataset, as it was an outlier with the dominant taxon being *Berberis* sp., a genus of flowering shrubs in the family *Berberidaceae*, which are frequently cultivated in domestic gardens.

For the taxa identified in the woodland faecal samples by DNA metabarcoding, a Non-Metric Multidimensional Scaling (NMDS) approach was used to visualise dissimilarity in taxonomic composition of the diet across seasons and woodland sites using the *metaMDS* function in the *vegan* package in R (Oksanen et al., 2022). This was also done for the vegetation survey data, separately for the quadrat ground flora and woody plant datasets due to differences in survey methodology. The Shannon Diversity Index (SDI) for the taxa identified in faecal samples from each woodland site and season was also calculated and plotted. In addition, a Permutational multivariate analysis of variance (PERMANOVA) test was carried out using the *adonis2* function in the *vegan* package to test whether woodland site or meteorological season was a significant predictor of taxa across 338 faecal samples from the consensus dataset across the three woodland sampling sites. Samples were split by season as follows: autumn (September, October, November), winter (December, January, February), spring (March, April, May) and summer (June, July, August). A similar approach with NMDS plots and a PERMANOVA test was used to explore whether woodland site

or season was more important for explaining variation in the percentage cover of ground flora species. The PERMANOVA used a binary presence / absence matrix of taxa from 79 individual site surveys across the ten woodlands during 2019-2021.

To visualise the relative contributions of plant taxa to the diet per month and per site, bipartite networks were constructed using the proportion of sequences per genus as a measure of relative abundance using the geom_alluvium function in the ggplot2 R package (Wickham, 2016). In addition, to test the specificity of the diet relative to resource availability, a preference analysis was carried out using the generate null net function from the econullnetr package in R (Vaughan et al., 2018). This package has been used previously to assess the plant foraging preferences of honeybees (Lowe et al., 2022) and giant tortoises (Moorhouse-Gann et al., 2022) in relation to plant availability. A preference analysis involves comparing the proportion of plant taxa in diet samples with the relative availability of taxa in the environment. A resource is deemed to be used more than expected if observed consumption is outside the central 95% confidence intervals of expected values derived from multiple iterations of the null model, indicating higher or lower percentage content in the diet than expected given availability in the landscape (Vaughan et al., 2018). In the present study, this methodology was applied separately for ground flora (dicot and monocot herbs, ferns, grasses, sedges, rushes, reeds and vines) and woody plants (trees and shrubs) as these groups were surveyed separately according to the methodology previously described. For the ground flora preference analysis, the diet data were aligned with the plant percentage cover data according to survey month (Oct-2019, Nov-2019 etc.).

I used ground flora survey data from all ten woodland study sites to quantify resource availability, as the fallow deer potentially have access to the whole landscape for foraging. A null model was generated using the *econullnetr* function *generate_null_net* with 500 iterations (Vaughan et al., 2018). This model used two matrices: 1) a consumer matrix which contained presence / absence data for all plant genera that were present in the diet (representing ≥ 1 % of reads in a sample) and ground flora surveys and 2) a resource matrix with proportional data of the total ground flora cover, split by survey month, across all ten woodland sites for each ground flora genus that was present in both the diet (representing ≥ 1 % of reads in a sample) and vegetation surveys. For the woody plant preference analysis, each woodland site had only been surveyed once for stem number by taxon, therefore I was unable to temporally link the diet data to woody plant availability. Instead, the proportional availabilities of woody plant genera were calculated using the total number of stems >

30 cm tall counted in all the surveys across all ten sites. Two matrices were used for this null model: 1) a consumer matrix with presence / absence data for all woody plant genera present in the diet (representing ≥ 1 % of reads in a sample) and field surveys and 2) a resource matrix containing a single row of proportional data per genus calculated relative to the total number of recorded stems across all included woody genera that were present in the diet (representing ≥ 1 % of reads in a sample) and field surveys.

To quantify differences in taxonomic composition of the diet across sites and seasons, post-hoc pairwise comparisons with a Bonferroni correction for multiple testing was carried out using the *pairwise.adonis* function from the *pairwiseAdonis* package in R (Martinez Arbizu, 2017), utilising the Bray-Curtis method with 1000 iterations.

Results

Sequencing products

Sequencing produced a total of 14,888,424 forward reads for ITS2 and rbcL combined. Of these forward reads, 4,428,309 were not assigned to any samples. Excluding these unassigned reads, the average number of reads per sample was $27,240 \pm 1048$ (SE). Following removal of primers and reads that did not contain primer sequences, 6,337,650 forward reads for ITS2 from 309 field samples and 4,868,694 forward reads for rbcL from 319 field samples remained.

A total of 3,273,487 merged reads for ITS2 and 2,387,737 forward reads for rbcL survived quality control. For ITS2, the mean number of sequences per sample was $10,594 \pm 537$ (SE) with a range of 126 to 41,544. For rbcL, the mean number of sequences per sample was 7485 ± 406 (SE). with a range of 107 to 33,444. The ITS2 marker identified a total of 77 unique taxa to genus level, while the rbcL marker identified a total of 155 unique taxa to genus level.

There was a significant positive correlation between the percentage read content of consensus taxa in faecal samples from ITS2 and rbcL (rho = 0.17, df = 2844, p < 0.001). The consensus dataset of the ITS2 and rbcL sequences from 338 field samples consisted of 177 unique identified genera. The dataset contained 5,661,026 reads with a mean of $17,139 \pm 805$ (SE) per sample with a range of 107 to 71,762 reads.

Diet diversity

In general, the fallow deer diet was most diverse in the autumn and least diverse in winter, although there was variation across the three sampling sites (Figure 6.2). The Shannon Diversity of the diet appeared to track the percentage content of bramble, with large increases in bramble content corresponding with lower diet diversity (Figures 6.3, 6.4). While there was variation in percentage bramble content (Figure 6.4), bramble remained an important dietary component in all three sites and four survey seasons (Figure 6.2).



Figure 6.2: Average proportion of reads obtained using DNA metabarcoding from plant genera that make up more than ten percent of reads in one or more samples, expressed as proportions of the whole plant community detected in the diet. This plot represents the consensus dataset for ITS2 and rbcL. Each column shows data from one of the sampling sites (BWN, HFD or WFR). The panels split the data by meteorological season (Autumn, Spring, Summer, Winter).



HFD





Figure 6.3. Violin plots of Shannon Diversity Index (SDI) against month for taxa identified using DNA metabarcoding from faecal samples collected at sites BWN, HFD and WFR. Blue = winter, yellow = spring, green = summer and orange = autumn. The central black lines show the median, the white boxes show the lower (25%) and upper (75%) quartiles, the tails show the minimum and the maximum values and the coloured "violins" show the density of samples spread across the range of SDI values.



Figure 6.4. Mean proportion of bramble (*Rubus fruticosus L. agg.*) present in faecal samples per month, split across sites. The error bars represent the standard error for each mean value. The fitted lines represent predicted values from generalised additive models (GAMs). The shaded area around the lines represents the 95% confidence intervals for the predicted values. Colour indicates season.

The PERMANOVA results showed that neither woodland site ($F_{(2,326)} = 1.22$, p = 0.22) nor pool concentration for ITS2 ($F_{(3,326)} = 1.02$, p = 0.41) or rbcL ($F_{(3,326)} = 1.07$, p = 0.33) were significant predictors of taxa present in diet samples at genus level. Conversely, meteorological season was a significant predictor of taxonomic composition ($F_{(3,326)} = 8.76$, p = 0.001). The post-hoc pairwise comparison with a Bonferroni correction showed that all seasons were significantly different from each other in their taxonomic composition (Table 6.3). Ordination of the diet data using NMDS illustrated how the samples clustered more strongly by season than by site. (Figure 6.5).

Table 6.3. Results from pairwise comparisons between seasons of the taxonomic composition by genus of the diet of fallow deer with Bonferroni-corrected p values. * = significant at 95% confidence level, ** = significant at 99% confidence level.

Pairwise comparison	F	Degrees of freedom	Adjusted P value
Autumn vs Winter	15.12	1	0.006 **
Autumn vs Spring	11.79	1	0.006 **
Autumn vs Summer	9.63	1	0.006 **
Winter vs Spring	2.02	1	0.05 *
Winter vs Summer	7.30	1	0.006 **
Spring vs Summer	5.21	1	0.006 **



Figure 6.5. NMDS plot showing community dissimilarity among fallow deer diet samples, split by month (colour) and the three woodland study sites (shape). Each point represents a sample.

Seasonal variation in diet composition

The bipartite network plots reiterate the dominance of bramble in the diet of fallow deer throughout the year, especially in January and February, for all three woodland study sites (Figure 6.6). The plots also highlight variation in the percentage composition of plant genera amongst the three sites, particularly in the second half of the year. While the annual percentage bramble content of samples from sites BWN and HFD was comparable across the seasons (Figure 6.6), the percentage content at site WFR declined sharply as the year progressed, with an average of 39% (SE \pm 13, n = 6) bramble in December, compared to 78% (SE \pm 3, n = 10) in samples from HFD and 73% (SE \pm 8, n = 10) from BWN. Across all sites, the periods of decline in dominance of bramble in the diet in were not associated with any other single genus displacing it but instead a diversity of other genera.

Grasses remained relatively scarce in the diet compared to woody genera. *Lolium* was the dominant grass genus, present in 72 samples and visible in the bipartite plots (Figure 6.6). This was most likely perennial ryegrass (*L. perenne*), a very common species in livestock pastures in Europe. The strongest peak in *Lolium* spp. consumption was in sample S208 in October at site BWN, making up 43% of the sample, but in the ten other samples from BWN that contained *Lolium*, the average monthly content was less than 4%. At site WFR, *Lolium* consumption spiked in November (mean = 34%, SE \pm 14, n = 5), March (mean = 24%, SE \pm 22, n = 2), and October (mean = 16% SE \pm 6, n = 4). *Lolium* content peaked at site HFD in April (mean = 28%, SE \pm 21, n = 2), but aside from one sample in August with an average content of 12%, the average monthly content of the remaining 23 samples that contained *Lolium* sp. was less than 6%.

Of the woody plant genera, oak was present in the diet in very small quantities from January until August but became present in larger quantities in September – October across all three sites (Figure 6.6). Oak content peaked in September at site BWN with an average percentage content of 30% (SE \pm 12.3, n = 7). The peak at site HFD was in October, with an average percentage content of 24% (SE \pm 10, n = 10). From November to December, the relative proportion of oak declined in samples from sites BWN and HFD but remained higher in samples from WFR, peaking at an average of 31% in December (SE \pm 10, n = 7). Other major woody components of the diet across all three sites included *Acer* spp. in May and June (probably mostly sycamore) and *Rosa* spp. in May – August (Figure 6.6). *Prunus* spp. consumption resurged throughout the spring and summer, likely to be mostly blackthorn (*P. spinosa*) with some wild cherry (*P. avium*). Sample S295 was removed from the dataset as it was an outlier with the dominant taxon being *Berberis* sp., a genus of flowering

173

shrubs. Common barberry (*Berberis vulgaris*) is sometimes included in ornamental plantings in the UK. This sample originated at site BWN and may reflect deer browsing of the horticultural gardens in the hotel grounds.









WFR

WFR



Figure 6.6. Bipartite plots showing the identity and proportion of plant genera (labels in the left panel) present in the fallow deer diet faecal samples from each of the three woodland study sites (denoted by three-letter codes in the right panel).

Resource availability: spatial and temporal variation in plant community composition

The seasonal ground vegetation surveys yielded a total of 113 plant species across 92 genera. Both woodland site (PERMANOVA, $F_{(9,66)} = 14.4$, p = 0.001) and meteorological season ($F_{(3,66)} = 6.5$, p = 0.001) had a significant influence on the taxonomic composition of the ground vegetation across the ten woodlands sampled. The post-hoc pairwise comparison with a Bonferroni correction showed that Winter vs Summer and Autumn vs Spring were significantly different from each other in their ground vegetation taxonomic composition (Table 6.4). In addition, a pairwise comparison amongst the sites indicated that most sites were significantly different from each other, but there were some exceptions. This was supported by ordination using NMDS, which showed distinct clustering for most sites (Figure 6.7). Notably, the three sites where diet content were sampled were significantly different from each other in their ground vegetation composition (Table 6.5). The relative proportions of different tree and shrub genera across the sites can be found in Figure 3.2.

Table 6.4. Results from pairwise comparison of taxonomic composition of ground vegetation per season across all ten woodland study sites. ** = significant at the 99% confidence level.

Pairwise comparison	F	Degrees of freedom	Adjusted P value
Autumn vs Winter	2.46	1	0.108
Autumn vs Spring	3.55	1	0.006 **
Autumn vs Summer	1.68	1	0.480
Winter vs Spring	1.87	1	0.509
Winter vs Summer	3.47	1	0.006 **
Spring vs Summer	2.19	1	0.072

Table 6.5. Partial results from pairwise comparison of diversity of ground flora per site across all seasons. * = significant at the 95% confidence level.

Pairwise comparison	F	Degrees of freedom	Adjusted P value
BWN vs HFD	14.54	1	0.045 *
BWN vs WFR	9.99	1	0.045 *
HFD vs WFR	12.72	1	0.045 *



Figure 6.7. Ordination of the ground flora survey data for the ten woodland study sites by survey month using NMDS. Deer faecal samples were collected from sites BWN, HFD and WFR.

Ground vegetation preference analysis

A total of 1275.85 m² of ground vegetation cover was recorded across the ten woodland sites. Mosses and liverworts were recorded in the ground vegetation but were excluded from further analysis as they were not present in the diet and could not be identified to genus level. In addition, tree and shrub seedlings were excluded from this analysis, as these genera were analysed separately in the woody plant preference analysis. A total of 292 faecal samples contained DNA from ground vegetation at ≥ 1 % of reads. Of the 74 herb, fern, rush, grass and vine genera that were present in the ground vegetation survey data, 24 were present and 50 were absent in the diet. Twelve genera that were present in the ground vegetation survey were also present in the consensus diet dataset at ≥ 1 % of reads in one or more samples. Therefore, the preference analysis was carried out on these 12 genera only. The preference analysis used a total of 124 faecal samples which were collected during the ground vegetation survey months and within which any of the 12 genera were present at ≥ 1 % of reads. The results showed that six genera were consumed at a higher proportion than their availability, although reliable confidence intervals could not be generated for the predicted values
for five of these genera due to their rarity in the field surveys (Figure 6.8). The strongest preference was for bramble *Rubus* sp. (Observed occurrences = 119, Null = 81, 95% CI = 73, 89). One genus, ivy *Hedera* sp. occurred in fewer samples than expected given its availability in the ground vegetation (Observed occurrences = 71, Null = 130, 95% CI = 121, 139). Five genera were consumed at a similar frequency to that predicted by the null model. Bramble and ivy were the most abundant resources in the ground vegetation (Figure 3.3), making up 17% and 23% of the total recorded cover, respectively and ivy also occurred frequently climbing on the stems of trees and shrubs (although this was not measured).



Number of samples containing taxa

Figure 6.8. Preference plot for the 12 ground vegetation genera that were present at \geq 1% content in one or more faecal samples and were also present in the concurrent ground vegetation surveys. Lines indicate the 95% confidence intervals for expected consumption given the null model. The coloured dots indicate the observed number of faecal samples in which each genus was present. White dots show the genus was consumed in proportion to its availability; blue shows the genus was consumed less than expected and orange indicates the genus was consumed more than expected given the null model in the preference analysis.

Tree and shrub preference analysis

A total of 20,555 tree and shrub stems of a range of sizes and 37 genera were recorded across the ten woodland study sites (Figure 3.2). A total of 337 faecal samples contained DNA from tree or shrub genera at $\geq 1\%$ of reads. Of the 37 unique tree and shrub genera that were present in the field survey, 13 were not present in the faecal samples. A total of 22 genera that were present in the tree and shrub survey were also present in the consensus diet dataset at $\geq 1\%$ of reads in one or more faecal samples. Therefore, the preference analysis was carried out for these 22 genera only. The preference analysis used a total of 258 faecal samples, in which any of the 22 genera represented \geq 1% of reads. Seven tree and shrub genera were consumed at a higher proportion than their availability (Figure 6.9). The strongest preferences were for Rosa (Observed = 82, Null = 8, 95% CI = 3, 13), Prunus (Observed = 96, Null = 13, 95% CI = 6, 20), oak Quercus (Observed = 100, Null = 25, 95% CI = 16, 33) and elm (*Ulmus*) (Observed = 60, Null = 10, 95% CI = 4, 16). A preference was recorded for horse chestnut (Aesculus), but this result should be treated with caution as this genus was found so rarely in the tree and shrub surveys that confidence intervals could not be generated for the null value (Observed = 4, Null = 0). Six genera were underrepresented in the faecal samples relative to their abundance in the tree and shrub survey: ash (*Fraxinus*) (Observed = 76, Null = 218, 95% CI = 195, 241), hazel (Corylus) (Observed = 15, Null = 95, 95% CI = 195, 241), birch (Betula) (Observed = 13, Null = 70, 95% CI = 55, 85), holly (Ilex) (Observed = 4, Null = 23, 95% CI = 14, 33) elder (*Sambucus*) (Observed = 2, Null = 16, 95% CI = 9,24) and hornbeam (*Carpinus*) (Observed = 2, Null = 13, 95% CI = 7, 20).



Figure 6.9. Preference plot for the 22 woody plant genera that were present at $\geq 1\%$ content in one or more faecal samples and were also present in the tree and shrub surveys. Lines indicate 95% confidence intervals for expected consumption given the null model. The coloured dots indicate the observed number of faecal samples where each genus was present. White dots show the genus was consumed in proportion to its availability; blue shows the genus was consumed less than expected and orange indicates the genus was consumed more than expected given the null model in the preference analysis.

Zoo samples

Of the six faecal samples included from the captive fallow deer population at the Welsh Mountain Zoo, all but one survived filtering for at least one marker and three survived filtering for both markers (Table 6.6). The ITS2 marker gave a total of 11,491 reads with a mean of 2873 (SD = 3972) reads per sample with a range of 663 to 8823 (n = 4). The rbcL marker gave a total of 12,265 reads, with a mean of 3066 = (4567) reads per sample with a range of 372 to 9898 (n = 4). The consensus dataset for the zoo samples contained a total of 23,756 reads with a mean of 5752 (SD = 7545) reads per sample with a range of 372 to 18,721 (n = 5). The consensus dataset consisted of 16 plant taxa identified to genus level. In contrast to the field samples from wild deer, the zoo samples were mostly dominated by grasses and small quantities of other plants typically associated with grasslands, such as thistles (*Cirsium* spp.), yarrow (*Achillea* spp.) and vetch (*Vicia* spp.) (Figure 6.10). Sample M2 contained 63% wheat (*Triticum*), which was probably present in animal feed. Woody species such as bramble and *Prunus* spp. may have come from the hedge adjacent to the enclosure fence.

Zoo samples	Sex	Survived filtering rbcL?	Survived filtering ITS2?
F1	Female	No	No
F2	Female	Yes	Yes
F3	Female	No	Yes
M1	Male	Yes	Yes
M2	Male	Yes	Yes
M3	Male	Yes	No

 Table 6.6. Zoo samples that survived quality filtering for rbcL and ITS2



Figure 6.10. Percentage read abundance of plant genera present in the zoo fallow deer faecal samples that survived filtering. This represents a consensus dataset containing combined data from ITS2 and rbcL markers. Sample F3 represents ITS2 data only, and M3 represents rbcL data only, as they did not survive filtering through both pipelines.

Field blanks

Of the five field blanks and two lab controls included in the sequencing run, only one survived filtering for the ITS2 marker, while three samples survived filtering for rbcL (Table 6.7). Neither of the laboratory control pools survived filtering. The ITS2 marker generated a total of 20,074 reads for the one surviving sample. The rbcL marker generated a total of 21,905 reads with an average of 7302 (SD = 6340) reads per sample with a range of 1845 to 14,256. The consensus dataset for the field blanks contained a total of 41,979 reads with a mean of 16,634 (SD = 10155) reads per sample with a range of 1845 to 25,878. The consensus dataset consisted of 11 taxa identified to genus level (Figure 6.11). The sequences from the November-December sampling period were 86% holly *Ilex* and 14 % oak *Quercus*. The sequences from the March-April sampling period were more diverse, perhaps partly because they included sequences from both markers, or because more species were releasing pollen in these months. The sequences were made up of 35% *Prunus*, 29% *Fraxinus* and 14% hawthorn (*Crataegus*).

Table 6.7. Field blanks that survived quality filtering for rbcL and ITS2



Figure 6.11. Percentage read abundance of plant genera present in the field blanks that survived filtering. The column for Apr - May contains consensus data for rbcL and ITS2. The Nov - Dec and Mar - Apr column contain data from rbcL only.

Discussion

This study aimed to characterise the diet of fallow deer in the Elwy Valley and identify how diet content varied with spatial and temporal variation in resource availability. The lack of grasses in the diet despite abundant pasture in the landscape indicates that graminoid productivity was not a driver of diet diversity, which contradicts our initial prediction. The only notable grass content was *Lolium*, appearing in moderate quantities in April at site HFD and in November at site WFR. Grasses were virtually absent from the diet of deer at site BWN. Overall, bramble was the dominant component of the diet across all three sites, although there was considerable variation in the relative proportion of bramble in samples across sites and seasons. The preference analysis for ground vegetation indicated that the deer disproportionately utilised bramble relative to its frequency in the resource availability surveys, despite bramble being among the most abundant taxa recorded in the landscape. The remainder of the diet was mainly composed of woody browse. Other studies have documented substantial seasonal variation in the diet of the fallow deer (Bruno and Apollonio, 1991; Borkowski and Obidziński, 2003; Morse et al., 2009), however this is the first study to use

DNA metabarcoding to identify seasonal variation in the diet of this species and relate this to seasonal resource availability and dietary preference.

The lack of grass in the diet of Elwy Valley fallow deer contradicts the findings of previous studies, which characterised the species as an intermediate grazer with high grass content in the diet supplemented by woody browse in winter (Borkowski & Obidziński, 2003; Caldwell et al., 1983; Kerridge & Bullock, 1991; Morse et al., 2009; Putman et al., 1993; Spitzer et al., 2020). Fallow deer are in fact highly flexible in their foraging habits and able to exploit resources which might not sustain other more specialist herbivores (Esattore et al., 2022; Hofmann, 1989). This may allow prioritisation of safety and convenience over a more palatable diet. In landscapes dominated by forest as opposed to grassland, fallow deer may adopt a heavily browse-dominated diet (Nugent, 1990). Notably, some previous studies of fallow deer diet were on deer estates in Essex (Caldwell et al., 1983) and Leicestershire, UK (Kerridge and Bullock, 1991) and an area in Poland where deer were fed supplementary hay (Borkowski and Obidziński, 2003). In these areas, graminoid availability is likely to be relatively high compared to woodland resources, and human activity more predictable (Recarte et al., 1998). Habituation to humans may permit more frequent foraging in open areas (Langbein & Putman, 1991). In contrast, the Elwy Valley population exists in a mosaic of woodlands and farmland where human activity is less predictable across the landscape. Woodlands may offer safe refuge from disturbance by humans and livestock (Gaudiano et al., 2021; Hood & Inglis, 1974; Khadka & James, 2016), which may lead to lower feeding rates in open areas (Ciuti et al., 2012; Jayakody et al., 2008; Stankowich, 2008) and reduced graminoid content in the diet. A study in the Scottish Highlands found that red deer faeces from recreation-disturbed sites contained less grassland species (grasses, sedges, herbs and rushes) and more browse (heather and trees) in the springtime compared to less disturbed sites (Jayakody et al., 2011). However, grassland species increased in recreation-disturbed sites in winter, possibly due to a reduction in recreation and the onset of the hunting season, which may drive deer to spend more time in fields away from hunters in woodlands (Jayakody et al., 2011). In addition, a study in Germany found that red deer used areas less frequently when they were grazed by cattle compared to non-grazed areas, even up to 21 days after relief from grazing (Weiss et al., 2022) In the Elwy Valley, where hunting took place in some woodlands and livestock grazing was widespread in the surrounding fields, woodland resources appeared to be dominant year-round, indicating that the fallow deer tend to avoid foraging in open fields across the seasons and that hunting did not deter deer foraging in woodlands compared to fields. This is also evident when contrasting the contents of the wild deer faecal

samples with samples from the zoo, where the enclosed fallow deer were constrained to grassland foraging. The findings of this study complement the larger-scale study of the Elwy Valley fallow deer, which found a positive effect of tree cover and negligible effects of hunting on deer woodland use at the landscape scale (Barton, 2023).

The diet was most diverse in the autumn season and least diverse in the winter months. The relative proportion of bramble consumed tracked diet diversity across site and season: as relative proportions of bramble in the diet decreased from January-February onwards, the diversity of the diet increased as alternative seasonal resources became available. Therefore, the diet diversity appears to be driven by availability of seasonal woody browse and woodland ground flora, with bramble as the keystone winter resource. The preference analysis for ground flora was limited to vegetation in woodlands, therefore I could not test for preferences of grassland and meadow species or crop plants. In addition, woodland plants that were missed by the ground flora surveys could not be tested for preference. Nonetheless, the preference for bramble was much stronger than for other ground flora genera that were tested. Even with their high availability in the landscape, evergreen ivy (*Hedera*) and holly (*Ilex*) were both consumed less than predicted by the preference analyses. Indeed, this was despite these species being moderately palatable to deer (González Hernández & Silva-Pando, 1999; Tixier et al., 1997) and previously recorded as significant components of the winter diet of fallow deer in the UK (Jackson, 1977).

The dominance of bramble over other evergreen resources contradicts the prediction that deer would become less selective in winter to maximise energy intake. Prolific vegetative growth and wide geographical distribution make bramble one of the most abundant understory plants in temperate forests (Balandier et al., 2013). This is especially true in the winter as bramble retains foliage throughout the year, while most other understory foliage is largely absent (Aerts, 1995). Previous studies have found that deer frequently consume bramble and woody browse outside of the plant growing season (Boulanger et al., 2009; Jackson, 1977; Kamler & Homolka, 2011; Tixier et al., 1997). Winter is an energetically costly period due to thermoregulatory demands. Therefore, deer may spend more time in sheltered environments such as woodlands and bulk browse on evergreen foliage to save energy (Mysterud et al., 2011; Nudds, 1980; Ossi et al., 2015). The relative decline in selectivity over the winter seems to be due to sole reliance on bramble as a common, reliable resource to ensure survival through the winter. Nonetheless, the ground flora preference analysis showed a strong overall preference for bramble across the seasons. Indeed,

188

bramble can be a highly palatable resource for browsing deer species (Harmer et al., 2010; Obidziński et al., 2013). New growth in the spring contains high concentrations of nitrogen, potassium and phosphorus, while more aged leaves have a higher concentration of calcium and intermediate levels of magnesium (Taylor, 1982). In addition, woodland resources such as bramble may provide a low-risk food option compared to grasses in open fields if human disturbance is high (Jayakody et al., 2011). These factors provide some possible explanations for the continuous consumption of bramble by fallow deer throughout the year in the present study.

The results of the tree and shrub preference analysis indicate that genera occurring at high localised stem densities were under-represented in the diet according to their availability. For example, ash sapling densities were exceptionally high at site LNH; birch was locally dominant throughout site EWD; and hornbeam saplings were locally abundant at site MRN (Figure 3.2). Similarly, hazel stems were usually recorded in clusters as they occurred as coppice shoots from the same stool (e.g., Figure 3.10). Although these species were abundant in the landscape, their distribution was more clustered and so the deer may have been less likely to encounter them while foraging. In contrast, woody genera that were more widespread but less locally dominant were designated as a preferred resource in the diet, such as oak *Quercus*, *Rosa* spp, *Prunus* spp, *Acer* spp. and elm *Ulmus* spp. Some care should be taken when drawing conclusions on the foraging preferences of the fallow deer for woody species based on this preference analysis, as the results may be an artefact of resource distribution in the environment (Duparc et al., 2020; Wang et al., 2010). Nonetheless, these "preferred" woody genera have been shown to be palatable for deer (Moore et al., 1999; Ohse, Seele, et al., 2017; Rupprecht et al., 2022). Blackthorn (Prunus spinosa) and dogrose (Rosa canina) are typically low shrubs, while elm and occasionally sycamore can produce suckers from the main stem (Bleay, 1987). These growth forms are more likely to present available foliage at browsing height, compared to more light demanding species such as birch and ash, which typically have a higher crown base and were recorded as under-represented in the diet. The presence of moderate quantities of oak in the diet from September – December suggests that the deer were primarily consuming acorns rather than browsing oaks directly. There was a particular spike in oak consumption across all three sites in October, which would typically be the peak month for acorn production (Hanley et al., 2018) and previous fallow deer diet studies have shown oak seeds to be an important component of the autumn and winter diet in this species (Azorit et al., 2012; Caldwell et al., 1983; Herrera, 1995). Oak masting (acorn production) varies substantially between years (Hanley et al., 2018) and Forestry England recorded autumn 2020 as a good mast year in the UK

(Forestry England, 2020). Another possible explanation is the late senescence of oak foliage compared to other deciduous species, which could still provide browse material into the winter months.

The site from which samples were collected did not have a significant influence on the taxonomic composition of the diet, however all seasons were significantly different from each other in taxonomic composition. Conversely, ground vegetation community composition did not substantially change with season but was very spatially variable amongst sites. There was also considerable spatial variation in the taxonomic composition of trees and shrubs (Figure 3.2), although temporal variation in browse availability from these taxa was not assessed. Taken together, these results indicate that while woodland site was the main determinant of variation in resource availability, it was not a driver of diet composition. Areas of the Elwy Valley vary in soil type, with base-rich limestone soils around Bodelwyddan and St Asaph and more acidic soils to the south and east. Soil moisture is also an important factor, as lower areas accumulate higher water content. This was evident in plant species communities across the valley, with drier limestone areas displaying more grassland species, while the wetter woodland areas showed more typical ancient woodland ground flora such as dog's mercury, wood anemone (Anemone nemorosa), wild garlic (Allium ursinum) and bluebells (Hyacinthoides non-scripta). This variation in soil type and moisture is also likely to influence nutritional quality and palatability of the ground flora, which could generate local variation in browsing preferences (Hundley, 1959; Dykes et al., 2018) but this was beyond the scope of the present study.

The spatial scale of deer foraging probably did not match the site-scale at which resource availability was measured. The home range of a fallow deer may be several times larger than the individual study woodlands (Borkowski & Pudełko, 2007). It is therefore very likely that the deer utilised multiple woodlands within their home range within a single bout of feeding. A recent camera trap study of roe deer habitat use in the Black Forest, Germany found that local forest structure aspects (100 x 100 m²) such as canopy cover and tree species richness were the greatest determinant of roe deer habitat use, while patch scale food availability (5 x 5 m²) had little effect (Schwegmann et al., 2023). In addition, a study in the east of England found that culling of smallbodied, sedentary deer species - roe deer and Reeve's muntjac (*Muntiacus reevesi*) - was effective at reducing browsing impacts at the individual woodland scale and the efficacy meaningfully increased up to a radius of 50 km for roe deer and 30 km for muntjac (Fattorini et al., 2020). In contrast, culling of fallow deer only became effective at the 5 km scale, doubled at the 70 km scale and was three times more effective at the 100 km scale (Fattorini et al., 2020). Taken together with the results of the present study, deer populations require management at a spatial scale that matches the scale of foraging and ranging behaviour of the species.

To successfully manage a growing population of browsing ungulates such as the Elwy Valley fallow deer, there is a necessity to preserve the ecological and socio-economic role of deer in the landscape (Reimoser & Putman, 2011; Vera et al., 2008; Weisberg & Bugmann, 2003), determine threshold levels at which browsing is problematic (Putman et al., 2011), and identify management interventions to successfully prevent or mediate impacts (Barton et al., 2022). While this study has highlighted considerable browse content in the diet, the lack of crop plants and grasses indicates minimal use of crop fields and grazing pasture, which is contrary to concerns that the deer may be reducing crop yield (Menichetti et al., 2019) or spending time in the vicinity of livestock with the possibility of disease transmission (Putman et al., 2011). If reductions in deer numbers are required for the benefit of tree regeneration, this is likely to require a landscape-scale effort due to displacement of deer out of hunted woodlands (Fattorini et al., 2020; Yamaguchi et al., 2020) - see Chapter 5. While modifying tree species composition to make a stand less palatable (Maltoni et al., 2019) or altering the availability of cover in the understory (Bobek et al., 2016; Borkowski & Ukalski, 2012) may deter herbivory at the woodland scale, it is unlikely to curtail problematic browsing pressure across the whole landscape without a coordinated effort, as deer foraging bouts are likely to overlap management units. Nonetheless, conversion of a whole landscape to be deliberately unsuitable for deer would be impractical and ecologically damaging. There is a balance to be struck between maintaining the ecological and economic value of deer populations while mitigating the consequences of intensive browsing for woodland health (Gordon et al., 2004; Valente et al., 2020).

Methodological considerations

Bramble dominance in the diet raises questions of contamination from the laboratory or the sampling environment, or biases in the primer sets used. However, the lack of bramble in the zoo samples and field blanks demonstrated that there was not ubiquitous contamination. While the field blanks indicated that pollen and fallen leaves are likely to contaminate faecal samples, the dominance of bramble in the diet with a peak in January – February strongly suggests that pollen contamination was not the main cause of bramble dominance. Furthermore, the dominance of

bramble in the diet at sites WFR and BWN - despite lack of bramble in the ground vegetation surveys at these two sites (Supplementary S4.3) - indicates that soil contamination is unlikely to be a significant contributor to relative read abundance. The primer pair combinations used in this study have been previously used by Lowe et al., (2022) and Jones et al., (2022) to study the foraging habits of honeybees *Apis melifera*. While bramble was a key component of the honey in certain survey months, it was not ubiquitous across their datasets, indicating that these primers accurately represented bramble use (Jones et al., 2022; Lowe et al., 2022).

The dominance of holly in DNA extracted from the field blanks placed in the field during the November-December sampling period was not surprising, considering the samples were positioned in and around a holly grove. The soil may have contained a high concentration of holly DNA from cumulative leaf fall. Although there were no larch or Douglas fir recorded within site WFR (see Chapter 3), sequences from the March-April blanks were entirely composed of these taxa. This strongly indicates that wind-blown pollen was the source of the detected sequences, as Douglas fir (Isaac & Dimock, 1958) and larch (Colas et al., 2008) both release pollen during those months. The April-May blanks were dominated by hawthorn, *Prunus* spp and ash, which are all in flower in the UK at this time (Sparks et al., 2000; Thomas, 2016). The results from the field blanks highlight the potential for environmental contamination to influence the results of DNA metabarcoding studies looking at herbivore diet from faecal samples. Future studies of deer diet could analyse intestinal faeces from culled individuals (Smith & Shandruk, 1979) to validate diet contents and to assess the degree of environmental contamination of samples collected from the field.

It would have been interesting to segregate the diet samples by sex to identify whether male and female deer vary in their dietary choices. Although protocols are available for sexing ungulate herbivores from faecal samples (Liu et al., 2015; Pajares et al., 2007), including deer (Yamauchi et al., 2000; Gurgul et al., 2010), there has been limited use of these in diet studies thus far. Nakahama et al., (2021) used the AMEL sexing primers developed by Yamauchi et al., (2000) to compare the diets of male and female sika deer, although DNA degradation prevented definitive identification for nearly a quarter of their samples. While previous studies have identified sex-specific patterns in diet relating to reproductive behaviour (Djaković et al., 2015; Pélabon & Komers, 1997; Soulsbury, 2019) or social segregation (Putman et al., 1993), this was beyond the scope of the present study.

Conclusions

The aim of this study was to characterise the dietary composition of the fallow deer in the Elwy Valley using DNA metabarcoding and identify how the diet changes with temporal and spatial variation in resource availability. Contrary to expectations in this woodland-pasture landscape, grasses were not a major component of the diet across seasons. The diet was largely dominated by bramble throughout the year, especially in the winter months. The diversity of the diet increased in the spring and peaked in the summer and autumn as availability of different browse material increased, corresponding with a reduction in percentage of bramble content. While availability of forage plants was mainly determined by spatial variation, diet composition was influenced by season. Therefore, deer foraging was not spatially restricted within individual woodland sites and varied according to seasonal woodland resource availability. This study further demonstrates the generalist nature of the fallow deer diet and exhibits DNA metabarcoding as a valuable tool to monitor regional deer foraging, which could help to inform landscape-scale, co-ordinated deer management.

Chapter 7

General Discussion

My thesis aimed to explore key drivers of deer habitat use and diet in woodlands within humanaltered landscapes using novel methodologies. A systematic map collated the existing literature on the effects of the six UK deer species and the North American elk (a close relative of the red deer) on vegetation in wooded habitats across the globe, addressing the methodological context of studies and whether deer species were studied alone or within a herbivore community. Focusing on a local fallow deer population in North Wales, the subsequent chapters brought together Terrestrial LiDAR, DNA metabarcoding and motion-activated cameras to explore how deer woodland use varied across the 24-hour period according to risk factors and habitat structure, and how seasonal deer diet varied with landscape-scale resource availability.

Deer are not a single generic species

To successfully manage expanding deer populations in the temperate zone, a sound understanding of the ecological roles of different deer species is crucial. Where multiple deer species exist in a landscape, they are often treated as a single entity when it comes to browsing impacts and management. In reality, body size, feeding strategy and habitat use are closely linked to resource selection, which will generate different effects on vegetation communities among deer species (Gordon, 2003; Johnson, 1980; J. Latham, 1999; Putman et al., 2011). For example, a recent review highlighted how roe deer were the most likely deer species to be overabundant in forestry in Europe, while red deer were most likely to be overabundant in protected areas (Carpio et al., 2021). Despite their differences, species often overlap in their diet content (Esattore et al., 2022; Kerridge & Bullock, 1991; Spitzer et al., 2020; Tixier & Duncan, 1996). Therefore, it can be difficult to separate out the ecological effects of coexisting deer populations (Faison et al., 2016). Without species-specific monitoring of behaviour and diet, disentangling the effects of coexisting herbivores may not be possible. The systematic map (**Chapter 2**) highlighted the huge range of effects that deer can exert on vegetation and found that most studies have been conducted within the context of a herbivore community, therefore there is very little information available on the effects of

individual deer species, even for red, roe and fallow deer which are widespread across the UK and Europe.

In order to understand how growing deer populations are affecting landscapes, there is a need for population or activity monitoring alongside documentation of ecological change. Many studies identified by the systematic map used a method of quantifying deer numbers to study effects on vegetation. The study of deer impacts on forests using exclosures is common (Stephan et al., 2017; Fujiki and Sakata, 2021). However, exclosures represent a scenario where deer are totally absent from a system and may therefore be most useful for studying potential ecological consequences of ungulate extinctions (Bakker, Gill, et al., 2016) or recovery of vulnerable vegetation communities following relief of grazing (Barrere et al., 2021; Otsu et al., 2019; Putman et al., 1989). For common, widespread ungulates such as the fallow deer, quantifying their habitat use and activity patterns provides a better picture of herbivory pressure and ecological impacts. In the systematic map (Chapter 2), the most common method for quantifying deer numbers was faecal pile counts, however error rates in deer species identification are frequent when using this method (Pfeffer et al., 2018; Spitzer et al., 2019). Survey techniques such as camera trapping or spotlight counts allow reliable species identification (Corlatti et al., 2016; Rowcliffe et al., 2008). However, without identification of individual animals, density estimates from cameras are often unreliable due to dispersal in and out of the survey area and deliberate placement of cameras to maximise species detection (Hofmeester et al., 2019; Rowcliffe et al., 2008). In addition, the frequency or effects of herbivory may not be linked to deer density in a linear way (Charro et al., 2018; Koda & Fujita, 2011), and the same deer density may be damaging in one habitat type but produce negligible impacts in another (Putman, 1996). Instead of focusing purely on species density, studying the behaviour and habitat use of different deer species can improve our understanding of their impacts on the environment (Putman et al., 2011).

Advancing deer ecology and behaviour research using novel methodologies

Rapid developments in Terrestrial LiDAR (TLS) technology have provided exciting opportunities to explore interactions between animal behaviour and habitat structure (Aben et al., 2018, Davies & Asner 2014). While TLS equipment requires significant financial investment, a single survey can supply multiple metrics of fine-scale habitat structure from a single dataset (Ryding et al., 2015). These include foliage density (Béland & Kobayashi, 2021; Greaves et al., 2015; Zhao et al., 2015), tree stem density and size (Bauwens et al., 2016; Dassot et al., 2011; Watt & Donoghue, 2005),

structural complexity (Maguire et al., 2019) and viewshed length (Lecigne et al., 2020; Olsoy et al., 2015). Habitat complexity metrics can be related to diversity of different animal guilds, such as birds or invertebrates (Acebes et al., 2021). In addition, resource availability or cover in the form of foliage could be quantified at different heights of the canopy or across seasons (Z. Li et al., 2018), as demonstrated in **Chapter 4** where Leaf Area Index (LAI) was compared between winter (leaf-off) and summer (leaf-on) scans. Habitat openness can influence the quality of cover for concealment and thermoregulation for animals at different heights within the canopy (Lecigne et al., 2020; Olsoy et al., 2015).

TLS data can be used to study the quality of cover for prey animals, which could improve our understanding of predator-prey relationships in wooded environments (Olsoy et al., 2015; Lecigne et al., 2020). As deer primarily influence their environment through herbivory, factors that affect their foraging behaviour will alter the ecological effects of different deer species. Habitat structure is a key driver of deer space use, as deer frequently select for dense cover when perceived predation risk is high (Mysterud and Ostbye, 1999; Uzal et al., 2013). Indeed, studies have shown that sika (Takada and Washida, 2020), fallow (Thirgood, 1996) and roe (San José et al., 1997; Pays et al., 2007) deer form larger social groups in more open habitats. When the physical structure of a habitat is sparser, concealment from predators is reduced, therefore increased group sizes boost vigilance capacity of the herd to compensate (Barja and Rosellini, 2008). In addition, red deer have been shown to alter their space use in response to the onset of the hunting season by selecting for habitats more dense vegetation cover (Lone et al., 2015; Meisingset et al., 2022). An experiment using enclosed red and roe deer found that both species exhibited stronger reactions to visual human disturbance stimuli than acoustic, although the two species exhibited differences in the magnitude and duration of their reactions (Reimoser, 2012). Visual concealment is therefore likely to be important for deer populations under human disturbance to buffer perceived risk and stress (Reimoser, 2012; Dixon et al., 2021).

In UK landscapes such as the Elwy Valley where management of the local fallow deer population is spatially patchy, quantifying woodland habitat structure may identify features which could allow deer to evade shooting and increase their tolerance to disturbance. **Chapter 4** of this thesis demonstrates the use of mobile TLS technology to quantify visibility (viewshed length) in the understory layer for forest-dwelling deer using high resolution, three-dimensional point cloud data. Horizontal visibility was lower in woodlands with higher densities of small-diameter tree stems,

indicating that these woodlands provided better horizontal cover than woodlands with lower stem densities. Shooting deer is likely to be more challenging in woodlands where small-diameter trees have grown past browsing height but remain in high density due to reduced sightlines (Gaynor et al., 2022; Lone et al., 2014). Consequently, woodlands with shorter sightlines may act as safe refuge (Meisingset et al., 2022) which may reduce the efficacy of shooting in neighbouring areas (Iijima, 2017; Yamaguchi et al., 2020).

Deer behavioural plasticity in response to perceived risk is likely to buffer effects of human disturbance on deer browsing pressure (Barton et al., 2022; Hewison et al., 2001). Lethal management of deer at the site level can displace deer into the surrounding landscape where shooting is absent (Iijima, 2017; Lone et al., 2015; Yamaguchi et al., 2020). While this displacement effect has been shown to reduce localised browsing intensity in other deer populations (Hothorn & Müller, 2010; Martin & Baltzinger, 2002; Mols et al., 2022), the results from Chapter 5 of this thesis indicated that the Elwy Valley fallow deer are compensating for fine-scale temporal variation in risk from hunters by adjusting their timing of woodland use. Site occupancy was reduced in the diurnal period - when hunters are most active - but hunting did not influence occupancy in the crepuscular or nocturnal period. In addition, diurnal detection probability was lower in areas with greater bramble cover, indicating that the fallow deer may have been using dense bramble banks as hiding cover during the riskiest part of the 24-hour cycle. This spatial and temporal displacement of deer habitat use is likely to be reducing the efficacy of existing lethal management by preventing removal of individuals from the population and temporarily shifting browsing pressure around the landscape (Bonnot et al., 2020; Ikeda et al., 2019; Yamaguchi et al., 2020). Hunting is therefore unlikely to significantly reduce regional and site-level browsing damage at present, even in regularly hunted woodlands. Monitoring deer responses to perceived risk in different woodland environments is key to successful, species-specific management.

Responses to predation risk of different deer species are traded off against their nutritional requirements, which are likely to generate differences in ecological effects of browsing across species. The UK deer species are a mix of small-bodied concentrate selectors for browse, forbs and herbs (roe deer, Reeve's muntjac and Chinese water deer) and large-bodied intermediate grazers (sika, red and fallow deer) (Hofmann, 1989). The general categorisation of deer species as primary grazers or browsers may in fact be unhelpful for deer management, as there are likely to be considerable regional differences in diet content within species according to seasonal resource

availability. For instance, the fallow deer is a generalist herbivore that can thrive on a wide variety of browse and grazing material, which has probably contributed to its success as an introduced species across the globe (Esattore et al., 2022). **Chapter 6** of this thesis demonstrates the use of DNA metabarcoding to monitor the seasonal diet of the Elwy Valley fallow deer population at the landscape scale. The results showed that the fallow deer in this region are primarily browsers across all seasons, which contradicts the typified categorisation of fallow deer as intermediate grazers (Hofmann, 1989) and confirms the huge dietary flexibility of the species (Esattore et al., 2022). Bramble formed a significant portion of the diet during winter, although the diet became more diverse as the seasons progressed with a greater proportion of deciduous browse and woodland ground flora. In addition, a preference analysis highlighted several woody plant genera that appeared to be actively selected for in the diet, including *Rosa, Prunus, Ulmus* and *Acer.* Given the rapid expansion of this population over the last 100 years, the high deciduous browse content in the diet relative to grasses suggests the Elwy Valley fallow deer may be problematic for woodland creation, restoration, and broadleaf forestry in the local area.

There is great potential to use molecular tools for improved management of ecosystems where ungulate herbivory is a key component (McShea et al., 2019). DNA metabarcoding, as used in Chapter 6, can provide highly detailed taxonomic information on the diets of large herbivore species, with the possibility to explore seasonal and spatial variation in the diet (Spitzer et al., 2020). This can be especially useful where the browsing impacts of co-existing deer species are difficult to tease out. Where dung is collected in the environment, the herbivore species and sex can be identified by sequencing DNA present from the animal (Ramón-Laca et al., 2014; Sugimoto et al., 2018), which opens the possibility of studying variation in foraging habits between the sexes due to differences in nutritional requirements (Hamasaki et al., 2009; Perez-Barberia & Gordon, 1998; Shannon et al., 2013) or thermal constraints (Conradt et al., 2000). In addition, seasonal diet content of culled animals from rumen contents (Nichols et al., 2016) can be related to body condition, providing information on the health of managed deer populations in relation to resource availability (Fløjgaard et al., 2017). Animal DNA can even be sequenced from the saliva on browsed branches to explore spatial overlap of feeding behaviour between coexisting ungulate species (Iacolina et al., 2020; Nichols et al., 2012). On a global scale, DNA metabarcoding can be used to study the diets of endangered ungulates (Kim et al., 2021; Leonard et al., 2017), or even track long-term climate-driven changes in large herbivore diets (Craine et al., 2016). The

widespread use of DNA sequencing to monitor deer diet and population dynamics could contribute valuable information towards a landscape-scale deer management plan in the UK.

Integrating novel methods with ungulate management and policy

The integration of new technologies to support data analysis and decision making is crucial for improvement of UK deer management. Population growth of generalist herbivores such as the fallow deer presents a significant barrier to expansion of native broadleaf woodland cover (Croft et al., 2019; Fuentes-Montemayor et al., 2022). In 2018, the Welsh Government published an update to their Woodlands for Wales action plan (Welsh Government, 2018). In addition, the UK government has published the England Trees Action Plan covering 2021-2024 (Defra, 2021). The primary objectives of these plans are to increase woodland cover in England and Wales to boost carbon storage and biodiversity, provide opportunities for local livelihoods in forestry and tourism, benefit human wellbeing and mitigate flood risk, using a "right tree, right place" approach (Defra, 2021; Welsh Government, 2018). These documents acknowledge that growing deer populations need to be managed and action plans are required but give no further detail on how this will be achieved. This reflects the lack of detailed knowledge on species-specific deer impacts identified by the systematic map (**Chapter 2**). There is an urgent need to build an informed, landscape-scale deer management strategy for the UK as deer populations continue to expand.

To build an efficient and sustainable plan for UK deer management, lessons should be learned from approaches in other countries. In European countries such as Norway and Poland, municipal deer management is informed by quantifying deer densities from hunter bag counts and citizen reports (Husek et al., 2021; Mysterud et al., 2007). Based on these counts, annual harvest quotas are calculated to maintain population densities at an 'acceptable' level. These decisions aim to balance maintaining a healthy population while mitigating against damage to crops and forestry, road traffic accidents and ecological damage (Putman et al., 2011). In Scandinavia, hunting is an actively encouraged public activity that is crucial to the management of ungulate populations (Brainerd & Kaltenborn, 2010). Encouraging a sense of public stewardship for the landscape and accessibility to wildlife as a common resource is key to maintaining the public engagement that supports this model of wildlife management (Hansson-Forman et al., 2020; Prager et al., 2018). Such landscape-scale deer monitoring and engagement with hunting is lacking in the UK, with most organised deer management taking place in closed deer parks for animal welfare reasons, or sport shooting on game estates and private land. Deer in the wider UK landscape are mainly managed on an informal

basis by landowners where deer are considered a barrier to management objectives, such as the growth of timber or woodland conservation. According to the behavioural observations in this thesis and the larger-scale study of the Elwy Valley fallow deer (Barton, 2023), this sporadic approach to management is unlikely to have any substantial effect on UK deer populations, and both native and introduced species are continuing to grow in number and range (Croft et al., 2019; Ward, 2005; Ward et al., 2021). The methodologies outlined in this thesis provide new tools to monitor regional woodland resource use and behavioural responses to management.

Conclusions

Large herbivores are integral components of terrestrial ecosystems in the temperate zone, but anthropogenic landscape changes are altering interactions between deer and vegetation communities. Deer species continue to be treated as a single entity when it comes to management, despite the considerable differences in their biology and feeding ecology. By using remote sensing technologies to monitor deer populations and their habitat use, we can improve our understanding of which woodlands are most vulnerable to browsing damage by different deer species, and how deer are likely to respond to management and disturbance. In addition, new molecular methods such as DNA metabarcoding can be used to identify the dietary components of deer species, which provides valuable information on the trophic interactions between growing populations and vegetation communities. The lack of a long-term, landscape scale, species-specific approach to deer management means that the health of UK woodlands and forests is facing a growing challenge. Increasing deer populations may impede woodland creation and expansion, which could jeopardise efforts to boost carbon storage, conserve biodiversity and promote sustainable forestry practices. There is clearly a balance to be struck: total removal or exclusion of deer is impractical and would be ecologically damaging in the long-term. However, rapidly increasing deer populations must be carefully managed if we are to mitigate ecological impacts in the UK and across the temperate zone. Studying the behavioural ecology of deer species is key to developing effective management strategies at the landscape scale.

References

- Abbas, F., Picot, D., Merlet, J., Cargnelutti, B., Lourtet, B., Angibault, J. M., Daufresne, T., Aulagnier, S., & Verheyden, H. (2013). A typical browser, the roe deer, may consume substantial quantities of grasses in open landscapes. *European Journal of Wildlife Research*, 59(1), 69–75. https://doi.org/10.1007/s10344-012-0648-9
- Aben, J., Pellikka, P., & Travis, J. M. J. (2018). A call for viewshed ecology: Advancing our understanding of the ecology of information through viewshed analysis. *Methods in Ecology and Evolution*, 9(3), 624–633. https://doi.org/10.1111/2041-210X.12902
- Aben, J., Signer, J., Heiskanen, J., Pellikka, P., & Travis, J. M. J. (2021). What you see is where you go: visibility influences movement decisions of a forest bird navigating a three-dimensional-structured matrix. *Biology Letters*, 17(20200478). https://doi.org/10.1098/rsbl.2020.0478rsbl20200478
- Abraham, A. J., Duvall, E., Ferraro, K., Webster, A. B., Doughty, C. E., le Roux, E., & Ellis-Soto, D. (2022). Understanding anthropogenic impacts on zoogeochemistry is essential for ecological restoration. *Restoration Ecology*, 31(3). https://doi.org/10.1111/rec.13778
- Acebes, P., Lillo, P., & Jaime-González, C. (2021). Disentangling LiDAR Contribution in Modelling Species-Habitat Structure Relationships in Terrestrial Ecosystems Worldwide. A Systematic Review and Future Directions. *Remote Sensing*, 13(17). https://doi.org/10.3390/rs13173447
- Acebes, P., Malo, J. E., & Traba, J. (2013). Trade-offs between food availability and predation risk in desert environments: The case of polygynous monomorphic guanaco (*Lama guanicoe*). *Journal of Arid Environments*, 97, 136–142. https://doi.org/10.1016/J.JARIDENV.2013.05.017
- Aebischer, N. J., Wheatley, C. J., & Rose, H. R. (2014). Factors associated with shooting accuracy and wounding rate of four managed wild deer species in the UK, based on anonymous field records from deer stalkers. *PLoS ONE*, *9*(10). https://doi.org/10.1371/JOURNAL.PONE.0109698
- Aerts, R. (1995). The advantages of being evergreen. Trends in Ecology & Evolution, 10(10), 402-407.
- Ager, A. A., Johnson, B. K., Kern, J. W., & Kie, J. G. (2003). Daily and Seasonal Movements and Habitat Use by Female Rocky Mountain Elk and Mule Deer. *Journal of Mammalogy*, 84(3), 1076– 1088. https://academic.oup.com/jmammal/article/84/3/1076/905056
- Agetsuma, N., Koda, R., Tsujino, R., & Agetsuma-Yanagihara, Y. (2016). Impact of anthropogenic disturbance on the density and activity pattern of deer evaluated with respect to spatial scaledependency. *Mammalian Biology*, 81(2), 130–137. https://doi.org/10.1016/j.mambio.2015.09.005

- Akashi, N., & Nakashizuka, T. (1999). Effects of bark-stripping by Sika deer (*Cervus nippon*) on population dynamics of a mixed forest in Japan. *Forest Ecology and Management*, 113(1), 75–82. https://doi.org/10.1016/S0378-1127(98)00415-0
- Akashi, N., Unno, A., & Terazawa, K. (2011). Effects of deer abundance on broad-leaf tree seedling establishment in the understory of *Abies sachalinensis* plantations. *Journal of Forest Research*, *16*(6), 500–508. https://doi.org/10.1007/s10310-010-0245-2
- Ali, A. H., Ford, A. T., Evans, J. S., Mallon, D. P., Hayes, M. M., King, J., Amin, R., & Goheen, J. R. (2017). Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. *Journal of Applied Ecology*, 54(6), 1720–1729. https://doi.org/10.1111/1365-2664.12856
- Allen, R. B., Forsyth, D. M., Allen, R. K. J., Affeld, K., & MacKenzie, D. I. (2015). Solar radiation determines site occupancy of coexisting tropical and temperate deer species introduced to New Zealand forests. *PLoS ONE*, 10(6). https://doi.org/10.1371/journal.pone.0128924
- Allen, R. B., Payton, I. J., & Knowlton, J. E. (1984). Effects of ungulates on structure and species composition in the Urewera forests as shown by exclosures. *New Zealand Journal of Ecology*, 7, 119–130.
- Allombert, S., Stockton, S., & Martin, J. L. (2005). A natural experiment on the impact of overabundant deer on songbird populations. *Conservation Biology*, 19(6), 1917–1929. https://doi.org/10.1111/j.1523-1739.2005.00280.x
- Alstad, K. P., Welker, J. M., Williams, S. A., & Trlica, M. J. (1999). Carbon and water relations of Salix monticola in response to winter browsing and changes in surface water hydrology: an isotopic study using delta-13C and delta-18O. *OECOLOGIA*, 120, 375–385. https://doi.org/10.1007/s004420050870
- Amar, A., Smith, K. W., Butler, S., Lindsell, J. A., Hewson, C. M., Fuller, R. J., & Charman, E. C. (2010). Recent patterns of change in vegetation structure and tree composition of British broadleaved woodland: Evidence from large-scale surveys. *Forestry*, 83(4), 345–356. https://doi.org/10.1093/forestry/cpq017
- Ambroz, R., Vacek, S., Vacek, Z., Král, J., & Štefančík, I. (2015). Current and simulated structure, growth parameters and regeneration of beech forests with different game management in the Lány Game Enclosure. *Forestry Journal*, 61(2), 78–88. https://doi.org/10.1515/forj-2015-0016
- Ameztegui, A., & Coll, L. (2015). Herbivory and seedling establishment in Pyrenean forests: Influence of micro- and meso-habitat factors on browsing pressure. *Forest Ecology and Management*, 342, 103–111. https://doi.org/10.1016/j.foreco.2015.01.021

- Anderson, E. M. (2007). Changes in Bird Communities and Willow Habitats Associated With Fed Elk. *The Wilson Journal of Ornithology*, *119*(3), 400–409. https://doi.org/10.1676/06-079.1
- Ando, M., Itaya, A., Yamamoto, S. I., & Shibata, E. (2006). Expansion of dwarf bamboo, Sasa nipponica, grassland under feeding pressure of sika deer, *Cervus nippon*, on subalpine coniferous forest in central Japan. *Journal of Forest Research*, 11(1), 51–55. https://doi.org/10.1007/s10310-005-0180-9
- Apollonio, M., Belkin, V. V., Borkowski, J., Borodin, O. I., Borowik, T., Cagnacci, F., Danilkin, A. A., Danilov, P. I., Faybich, A., Ferretti, F., Gaillard, J. M., Hayward, M., Heshtaut, P., Heurich, M., Hurynovich, A., Kashtalyan, A., Kerley, G. I. H., Kjellander, P., Kowalczyk, R., ... Yanuta, G. (2017). Challenges and science-based implications for modern management and conservation of European ungulate populations. *Mammal Research*, *62*(3), 209–217. https://doi.org/10.1007/s13364-017-0321-5
- Apollonio, M., de Cena, F., Bongi, P., & Ciuti, S. (2014). Female preference and predation risk models can explain the maintenance of a fallow deer (Dama dama) lek and its "handy" location. *PLoS ONE*, 9(3). https://doi.org/10.1371/journal.pone.0089852
- Apollonio, M., Festa-Bianchet, M., Franco, M., Mattioli, M., & Sarno, B. (1992). To lek or not to lek: mating strategies of male fallow deer. *Behavioural Ecology*, *3*(1), 25–31.
- Apollonio, M., Focardi, S., Toso, S., & Nacci, L. (1998). Habitat selection and group formation pattern of fallow deer Dama dama in a submediterranean environment. *Oikos*, 21(3), 225–234. https://www.jstor.org/stable/pdf/3682973.pdf?refreqid=excelsior%3A979079474bcf14ea6b10da5f9 9d591c5
- Arnold, J. M., Gerhardt, P., Steyaert, S. M. J. G., Hochbichler, E., & Hackländer, K. (2018). Diversionary feeding can reduce red deer habitat selection pressure on vulnerable forest stands, but is not a panacea for red deer damage. *Forest Ecology and Management*, 407, 166–173. https://doi.org/10.1016/j.foreco.2017.10.050
- Atkins, J. W., Fahey, R. T., Hardiman, B. H., & Gough, C. M. (2018). Forest Canopy Structural Complexity and Light Absorption Relationships at the Subcontinental Scale. *Journal of Geophysical Research: Biogeosciences*, 123(4), 1387–1405. https://doi.org/10.1002/2017JG004256
- Attiwill, P. M. (1994). The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management*, *63*(2–3), 247–300. https://doi.org/10.1016/0378-1127(94)90114-7
- Augustine, D. J., & McNaughton, S. J. (1998). Ungulate effects on the functional species composition of plant communities. *Journal of Wildlife Management*, 62(4), 1165–1183.

- Augustine, D. J., & Mcnaughton, S. J. (2004). Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*, 41(1), 45–58. https://doi.org/10.1111/j.1365-2664.2004.00864.x
- Azorit, C., Tellado, S., Oya, A., & Moro, J. (2012). Seasonal and specific diet variations in sympatric red and fallow deer of southern Spain: A preliminary approach to feeding behaviour. *Animal Production Science*, 52(8), 720–727. https://doi.org/10.1071/AN12016
- Bailey, J. K., & Whitham, T. G. (2002). Interactions among fire, aspen, and elk affect insect diversity: Reversal of a community response. *Ecology*, 83(6), 1701–1712. https://doi.org/10.1890/0012-9658(2002)083[1701:IAFAAE]2.0.CO;2
- Baker, W. L., Munroe, J. A., & Hessl, A. E. (1997). The effects of elk on aspen in the winter range in Rocky Mountain National Park. *Ecography*, 20(2), 155–165. https://doi.org/10.1111/j.1600-0587.1997.tb00358.x
- Bakker, E. S., Gill, J. L., Johnson, C. N., Vera, F. W. M., Sandom, C. J., Asner, G. P., & Svenning, J. C. (2016). Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proceedings of the National Academy of Sciences of the United States of America*, 113(4), 847–855. https://doi.org/10.1073/pnas.1502545112
- Bakker, E. S., Pagès, J. F., Arthur, R., & Alcoverro, T. (2016). Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems. *Ecography*, *39*(2), 162–179. https://doi.org/10.1111/ecog.01651
- Balandier, P., Marquier, A., Casella, E., Kiewitt, A., Coll, L., Wehrlen, L., & Harmer, R. (2013). Architecture, cover and light interception by bramble (*Rubus fruticosus*): A common understorey weed in temperate forests. *Forestry*, 86(1), 39–46. https://doi.org/10.1093/forestry/cps066
- Baltzinger, M., Mårell, A., Archaux, F., Pérot, T., Leterme, F., & Deconchat, M. (2016). Overabundant ungulates in French Sologne? Increasing red deer and wild boar pressure may not threaten woodland birds in mature forest stands. *Basic and Applied Ecology*, 17(6), 552–563. https://doi.org/10.1016/j.baae.2016.04.005
- Bardgett, R. D., & Wardle, D. A. (2003). Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, *84*(9), 2258–2268. https://doi.org/10.1890/02-0274
- Baril, L. M., Hansen, A. J., Renkin, R., & Lawrence, R. (2011). Songbird response to increased willow (Salix spp.) growth in Yellowstone's northern range. *Ecological Applications*, 21(6), 2283–2296. https://doi.org/10.1890/10-0169.1
- Barja, I., & Rosellini, S. (2008). Does habitat type modify group size in roe deer and red deer under predation risk by Iberian wolves? *Canadian Journal of Zoology*, 86(3), 170–176. https://doi.org/10.1139/z07-129

- Barnett, D. T., & Stohlgren, T. J. (2001). Aspen persistence near the National Elk Refuge and Gros Ventre Valley elk feedgrounds of Wyoming, USA. *Landscape Ecology*, 16(6), 569–580. https://doi.org/10.1023/A:1013158511225
- Barrere, J., Petersson, L. K., Boulanger, V., Collet, C., Felton, A. M., Löf, M., & Saïd, S. (2021). Canopy openness and exclusion of wild ungulates act synergistically to improve oak natural regeneration. *Forest Ecology and Management*, 487. https://doi.org/10.1016/j.foreco.2021.118976
- Barrere, J., Saïd, S., Morin, X., Boulanger, V., Rowe, N., Amiaud, B., & Bernard, M. (2019). The cost of deer to trees: changes in resource allocation from growth- related traits and phenolic content to structural defence. *Plant Ecology and Evolution*, 152(3), 417–425. https://doi.org/10.5091/plecevo.2019.1593
- Barrios-Garcia, M. N., Relva, M. A., & Kitzberger, T. (2012). Patterns of use and damage by exotic deer on native plant communities in northwestern Patagonia. *European Journal of Wildlife Research*, 58(1), 137–146. https://doi.org/10.1007/s10344-011-0554-6
- Bartolomé, J., Molina-Alcaide, E., Cassinello, J., Gálvez-Bravo, L., Sicilia, M., & Miranda, M. (2012). Foraging sexual segregation in a Mediterranean environment: Summer drought modulates sexspecific resource selection. *Journal of Arid Environments*, 85, 97–104. https://doi.org/10.1016/j.jaridenv.2012.05.011
- Bartoń, K. (2022). MuMIn: Multi-Model Inference. https://CRAN.R-project.org/package=MuMIn
- Barton, O. (2023). Assessing landscape-scale patterns of activity and habitat-use by fallow deer (Dama dama) in the Elwy Valley region of North Wales, UK [PhD Thesis]. Bangor University.
- Barton, O., Gresham, A., Healey, J. R., Cordes, L. S., & Shannon, G. (2022). The effects of population management on wild ungulates: A systematic map of evidence for UK species. *PLOS ONE*, 1–26. https://doi.org/10.1371/journal.pone.0267385
- Bartos, L., Vankova, D., Miller, K. v., & Siler, J. (2002). Interspecific Competition between White-Tailed, Fallow, Red, and Roe Deer. *The Journal of Wildlife Management*, 66(2), 522–527.
- Baruzzi, C., & Krofel, M. (2017). Friends or foes? Importance of wild ungulates as ecosystem engineers for amphibian communities. *North-Western Journal of Zoology*, 13(2), 320–325. https://doi.org/10.1016/j.bioorg.2014.12.001
- Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J. D. C., Odden, J., Andersen, R., Arild Høgda, K., & Gaillard, J. M. (2009). What shapes Eurasian lynx distribution in human dominated landscapes: Selecting prey or avoiding people? *Ecography*, 32(4), 683–691. https://doi.org/10.1111/j.1600-0587.2009.05712.x

- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48. https://doi.org/10.18637/jss.v067.i01
- Bauwens, S., Bartholomeus, H., Calders, K., & Lejeune, P. (2016). Forest inventory with terrestrial LiDAR: A comparison of static and hand-held mobile laser scanning. *Forests*, 7(6), 127. https://doi.org/10.3390/f7060127
- Becklin, K. M., & Kirkpatrick, H. E. (2006). Compensation through rosette formation: The response of scarlet gilia (*Ipomos aggregata: Polemoniaceae*) to mammalian herbivory. *Canadian Journal of Botany*, 84(8), 1298–1303. https://doi.org/10.1139/B06-099
- Bee, J. N., Tanentzap, A. J., Lee, W. G., Lavers, R. B., Mark, A. F., Mills, J. A., & Coomes, D. A. (2009). The benefits of being in a bad neighbourhood: Plant community composition influences red deer foraging decisions. *Oikos*, 118(1), 18–24. https://doi.org/10.1111/j.1600-0706.2008.16756.x
- Bee, J. N., Tanentzap, A. J., Lee, W. G., Lavers, R. B., Mark, A. F., Mills, J. A., & Coomes, D. A. (2011). Influence of foliar traits on forage selection by introduced red deer in New Zealand. *Basic* and Applied Ecology, 12(1), 56–63. https://doi.org/10.1016/J.BAAE.2010.09.010
- Béland, M., & Kobayashi, H. (2021). Mapping forest leaf area density from multiview terrestrial lidar. *Methods in Ecology and Evolution*, 2021(June 2020), 1–15. https://doi.org/10.1111/2041-210X.13550
- Bellamy, P. E., Burgess, M. D., Mallord, J. W., Cristinacce, A., Orsman, C. J., Davis, T., Grice, P. v., & Charman, E. C. (2018). Nest predation and the influence of habitat structure on nest predation of Wood Warbler *Phylloscopus sibilatrix*, a ground-nesting forest passerine. *Journal of Ornithology*, 159(2), 493–506. https://doi.org/10.1007/s10336-017-1527-7
- Bellingham, P. J., Richardson, S. J., Mason, N. W. H., Veltman, C. J., Allen, R. B., Allen, W. J., Barker, R. J., Forsyth, D. M., Nicol, S. J., & Ramsey, D. S. L. (2016). Introduced deer at low densities do not inhibit the regeneration of a dominant tree. *Forest Ecology and Management*, 364, 70–76. https://doi.org/10.1016/j.foreco.2015.12.013
- Belotti, E., Červený, J., Šustr, P., Kreisinger, J., Gaibani, G., & Bufka, L. (2013). Foraging sites of Eurasian lynx Lynx lynx: Relative importance of microhabitat and prey occurrence. Wildlife Biology, 19(2), 188–201. https://doi.org/10.2981/12-077
- Berger-Tal O., Greggor, A. L., Macura, B., Adams, C. A., Blumenthal, A., Bouskila, A., Candolin, U., Doran, C., Fernández-Juricic, E., Gotanda, K. M., Price, C., Putman, B. J., Segoli, M., Snijders, L., Wong, B. B. M., & Blumstein, D. T. (2019) Systematic reviews and maps as tools for applying behavioral ecology to management and policy. *Behavioral Ecology, 30*(1), 1-8. Bergquist, J., Bergström, R., & Zakharenka, A. (2003). Responses of young Norway spruce (Picea abies) to winter browsing by roe deer (*Capreolus capreolus*): Effects on height growth and stem

morphology. *Scandinavian Journal of Forest Research*, *18*(4), 368–376. https://doi.org/10.1080/0282758031005431

- Bergquist, J., Löf, M., & Örlander, G. (2009). Effects of roe deer browsing and site preparation on performance of planted broadleaved and conifer seedlings when using temporary fences. *Scandinavian Journal of Forest Research*, 24(4), 308–317. https://doi.org/10.1080/02827580903117420
- Bergquist, J., Örlander, G., & Nilsson, U. (1999). Deer browsing and slash removal affect field vegetation on south Swedish clearcuts. *Forest Ecology and Management*, *115*(2–3), 171–182. https://doi.org/10.1016/S0378-1127(98)00397-1
- Bergström, R., & Bergqvist, G. (1997). Frequencies and patterns of browsing by large herbivores on conifer seedlings. *Scandinavian Journal of Forest Research*, 12(3), 288–294. https://doi.org/10.1080/02827589709355412
- Bergvall, U. A. (2009). Development of feeding selectivity and consistency in food choice over 5 years in fallow deer. *Behavioural Processes*, 80(2), 140–146. https://doi.org/10.1016/j.beproc.2008.11.004
- Bergvall, U. A., Schäpers, A., Kjellander, P., & Weiss, A. (2011). Personality and foraging decisions in fallow deer, *Dama dama. Animal Behaviour*, 81(1), 101–112. https://doi.org/10.1016/j.anbehav.2010.09.018
- Berman, T. S., Ben-Ari, M., Henkin, Z., & Inbar, M. (2018). Immediate and long-term facilitative effects of cattle grazing on a polyphagous caterpillar. *Agriculture, Ecosystems and Environment*, 261, 45–53. https://doi.org/10.1016/j.agee.2018.03.019
- Bernard, M., Boulanger, V., Dupouey, J. L., Laurent, L., Montpied, P., Morin, X., Picard, J. F., & Saïd, S. (2017). Deer browsing promotes Norway spruce at the expense of silver fir in the forest regeneration phase. *Forest Ecology and Management*, 400, 269–277. https://doi.org/10.1016/j.foreco.2017.05.040
- Bernes, C., Macura, B., Jonsson, B. G., Junninen, K., Müller, J., Sandström, J., Lõhmus, A., & Macdonald, E. (2018). Manipulating ungulate herbivory in temperate and boreal forests: Effects on vegetation and invertebrates. A systematic review. *Environmental Evidence*, 7(13). https://doi.org/10.1186/s13750-018-0125-3
- Beschta, R. L. (2005). Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's Northern Range. *Ecology*, 86(2), 391–403. https://doi.org/10.1890/04-0964
- Beschta, R. L., & Ripple, W. J. (2007). Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Canadian Journal of Forest Research*, *37*(10), 1873–1885. https://doi.org/10.1139/X07-017

- Beschta, R. L., & Ripple, W. J. (2010). Mexican wolves, elk, and aspen in Arizona: Is there a trophic cascade? *Forest Ecology and Management*, 260(5), 915–922. https://doi.org/10.1016/j.foreco.2010.06.012
- Beschta, R. L., & Ripple, W. J. (2013). Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology*, *94*(6), 1420–1425. https://doi.org/10.1890/11-0063.1
- Beschta, R. L., & Ripple, W. J. (2015). Divergent patterns of riparian cottonwood recovery after the return of wolves in Yellowstone, USA. *Ecohydrology*, 8(1), 58–66. https://doi.org/10.1002/eco.1487
- Beschta, R. L., & Ripple, W. J. (2016). Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction. *Biological Conservation*, 198, 93–103. https://doi.org/10.1016/j.biocon.2016.03.031
- Beschta, R. L., & Ripple, W. J. (2019). Can large carnivores change streams via a trophic cascade? *Ecohydrology*, *12*(1), 1–13. https://doi.org/10.1002/eco.2048
- Best, J. N., Bork, E. W., & Cool, N. L. (2003). Initial beaked hazel growth responses following protection from ungulate browsing. *Journal of Range Management*, 56(5), 455–460. https://doi.org/10.2307/4003836
- Bideau, E., Maublanc, M. L., Picot, D., Hamard, J. P., Ballon, P., & Gerard, J. F. (2016). Short-term browsing by roe deer has little effect on survival and growth of sessile oak seedlings. *Scandinavian Journal of Forest Research*, 31(1), 40–45. https://doi.org/10.1080/02827581.2015.1054873
- Biggs, J. R., VanLeeuwen, D. M., Holechek, J. L., Sherwood, S. L., & Valdez, R. (2016). Characteristics of browsed aspen forests following wildfire and implications for management: a case study. *Journal* of Plant Ecology, 10(6), 949–957. https://doi.org/10.1093/jpe/rtw101
- Biuw, M., Jepsen, J. U., Cohen, J., Ahonen, S. H., Tejesvi, M., Aikio, S., Wäli, P. R., Vindstad, O. P. L., Markkola, A., Niemelä, P., & Ims, R. A. (2014). Long-term Impacts of Contrasting Management of Large Ungulates in the Arctic Tundra-Forest Ecotone: Ecosystem Structure and Climate Feedback. *Ecosystems*, 17(5), 890–905. https://doi.org/10.1007/s10021-014-9767-3
- Bjørneraas, K., Solberg, E. J., Herfindal, I., Moorter, B. Van, Rolandsen, C. M., Tremblay, J.-P., Skarpe, C., Sæther, B.-E., Eriksen, R., & Astrup, R. (2011). Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. *Wildlife Biology*, 17(1), 44–54. https://doi.org/10.2981/10-073
- Bleay, N. J. (1987). *The ecology of sycamore in British Woodland* [Master's Thesis]. Middlesex University.

- Bobek, B., Merta, D., & Furtek, J. (2016). Winter food and cover refuges of large ungulates in lowland forests of south-western Poland. *Forest Ecology and Management*, 359, 247–255. https://doi.org/10.1016/j.foreco.2015.09.050
- Bobrowski, M., Gillich, B., & Stolter, C. (2020). Nothing else matters? Food as a driving factor of habitat use by red and roe deer in winter? *Wildlife Biology*, 2020(4). https://doi.org/10.2981/wlb.00723
- Bongi, P., Ciuti, S., Grignolio, S., del Frate, M., Simi, S., Gandelli, D., & Apollonio, M. (2008). Antipredator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. *Journal of Zoology*, 276(3), 242–251. https://doi.org/10.1111/j.1469-7998.2008.00481.x
- Bonnot, N. C., Couriot, O., Berger, A., Cagnacci, F., Ciuti, S., De Groeve, J. E., Gehr, B., Heurich, M., Kjellander, P., Kröschel, M., Morellet, N., Sönnichsen, L., Hewison, A. J. M., Park, N., & Ecology, W. (2020). Fear of the dark? Contrasting impacts of humans vs lynx on diel activity of roe deer across Europe. *Journal of Animal Ecology*, *89*, 132–145. https://doi.org/10.1111/1365-2656.13161
- Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., & Hewison, A. J. M. (2013). Habitat use under predation risk: Hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife Research*, 59(2), 185–193. https://doi.org/10.1007/s10344-012-0665-8
- Bork, E. W., Carlyle, C. N., Cahill, J. F., Haddow, R. E., & Hudson, R. J. (2013). Disentangling herbivore impacts on *Populus tremuloides*: A comparison of native ungulates and cattle in Canada's Aspen Parkland. *Oecologia*, *173*(3), 895–904. https://doi.org/10.1007/s00442-013-2676-x
- Bork, E. W., Hudson, R. J., & Bailey, A. W. (1997). Populus forest characterization in Elk Island National Park relative to herbivory, prescribed fire, and topography. *Canadian Journal of Botany*, 75(9), 1518–1526. https://doi.org/10.1139/b97-866
- Borkowski, J., & Obidziński, A. (2003). The composition of the autumn and winter diets in two Polish populations of fallow deer. *Acta Theriologica*, 48(4), 539–546. https://doi.org/10.1007/BF03192499
- Borkowski, J., & Pudełko, M. (2007). Forest habitat use and home-range size in radio-collared fallow deer. *Ann. Zool. Fennici*, 44, 107–114. http://www.sekj.org/PDF/anz44-free/anz44-107.pdf
- Borkowski, J., & Ukalska, J. (2008). Winter habitat use by red and roe deer in pine-dominated forest. *Forest Ecology and Management*, 255, 468–475. https://doi.org/10.1016/j.foreco.2007.09.013
- Borkowski, J., Ukalska, J., Jurkiewicz, J., & Chećko, E. (2016). Living on the boundary of a postdisturbance forest area: The negative influence of security cover on red deer home range size. *Forest Ecology and Management*, 381, 247–257. https://doi.org/10.1016/J.FORECO.2016.09.009

- Borkowski, J., & Ukalski, K. (2012). Bark stripping by red deer in a post-disturbance area: The importance of security cover. *Forest Ecology and Management*, *263*, 17–23. https://doi.org/10.1016/j.foreco.2011.09.029
- Borowski, Z., Bałazy, R., Ciesielski, M., & Korzeniewski, K. (2019). Does winter supplementary feeding affect deer damage in a forest ecosystem? A field test in areas with different levels of deer pressure. *Pest Management Science*, 75(4), 893–899. https://doi.org/10.1002/ps.5131
- Borowski, Z., Gil, W., Bartoń, K., Zajączkowski, G., Łukaszewicz, J., Tittenbrun, A., & Radliński, B. (2021). Density-related effect of red deer browsing on palatable and unpalatable tree species and forest regeneration dynamics. *Forest Ecology and Management*, 496. https://doi.org/10.1016/j.foreco.2021.119442
- Bose, S., Forrester, T. D., Casady, D. S., & Wittmer, H. U. (2018). Effect of activity states on habitat selection by black-tailed deer. *Journal of Wildlife Management*, 82(8), 1711–1724. https://doi.org/10.1002/jwmg.21529
- Boulanger, V., Baltzinger, C., Saïd, S., Ballon, P., Picard, J. F., & Dupouey, J. L. (2009). Ranking temperate woody species along a gradient of browsing by deer. *Forest Ecology and Management*, 258(7), 1397–1406. https://doi.org/10.1016/j.foreco.2009.06.055
- Boulanger, V., Baltzinger, C., Saïd, S., Ballon, P., Picard, J. F., & Dupouey, J. L. (2015). Decreasing deer browsing pressure influenced understory vegetation dynamics over 30 years. *Annals of Forest Science*, 72(3), 367–378. https://doi.org/10.1007/s13595-014-0431-z
- Boulanger, V., Dupouey, J. L., Archaux, F., Badeau, V., Baltzinger, C., Chevalier, R., Corcket, E., Dumas, Y., Forgeard, F., Mårell, A., Montpied, P., Paillet, Y., Picard, J. F., Saïd, S., & Ulrich, E. (2018). Ungulates increase forest plant species richness to the benefit of non-forest specialists. *Global Change Biology*, 24(2), e485–e495. https://doi.org/10.1111/gcb.13899
- Brainerd, S. M., & Kaltenborn, B. (2010). The Scandinavian model: A different path to wildlife management. *The Wildlife Professional*, 4(3), 52–56.
- Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Fauchald, P., Tveraa, T., & Hausner, V. H. (2007). Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems*, *10*(5), 773–789. https://doi.org/10.1007/s10021-007-9058-3
- Brennan, G. L., Potter, C., de Vere, N., Griffith, G. W., Skjøth, C. A., Osborne, N. J., Wheeler, B. W., McInnes, R. N., Clewlow, Y., Barber, A., Hanlon, H. M., Hegarty, M., Jones, L., Kurganskiy, A., Rowney, F. M., Armitage, C., Adams-Groom, B., Ford, C. R., Petch, G. M., ... Creer, S. (2019). Temperate airborne grass pollen defined by spatio-temporal shifts in community composition. *Nature Ecology and Evolution*, *3*(5), 750–754. https://doi.org/10.1038/s41559-019-0849-7

- British Deer Society. (2022). *Deer Species*. Available from: https://bds.org.uk/information-advice/about-deer/deer-species/
- Brodie, J., Post, E., Watson, F., & Berger, J. (2012). Climate change intensification of herbivore impacts on tree recruitment. *Proceedings of the Royal Society B: Biological Sciences*, 279(1732), 1366– 1370. https://doi.org/10.1098/rspb.2011.1501
- Brousseau, M., Thiffault, N., Beguin, J., Roy, V., & Tremblay, J. P. (2017). Deer browsing outweighs the effects of site preparation and mechanical release on balsam fir seedlings performance: Implications to forest management. *Forest Ecology and Management*, 405, 360–366. https://doi.org/10.1016/j.foreco.2017.09.024
- Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, 22(1), 37–47. https://doi.org/10.1007/BF00395696
- Brüllhardt, M., Risch, A. C., Filli, F., Haller, R. M., & Schütz, M. (2015). Spatiotemporal dynamics of natural tree regeneration in unmanaged subalpine conifer forests with high wild ungulate densities. *Canadian Journal of Forest Research*, 45(6), 607–614. https://doi.org/10.1139/cjfr-2014-0358
- Bruno, E., & Apollonio, M. (1991). Seasonal variations in the diet of adult male fallow deer in a submediterranean coastal area. *Revue d'Ecologie (Terre et La Vie)*, 46(4), 349–362.
- Bryant, J. P., Reichardt, P. B., & Clausen, T. P. (1992). Chemically mediated interactions between woody plants and browsing mammals. *Journal of Range Management*, 45(January), 18–24. https://doi.org/10.2307/4002520
- Buchanan, C. B., Beck, J. L., Bills, T. E., & Miller, S. N. (2014). Seasonal resource selection and distributional response by elk to development of a natural gas field. *Rangeland Ecology and Management*, 67(4), 369–379. https://doi.org/10.2111/REM-D-13-00136.1
- Buckley, G. P. (1992). *Ecology and Management of Coppice Woodlands* (G. P. Buckley, Ed.). Springer Dordrecht.
- Buesching, C. D., Newman, C., Jones, J. T., & Macdonald, D. W. (2011). Testing the effects of deer grazing on two woodland rodents, bankvoles and woodmice. *Basic and Applied Ecology*, 12(3), 207–214. https://doi.org/10.1016/j.baae.2011.02.007
- Burkepile, D. E., Fynn, R. W. S., Thompson, D. I., Lemoine, N. P., Koerner, S. E., Eby, S., Hagenah, N., Wilcox, K. R., Collins, S. L., Kirkman, K. P., Knapp, A. K., & Smith, M. D. (2017). Herbivore size matters for productivity–richness relationships in African savannas. *Journal of Ecology*, 105(3), 674–686. https://doi.org/10.1111/1365-2745.12714

- Bush, E. R., Buesching, C. D., Slade, E. M., & Macdonald, D. W. (2012). Woodland recovery after suppression of deer: Cascade effects for small mammals, wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*). *PLoS ONE*, 7(2), e31404. https://doi.org/10.1371/journal.pone.0031404
- Caldwell, J. F., Chapman, D. I., & Chapman, N. (1983). Observations on the autumn and winter diet of Fallow deer (*Dama dama*). *Journal of Zoology*, 47, 559–563.
- Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., & Holmes, S. P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. *Nature Methods*, 13(7), 581–583. https://doi.org/10.1038/nmeth.3869
- Camarretta, N., Harrison, P. A., Lucieer, A., Potts, B. M., Davidson, N., & Hunt, M. (2021). Handheld Laser Scanning Detects Spatiotemporal Differences in the Development of Structural Traits among Species in Restoration Plantings. *Remote Sensing*, 13(9), 1706. https://doi.org/10.3390/rs13091706
- Campbell, M. J., Dennison, P. E., Hudak, A. T., Parham, L. M., & Butler, B. W. (2018). Quantifying understory vegetation density using small-footprint airborne lidar. *Remote Sensing of Environment*, 215, 330–342. https://doi.org/10.1016/j.rse.2018.06.023
- Caravaggi, A., Burton, A. C., Clark, D. A., Fisher, J. T., Grass, A., Green, S., Hobaiter, C., Hofmeester, T. R., Kalan, A. K., Rabaiotti, D., & Rivet, D. (2020). A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. *Conservation Science and Practice*, 2(8). https://doi.org/10.1111/csp2.239
- Carline, K. A., Jones, H. E., & Bardgett, R. D. (2005). Large herbivores affect the stoichiometry of nutrients in a regenerating woodland ecosystem. *Oikos*, 110(3), 453–460. https://doi.org/10.1111/j.0030-1299.2005.13550.x
- Carpio, A. J., Apollonio, M., & Acevedo, P. (2021). Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. *Mammal Review*, 51(1), 95–108. https://doi.org/10.1111/mam.12221
- Carranza, J., & Mateos-Quesada, P. (2001). Habitat modification when scent marking: Shrub clearance by roe deer bucks. *Oecologia*, *126*(2), 231–238. https://doi.org/10.1007/s004420000511
- Case, R. L., & Kauffman, J. B. (1997). Wild ungulate influences on the recovery of willows, black cottonwood and thin-leaf alder following cessation of cattle grazing in northeastern Oregon. *Northwest Science*, 71(2), 115–126.
- Cellura, M., lo Brano, V., Mistretta, M., & Orioli, A. (2010). Influence of management practices on large herbivore diet - Case of European bison in Bialowieza Primeval Forest (Poland). ASHRAE Transactions, 116(PART 2), 585–596. https://doi.org/10.1016/j.foreco.2010.11.026

- Čermák, P., Beranová, P., Orálková, J., Horsák, P., & Plšek, J. (2011). Relationships between browsing damage and the species dominance by the highly-food-attractive and less food-attractive trees. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis*, *59*(1), 29–36. https://doi.org/10.11118/actaun201159010029
- Champagne, E., Dumont, A., Tremblay, J. P., & Côté, S. D. (2018). Forage diversity, type and abundance influence winter resource selection by white-tailed deer. *Journal of Vegetation Science*, 29(4), 619–628. https://doi.org/10.1111/jvs.12643
- Champagne, E., Perroud, L., Dumont, A., Tremblay, J. P., & Côté, S. D. (2018). Neighbouring plants and perception of predation risk modulate winter browsing by white-tailed deer (*Odocoileus virginianus*). *Canadian Journal of Zoology*, 96(2), 117–125. https://doi.org/10.1139/cjz-2017-0063
- Chapman, D., & Chapman, N. G. (1997). *Fallow deer: their history, distribution, and biology* (2nd ed.). Coch-y-Bonddu Books.
- Chapman, N. G. (2021). History of introduction of Reeves' muntjac in Great Britain and ecological characteristics facilitating expansion of feral populations. *European Journal of Wildlife Research*, 67(3), 1–7. https://doi.org/10.1007/s10344-021-01477-3
- Charco, J., Perea, R., Gil, L., & Nanos, N. (2016). Impact of deer rubbing on pine forests: implications for conservation and management of *Pinus pinaster* populations. *European Journal of Forest Research*, *135*(4), 719–729. https://doi.org/10.1007/s10342-016-0967-6
- Charro, J. L., López-Sánchez, A., & Perea, R. (2018). Traditional cattle vs. introduced deer management in Chaco Serrano woodlands (Argentina): Analysis of environmental sustainability at increasing densities. *Journal of Environmental Management*, 206, 642–649. https://doi.org/10.1016/j.jenvman.2017.11.007
- Chauchard, S., Carcaillet, C., & Guibal, F. (2018). Fir expansion not controlled by moderate densities of large herbivores: a Mediterranean mountain grassland conservation issue. *Annals of Forest Science*, 75(4). https://doi.org/10.1007/s13595-018-0774-y
- Chen, S., Yao, H., Han, J., Liu, C., Song, J., Shi, L., Zhu, Y., Ma, X., Gao, T., Pang, X., Luo, K., Li, Y., Li, X., Jia, X., Lin, Y., & Leon, C. (2010). Validation of the ITS2 region as a novel DNA barcode for identifying medicinal plant species. *PLoS ONE*, 5(1), 1–8. https://doi.org/10.1371/journal.pone.0008613
- Chollet, S., & Martin, J. L. (2013). Declining woodland birds in North America: Should we blame Bambi? *Diversity and Distributions*, *19*(4), 481–483. https://doi.org/10.1111/ddi.12003
- Chollet, S., Padié, S., Stockton, S., Allombert, S., Gaston, A. J., & Martin, J. L. (2016). Positive plant and bird diversity response to experimental deer population reduction after decades of uncontrolled browsing. *Diversity and Distributions*, 22(3), 274–287. https://doi.org/10.1111/ddi.12393

- Churski, M., Bubnicki, J. W., Jędrzejewska, B., Kuijper, D. P. J., & Cromsigt, J. P. G. M. (2017). Brown world forests: increased ungulate browsing keeps temperate trees in recruitment bottlenecks in resource hotspots. *New Phytologist*, 214(1), 158–168. https://doi.org/10.1111/nph.14345
- Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012). Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *PLoS ONE*, 7(11). https://doi.org/10.1371/journal.pone.0050611
- Claridge, A. W., Hunt, R., Thrall, P. H., & Mills, D. J. (2016). Germination of native and introduced plants from scats of Fallow Deer (Dama dama) and Eastern Grey Kangaroo (*Macropus giganteus*) in a south-eastern Australian woodland landscape. *Ecological Management and Restoration*, 17(1), 56–62. https://doi.org/10.1111/emr.12193
- Clements, G. M., Hygnstrom, S. E., Gilsdorf, J. M., Baasch, D. M., Clements, M. J., & Vercauteren, K. C. (2011). Movements of white-tailed deer in riparian habitat: Implications for infectious diseases. *Journal of Wildlife Management*, 75(6), 1436–1442. https://doi.org/10.1002/jwmg.183
- Clutton-Brock, T. H., Green, D., Hiraiwa-Hasegawa, M., & Albon, S. D. (1988). Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behavioral Ecology and Sociobiology*, 23(5), 281–296. https://doi.org/10.1007/BF00300575
- Clutton-Brock, T. H., Iason, G. R., Albon, S. D., & Guiness, F. E. (1982). The effects of lactation on feeding behavior and habitat use in wild red deer hinds. *Journal of Zoology*, *198*, 227–236. https://zslpublications.onlinelibrary.wiley.com/doi/pdf/10.1111/j.1469-7998.1982.tb02072.x
- Colas, F., Perron, M., Tousignant, D., Parent, C., Pelletier, M., & Lemay, P. (2008). A novel approach for the operational production of hybrid larch seeds under northern climatic conditions. *The Forestry Chronicle*, 84(1), 95–104.
- Conradt, L., Clutton-Brock, T. H., & Guinness, F. E. (2000). Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Animal Behavior*, 59, 1049–1060. https://doi.org/10.1006/anbe.2000.1409
- Cooke, A. S. (1998). Colonisation of Holme Fen National Nature Reserve by Chinese water deer and muntjac, 1976-1997. *Deer*, *10*, 414-416.
- Cooke, A. S. (2006). Monitoring muntjac deer Muniacus reevesi and their impacts in Monks Wood National Nature Reserve. *English Nature Research Reports*, 681.
- Cooke, A. S. (2021). Colonisation, impacts in conservation woodland and management of Reeves' muntjac (*Muntiacus reevesi*) in an English county. *European Journal of Wildlife Research*, 67(3). https://doi.org/10.1007/s10344-021-01480-8

- Cooke, A. S., & Farrell, L. (2001). Impact of muntjac deer (*Muntiacus reevesi*) at Monks Wood National Nature Reserve, Cambridgeshire, eastern England. *Forestry*, 74(3), 241–250. https://doi.org/10.1093/forestry/74.3.241
- Cooke, A. S., & Lakhani, K. H. (1996). Damage to coppice regrowth by muntjac deer *Muntiacus reevesi* and protection with electric fencing. *Biological Conservation*, 75(3), 231–238. https://doi.org/10.1016/0006-3207(95)00070-4
- Coomes, D. A., Allen, R. B., Bentley, W. A., Burrows, L. E., Canham, C. D., Fagan, L., Forsyth, D. M., Gaxiola-Alcantar, A., Parfitt, R. L., Ruscoe, W. A., Wardle, D. A., Wilson, D. J., & Wright, E. F. (2005). The hare, the tortoise and the crocodile: The ecology of angiosperm dominance, conifer persistence and fern filtering. *Journal of Ecology*, 93(5), 918–935. https://doi.org/10.1111/j.1365-2745.2005.01012.x
- Coppes, J., Burghardt, F., Hagen, R., Suchant, R., & Braunisch, V. (2017). Human recreation affects spatio-temporal habitat use patterns in red deer (*Cervus elaphus*). *PLoS ONE*, *12*(5), e0175134. https://doi.org/10.1371/journal.pone.0175134
- Corgatelli, G., Mattiello, S., Colombini, S., & Crovetto, G. M. (2019). Impact of red deer (*Cervus elaphus*) on forage crops in a protected area. *Agricultural Systems*, 169, 41–48. https://doi.org/10.1016/j.agsy.2018.11.009
- Corlatti, L., Gugiatti, A., & Pedrotti, L. (2016). Spring spotlight counts provide reliable indices to track changes in population size of mountain-dwelling red deer *Cervus elaphus*. *Wildlife Biology*, 22, 268–276. https://doi.org/10.2981/wlb.00244
- Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics*, 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725
- Coverdale, T. C., Goheen, J. R., Palmer, T. M., & Pringle, R. M. (2018). Good neighbors make good defenses: associational refuges reduce defense investment in African savanna plants. *Ecology*, 99(8), 1724–1736. https://doi.org/10.1002/ecy.2397
- Coverdale, T. C., Kartzinel, T. R., Grabowski, K. L., Shriver, R. K., Hassan, A. A., Goheen, J. R., & Palmer, T. M. (2016). Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. *Ecology*, 97(11), 3219–3230. https://doi.org/http://dx.doi.org/10.1002/ecy.1557
- Craine, J. M., Angerer, J. P., Elmore, A., & Fierer, N. (2016). Continental-scale patterns reveal potential for warming-induced shifts in cattle diet. *PLoS ONE*, 11(8), e0161511. https://doi.org/10.1371/journal.pone.0161511
- Croft, S., Ward, A. I., Aegerter, J. N., & Smith, G. C. (2019). Modeling current and potential distributions of mammal species using presence-only data: A case study on British deer. *Ecology* and Evolution, 9(15), 8724–8735. https://doi.org/10.1002/ece3.5424
- Csányi, E., Tari, T., Németh, S., & Sándor, G. (2022). Move or Not to Move—Red Deer Stags Movement Activity during the Rut. *Animals*, *12*(5). https://doi.org/10.3390/ani12050591
- Cukor, J., Vacek, Z., Linda, R., Sharma, R. P., & Vacek, S. (2019). Afforested farmland vs. forestland: Effects of bark stripping by *Cervus elaphus* and climate on production potential and structure of Picea abies forests. *Plos One*, *14*(8), e0221082. https://doi.org/10.1371/journal.pone.0221082
- Cukor, J., Vacek, Z., Linda, R., Vacek, S., Marada, P., Šimůnek, V., & Havránek, F. (2019). Effects of bark stripping on timber production and structure of Norway Spruce forests in relation to climatic factors. *Forests*, 10(4). https://doi.org/10.3390/f10040320
- Cusack, J. J., Dickman, A. J., Rowcliffe, J. M., Carbone, C., Macdonald, D. W., & Coulson, T. (2015). Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS ONE*, 10(5). https://doi.org/10.1371/journal.pone.0126373
- Cutini, A., Bongi, P., Chianucci, F., Pagon, N., Grignolio, S., Amorini, E., & Apollonio, M. (2011). Roe deer (*Capreolus capreolus L.*) browsing effects and use of chestnut and Turkey oak coppiced areas. *Annals of Forest Science*, 68(4), 667–674. https://doi.org/10.1007/s13595-011-0072-4
- Czernik, M., Taberlet, P., Świsłocka, M., Czajkowska, M., Duda, N., & Ratkiewicz, M. (2013). Fast and efficient DNA-based method for winter diet analysis from stools of three cervids: Moose, red deer, and roe deer. *Acta Theriologica*, *58*(4), 379–386. https://doi.org/10.1007/s13364-013-0146-9
- D'Aprile, D., Vacchiano, G., Meloni, F., Garbarino, M., Motta, R., Ducoli, V., & Partel, P. (2020). Effects of twenty years of ungulate browsing on forest regeneration at Paneveggio reserve, Italy. *Forests*, 11(6), 1–12. https://doi.org/10.3390/F11060612
- Das, A. J., Stephenson, N. L., & Davis, K. P. (2016). Why do trees die? Characterizing the drivers of background tree mortality. *Ecology*, 97(10), 2616–2627. https://doi.org/10.1002/ecy.1497
- Daskin, J. H., Stalmans, M., & Pringle, R. M. (2016). Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *Journal of Ecology, 104,* 79-89. https://doi.org/10.1111/1365-2745.12483
- Dassot, M., Constant, T., & Fournier, M. (2011). The use of terrestrial LiDAR technology in forest science: Application fields, benefits and challenges. *Annals of Forest Science*, 68(5), 959–974. https://doi.org/10.1007/s13595-011-0102-2

- Davies, A. B., & Asner, G. P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology and Evolution*, 29(12), 681–691. https://doi.org/10.1016/j.tree.2014.10.005
- Davini, S., Ciuti, S., Luccarini, S., & Apollonio, M. (2004). Home range patterns of male fallow deer Dama dama in a sub-Mediterranean habitat. *Acta Theriologica*, 49(3), 393–404. https://doi.org/10.1007/BF03192537
- Davis, N. E., Bennett, A., Forsyth, D. M., Bowman, D. M. J. S., Lefroy, E. C., Wood, S. W.,
 Woolnough, A. P., West, P., Hampton, J. O., & Johnson, C. N. (2016). A systematic review of the impacts and management of introduced deer (family *Cervidae*) in Australia. *Wildlife Research*, 43(6), 515–532. https://doi.org/10.1071/WR16148
- de Almeida, D. R. A., Stark, S. C., Silva, C. A., Hamamura, C., & Valbuena, R. (2021). *leafR: Calculates the Leaf Area Index (LAD) and Other Related Functions*. (0.3.5). https://CRAN.R-project.org/package=leafR
- de Chantal, M., & Granström, A. (2007). Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. *Forest Ecology and Management*, 250(1–2), 3–8. https://doi.org/10.1016/j.foreco.2007.03.035
- de Vere, N., Jones, L. E., Gilmore, T., Moscrop, J., Lowe, A., Smith, D., Hegarty, M. J., Creer, S., & Ford, C. R. (2017). Using DNA metabarcoding to investigate honeybee foraging reveals limited flower use despite high floral availability. *Scientific Reports*, 7(1), 42838. https://doi.org/10.1038/srep42838
- de Vere, N., Rich, T. C. G., Ford, C. R., Trinder, S. A., Long, C., Moore, C. W., Satterthwaite, D., Davies, H., Allainguillaume, J., Ronca, S., Tatarinova, T., Garbett, H., Walker, K., & Wilkinson, M. J. (2012). DNA barcoding the native flowering plants and conifers of Wales. *PLoS ONE*, 7(6), e37945. https://doi.org/10.1371/journal.pone.0037945
- Defra. (2021). *The England Trees Action Plan 2021-2024*. Available at: https://www.gov.uk/government/publications/england-trees-action-plan-2021-to-2024
- Deiner, K., Bik, H. M., Mächler, E., Seymour, M., Lacoursière-Roussel, A., Altermatt, F., Creer, S., Bista, I., Lodge, D. M., de Vere, N., Pfrender, M. E., & Bernatchez, L. (2017). Environmental DNA metabarcoding: Transforming how we survey animal and plant communities. *Molecular Ecology*, 26(21), 5872–5895. https://doi.org/10.1111/mec.14350
- Dixon, G., Marriott, A. S., Stelfox, G., Dunkerley, C., & Batke, S. P. (2021). How do red deer react to increased visitor numbers? A case study on human-deer encounter probability and its effect on cortisol stress responses. *Nature Conservation*, 43, 55–78. https://doi.org/10.3897/NATURECONSERVATION.43.56266

- Djaković, N., Holand, O., Hovland, A. L., Weladji, R. B., Røed, K. H., & Nieminen, M. (2015). Effects of males presence on female behaviour during the rut. *Ethology Ecology and Evolution*, 27(2), 148–160. https://doi.org/10.1080/03949370.2014.905498
- Dobrowolska, D., Załuski, D., Dąbrowski, W., Banul, R., & Borkowski, J. (2020). Factors affecting admixed pedunculate oak growth under heavy browsing by deer: benefits from inter- and intraspecific neighbourhoods. *European Journal of Forest Research*, *139*(2), 155–167. https://doi.org/10.1007/s10342-020-01268-6
- Drexhage, M., & Colin, F. (2003). Effects of browsing on shoots and roots of naturally regenerated sessile oak seedlings. *Annals of Forest Science*, 60, 173–178. https://doi.org/10.1051/forest
- du Toit, J. T., & Olff, H. (2014). Generalities in grazing and browsing ecology: Using across-guild comparisons to control contingencies. *Oecologia*, *174*(4), 1075–1083. https://doi.org/10.1007/s00442-013-2864-8
- Dubost, G., Charron, F., Courcoul, A., & Rodier, A. (2011). The Chinese water deer, *Hydropotes inermis* A fast-growing and productive ruminant. *Mammalian Biology*, 76(2), 190–195. https://doi.org/10.1016/j.mambio.2010.04.001
- Dumont, B., Renaud, P. C., Morellet, N., Mallet, C., Anglard, F., & Verheyden-Tixier, H. (2005). Seasonal variations of Red Deer selectivity on a mixed forest edge. *Animal Research*, 54(5), 369–381. https://doi.org/10.1051/animres:2005030
- Duncan, A. J., & Gordon, I. J. (1999). Habitat selection according to the ability of animals to eat, digest and detoxify foods. *Proceedings of the Nutrition Society*, 58(4), 799–805. https://doi.org/10.1017/S0029665199001081
- Duparc, A., Garel, M., Marchand, P., Dubray, D., Maillard, D., & Loison, A. (2020). Through the taste buds of a large herbivore: foodscape modelling contributes to an understanding of forage selection processes. *Oikos*, *129*(2), 170–183. https://doi.org/10.1111/oik.06386
- Dupke, C., Bonenfant, C., Reineking, B., Hable, R., Zeppenfeld, T., Ewald, M., & Heurich, M. (2017). Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. *Ecography*, 40(8), 1014–1027. https://doi.org/10.1111/ecog.02152
- Durham, D. A. (2010). Aspen Response to Prescribed Fire under Managed Cattle Grazing and Low Elk Densities in Southwest Montana. *Northwest Science*, *84*(1), 141. https://doi.org/10.3955/046.084.0203
- Dykes, J. L., Strickland, B. K., Demarais, S., Reynolds, D. B., & Lashley, M. A. (2018) Soil nutrients indirectly influence intraspecific plant selection in white-tailed deer. *Basic and Applied Ecology*, *32*, 103-109.

- Eichhorn, M. P., Ryding, J., Smith, M. J., Gill, R. M. A., Siriwardena, G. M., & Fuller, R. J. (2017). Effects of deer on woodland structure revealed through terrestrial laser scanning. *Journal of Applied Ecology*, 54(6), 1615–1626. https://doi.org/10.1111/1365-2664.12902
- Eldegard, K., Lyngved, J. T., & Hjeljord, O. (2012). Coping in a human-dominated landscape: Trade-off between foraging and keeping away from roads by moose (*Alces alces*). *European Journal of Wildlife Research*, 58(6), 969–979. https://doi.org/10.1007/s10344-012-0640-4
- Ellenberg, H. H. (1988). Vegetation Ecology of Central Europe. In *Cambridge University Press* (4th ed.). Cambridge University Press.
- Endress, B. A., & Averett, J. P. (2020). Ungulate herbivores reduce fruit production of shrubs in dry conifer forests of the interior Pacific Northwest, USA. *Food Webs*, 25, e00172. https://doi.org/10.1016/j.fooweb.2020.e00172
- Endress, B. A., Naylor, B. J., Pekin, B. K., & Wisdom, M. J. (2016). Aboveground and belowground mammalian herbivores regulate the demography of deciduous woody species in conifer forests. *Ecosphere*, 7(10), 1–18. https://doi.org/10.1002/ecs2.1530
- Ensing, E. P., Ciuti, S., de Wijs, F. A. L. M., Lentferink, D. H., Hoedt, A., Boyce, M. S., & Hut, R. A. (2014). GPS based daily activity patterns in European red deer and North American elk (*Cervus elaphus*): Indication for a weak circadian clock in ungulates. *PLoS ONE*, 9(9). https://doi.org/10.1371/journal.pone.0106997
- Erickson, D. L., Reed, E., Ramachandran, P., Bourg, N. A., McShea, W. J., & Ottesen, A. (2017). Reconstructing a herbivore's diet using a novel rbcL DNA mini-barcode for plants. *AoB PLANTS*, 9(3). https://doi.org/10.1093/aobpla/plx015
- Esattore, B., Saggiomo, L., Sensi, M., Francia, V., & Cherin, M. (2022). Tell me what you eat and I'll tell you...where you live: an updated review of the worldwide distribution and foraging ecology of the fallow deer (Dama dama). *Mammalian Biology*, *102*(2), 321–338. https://doi.org/10.1007/s42991-022-00250-6
- Estes, J. A., & Duggins, D. O. (1995). Sea Otters and Kelp Forests in Alaska: Generality and Variation in a Community Ecological Paradigm. *Ecological Society of America*, 65(1), 75–100. https://doi.org/10.2307/2937159
- Ewald, M., Dupke, C., Heurich, M., Müller, J., & Reineking, B. (2014). LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of european roe deer. *Forests*, 5(6), 1374–1390. https://doi.org/10.3390/f5061374
- Eycott, A. E., Watkinson, A. R., Hemami, M. R., & Dolman, P. M. (2007). The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. *Oecologia*, *154*(1), 107–118. https://doi.org/10.1007/s00442-007-0812-1

- Fairweather, M. L., Rokala, E. A., & Mock, K. E. (2014). Aspen seedling establishment and growth after wildfire in central arizona: An instructive case history. *Forest Science*, 60(4), 703–712. https://doi.org/10.5849/forsci.13-048
- Faison, E. K., DeStefano, S., Foster, D. R., Motzkin, G., & Rapp, J. M. (2016). Ungulate browsers promote herbaceous layer diversity in logged temperate forests. *Ecology and Evolution*, 6(13), 4591–4602. https://doi.org/10.1002/ece3.2223
- Fattorini, N., Lovari, S., Watson, P., & Putman, R. (2020). The scale-dependent effectiveness of wildlife management: A case study on British deer. *Journal of Environmental Management*, 276(July). https://doi.org/10.1016/j.jenvman.2020.111303
- Ferraro, K. M., Schmitz, O. J., & McCary, M. A. (2022). Effects of ungulate density and sociality on landscape heterogeneity: a mechanistic modeling approach. *Ecography*, 2022(2). https://doi.org/10.1111/ecog.06039
- Fløjgaard, C., De Barba, M., Taberlet, P., & Ejrnæs, R. (2017). Body condition, diet and ecosystem function of red deer (*Cervus elaphus*) in a fenced nature reserve. *Global Ecology and Conservation*, 11, 312–323. https://doi.org/10.1016/j.gecco.2017.07.003
- Fløjgaard, C., Pedersen, P. B. M., Sandom, C. J., Svenning, J. C., & Ejrnæs, R. (2021). Exploring a natural baseline for large-herbivore biomass in ecological restoration. *Journal of Applied Ecology*, 59(1), 18–24. https://doi.org/10.1111/1365-2664.14047
- Flowerdew, J. R., & Ellwood, S. A. (2001). Impacts of woodland deer on small mammal ecology. *Forestry*, 74(3), 277–287. https://doi.org/10.1093/forestry/74.3.277
- Foley, A. M., Deyoung, R. W., Hewitt, D. G., Hellickson, M. W., Gee, K. L., Wester, D. B., Lockwood, M. A., & Miller, K. v. (2015). Purposeful wanderings: Mate search strategies of male white-tailed deer. *Journal of Mammalogy*, 96(2), 279–286. https://doi.org/10.1093/jmammal/gyv004
- Forbes, E. S., Cushman, J. H., Burkepile, D. E., Young, T. P., Klope, M., & Young, H. S. (2019). Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Functional Ecology*, 33(9), 1597–1610. https://doi.org/10.1111/1365-2435.13376
- Forester, J. D., Anderson, D. P., & Turner, M. G. (2007). Do high-density patches of coarse wood and regenerating saplings create browsing refugia for aspen (*Populus tremuloides Michx.*) in Yellowstone National Park (USA)? *Forest Ecology and Management*, 253(1–3), 211–219. https://doi.org/10.1016/j.foreco.2007.07.019
- Forestry England. (2020). *It's been a bumper year for fruits and nuts say Forestry England experts*. Available from: https://tinyurl.com/25mtw6bu

- Forsyth, D. M., Coomes, D. A., Hall, G. M. J., & Nugent, G. (2002). Diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand. *New Zealand Journal of Zoology*, 29(4), 323–343. https://doi.org/10.1080/03014223.2002.9518316
- Forsyth, D. M., Wilson, D. J., Easdale, T. A., Kunstler, G., Canham, C. D., Ruscoe, W. A., Wright, E. F., Murphy, L., Gormley, A. M., Gaxiola, A., & Coomes, D. A. (2015). Century-scale effects of invasive deer and rodents on the dynamics of forests growing on soils of contrasting fertility. *Ecological Monographs*, 85(2), 157–180. https://doi.org/10.1890/14-0389.1
- Foster, C. N., Barton, P. S., & Lindenmayer, D. B. (2014). Effects of large native herbivores on other animals. *Journal of Applied Ecology*, *51*(4), 929–938. https://doi.org/10.1111/1365-2664.12268
- Fuentes-Montemayor, E., Park, K. J., Cordts, K., & Watts, K. (2022). The long-term development of temperate woodland creation sites: from tree saplings to mature woodlands. *Forestry*, 95, 28–37. https://doi.org/10.1093/forestry/cpab027
- Fujiki, D., Kishimoto, Y., & Sakata, H. (2010). Assessing decline in physical structure of deciduous hardwood forest stands under sika deer grazing using shrub-layer vegetation cover. *Journal of Forest Research*, 15(2), 140–144. https://doi.org/10.1007/s10310-009-0172-2
- Fuller, R. J. (2001). Responses of woodland birds to increasing numbers of deer: A review of evidence and mechanisms. *Forestry*, 74(3), 289–298. https://doi.org/10.1093/forestry/74.3.289
- Fuller, R. J., & Gill, R. M. A. (2001). Ecological impacts of increasing numbers of deer in British woodland. *Forestry*, 74(3), 193–199. https://doi.org/10.1093/forestry/74.3.193
- Furusawa, H., Hino, T., Takahashi, H., & Kaneko, S. (2016). Nitrogen leaching from surface soil in a temperate mixed forest subject to intensive deer grazing. *Landscape and Ecological Engineering*, 12(2), 223–230. https://doi.org/10.1007/s11355-016-0296-4
- Garnick, S., Barboza, P. S., & Walker, J. W. (2018). Assessment of Animal-Based Methods Used for Estimating and Monitoring Rangeland Herbivore Diet Composition. *Rangeland Ecology and Management*, 71(4), 449–457. https://doi.org/10.1016/j.rama.2018.03.003
- Gass, T. M., & Binkley, D. (2011). Soil nutrient losses in an altered ecosystem are associated with native ungulate grazing. *Journal of Applied Ecology*, *48*(4), 952–960. https://doi.org/10.1111/j.1365-2664.2011.01996.x
- Gaston, K. J. (2019). Nighttime ecology: the "nocturnal problem" revisited. *The American Naturalist*, *193*, 481–502.

- Gaudiano, L., Pucciarelli, L., & Mori, E. (2021). Livestock grazing affects movements and activity pattern of Italian roe deer in Southern Italy. *European Journal of Wildlife Research*, 67(4). https://doi.org/10.1007/s10344-021-01506-1
- Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology and Evolution*, 34(4), 355–368. https://doi.org/10.1016/j.tree.2019.01.004
- Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*, 1232–1235.
- Gaynor, K. M., McInturff, A., & Brashares, J. S. (2022). Contrasting patterns of risk from human and non-human predators shape temporal activity of prey. *Journal of Animal Ecology*, *91*(1), 46–60. https://doi.org/10.1111/1365-2656.13621
- Geary, A. B., Merrill, E. H., Cook, J. G., Cook, R. C., & Irwin, L. L. (2017). Elk nutritional resources: Herbicides, herbivory and forest succession at Mount St. Helens. *Forest Ecology and Management*, 401, 242–254. https://doi.org/10.1016/j.foreco.2017.06.028
- Gebremedhin, B., Flagstad, O., Bekele, A., Chala, D., Bakkestuen, V., Boessenkool, S., Popp, M., Gussarova, G., Schrøder-Nielsen, A., Nemomissa, S., Brochmann, C., Stenseth, N. Chr., & Epp, L. S. E. (2016). DNA metabarcoding reveals diet overlap between the endangered walia ibex and domestic goats Implications for conservation. *PLoS ONE*, *11*(7), e0159133. https://doi.org/10.1371/journal.pone.0159133
- Gerber, R., & Schmidt, W. (1996). Influence of roe deer on the vegetation of oak-hornbeam-forests in the southern Steigerwald. *Verhandlungen Der Gesellschaft Für Ökologie*, *26*, 345–353.
- Gerhardt, P., Arnold, J. M., Hackländer, K., & Hochbichler, E. (2013). Determinants of deer impact in European forests – A systematic literature analysis. *Forest Ecology and Management*, 310, 173– 186. https://doi.org/10.1016/J.FORECO.2013.08.030
- Gill, R. M. A. (1992). A review of damage by mammals in North temperate forests: 1. Deer. *Forestry*, 65(2), 145–169. https://doi.org/10.1093/forestry/65.2.145
- Gill, R. M. A., & Beardall, V. (2001). The impact of deer on woodlands: The effects of browsing and seed dispersal on vegetation structure and composition. *Forestry*, 74(3), 209–218. https://doi.org/, doi:
- Gill, R. M. A., & Fuller, R. J. (2007). The effects of deer browsing on woodland structure and songbirds in lowland Britain. *Ibis*, *149*, 119–127. https://doi.org/10.1093/forestry/65.2.145

- Gill, R. M. A., & Morgan, G. (2010). The effects of varying deer density on natural regeneration in woodlands in lowland Britain. *Forestry*, 83(1), 53–63. https://doi.org/10.1093/forestry/cpp031
- Giralt-Rueda, J. M., & Santamaria, L. (2021). Complementary differences in primary production and phenology among vegetation types increase ecosystem resilience to climate change and grazing pressure in an iconic Mediterranean ecosystem. *Remote Sensing*, *13*(19), 1–26. https://doi.org/10.3390/rs13193920
- Glass, T. W., Breed, G. A., Robards, M. D., Williams, C. T., & Kielland, K. (2021). Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore. *Animal Behaviour*, 175, 163–174. https://doi.org/10.1016/J.ANBEHAV.2021.02.017
- Goetz, S. J., Sun, M., Zolkos, S., Hansen, A., & Dubayah, R. (2014). The relative importance of climate and vegetation properties on patterns of North American breeding bird species richness. *Environmental Research Letters*, 9(3). https://doi.org/10.1088/1748-9326/9/3/034013
- González Hernández, M. P., & Silva-Pando, F. J. (1999). Nutritional attributes of understory plants known as components of deer diets. *Journal of Range Management*, 52, 132–138.
- Gordon, I. J. (2003). Browsing and grazing ruminants: Are they different beasts? In *Forest Ecology and Management* (Vol. 181, Issues 1–2, pp. 13–21). https://doi.org/10.1016/S0378-1127(03)00124-5
- Gordon, I. J., Hester, A. J., & Festa-Bianchet, M. (2004). The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, *41*(6), 1021–1031. https://doi.org/10.1111/j.0021-8901.2004.00985.x
- Greaves, H. E., Vierling, L. A., Eitel, J. U. H., Boelman, N. T., Magney, T. S., Prager, C. M., & Griffin, K. L. (2015). Estimating aboveground biomass and leaf area of low-stature Arctic shrubs with terrestrial LiDAR. *Remote Sensing of Environment*, 164, 26–35. https://doi.org/10.1016/j.rse.2015.02.023
- Green, D., & Stowe, J. P. (2000). Quality deer management: Ethical and social issues. *Human Dimensions of Wildlife*, 5(4), 62–71. https://doi.org/10.1080/10871200009359195
- Green, S. E., Rees, J. P., Stephens, P. A., Hill, R. A., & Giordano, A. J. (2020). Innovations in camera trapping technology and approaches: The integration of citizen science and artificial intelligence. *Animals*, 10(1). https://doi.org/10.3390/ani10010132
- Griffiths, C. J., Jones, C. G., Hansen, D. M., Puttoo, M., Tatayah, R. v., Müller, C. B., & Harris, S. (2010). The use of extant non-indigenous tortoises as a restoration tool to replace extinct ecosystem engineers. *Restoration Ecology*, 18(1), 1–7. https://doi.org/10.1111/j.1526-100X.2009.00612.x

- Gunn, A. 2016. *Rangifer tarandus*. The IUCN Red List of Threatened Species 2016: e.T29742A22167140. https://dx.doi.org/10.2305/IUCN.UK.2016 1.RLTS.T29742A22167140.en.
- Gurgul, A., Radko, A., & Słota, E. (2010). Characteristics of X- and Y-chromosome specific regions of the amelogenin gene and a PCR-based method for sex identification in red deer (*Cervus elaphus*). *Molecular Biology Reports*, 37(6), 2915–2918. https://doi.org/10.1007/s11033-009-9852-4
- Haddaway, N. R., Macura, B., Whaley, P., & Pullin, A. S. (2017). ROSES Flow diagram for Systematic Reviews. Version 1.0.
- Hagen, R., Haydn, A., & Suchant, R. (2018). Estimating red deer (*Cervus elaphus*) population size in the Southern Black Forest: the role of hunting in population control. *European Journal of Wildlife Research*, 64(4), 42. https://doi.org/10.1007/s10344-018-1204-z
- Hagen, R., & Suchant, R. (2020). Evidence of a spatial auto-correlation in the browsing level of four major European tree species. *Ecology and Evolution*, 10(15), 8517–8527. https://doi.org/10.1002/ece3.6577
- Hall Defrees, D., Averett, J. P., & Endress, B. A. (2021). Understory physical structures reduce browsing damage to palatable shrubs in a dry conifer forest, western North America. *Plant Ecology*, 222(7), 807–817. https://doi.org/10.1007/s11258-021-01144-2
- Hall Defrees, D., Averett, J. P., Wisdom, M. J., & Endress, B. A. (2020). Interactive effects of fuels reduction and large herbivores on shrub assemblages in dry conifer forests of the interior west, USA. Forest Ecology and Management, 463, 118031. https://doi.org/10.1016/j.foreco.2020.118031
- Hamasaki, S., Takatsuki, S., Kishimoto, M., Kitahara, M., & Jiang, Z. (2009). Seasonal and Sexual Variation in the Diet and Gastrointestinal Features of the Sika Deer in Western Japan: Implications for the Feeding Strategy. *Zoological Science*, *26*(10), 691–697. https://doi.org/10.2108/zsj.26.691
- Hanberry, B. & Faison, E. (2023) Re-framing deer herbivory as a natural disturbance regime with ecological and socioeconomic outcomes in the eastern United States. *Science of the Total Environment*, 868, 161669
- Hanley, M. E., Cook, B. I., & Fenner, M. (2018). Climate variation, reproductive frequency and acorn yield in English Oaks. *Journal of Plant Ecology*, *12*(3), 542–549. https://doi.org/10.1093/jpe/rty046
- Hannah, D. M., Brown, L. E. E. E., & Milner, A. M. (2007). Willow (*Salix* spp.) and aspen (*Populus tremula*) regrowth after felling by the Eurasian beaver (*Castor fiber*): implications for riparian woodland conservation in Scotland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 656(October 2006), 636–656. https://doi.org/10.1002/aqc

- Hansson-Forman, K., Sandström, C., & Ericsson, G. (2020). What influences hunting participation of potential new hunters? Qualitative insights from Sweden. *Wildlife Biology*, 2020(4). https://doi.org/10.2981/wlb.00721
- Harada, K., Ang Meng Ann, J., & Suzuki, M. (2020). Legacy effects of sika deer overpopulation on ground vegetation and soil physical properties. *Forest Ecology and Management*, 474(March), 118346. https://doi.org/10.1016/j.foreco.2020.118346
- Harmer, R., Kiewitt, A., Morgan, G., & Gill, R. (2010). Does the development of bramble (*Rubus fruticosus L. agg.*) facilitate the growth and establishment of tree seedlings in woodlands by reducing deer browsing damage? *Forestry*, 83(1), 93–102. https://doi.org/10.1093/forestry/cpp032
- Harris, R. B., & Duckworth, J. W. (2015). Hydropotes inermis. The IUCN Red List of Threatened Species 2015: e.T10329A22163569. https://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T10329A22163569.en. Downloaded on 01 May 2020. https://www.iucnredlist.org/species/10329/22163569
- Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2303–2312. https://doi.org/10.1098/rstb.2010.0087
- Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., Bayley, S. E., & Paquet, P. C. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, 86(8), 2135–2144. https://doi.org/10.1890/04-1269
- Hegland, S. J., & Rydgren, K. (2016). Eaten but not always beaten: Winners and losers along a red deer herbivory gradient in boreal forest. *Journal of Vegetation Science*, 27(1), 111–122. https://doi.org/10.1111/jvs.12339
- Hegland, S. J., Rydgren, K., & Seldal, T. (2005). The response of Vaccinium myrtillus to variations in grazing intensity in a Scandinavian pine forest on the island of Svanøy. *Canadian Journal of Botany*, 83(12), 1638–1644. https://doi.org/10.1139/b05-132
- Hegland, S. J., Seldal, T., Lilleeng, M. S., & Rydgren, K. (2016). Can browsing by deer in winter induce defence responses in bilberry (*Vaccinium myrtillus*)? *Ecological Research*, 31(3), 441–448. https://doi.org/10.1007/s11284-016-1351-1
- Heinen, J. T., & Castillo, B. (2019). Browse-Mediated Succession by Deer and Elk 40 y after a Clearcut in Northern Lower Michigan. *American Midland Naturalist*, 181(1), 81–91. https://doi.org/10.1674/0003-0031-181.1.81
- Heinen, J. T., & Currey, R. C. D. (2000). A 22-Year Study on the Effects of Mammalian Browsing on Forest Succession Following a Clearcut in Northern Lower Michigan. *The American Midland Naturalist*, 144(2), 243–252. https://doi.org/10.1674/0003-0031(2000)144[0243:aysote]2.0.co;2

- Heinze, E., Boch, S., Fischer, M., Hessenmöller, D., Klenk, B., Müller, J., Prati, D., Schulze, E. D., Seele, C., Socher, S., & Halle, S. (2011). Habitat use of large ungulates in northeastern Germany in relation to forest management. *Forest Ecology and Management*, 261(2), 288–296. https://doi.org/10.1016/j.foreco.2010.10.022
- Hemami, M. R. (2003). *The ecology of roe deer (Capreolus capreolus) and muntjac (Muntiacus reevesi) in a forested landscape in eastern England.* [PhD Thesis]. University of East Anglia.
- Herrera, J. (1995). Acorn predation and seedling production in a low-density population of cork oak (*Quercus suber L.*). Forest Ecology and Management, 76(1–3), 197–201. https://doi.org/10.1016/0378-1127(95)03566-S
- Herrero, A., Almaraz, P., Zamora, R., Castro, J., & Hódar, J. A. (2016). From the individual to the landscape and back: Time-varying effects of climate and herbivory on tree sapling growth at distribution limits. *Journal of Ecology*, *104*(2), 430–442. https://doi.org/10.1111/1365-2745.12527
- Hessl, A. E., & Graumlich, L. J. (2002). Interactive effects of human activities, herbivory and fire on quaking aspen (Populus tremuloides) age structures in western Wyoming. *Journal of Biogeography*, 29(7), 889–902. https://doi.org/10.1046/j.1365-2699.2002.00703.x
- Hester, A. J., Gordon, I. J., Baillie, G. J., & Tappin, E. (1999). Foraging behaviour of sheep and red deer within natural heather/grass mosaics. *Journal of Applied Ecology*, 36(1), 133–146. https://doi.org/10.1046/j.1365-2664.1999.00387.x
- Hester, A. J., Mitchell, F. J. G., & Kirby, K. J. (1996). Effects of season and intensity of sheep grazing on tree regeneration in a British upland woodland. *Forest Ecology and Management*, 88(1–2), 99–106. https://doi.org/10.1016/S0378-1127(96)03815-7
- Heuze, P., Schnitzler, A., & Klein, F. (2005). Consequences of increased deer browsing winter on silver fir and spruce regeneration in the Southern Vosges mountains: Implications for forest management. *Annals of Forest Science*, 62(4), 313–323. https://doi.org/DOI: 10.1051/forest:2005009
- Hewison, A. J. M., Joachim, J., Vincent, J. P., Angibault, J. M., Cargnelutti, B., & Cibien, C. (2001). The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. *Canadian Journal of Zoology*, 79(4), 679–689. https://doi.org/10.1139/cjz-79-4-679
- Hibert, F., Taberlet, P., Chave, J., Scotti-Saintagne, C., Sabatier, D., & Richard-Hansen, C. (2013). Unveiling the Diet of Elusive Rainforest Herbivores in Next Generation Sequencing Era? The Tapir as a Case Study. *PLoS ONE*, 8(4), e60799. https://doi.org/10.1371/journal.pone.0060799
- Hill, R. A., & Broughton, R. K. (2009). Mapping the understorey of deciduous woodland from leaf-on and leaf-off airborne LiDAR data: A case study in lowland Britain. *ISPRS Journal of Photogrammetry and Remote Sensing*, 64(2), 223–233. https://doi.org/10.1016/j.isprsjprs.2008.12.004

- Hobbs, N. T. (1996). Modification of Ecosystems by Ungulates. *The Journal of Wildlife Management*, 60(4), 695–713. https://doi.org/10.2307/3802368
- Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, 78, 443–457. https://link.springer.com/content/pdf/10.1007/BF00378733.pdf
- Hofmeester, T. R., Cromsigt, J. P. G. M., Odden, J., Andrén, H., Kindberg, J., & Linnell, J. D. C. (2019). Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution*, 9(4), 2320–2336. https://doi.org/10.1002/ece3.4878
- Hofmeester, T. R., Rowcliffe, J. M., & Jansen, P. A. (2017). A simple method for estimating the effective detection distance of camera traps. *Remote Sensing in Ecology and Conservation*, 3(2), 81–89. https://doi.org/10.1002/rse2.25
- Hofmeester, T. R., Thorsen, N. H., Cromsigt, J. P. G. M., Kindberg, J., Andrén, H., Linnell, J. D. C., & Odden, J. (2021). Effects of camera-trap placement and number on detection of members of a mammalian assemblage. *Ecosphere*, 12(7). https://doi.org/10.1002/ecs2.3662
- Holík, J., Janík, D., Hort, L., & Adam, D. (2021). Neighbourhood effects modify deer herbivory on tree seedlings. *European Journal of Forest Research*, 140(2), 403–417. https://doi.org/10.1007/s10342-020-01339-8
- Hollingsworth, P. M. (2011). Refining the DNA barcode for land plants. *Proceedings of the National Academy of Sciences*, *108*(49), 19451–19452. https://doi.org/10.1073/pnas.1116812108
- Holloway, C. W. (1967). The effect of red deer and other animals on naturally regenerated Scots pine. [PhD Thesis]. University of Aberdeen.
- Holt, C. A., Fuller, R. J., & Dolman, P. M. (2011). Breeding and post-breeding responses of woodland birds to modification of habitat structure by deer. *Biological Conservation*, 144(9), 2151–2162. https://doi.org/10.1016/j.biocon.2011.05.004
- Hood, R. E., & Inglis, J. M. (1974). Behavioral Responses of White-Tailed Deer to Intensive Ranching Operations. *The Journal of Wildlife Management*, *38*(3), 488–498. https://about.jstor.org/terms
- Hothorn, T., & Müller, J. (2010). Large-scale reduction of ungulate browsing by managed sport hunting. *Forest Ecology and Management*, 260(9), 1416–1423. https://doi.org/10.1016/j.foreco.2010.07.019
- Hothorn, T., Müller, J., Held, L., Möst, L., & Mysterud, A. (2015). Temporal patterns of deer–vehicle collisions consistent with deer activity pattern and density increase but not general accident risk. *Accident Analysis & Prevention*, 81, 143–152. https://doi.org/10.1016/J.AAP.2015.04.037

- Huffman, D. W., & Moore, M. M. (2003). Ungulate herbivory on buckbrush in an Arizona ponderosa pine forest. *Journal of Range Management*, 56(4), 358–363. https://doi.org/10.2307/4004039
- Huffman, D. W., & Moore, M. M. (2004). Responses of *Fendler ceanothus* to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest. *Forest Ecology and Management*, 198(1–3), 105–115. https://doi.org/10.1016/j.foreco.2004.03.040
- Hull, I. T., & Shipley, L. A. (2019). Testing the Ability of Airborne LiDAR to Measure Forage Resources for Wild Ungulates in Conifer Forests. *Journal of Forestry*, 117(5), 492–503. https://doi.org/10.1093/jofore/fvz040
- Hundley, L. R. (1959) Available Nutrients in Selected Deer-Browse Species Growing on Different Soils. *The Journal of Wildlife Management*, 23(1), 81-90.
- Husek, J., Boudreau, M. R., & Panek, M. (2021). Hunter estimates of game density as a simple and efficient source of information for population monitoring: A comparison to targeted survey methods. *PLoS ONE*, 16(8 August). https://doi.org/10.1371/journal.pone.0256580
- Husheer, S. W. (2007). Introduced red deer reduce tree regeneration in Pureora forest, central North Island, New Zealand. *New Zealand Journal of Ecology*, *31*(1), 79–87.
- Husheer, S. W., Coomes, D. A., & Robertson, A. W. (2003). Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. *Forest Ecology and Management*, 181(1–2), 99–117. https://doi.org/10.1016/S0378-1127(03)00120-8
- Husheer, S. W., & Frampton, C. M. (2005). Fallow deer impacts on Wakatipu beech forest. *New Zealand Journal of Ecology*, 29(1), 83–94.
- Husheer, S. W., & Robertson, A. W. (2005). High-intensity deer culling increases growth of mountain beech seedlings in New Zealand. *Wildlife Research*, 32(4), 273–280. https://doi.org/10.1071/WR04006
- Iacolina, L., Corlatti, L., Buzan, E., Safner, T., & Šprem, N. (2019). Hybridisation in European ungulates: an overview of the current status, causes, and consequences. *Mammal Review*, 49(1), 45– 59. https://doi.org/10.1111/mam.12140
- Iacolina, L., Lukassen, M. B., Fløjgaard, C., Buttenschøn, R., Nielsen, J. L., & Pertoldi, C. (2020). eDNA and metabarcoding for rewilding projects monitoring, a dietary approach. *Mammalian Biology*, 100(4), 411–418. https://doi.org/10.1007/s42991-020-00032-y
- Iida, T., Soga, M., Hiura, T., & Koike, S. (2016). Life history traits predict insect species responses to large herbivore overabundance: a multitaxonomic approach. *Journal of Insect Conservation*, 20(2), 295–304. https://doi.org/10.1007/s10841-016-9866-x

- Iida, T., Soga, M., & Koike, S. (2018). Large herbivores affect forest ecosystem functions by altering the structure of dung beetle communities. *Acta Oecologica*, 88, 65–70. https://doi.org/10.1016/j.actao.2018.03.003
- Iijima, H. (2017). The Effects of Landscape Components, Wildlife Behavior and Hunting Methods on Hunter Effort and Hunting Efficiency of Sika Deer. Wildlife Biology, 2017(1), wlb.00329. https://doi.org/10.2981/wlb.00329
- Iijima, H., & Iijima, H. (2018). Seasonal Change of Deer Occurrence and Damage of Plant Biomass in the Mosaic Landscape of Artificial Grasslands and Forests. *Mammal Study*, 43(2), 1–7. https://doi.org/10.3106/ms2017-0087
- Iijima, H., & Nagaike, T. (2015). Appropriate vegetation indices for measuring the impacts of deer on forest ecosystems. *Ecological Indicators*, 48, 457–463. https://doi.org/10.1016/j.ecolind.2014.09.009
- Ikeda, T., Takahashi, H., Igota, H., Matsuura, Y., Azumaya, M., Yoshida, T., & Kaji, K. (2019). Effects of culling intensity on diel and seasonal activity patterns of sika deer (Cervus nippon). *Scientific Reports*, 9(1), 1–8. https://doi.org/10.1038/s41598-019-53727-9
- Inagaki, A., Allen, M. L., Naganuma, T., & Koike, S. (2022). Vertebrate Scavenging on Sika Deer Carcasses and Its Effects on Ecological Processes. In Sika Deer: Life History Plasticity and Management (pp. 375–385). Springer, Singapore. https://doi.org/10.1007/978-981-16-9554-4_21
- Irby, L. R., Norland, J. E., Westfall, J. A., & Sullivan, M. A. (2002). Evaluation of a forage allocation model for Theodore Roosevelt National Park. *Journal of Environmental Management*, 64(2), 153– 169. https://doi.org/10.1006/jema.2001.0514
- Isaac, L. A., & Dimock, E. J. (1958). *Silvical Characteristics of Douglas-fir (var. Menziesii)*. Pacific Northwest Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service.
- Ismaili, B., Diouri, M., & Ouijja, A. (2018). Getting the dietary knowledge to restore a missing species: seasonal diet of Atlas deer *Cervus elaphus barbarus* in Tazekka National Park, Morocco. *Wildlife Biology*, 2018(1), wlb.00387. https://doi.org/10.2981/wlb.00387
- Itô, H., & Hino, T. (2004). Effects of deer, mice and dwarf bamboo on the emergence, survival and growth of *Abies homolepis* (Piceaceae) seedlings. *Ecological Research*, 19(2), 217–223. https://doi.org/10.1111/j.1440-1703.2004.00626.x
- Itô, H., & Hino, T. (2005). How do deer affect tree seedlings on a dwarf bamboo-dominated forest floor? *Ecological Research*, 20(2), 121–128. https://doi.org/10.1007/s11284-004-0023-8

- Itô, H., & Hino, T. (2008). Effects of deer and mice on seedling survival in a temperate mixed forest of Japan. *Forest Ecology and Management*, 256(1–2), 129–135. https://doi.org/10.1016/j.foreco.2008.04.016
- Jackson, J. (1977). The annual diet of the Fallow deer (*Dama dama*) in the New Forest, Hampshire, as determined by rumen content analysis. *Journal of Zoology*, *181*(4), 465–473. https://doi.org/10.1111/j.1469-7998.1977.tb03257.x
- Jackson, J. (1980). The annual diet of the Roe deer (*Capreolus capreolus*) in the New Forest, Hampshire, as determined by rumen content analysis. *Journal of Zoology*, 192(1), 71–83. https://doi.org/10.1111/j.1469-7998.1980.tb04220.x
- Jarnemo, A., Widén, A., Månsson, J., & Felton, A. M. (2022). The proximity of rapeseed fields influences levels of forest damage by red deer. *Ecological Solutions and Evidence*, *3*(2). https://doi.org/10.1002/2688-8319.12156
- Jayakody, S., Sibbald, A. M., Gordon, I. J., & Lambin, X. (2008). Red deer (*Cervus elaphus*) vigilance behaviour differs with habitat and type of human disturbance. WILDLIFE BIOLOGY-1, 14(1), 81– 91. https://doi.org/10.2981/0909-6396(2008)14[81:RDCEVB]2.0.CO;2
- Jayakody, S., Sibbald, A. M., Mayes, R. W., Hooper, R. J., Gordon, I. J., & Lambin, X. (2011). Effects of human disturbance on the diet composition of wild red deer (*Cervus elaphus*). *European Journal of Wildlife Research*, 57(4), 939–948. https://doi.org/10.1007/s10344-011-0508-z
- Jensen, A. M., Götmark, F., & Löf, M. (2012). Shrubs protect oak seedlings against ungulate browsing in temperate broadleaved forests of conservation interest: A field experiment. *Forest Ecology and Management*, 266, 187–193. https://doi.org/10.1016/j.foreco.2011.11.022
- Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., & Luskin, M. S. (2018). Global signal of top-down control of terrestrial plant communities by herbivores. *Proceedings of the National Academy of Sciences*, 115(24), 6237–6242. https://doi.org/10.1073/pnas.1707984115
- Jiang, Z. G., Ma, Y., Wu, Y., Wang, Y. X., Zhou, K. Y., Liu, S. Y., & Feng, Z. J. (2015). *China's Mammal Diversity and Geographic Distribution.*
- Jobe, J. G. D., & Gedan, K. (2021). Species-specific responses of a marsh-forest ecotone plant community responding to climate change. *Ecology*, *102*(4), 1–11. https://doi.org/10.1002/ecy.3296
- Johnson, C. J., Parker, K. L., & Heard, D. C. (2001). Foraging across a variable landscape: Behavioral decisions made by woodland caribou at multiple spatial scales. *Oecologia*, 127(4), 590–602. https://doi.org/10.1007/s004420000573

- Johnson, C. N., Prior, L. D., Archibald, S., Poulos, H. M., Barton, A. M., Williamson, G. J., & Bowman, D. M. J. S. (2018). Can trophic rewilding reduce the impact of fire in a more flammable world? In *Philosophical Transactions of the Royal Society B: Biological Sciences* (Vol. 373, Issue 1761). https://doi.org/10.1098/rstb.2017.0443
- Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, *61*(1), 65–71. https://doi.org/10.2307/1937156
- Johnston, D. B., Cooper, D. J., & Hobbs, N. T. (2007). Elk browsing increases aboveground growth of water-stressed willows by modifying plant architecture. *Oecologia*, 154(3), 467–478. https://doi.org/10.1007/s00442-007-0854-4
- Jones, L., Lowe, A., Ford, C. R., Christie, L., Creer, S., & de Vere, N. (2022). Temporal Patterns of Honeybee Foraging in a Diverse Floral Landscape Revealed Using Pollen DNA Metabarcoding of Honey. *Integrative and Comparative Biology*, 62(2), 199–210. https://doi.org/10.1093/icb/icac029
- Jones, L., Twyford, A. D., Ford, C. R., Rich, T. C. G., Davies, H., Forrest, L. L., Hart, M. L., McHaffie, H., Brown, M. R., Hollingsworth, P. M., & de Vere, N. (2021). Barcode UK: A complete DNA barcoding resource for the flowering plants and conifers of the United Kingdom. *Molecular Ecology Resources*, 21, 2050–2062.
- Joys, A. C., Fuller, R. J., & Dolman, P. M. (2004). Influences of deer browsing, coppice history, and standard trees on the growth and development of vegetation structure in coppiced woods in lowland England. *Forest Ecology and Management*, 202(1–3), 23–37. https://doi.org/10.1016/j.foreco.2004.06.035
- Kalb, D. M., Bowman, J. L., & DeYoung, R. W. (2018). Dietary resource use and competition between white-tailed deer and introduced sika deer. *Wildlife Research*, 45(5), 457. https://doi.org/10.1071/wr17125
- Kalisz, S., Spigler, R. B., & Horvitz, C. C. (2014). In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. *PNAS*, 111(12), 4501–4506. https://doi.org/10.5061/dryad.bk272
- Kamler, J., & Homolka, M. (2011). Needles in faeces: An index of quality of wild ungulate winter diet. *Folia Zoologica*, *60*(1), 63–69. https://doi.org/10.25225/fozo.v60.i1.a10.2011
- Kamler, J., Homolka, M., Barančeková, M., & Krojerová-Prokešová, J. (2010). Reduction of herbivore density as a tool for reduction of herbivore browsing on palatable tree species. *European Journal of Forest Research*, 129(2), 155–162. https://doi.org/10.1007/s10342-009-0309-z
- Kämmerle, J.-L., Brieger, F., Kröschel, M., Hagen, R., Storch, I., & Suchant, R. (2017). Temporal patterns in road crossing behaviour in roe deer (*Capreolus capreolus*) at sites with wildlife warning reflectors. *PLOS ONE*, 12(9), e0184761. https://doi.org/10.1371/journal.pone.0184761

- Karimi, S., Hemami, M. R., Tarkesh Esfahani, M., Akhani, H., & Baltzinger, C. (2018). Complementary endozoochorous seed dispersal by large mammals in the Golestan National Park, Iran. *Seed Science Research*, 28(4), 294–302. https://doi.org/10.1017/S0960258518000351
- Kartzinel, T. R., Chen, P. A., Coverdale, T. C., Erickson, D. L., John Kress, W., Kuzmina, M. L., Rubenstein, D. I., Wang, W., & Pringle, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. 112(26), 8019–8024. https://doi.org/10.5061/dryad.2fg10
- Katagiri, N., & Hijii, N. (2015). Effects of sika deer browsing on the arthropod communities on understory vegetation in a thinned Japanese cypress plantation. *Journal of Forest Research*, 20(3), 347–356. https://doi.org/10.1007/s10310-015-0486-1
- Katagiri, N., & Hijii, N. (2017). Effects of sika deer browsing on soil mesofauna in a thinned Japanese cypress plantation. *Journal of Forest Research*, 22(3), 169–176. https://doi.org/10.1080/13416979.2017.1317228
- Kay, C. E. (1997). The condition and trend of aspen, *Populus tremuloides*, in Kootenay and Yoho National Parks: Implications for ecological integrity. *Canadian Field-Naturalist*, *111*(4), 607–616.
- Kay, C. E. (2001). Long-Term Aspen Exclosures in the Yellowstone Ecosystem. USDA Forest Service Proceedings, 18, 225–240.
- Kay, C. E., & Bartos, D. L. (2000). Ungulate herbivory on Utah aspen: Assessment of long-term exclosures. *Journal of Range Management*, 53(2), 145–153. https://doi.org/10.2307/4003274
- Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478
- Keesing, F., & Young, T. P. (2014). Cascading Consequences of the Loss of Large Mammals in an African Savanna. *BioScience*, *64*(6), 487–495. https://doi.org/10.1093/biosci/biu059
- Kelly, D. L. (2002). The regeneration of *Quercus petraea* (sessile oak) in southwest Ireland: A 25-year experimental study. *Forest Ecology and Management*, *166*(1–3), 207–226. https://doi.org/10.1016/S0378-1127(01)00670-3
- Kerridge, F. J., & Bullock, D. J. (1991). Diet and dietary quality of red deer and fallow deer in late summer. *Journal of Zoology*, 224(2), 333–337. https://doi.org/10.1111/j.1469-7998.1991.tb04812.x
- Khadka, K. K., & James, D. A. (2016). Habitat selection by endangered Himalayan musk deer (*Moschus chrysogaster*) and impacts of livestock grazing in Nepal Himalaya: Implications for conservation. *Journal for Nature Conservation*, 31, 38–42. https://doi.org/10.1016/j.jnc.2016.03.002

- Khanam, S., Howitt, R., Mushtaq, M., & Russell, J. C. (2016). Diet analysis of small mammal pests: A comparison of molecular and microhistological methods. *Integrative Zoology*, 11(2), 98–110. https://doi.org/10.1111/1749-4877.12172
- Kienast, F., Fritschi, J., Bissegger, M., & Abderhalden, W. (1999). Modelling successional patterns of high-elevation forests under changing herbivore pressure - Responses at the landscape level. *Forest Ecology and Management*, 120(1–3), 35–46. https://doi.org/10.1016/S0378-1127(98)00541-6
- Kiffner, C., Rößiger, E., Trisl, O., Schulz, R., & Rühe, F. (2008). Probability of recent bark stripping damage by red deer (*Cervus elaphus*) on Norway spruce (*Picea abies*) in a low mountain range in Germany - A preliminary analysis. *Silva Fennica*, 42(1), 125–134. https://doi.org/10.14214/sf.269
- Kilpatrick, S., Clause, D., & Scott, D. (2003). Aspen Response to Prescribed Fire, Mechanical Treatments, and Ungulate Herbivory. *USDA Forest Service Proceedings*, *29*, 93–102.
- Kim, J., Joo, S., & Park, S. (2021). Diet composition of Korean water deer (*Hydropotes inermis argyropus*) from the Han River Estuary Wetland in Korea using fecal DNA. *Mammalia*, 85(6), 487–493. https://doi.org/10.1515/mammalia-2021-0010
- Kimble, D. S., Tyers, D. B., Robison-Cox, J., & Sowell, B. F. (2011). Aspen recovery since wolf reintroduction on the Northern Yellowstone winter range. *Rangeland Ecology and Management*, 64(2), 119–130. https://doi.org/10.2111/REM-D-10-00018.1
- Kingery, J. L., & Graham, R. T. (1991). The effect of cattle grazing on ponderosa pine regeneration. *Forestry Chronicle*, 67(3), 245–248. https://doi.org/10.5558/tfc67245-3
- Kjellander, P., Svartholm, I., Bergvall, U. A., & Jarnemo, A. (2012). Habitat use, bed-site selection and mortality rate in neonate fallow deer *Dama dama*. *Wildlife Biology*, 18(3), 280–291. https://doi.org/10.2981/10-093
- Kjøstvedt, J. H., Mysterud, A., & Østbye, E. (2018). Roe deer *Capreolus capreolus* use of agricultural crops during winter in the Lier valley, Norway. *Wildlife Biology*, *4*(1), 23–31. https://doi.org/10.2981/wlb.1998.012
- Klopcic, M., Jerina, K., & Boncina, A. (2010). Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: Are red deer an important factor? *European Journal of Forest Research*, 129(3), 277–288. https://doi.org/10.1007/s10342-009-0325-z
- Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C., & Towne, E. G. (1999). The Keystone Role of Bison in North American Tallgrass Prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience*, 49(1), 39–50. https://doi.org/10.1525/bisi.1999.49.1.39

- Koda, R., & Fujita, N. (2011). Is deer herbivory directly proportional to deer population density? Comparison of deer feeding frequencies among six forests with different deer density. *Forest Ecology and Management*, 262(3), 432–439. https://doi.org/10.1016/j.foreco.2011.04.009
- Koda, R., Noma, N., Tsujino, R., Umeki, K., & Fujita, N. (2008). Effects of sika deer (*Cervus nippon yakushimae*) population growth on saplings in an evergreen broad-leaved forest. *Forest Ecology and Management*, 256(3), 431–437. https://doi.org/10.1016/j.foreco.2008.04.044
- Koerner, S. E., Smith, M. D., Burkepile, D. E., Hanan, N. P., Avolio, M. L., Collins, S. L., Knapp, A. K., Lemoine, N. P., Forrestel, E. J., Eby, S., Thompson, D. I., Aguado-Santacruz, G. A., Anderson, J. P., Anderson, T. M., Angassa, A., Bagchi, S., Bakker, E. S., Bastin, G., Baur, L. E., ... Zelikova, T. J. (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology and Evolution*, 2(12), 1925–1932. https://doi.org/10.1038/s41559-018-0696-y
- Koike, S., Soga, M., Nemoto, Y., & Kozakai, C. (2014). How are dung beetle species affected by deer population increases in a cool temperate forest ecosystem? *Journal of Zoology*, 293(4), 227–233. https://doi.org/10.1111/jzo.12138
- Kowalczyk, R., Kamiński, T., & Borowik, T. (2021). Do large herbivores maintain open habitats in temperate forests? Forest Ecology and Management, 494. https://doi.org/10.1016/j.foreco.2021.119310
- Kowalczyk, R., Wójcik, J. M., Taberlet, P., Kamiński, T., Miquel, C., Valentini, A., Craine, J. M., & Coissac, E. (2019). Foraging plasticity allows a large herbivore to persist in a sheltering forest habitat: DNA metabarcoding diet analysis of the European bison. *Forest Ecology and Management*, 449. https://doi.org/10.1016/j.foreco.2019.117474
- Krishna, Y. C., Kumar, A., & Isvaran, K. (2016). Wild ungulate decision-making and the role of tiny refuges in human-dominated landscapes. *PLoS ONE*, 11(3). https://doi.org/10.1371/journal.pone.0151748
- Kristensen, J. A., Svenning, J. C., Georgiou, K., & Malhi, Y. (2022). Can large herbivores enhance ecosystem carbon persistence? *Trends in Ecology and Evolution*, *37*(2), 117–128. https://doi.org/10.1016/j.tree.2021.09.006
- Kuijper, D. P. J. (2011). Lack of natural control mechanisms increases wildlife-forestry conflict in managed temperate European forest systems. *European Journal of Forest Research*, 130(6), 895– 909. https://doi.org/10.1007/s10342-011-0523-3
- Kuijper, D. P. J., de Kleine, C., Churski, M., van Hooft, P., Bubnicki, J., & Jedrzejewska, B. (2013). Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Bialowieża Primeval Forest, Poland. *Ecography*, 36(12), 1263–1275. https://doi.org/10.1111/j.1600-0587.2013.00266.x

- Kuijper, D. P. J., Jedrzejewska, B., Brzeziecki, B., Churski, M., Jedrzejewski, W., & Zybura, H. (2010). Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland. *Journal of Vegetation Science*, 21(6), 1082–1098. https://doi.org/10.1111/J.1654-1103.2010.01217.X
- Kuijper, D. P. J., Verwijmeren, M., Churski, M., Zbyryt, A., Schmidt, K., Jedrzejewska, B., & Smit, C. (2014). What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS ONE*, 9(1), 1–12. https://doi.org/10.1371/journal.pone.0084607
- Kuiters, A. T., & Slim, P. A. (2002). Regeneration of mixed deciduous forest in a Dutch forestheathland, following a reduction of ungulate densities. *Biological Conservation*, 105(1), 65–74. https://doi.org/10.1016/S0006-3207(01)00204-X
- Kumar, S., Takeda, A., & Shibata, E. (2006). Effects of 13-year fencing on browsing by sika deer on seedlings on Mt. Ohdaigahara, central Japan. *Journal of Forest Research*, 11(5), 337–342. https://doi.org/10.1007/s10310-006-0216-9
- Kupferschmid, A. D., Wasem, U., & Bugmann, H. (2015). Browsing regime and growth response of Abies alba saplings planted along light gradients. *European Journal of Forest Research*, 134(1), 75–87. https://doi.org/10.1007/s10342-014-0834-2
- Kurzel, B. P., Veblen, T. T., & Kulakowski, D. (2007). A typology of stand structure and dynamics of Quaking aspen in northwestern Colorado. *Forest Ecology and Management*, 252(1–3), 176–190. https://doi.org/10.1016/j.foreco.2007.06.027
- Langbein, J., & Putman, R. J. (1991). Behavioural Responses of Park Red and Fallow Deer to Disturbance and Effects on Population Performance. *Animal Welfare*, *1*(1), 19–38.
- Langbein, J., & Thirgood, S. J. (1989). Variation in Mating Systems of Fallow Deer (*Dama dama*) in Relation to Ecology. *Ethology*, 83(3), 195–214. https://doi.org/10.1111/j.1439-0310.1989.tb00529.x
- Larsen, E. J., & Ripple, W. J. (2003). Aspen age structure in the northern Yellowstone ecosystem: USA. *Forest Ecology and Management*, *179*(1–3), 469–482. https://doi.org/10.1016/S0378-1127(02)00532-7
- Larsen, E. J., & Ripple, W. J. (2011). Aspen Overstory Recruitment in Northern Yellowstone National Park During the Last 200 Years. USDA Forest Service Proceedings RMRS-P-18. www.cof.orst.edu/cof/fr/research/aspen/.
- Latham, A. D. M., Herries, D., & Latham, C. M. (2015). Seasonal patterns of resource selection by introduced sika deer (*Cervus nippon*) in Kaweka Forest Park Recreational Hunting Area, New Zealand. *New Zealand Journal of Ecology*, *39*(2), 291–302. http://www.newzealandecology.org/nzje/

- Latham, J. (1999). Interspecific interactions of ungulates in European forests: An overview. *Forest Ecology and Management*, 120(1–3), 13–21. https://doi.org/10.1016/S0378-1127(98)00539-8
- Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: re-establishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, 79, 1401–1409. https://doi.org/10.1139/z01-094
- Laurent, L., Mårell, A., Balandier, P., Holveck, H., & Saïd, S. (2017). Understory vegetation dynamics and tree regeneration as affected by deer herbivory in temperate hardwood forests. *IForest*, 10(5), 837–844. https://doi.org/10.3832/ifor2186-010
- Lecigne, B., & Eitel, J. (2022). *viewshed3d: Compute Viewshed in 3D Point Clouds of Ecosystems*. https://rdrr.io/cran/viewshed3d/
- Lecigne, B., Eitel, J. U. H., & Rachlow, J. L. (2020). viewshed3d: An r package for quantifying 3D visibility using terrestrial lidar data. *Methods in Ecology and Evolution*, *11*(6), 733–738. https://doi.org/10.1111/2041-210X.13385
- Lecomte, X., Caldeira, M. C., Catry, F. X., Fernandes, P. M., Jackson, R. B., & Bugalho, M. N. (2019). Ungulates mediate trade-offs between carbon storage and wildfire hazard in Mediterranean oak woodlands. *Journal of Applied Ecology*, 56(3), 699–710. https://doi.org/10.1111/1365-2664.13310
- Leonard, J. L., Perkins, L. B., Lammers, D. J., & Jenks, J. A. (2017). Are Bison Intermediate Feeders? Unveiling Summer Diet Selection at the Northern Fringe of Historical Distribution. *Rangeland Ecology and Management*, 70(4), 405–410. https://doi.org/10.1016/j.rama.2017.01.005
- Leonardsson, J., Löf, M., & Götmark, F. (2015). Exclosures can favour natural regeneration of oak after conservation-oriented thinning in mixed forests in Sweden: A 10-year study. *Forest Ecology and Management*, 354, 1–9. https://doi.org/10.1016/j.foreco.2015.07.004
- Leopold, C. R., & Hess, S. C. (2017). Conversion of native terrestrial ecosystems in Hawai'i to novel grazing systems: a review. *Biological Invasions*, 19(1), 161–177. https://doi.org/10.1007/s10530-016-1270-7
- Lewis, J. S., Logan, K. A., Alldredge, M. W., Bailey, L. L., Vandewoude, S., & Crooks, K. R. (2015). The effects of urbanization on population density, occupancy, and detection probability of wild felids. *Ecological Applications*, 25(7), 1880–1895. http://www.ncdc.noaa.gov/data-access/landbased-station-
- Lewis, J. S., Spaulding, S., Swanson, H., Keeley, W., Gramza, A. R., VandeWoude, S., & Crooks, K. R. (2021). Human activity influences wildlife populations and activity patterns: implications for spatial and temporal refuges. *Ecosphere*, 12(5). https://doi.org/10.1002/ecs2.3487

- Li, S., Hou, Z., Ge, J., & Wang, T. (2022). Assessing the effects of large herbivores on the threedimensional structure of temperate forests using terrestrial laser scanning. *Forest Ecology and Management*, 507(January), 119985. https://doi.org/10.1016/j.foreco.2021.119985
- Li, X. Y., Bleisch, W. v., Liu, X. W., Hu, W. Q., & Jiang, X. L. (2020). Human disturbance and prey occupancy as predictors of carnivore richness and biomass in a Himalayan hotspot. *Animal Conservation*, 1–9. https://doi.org/10.1111/acv.12600
- Li, Z., Strahler, A., Schaaf, C., Jupp, D., Schaefer, M., & Olofsson, P. (2018). Seasonal change of leaf and woody area profiles in a midlatitude deciduous forest canopy from classified dual-wavelength terrestrial lidar point clouds. *Agricultural and Forest Meteorology*, 262, 279–297. https://doi.org/10.1016/j.agrformet.2018.07.014
- Licoppe, A. M. (2006). The diurnal habitat used by red deer (*Cervus elaphus L.*) in the Haute Ardenne. *Eur J Wildl Res*, 52, 164–170. https://doi.org/10.1007/s10344-006-0027-5
- Lilleeng, M. S., Hegland, S. J., Rydgren, K., & Moe, S. R. (2016). Red deer mediate spatial and temporal plant heterogeneity in boreal forests. *Ecological Research*, 31(6), 777–784. https://doi.org/10.1007/s11284-016-1391-6
- Lilleeng, M. S., Rydgren, K., Halvorsen, R., Moe, S. R., & Hegland, S. J. (2018). Red deer structure the ground-dwelling beetle community in boreal forest. *Biodiversity and Conservation*, 27(10), 2507– 2525. https://doi.org/10.1007/s10531-018-1550-x
- Linnell, J. D. C., Cretois, B., Nilsen, E. B., Rolandsen, C. M., Solberg, E. J., Veiberg, V., Kaczensky, P., Van Moorter, B., Panzacchi, M., Rauset, G. R., & Kaltenborn, B. (2020). The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biological Conservation*, 244, 108500. https://doi.org/10.1016/j.biocon.2020.108500
- Little, A. R., Webb, S. L., Demarais, S., Gee, K. L., Riffell, S. K., & Gaskamp, J. A. (2016). Hunting intensity alters movement behaviour of white-tailed deer. *Basic and Applied Ecology*, 17(4), 360– 369. https://doi.org/10.1016/j.baae.2015.12.003
- Little, E. L. (1971). *Atlas of United States trees, vol. 1., Conifers and important hardwoods* (Vol. 1). U.S Department of Agriculture.
- Liu, X., Yang, Y. Y., Wang, X. M., Liu, Z. S., Wang, Z. H., & Ding, Y. Z. (2015). Sex identification based on AMEL gene PCR amplification from blue sheep (*Pseudois nayaur*) fecal DNA samples. *Genetics and Molecular Research*, 14(3), 9045–9052. https://doi.org/10.4238/2015.August.7.13
- Loarie, S. R., Tambling, C. J., & Asner, G. P. (2013). Lion hunting behaviour and vegetation structure in an African savanna. *Animal Behaviour*, 85(5), 899–906. https://doi.org/10.1016/j.anbehav.2013.01.018

- Lone, K., Loe, L. E., Gobakken, T., Linnell, J. D. C., Odden, J., Remmen, J., & Mysterud, A. (2014). Living and dying in a multi-predator landscape of fear: Roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos*, *123*(6), 641–651. https://doi.org/10.1111/j.1600-0706.2013.00938.x
- Lone, K., Loe, L. E., Meisingset, E. L., Stamnes, I., & Mysterud, A. (2015). An adaptive behavioural response to hunting: Surviving male red deer shift habitat at the onset of the hunting season. *Animal Behaviour*, 102, 127–138. https://doi.org/10.1016/j.anbehav.2015.01.012
- Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., Findholt, S. L., Dick, B. L., & Kie, J. G. (2016). Linking habitat selection to fitness-related traits in herbivores: the role of the energy landscape. *Oecologia*, 181(3), 709–720. https://doi.org/10.1007/s00442-016-3604-7
- Long, Z. T., Pendergast IV, T. H., & Carson, W. P. (2007). The impact of deer on relationships between tree growth and mortality in an old-growth beech-maple forest. *Forest Ecology and Management*, 252(1–3), 230–238. https://doi.org/10.1016/j.foreco.2007.06.034
- Lovari, S., Cuccus, P., Murgia, A., Murgia, C., Soi, F., & Plantamura, G. (2007). Space use, habitat selection and browsing effects of red deer in Sardinia. *Italian Journal of Zoology*, 74(2), 179–189. https://doi.org/10.1080/11250000701249777
- Lowe, A., Jones, L., Brennan, G., Creer, S., Christie, L., & de Vere, N. (2022). Temporal change in floral availability leads to periods of resource limitation and affects diet specificity in a generalist pollinator. *Molecular Ecology*. https://doi.org/10.1111/mec.16719
- Lyly, M., Klemola, T., Koivisto, E., Huitu, O., Oksanen, L., & Korpimäki, E. (2014). Varying impacts of cervid, hare and vole browsing on growth and survival of boreal tree seedlings. *Oecologia*, 174(1), 271–281. https://doi.org/10.1007/s00442-013-2761-1
- Maas-Hebner, K. G., Emmingham, W. H., Larson, D. J., & Chan, S. S. (2005). Establishment and growth of native hardwood and conifer seedlings underplanted in thinned Douglas-fir stands. *Forest Ecology and Management*, 208(1–3), 331–345. https://doi.org/10.1016/j.foreco.2005.01.013
- MacDougall, A. S. (2008). Herbivory, hunting, and long-term vegetation change in degraded savanna. *Biological Conservation*, 141(9), 2174–2183. https://doi.org/10.1016/j.biocon.2008.07.003
- Machar, I., Cermak, P., & Pechanec, V. (2018). Ungulate browsing limits bird diversity of the Central European hardwood floodplain forests. *Forests*, *9*(7), 1–14. https://doi.org/10.3390/f9070373

MacKenzie, D., & Hines, J. (2023). RPresence: R Interface for Program PRESENCE.

- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. H. (2017). Chapter 14 - Species Co-Occurrence. In *Occupancy Estimation and Modeling* (2nd ed., pp. 509– 556). Academic Press. https://doi.org/10.1016/C2012-0-01164-7
- Macmillan, D. C., & Phillip, S. (2008). Consumptive and non-consumptive values of wild mammals in Britain. *Mammal Review*, *38*(2–3), 189–204. https://doi.org/10.1111/j.1365-2907.2008.00124.x
- MacSween, J., Leroux, S. J., & Oakes, K. D. (2018). Cross-ecosystem effects of a large terrestrial herbivore on stream ecosystem functioning. *Oikos*. https://doi.org/10.1111/oik.05331
- Maguire, A. J., Eitel, J. U. H., Vierling, L. A., Johnson, D. M., Griffin, K. L., Boelman, N. T., Jensen, J. E., Greaves, H. E., & Meddens, A. J. H. (2019). Terrestrial lidar scanning reveals fine-scale linkages between microstructure and photosynthetic functioning of small-stature spruce trees at the forest-tundra ecotone. *Agricultural and Forest Meteorology*, 269–270(November 2018), 157–168. https://doi.org/10.1016/j.agrformet.2019.02.019
- Mahon, M. B., Campbell, K. U., & Crist, T. O. (2019). Experimental effects of white-tailed deer and an invasive shrub on forest ant communities. *Oecologia*, 191(3), 633–644. https://doi.org/10.1007/s00442-019-04516-8
- Malhi, Y., Jackson, T., Bentley, L. P., Lau, A., Shenkin, A., Herold, M., Calders, K., Bartholomeus, H., & Disney, M. I. (2018). New perspectives on the ecology of tree structure and tree communities through terrestrial laser scanning. *Interface Focus*, 8(2). https://doi.org/10.1098/rsfs.2017.0052
- Malo, J. E., Jiménez, B., & Suarez, F. (2000). Herbivore dunging and endozoochorous seed deposition in a Mediterranean dehesa. *Journal of Range Management*, 53(3), 322–328. https://doi.org/10.2307/4003440
- Maltoni, A., Mariotti, B., Tani, A., Martini, S., Jacobs, D. F., & Tognetti, R. (2019). Natural regeneration of Pinus pinaster facilitates *Quercus ilex* survival and growth under severe deer browsing pressure. *Forest Ecology and Management*, 432, 356–364. https://doi.org/10.1016/j.foreco.2018.09.045
- Mårell, A., Hamard, J. P., Pérot, T., Perret, S., & Korboulewsky, N. (2018). The effect of deer browsing and understory light availability on stump mortality and sprout growth capacity in sessile oak. *Forest Ecology and Management*, 430, 134–142. https://doi.org/10.1016/j.foreco.2018.08.015
- Marion, S., Demšar, U., Davies, A. L., Stephens, P. A., Irvine, R. J., & Long, J. A. (2021). Red deer exhibit spatial and temporal responses to hiking activity. *Wildlife Biology*, 2021(3). https://doi.org/10.2981/wlb.00853

- Marion, S., Demšar, U., Davies, A. L., Stephens, P. A., Irvine, R. J., & Long, J. A. (2022). Red deer behavioural response to hiking activity: a study using camera traps. *Journal of Zoology*, 317(4), 249–261. https://doi.org/10.1111/jzo.12976
- Mark, A. F., Baylis, G. T. S., & Dickinson, K. J. M. (1991). Monitoring the impacts of deer on vegetation condition of Secretary Island, Fiordland National Park, New Zealand: A clear case for deer control and ecological restoration. *Journal of the Royal Society of New Zealand*, 21(1), 43–54. https://doi.org/10.1080/03036758.1991.10416109
- Marozas, V., Baranauskaitė, J., & Pételis, K. (2011). The Fallow Deer Influence on Enclose Forest Vegetation. The Fifth International Scientific Conference: Rural Development, Proceedings II. Volume 5, Book 2, 82–85.
- Marozas, V., Petelis, K., Brazaitis, G., & Baranauskaite, J. (2009). Early changes of ground vegetation in fallow deer enclosure. *Baltic Forestry*, 15(2), 268–272.
- Martin, J., Chamaillé-jammes, S., Waller, D. M., Fonctionnelle, É., Montpellier, U. de, Paul, U., Montpellier, V., & Psl, E. (2020). Deer, wolves, and people: costs, benefits and challenges of living together. *Biological Reviews*, 4, 000–000. https://doi.org/10.1111/brv.12587
- Martin, J. L., Stockton, S. A., Allombert, S., & Gaston, A. J. (2010). Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: Lessons from a deer introduction. *Biological Invasions*, 12(2), 353–371. https://doi.org/10.1007/s10530-009-9628-8
- Martin, J. & Baltzinger, C. (2002). Interaction among deer browsing, hunting, and tree regeneration. *Canadian Journal of Forest Research, 32*, 1254-1264. https://doi.org/10.1139/X02-043
- Martin, M. (2011). Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet.Journal*, *17*(1), 10–11. https://doi.org/10.14806/ej.17.1.200
- Martin, T. E. (2015). Consequences of habitat change and resource selection specialization for population limitation in cavity-nesting birds. *Journal of Applied Ecology*, 52(2), 475–485. https://doi.org/10.1111/1365-2664.12375
- Martin, T. E., & Maron, J. L. (2012). Climate impacts on bird and plant communities from altered animal-plant interactions. *Nature Climate Change*, *2*(3), 195–200. https://doi.org/10.1038/nclimate1348

Martinez Arbizu, P. (2017). pairwiseAdonis: Pairwise Multilevel Comparison using Adonis.

Maschinski, J. (2001). Impacts of ungulate herbivores on a rare willow at the southern edge of its range. *Biological Conservation*, *101*(1), 119–130. https://doi.org/10.1016/S0006-3207(01)00029-5

- Massei, G., & Bowyer, R. T. (1999). Scent Marking in Fallow Deer: Effects of Lekking Behavior on Rubbing and Wallowing. *Journal of Mammalogy*, *80*(2), 633–638. https://doi.org/10.2307/1383307
- Mathisen, K. M., Wójcicki, A., & Borowski, Z. (2018). Effects of forest roads on oak trees via cervid habitat use and browsing. *Forest Ecology and Management*, 424, 378–386. https://doi.org/10.1016/j.foreco.2018.04.057
- Maublanc, M. L., Gerard, J. F., Picot, D., Goulard, M., Ballon, P., Hamard, J. P., & Bideau, É. (2021). Using Shrubs as Nurse-plants to Reduce Browsing and Rubbing Damage by Roe Deer: An Experimental Approach. *Journal of Sustainable Forestry*, 00(00), 1–14. https://doi.org/10.1080/10549811.2021.1980053
- Maxwell, J. D., Rhodes, A. C., & St. Clair, S. B. (2019). Human altered disturbance patterns and forest succession: impacts of competition and ungulate herbivory. *Oecologia*. https://doi.org/10.1007/s00442-019-04370-8
- McMurdie, P. J., & Holmes, S. (2013). phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. *PLoS ONE*, 8(4), e61217. http://dx.plos.org/10.1371/journal.pone.0061217
- McNaughton, S. J. (1984). Grazing Lawns: Animals in Herds, Plant Form, and Coevolution. *The American Naturalist*, 124(6), 863–886. https://about.jstor.org/terms
- McShea, W. J., Sukmasuang, R., Erickson, D. L., Herrmann, V., Ngoprasert, D., Bhumpakphan, N., & Davies, S. J. (2019). Metabarcoding reveals diet diversity in an ungulate community in Thailand. *Biotropica*, 51(6), 923–937. https://doi.org/10.1111/btp.12720
- Meier, M., Stöhr, D., Walde, J., & Tasser, E. (2017). Influence of ungulates on the vegetation composition and diversity of mixed deciduous and coniferous mountain forest in Austria. *European Journal of Wildlife Research*, 63(1). https://doi.org/10.1007/s10344-017-1087-4
- Meisingset, E. L., Gusevik, J., Skjørestad, A., Brekkum, Ø., Mysterud, A., & Rosell, F. (2022). Impacts of human disturbance on flight response and habitat use of red deer. *Ecosphere*, *13*(11). https://doi.org/10.1002/ecs2.4281
- Melin, M., Matala, J., Mehtätalo, L., Tiilikainen, R., Tikkanen, O. P., Maltamo, M., Pusenius, J., & Packalen, P. (2014). Moose (Alces alces) reacts to high summer temperatures by utilizing thermal shelters in boreal forests - an analysis based on airborne laser scanning of the canopy structure at moose locations. *Global Change Biology*, 20(4), 1115–1125. https://doi.org/10.1111/gcb.12405
- Melis, C., Buset, A., Aarrestad, P. A., Hanssen, O., Meisingset, E. L., Andersen, R., Moksnes, A., & Røskaft, E. (2006). Impact of red deer Cervus elaphus grazing on bilberry Vaccinium myrtillus and composition of ground beetle (Coleoptera, Carabidae) assemblage. *Biodiversity and Conservation*, 15(6), 2049–2059. https://doi.org/10.1007/s10531-005-2005-8

- Menezes, R. S. C., Elliott, E. T., Valentine, D. W., & Williams, S. A. (2001). Carbon and nitrogen dynamics in elk winter ranges. *Journal of Range Management*, 54(4), 400–408. https://doi.org/10.2307/4003110
- Menichetti, L., Touzot, L., Elofsson, K., Hyvönen, R., Kätterer, T., & Kjellander, P. (2019) Interactions between a population of fallow deer (Dama dama), humans and crops in a managed composite temperate landscape in southern Sweden: Conflict or opportunity? *PLoS ONE*, *14*(4), e0215594
- Millett, J., Hester, A. J., Millard, P., & McDonald, A. J. S. (2006). How do different competing species influence the response of *Betula pubescens Ehrh*. to browsing? *Basic and Applied Ecology*, 7(2), 123–132. https://doi.org/10.1016/j.baae.2005.05.004
- Milne-Rostkowska, F., Holeksa, J., Bogdziewicz, M., Piechnik, Ł., Seget, B., Kurek, P., Buda, J., & Żywiec, M. (2020). Where can palatable young trees escape herbivore pressure in a protected forest? *Forest Ecology and Management*, 472(May). https://doi.org/10.1016/j.foreco.2020.118221
- Minder, I. (2012). Local and seasonal variations of roe deer diet in relation to food resource availability in a Mediterranean environment. *European Journal of Wildlife Research*, 58(1), 215–225. https://doi.org/10.1007/s10344-011-0566-2
- Mitchell, B., Staines, B. W., & Welch, D. (1977). Ecology of Red Deer: A research review relevant to their management in Scotland Institute of Terrestrial Ecology Natural Environment Research Council. http://nora.nerc.ac.uk/id/eprint/5137/1/Ecology_Red_Deer_Scotland_.pdf
- Miyashita, T., Takada, M., & Shimazaki, A. (2004). Indirect effects of herbivory by deer reduce abundance and species richness of web spiders. *Ecoscience*, 11(1), 74–79. https://doi.org/10.1080/11956860.2004.11682811
- Moe, S. R., Gjørvad, I. R., Eldegard, K., & Hegland, S. J. (2018). Ungulate browsing affects subsequent insect feeding on a shared food plant, bilberry (*Vaccinium myrtillus*). *Basic and Applied Ecology*, 31, 44–51. https://doi.org/10.1016/j.baae.2018.05.015
- Mohr, D., Cohnstaedt, L. W., & Topp, W. (2005). Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. *Soil Biology and Biochemistry*, 37(4), 693–700. https://doi.org/10.1016/j.soilbio.2004.10.002
- Mohr, D., & Topp, W. (2005). Influence of deer exclusion on soil nutrients in oak forests of a central European low mountain range. *Land Degradation and Development*, 16(3), 303–309. https://doi.org/10.1002/ldr.654
- Mols, B., Lambers, E., Cromsigt, J. P. G. M., Kuijper, D. P. J., & Smit, C. (2022). Recreation and hunting differentially affect deer behaviour and sapling performance. *Oikos*, 2022(1), 1–13. https://doi.org/10.1111/oik.08448

- Montgomery, R. A., Roloff, G. J., & Millspaugh, J. J. (2012). Importance of visibility when evaluating animal response to roads. *Wildlife Biology*, *18*(4), 393–405. https://doi.org/10.2981/11-123
- Moore, N. P., Hart, J. D., & Langton, S. D. (1999). Factors influencing browsing by fallow deer *Dama dama* in young broad-leaved plantations. *Biological Conservation*, 87(2), 255–260. https://doi.org/10.1016/S0006-3207(98)00055-X
- Moore, O., & Crawley, M. J. (2014). The natural exclusion of red deer from large boulder grazing refugia and the consequences for saxicolous bryophyte and lichen ecology. *Biodiversity and Conservation*, 23(9), 2305–2319. https://doi.org/10.1007/s10531-014-0725-3
- Moorhouse-Gann, R. J., Dunn, J. C., de Vere, N., Goder, M., Cole, N., Hipperson, H., & Symondson, W. O. C. (2018). New universal ITS2 primers for high-resolution herbivory analyses using DNA metabarcoding in both tropical and temperate zones. *Scientific Reports*, 8(1), 8542. https://doi.org/10.1038/s41598-018-26648-2
- Moorhouse-Gann, R. J., Vaughan, I. P., Cole, N. C., Goder, M., Tatayah, V., Jones, C. G., Mike, D., Young, R. P., Bruford, M. W., Rivers, M. C., Hipperson, H., Russo, I. R. M., Stanton, D. W. G., & Symondson, W. O. C. (2022). Impacts of herbivory by ecological replacements on an island ecosystem. *Journal of Applied Ecology*, 59(9), 2245–2261. https://doi.org/10.1111/1365-2664.14096
- Morecroft, M. D., Taylor, M. E., Ellwood, S. A., & Quinn, S. A. (2001). Impacts of deer herbivory on ground vegetation at Wytham Woods, central England. *Forestry*, 74(3), 251–257. https://doi.org/10.1093/forestry/74.3.251
- Morellet, N., Gaillard, J. Hewison, A., Ballon, P., Boscardin, Y., Duncan, P., Klein, F., & Maillard, D. (2007) Indicators of ecological change: New tools for managing populations of large herbivores. *Journal of Applied ecology*, 44(3), 634-643
- Morellet, N., & Guibert, B. (1999). Spatial heterogeneity of winter forest resources used by deer. *Forest Ecology and Management, 123,* 11-20. https://doi.org/10.1016/S0378-1127(99)00007-9
- Morimoto, J., Sugiura, M., Morimoto, M., & Nakamura, F. (2021). Restoration of Natural Forests After Severe Wind Disturbance in a Cold, Snowy Region With a Deer Population: Implications From 15 Years of Field Experiments. *Frontiers in Forests and Global Change*, 4(July), 1–11. https://doi.org/10.3389/ffgc.2021.675475
- Morse, B. W., McElroy, M. L., & Miller, K. V. (2009). Seasonal Diets of an Introduced Population of Fallow Deer on Little St. Simons Island, Georgia. *Southeastern Naturalist*, 8(4), 571–586. https://doi.org/10.1656/058.008.0401

- Motta, R. (1996). Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. *Forest Ecology and Management*, 88(1–2), 93–98. https://doi.org/10.1016/S0378-1127(96)03814-5
- Motta, R. (2003). Ungulate impact on rowan (*Sorbus aucuparia L.*) and Norway spruce (*Picea abies L.*) Karst.) height structure in mountain forests in the eastern Italian Alps. *Forest Ecology and Management*, 181(1–2), 139–150. https://doi.org/10.1016/S0378-1127(03)00128-2
- Murray, B. D., Webster, C. R., & Bump, J. K. (2013). Broadening the ecological context of ungulateecosystem interactions: The importance of space, seasonality, and nitrogen. *Ecology*, 94(6), 1317– 1326. https://doi.org/10.1890/12-1582.1
- Mysterud, A., Lian, L.-B., & Hjermann, D. Ø. (2011). Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. *Canadian Journal of Zoology*, 77(9), 1486–1493. https://doi.org/10.1139/z99-118
- Mysterud, A., Meisingset, E. L., Veiberg, V., Langvatn, R., Solberg, E. J., Loe, L. E., & Stenseth, N. C. (2007). Monitoring population size of red deer *Cervus elaphus*: An evaluation of two types of census data from Norway. *Wildlife Biology*, 13(3), 285–298. https://doi.org/10.2981/0909-6396(2007)13[285:MPSORD]2.0.CO;2
- Mysterud, A., & Ostbye, E. (1999). Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildlife Society Bulletin*, 27(2), 385–394. https://doi.org/10.2307/3783905
- Mysterud, A., Pérez-Barbería, F. J., & Gordon, I. J. (2001). The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia*, *127*(1), 30–39. https://doi.org/10.1007/s004420000562
- Naaf, T., & Wulf, M. (2007). Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. *Forest Ecology and Management*, 244(1–3), 141–149. https://doi.org/10.1016/j.foreco.2007.04.020
- Nagaike, T. (2020). Effects of heavy, repeated bark stripping by *Cervus nippon* on survival of *Abies veitchii* in a subalpine coniferous forest in central Japan. *Journal of Forestry Research*, *31*(4), 1139–1145. https://doi.org/10.1007/s11676-019-00940-x
- Nakahama, N., Furuta, T., Ando, H., Setsuko, S., Takayanagi, A., & Isagi, Y. (2021). DNA metabarcoding revealed that sika deer foraging strategies vary with season in a forest with degraded understory vegetation. *Forest Ecology and Management*, 484. https://doi.org/10.1016/j.foreco.2020.118637

- Ndaimani, H., Murwira, A., & Kativu, S. (2013). Comparing terrain and vegetation-based visibility for explaining sable flight behaviour in a Southern African savanna. *Geocarto International*, 28(2), 130–143. https://doi.org/10.1080/10106049.2012.677481
- Neilson, E. W., Avgar, T., Cole Burton, A., Broadley, K., & Boutin, S. (2018). Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere*, 9(1). https://doi.org/10.1002/ecs2.2092
- Neumann, W., Martinuzzi, S., Estes, A. B., Pidgeon, A. M., Dettki, H., Ericsson, G., & Radeloff, V. C. (2015). Opportunities for the application of advanced remotely-sensed data in ecological studies of terrestrial animal movement. *Movement Ecology*, 3(1). https://doi.org/10.1186/s40462-015-0036-7
- Newman, M., Mitchell, F. J. G., & Kelly, D. L. (2014). Exclusion of large herbivores: Long-term changes within the plant community. *Forest Ecology and Management*, *321*, 136–144. https://doi.org/10.1016/j.foreco.2013.09.010
- Newson, S. E., Johnston, A., Renwick, A. R., Baillie, S. R., & Fuller, R. J. (2012). Modelling large-scale relationships between changes in woodland deer and bird populations. *Journal of Applied Ecology*, *49*(1), 278–286. https://doi.org/10.1111/j.1365-2664.2011.02077.x
- Newton, E. J., Pond, B. A., Brown, G. S., Abraham, K. F., & Schaefer, J. A. (2014). Remote sensing reveals long-term effects of caribou on tundra vegetation. *Polar Biology*, 37(5), 715–725. https://doi.org/10.1007/s00300-014-1472-3
- Nichols, R. V, Åkesson, M., & Kjellander, P. (2016). Diet assessment based on rumen contents: A comparison between DNA metabarcoding and macroscopy. *PLoS ONE*, *11*(6). https://doi.org/10.1371/journal.pone.0157977
- Nichols, R. v., Cromsigt, J. P. G. M., & Spong, G. (2015). DNA left on browsed twigs uncovers bitescale resource use patterns in European ungulates. *Oecologia*, 178(1), 275–284. https://doi.org/10.1007/s00442-014-3196-z
- Nichols, R. V., Königsson, H., Danell, K., & Spong, G. (2012). Browsed twig environmental DNA: diagnostic PCR to identify ungulate species. *Molecular Ecology Resources*, *12*(6), 983–989. https://doi.org/10.1111/j.1755-0998.2012.03172.x
- Nichols, R. v, & Spong, G. (2014). Ungulate browsing on conifers during summer as revealed by DNA. *Scandinavian Journal of Forest Research*, 29(7), 650–652. https://doi.org/10.1080/02827581.2014.960895
- Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, 7(12), 1457–1462.

- Niwa, H. (2021). Assessing the activity of deer and their influence on vegetation in a wetland using automatic cameras and low altitude remote sensing (LARS). *European Journal of Wildlife Research*, 67(1). https://doi.org/10.1007/s10344-020-01450-6
- Niwa, S., N. Kaneko, H. Okada, and K. Sakamoto. 2008. Effects of fine-scale simulation of deer browsing on soil micro-foodweb structure and N mineralization rate in a temperate forest. Soil Biol Biochem. 40:699–708. doi:10.1016/j.soilbio.2007.10.004.
- Niwa, S., Mariani, L., Kaneko, N., Okada, H., & Sakamoto, K. (2011). Early-stage impacts of sika deer on structure and function of the soil microbial food webs in a temperate forest: A large-scale experiment. *Forest Ecology and Management*, 261(3), 391–399. https://doi.org/10.1016/j.foreco.2010.10.024
- Nomiya, H., Suzuki, W., Kanazashi, T., Shibata, M., Tanaka, H., & Nakashizuka, T. (2003). The response of forest floor vegetation and tree regeneration to deer exclusion and disturbance in a riparian deciduous forest, central Japan. *Plant Ecology*, *164*(2), 263–276. https://doi.org/10.1023/A:1021294021438
- Nopp-Mayr, U., Reimoser, S., Reimoser, F., Sachser, F., Obermair, L., & Gratzer, G. (2020). Analyzing long-term impacts of ungulate herbivory on forest-recruitment dynamics at community and species level contrasting tree densities versus maximum heights. *Scientific Reports*, 10(1), 1–13. https://doi.org/10.1038/s41598-020-76843-3
- Norbury, G. L., & Sanson, G. D. (1992). Problems with measuring diet selection of terrestrial, mammalian herbivores. *Australian Journal of Ecology*, *17*(1), 1–7. https://doi.org/10.1111/j.1442-9993.1992.tb00774.x
- Norum, J. K., Lone, K., Linnell, J. D. C., Odden, J., Loe, L. E., & Mysterud, A. (2015). Landscape of risk to roe deer imposed by lynx and different human hunting tactics. *European Journal of Wildlife Research*, *61*(6), 831–840. https://doi.org/10.1007/s10344-015-0959-8
- Nudds, T. D. (1980). Forage "Preference": Theoretical Considerations of Diet Selection by Deer. *The Journal of Wildlife Management*, 44(3), 735–740. https://about.jstor.org/terms
- Nugent, G. (1990). Forage availability and the diet of fallow deer (*Dama dama*) in the Blue Mountains, Otago. *New Zealand Journal of Ecology*, *13*(1), 83–95. https://newzealandecology.org/nzje/1878.pdf
- Nuttle, T., Royo, A. A., Adams, M. B., & Carson, W. P. (2013). Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs*, 83(1), 3–17. https://doi.org/10.1890/11-2263.1

- Oberosler, V., Groff, C., Iemma, A., Pedrini, P., & Rovero, F. (2017). The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. *Mammalian Biology*, 87, 50–61. https://doi.org/10.1016/j.mambio.2017.05.005
- Obidziński, A., Kiełtyk, P., Borkowski, J., Bolibok, L., & Remuszko, K. (2013). Autumn-winter diet overlap of fallow, red, and roe deer in forest ecosystems, Southern Poland. *Central European Journal of Biology*, 8(1), 8–17. https://doi.org/10.2478/s11535-012-0108-2
- O'Connor, T. G. (2017). Demography of woody species in a semi-arid African savanna reserve following the re-introduction of elephants. *Acta Oecologica*, 78, 61–70. https://doi.org/10.1016/j.actao.2016.12.009
- O'Connor, T. G., & Page, B. R. (2014). Simplification of the composition, diversity and structure of woody vegetation in a semi-arid African savanna reserve following the re-introduction of elephants. *Biological Conservation*, *180*, 122–133. https://doi.org/10.1016/j.biocon.2014.09.036
- Ohashi, H., & Hoshino, Y. (2014). Disturbance by large herbivores alters the relative importance of the ecological processes that influence the assembly pattern in heterogeneous meta-communities. *Ecology and Evolution*, 4(6), 766–775. https://doi.org/10.1002/ece3.987
- Ohse, B., Hammerbacher, A., Seele, C., Meldau, S., Reichelt, M., Ortmann, S., & Wirth, C. (2017). Salivary cues: simulated roe deer browsing induces systemic changes in phytohormones and defence chemistry in wild-grown maple and beech saplings. *Functional Ecology*, *31*(2), 340–349. https://doi.org/10.1111/1365-2435.12717
- Ohse, B., Seele, C., Holzwarth, F., & Wirth, C. (2017). Different facets of tree sapling diversity influence browsing intensity by deer dependent on spatial scale. *Ecology and Evolution*, 7(17), 6779–6789. https://doi.org/10.1002/ece3.3217
- Oishi, Y., & Doei, H. (2019). The effect of Sika deer herbivory on epiphyte diversity changes. *The Bryologist*, *122*(3), 384. https://doi.org/10.1639/0007-2745-122.3.384
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., de Caceres, M., Durand, S., ... Weedon, J. (2022). *vegan: Community Ecology Package*. https://CRAN.R-project.org/package=vegan
- Olff, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology* & *Evolution*, *13*(7), 261–265. https://doi.org/10.1016/S0169-5347(98)01364-0
- Olsoy, P. J., Forbey, J. S., Rachlow, J. L., Nobler, J. D., Glenn, N. F., & Shipley, L. A. (2015). Fearscapes: Mapping functional properties of cover for prey with terrestrial LiDAR. *BioScience*, 65(1), 74–80. https://doi.org/10.1093/biosci/biu189

- Ordiz, A., Aronsson, M., Persson, J., Støen, O. G., Swenson, J. E., & Kindberg, J. (2021). Effects of human disturbance on terrestrial apex predators. *Diversity*, *13*(2), 1–18. https://doi.org/10.3390/d13020068
- O'Reilly-Wapstra, J. M., Moore, B. D., Brewer, M., Beaton, J., Sim, D., Wiggins, N. L., & Iason, G. R. (2014). *Pinus sylvestris* sapling growth and recovery from mammalian browsing. *Forest Ecology* and Management, 325, 18–25. https://doi.org/10.1016/j.foreco.2014.03.038
- Ossi, F., Gaillard, J. M., Hebblewhite, M., & Cagnacci, F. (2015). Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. *European Journal of Wildlife Research*, *61*(1), 111–124. https://doi.org/10.1007/s10344-014-0879-z
- Otsu, C., Iijima, H., & Nagaike, T. (2019). Plant community recovery from intense deer grazing depends on reduction of graminoids and the time after exclosure installation in a semi-natural grassland. *PeerJ*, 7, e7833. https://doi.org/10.7717/peerj.7833
- Painter, L. E., Beschta, R. L., Larsen, E. J., & Ripple, W. J. (2014). After long-term decline, are aspen recovering in northern Yellowstone? *Forest Ecology and Management*, 329, 108–117. https://doi.org/10.1016/j.foreco.2014.05.055
- Pajares, G., Álvarez, I., Fernández, I., Pérez-Pardal, L., Goyache, F., & Royo, L. J. (2007). A sexing protocol for wild ruminants based on PCR amplification of amelogenin genes AMELX and AMELY (short communication). *Archives Animal Breeding*, 50(5), 442–446. https://doi.org/10.5194/aab-50-442-2007
- Palmer, G., Stephens, P. A., Ward, A. I., & Willis, S. G. (2015). Nationwide trophic cascades: Changes in avian community structure driven by ungulates. *Scientific Reports*, 5. https://doi.org/10.1038/srep15601
- Palmer, M. S., Gaynor, K. M., Becker, J. A., Abraham, J. O., Mumma, M. A., & Pringle, R. M. (2022). Dynamic landscapes of fear: understanding spatiotemporal risk. *Trends in Ecology & Evolution*. https://doi.org/10.1016/j.tree.2022.06.007
- Palmer, S. C. F., Mitchell, R. J., Truscott, A. M., & Welch, D. (2004). Regeneration failure in Atlantic oakwoods: The roles of ungulate grazing and invertebrates. *Forest Ecology and Management*, 192(2–3), 251–265. https://doi.org/10.1016/j.foreco.2004.01.038
- Palmer, S. C. F., & Truscott, A. M. (2003). Browsing by deer on naturally regenerating Scots pine (*Pinus sylvestris L.*) and its effects on sapling growth. *Forest Ecology and Management*, 182(1–3), 31–47. https://doi.org/10.1016/S0378-1127(03)00026-4

- Palmer, S. C. F., & Trustcott, A. M. (2003). Seasonal habitat use and browsing by deer in Caledonian pinewoods. *Forest Ecology and Management*, *174*(1–3), 149–166. https://doi.org/10.1016/S0378-1127(02)00032-4
- Palmer, T. M., Stanton, M. L., Young, T. P., Goheen, J. R., Pringle, R. M., & Karban, R. (2008). Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African Savanna. *Science*, 319(5860), 192–195. https://doi.org/10.1126/science.1151579
- Panzacchi, M., Herfindal, I., Linnell, J. D. C., Odden, M., Odden, J., & Andersen, R. (2010). Trade-offs between maternal foraging and fawn predation risk in an income breeder. *Behavioral Ecology and Sociobiology*, 64(8), 1267–1278. https://doi.org/10.1007/s00265-010-0941-0
- Parks, C. G., Forest, U., Bednar, L., & Forest, U. (1998). Browsing Ungulates-An Important Consideration in Dieback and Mortality of Pacific Yew (*Taxus brevifolia*) in a Northeastern Oregon Stand. *Northwest Science*, 72(3), 190–197.
- Parsons, B. M., Coops, N. C., Kearney, S. P., Burton, A. C., Nelson, T. A., & Stenhouse, G. B. (2021). Road visibility influences habitat selection by grizzly bears (*Ursus arctos horribilis*). *Canadian Journal of Zoology*, 99(3), 161–171. https://doi.org/10.1139/cjz-2020-0125
- Parsons, B. M., Coops, N. C., Stenhouse, G. B., Burton, A. C., & Nelson, T. A. (2020). Building a perceptual zone of influence for wildlife: delineating the effects of roads on grizzly bear movement. *European Journal of Wildlife Research*, 66(4). https://doi.org/10.1007/s10344-020-01390-1
- Pastor, J., Dewey, B., Moen, R., Mladenoff, D. J., & White, M. (1998). Spatial Patterns in the Moose-Forest-Soil Ecosystem on Isle Royale, Michigan, USA. *Ecological Applications*, 8(2), 411–424. https://doi.org/10.1890/1051-0761(1998)008[0411:SPITMF]2.0.CO;2
- Pays, O., Benhamou, S., Helder, R., & Gerard, J.-F. (2007). The dynamics of group formation in large mammalian herbivores: an analysis in the European roe deer. *Animal Behaviour*, 74(5), 1429–1441. https://doi.org/10.1016/J.ANBEHAV.2007.02.012
- Pecorella, I., Fattorini, N., Macchi, E., & Ferretti, F. (2019). Sex/age differences in foraging, vigilance and alertness in a social herbivore. *Acta Ethologica*, 22(1), 1–8. https://doi.org/10.1007/s10211-018-0300-0
- Pecorella, I., Ferretti, F., Sforzi, A., & Macchi, E. (2016). Effects of culling on vigilance behaviour and endogenous stress response of female fallow deer. *Wildlife Research*, *43*(3), 189–196. https://doi.org/10.1071/WR15118
- Peinetti, H. R., Kalkhan, M. A., & Coughenour, M. B. (2002). Long-term changes in willow spatial distribution on the elk winter range of Rocky Mountain National Park (USA). *Landscape Ecology*, 17(4), 341–354. https://doi.org/10.1023/A:1020530710891

- Peinetti, H. R., Menezes, R. S. C., & Coughenour, M. B. (2001). Changes induced by elk browsing in the aboveground biomass production and distribution of willow (*Salix monticola Bebb*): Their relationships with plant water, carbon, and nitrogen dynamics. *Oecologia*, 127(3), 334–342. https://doi.org/10.1007/s004420000593
- Pekin, B. K., Endress, B. A., Wisdom, M. J., Naylor, B. J., & Parks, C. G. (2015). Impact of ungulate exclusion on understorey succession in relation to forest management in the Intermountain Western United States. *Applied Vegetation Science*, *18*(2), 252–260. https://doi.org/10.1111/avsc.12145
- Pekin, B. K., Wisdom, M. J., Endress, B. A., Naylor, B. J., & Parks, C. G. (2014). Ungulate browsing maintains shrub diversity in the absence of episodic disturbance in seasonally-arid conifer forest. *PLoS ONE*, 9(1). https://doi.org/10.1371/journal.pone.0086288
- Pekin, B. K., Wisdom, M. J., Parks, C. G., Endress, B. A., & Naylor, B. J. (2016). Response of native versus exotic plant guilds to cattle and elk herbivory in forested rangeland. *Applied Vegetation Science*, 19(1), 31–39. https://doi.org/10.1111/avsc.12194
- Pélabon, C., & Komers, P. E. (1997). Time-budget variations in relation to density- dependent social interactions in female and yearling male fallow deer during the rut. *Canadian Journal of Zoology*, 75(March 2015), 971–977. https://doi.org/10.1139/z97-118
- Pellerin, M., Saïd, S., Richard, E., Hamann, J. L., Dubois-Coli, C., & Hum, P. (2010). Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. *Forest Ecology and Management*, 260(4), 429–437. https://doi.org/10.1016/j.foreco.2010.04.031
- Peltzer, D. A., Allen, R. B., Bellingham, P. J., Richardson, S. J., Wright, E. F., Knightbridge, P. I., & Mason, N. W. H. (2014). Disentangling drivers of tree population size distributions. *Forest Ecology* and Management, 331, 165–179. https://doi.org/10.1016/j.foreco.2014.06.037
- Pelz, K. A., & Smith, F. W. (2018). Effects of stand structure, browsing, and biophysical conditions on regeneration following Mountain Pine Beetle in mixed lodgepole pine and aspen forests of the Southern Rockies. *Forests*, 9(9), 1–12. https://doi.org/10.3390/f9090525
- Pépin, D., Morellet, N., & Goulard, M. (2009). Seasonal and daily walking activity patterns of freeranging adult red deer (*Cervus elaphus*) at the individual level. *European Journal of Wildlife Research*, 55(5), 479–486. https://doi.org/10.1007/s10344-009-0267-2
- Pépin, D., Renaud, P. C., Boscardin, Y., Goulard, M., Mallet, C., Anglard, F., & Ballon, P. (2006). Relative impact of browsing by red deer on mixed coniferous and broad-leaved seedlings - An enclosure-based experiment. *Forest Ecology and Management*, 222(1–3), 302–313. https://doi.org/10.1016/j.foreco.2005.10.034

- Perea, R., & Gil, L. (2014a). Shrubs facilitating seedling performance in ungulate-dominated systems: Biotic versus abiotic mechanisms of plant facilitation. *European Journal of Forest Research*, *133*(3), 525–534. https://doi.org/10.1007/s10342-014-0782-x
- Perea, R., & Gil, L. (2014b). Tree regeneration under high levels of wild ungulates: The use of chemically vs. physically-defended shrubs. *Forest Ecology and Management*, *312*, 47–54. https://doi.org/10.1016/j.foreco.2013.10.022
- Perea, R., Girardello, M., & San Miguel, A. (2014). Big game or big loss? High deer densities are threatening woody plant diversity and vegetation dynamics. *Biodiversity and Conservation*, 23(5), 1303–1318. https://doi.org/10.1007/s10531-014-0666-x
- Perea, R., Perea-García-Calvo, R., Díaz-Ambrona, C. G., & San Miguel, A. (2015). The reintroduction of a flagship ungulate *Capra pyrenaica*: Assessing sustainability by surveying woody vegetation. *Biological Conservation*, 181, 9–17. https://doi.org/10.1016/j.biocon.2014.10.018
- Perez-Barberia, F. J., & Gordon, I. J. (1998). The influence of sexual dimorphism in body size and mouth morphology on diet selection and sexual segregation in cervids. *Acta Veterinaria Hungarica*, 46(3), 357–367.
- Perrin, P. M., Mitchell, F. J. G., & Kelly, D. L. (2011). Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: Changes in ground flora and species diversity. *Forest Ecology and Management*, 262(12), 2328–2337. https://doi.org/10.1016/j.foreco.2011.08.028
- Petersson, L. K., Milberg, P., Bergstedt, J., Dahlgren, J., Felton, A. M., Götmark, F., Salk, C., & Löf, M. (2019). Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: Six decades of landscape-scale evidence. *Forest Ecology and Management*, 444, 299–307. https://doi.org/10.1016/j.foreco.2019.04.037
- Pfeffer, S. E., Spitzer, R., Allen, A. M., Hofmeester, T. R., Ericsson, G., Widemo, F., Singh, N. J., & Cromsigt, J. P. G. M. (2018). Pictures or pellets? Comparing camera trapping and dung counts as methods for estimating population densities of ungulates. *Remote Sensing in Ecology and Conservation*, 4(2), 173–183. https://doi.org/10.1002/rse2.67
- Phillip, S., Dandy, N., Gill, R., & MacMillan, D. C. (2009). Is legislation a barrier to the sustainable management of game species? A case study of wild deer in Britain. *Journal of Environmental Planning and Management*, 52(8), 993–1012. https://doi.org/10.1080/09640560903327351
- Picardi, S., Basille, M., Peters, W., Ponciano, J. M., Boitani, L., & Cagnacci, F. (2019). Movement responses of roe deer to hunting risk. *Journal of Wildlife Management*, 83(1), 43–51. https://doi.org/10.1002/jwmg.21576
- Pollard, E., & Cooke, A. S. (1994). Impact of muntjac deer *Muntiacus reevesi* on egg-laying sites of the white admiral butterfly *Ladoga camilla* in a Cambridgeshire wood. *Biological Conservation*, 70(2), 189–191. https://doi.org/10.1016/0006-3207(94)90287-9
- Pompanon, F., Deagle, B. E., Symondson, W. O. C., Brown, D. S., Jarman, S. N., & Taberlet, P. (2012). Who is eating what: Diet assessment using next generation sequencing. *Molecular Ecology*, 21(8), 1931–1950. https://doi.org/10.1111/j.1365-294X.2011.05403.x
- Potts A, J. M., Beeton B,C, N. J., Bowman B, D. M. J. S., Williamson B, G. J., Lefroy, E. C., & Johnson, C. N. (2015). Predicting the future range and abundance of fallow deer in Tasmania, Australia. *Wildlife Research*. https://doi.org/10.1071/WR13206
- Prager, K., Lorenzo-Arribas, A., Bull, H., Kvernstuen, M. S., Loe, L. E., & Mysterud, A. (2018). Social constraints in cross-boundary collaborative deer management. *Ecology and Society*, 23(4). https://doi.org/10.5751/ES-10549-230429
- Pringle, R. M. (2008). Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology*, 89(1), 26–33. https://doi.org/10.1890/07-0776.1
- Putman, R. J., & Flueck, W. T. (2011). Intraspecific variation in biology and ecology of deer: Magnitude and causation. *Animal Production Science*, *51*(4), 277–291. https://doi.org/10.1071/AN10168
- Putman, R. J. (1986a). Food and Feeding Behaviour of the Forest Deer. In *Grazing in Temperate Ecosystems Large Herbivores and the Ecology of the New Forest* (pp. 116–133). Springer Netherlands. https://doi.org/10.1007/978-94-011-6081-0_6
- Putman, R. J. (1986b). The Pressure of Grazing and its Impact Upon the Vegetation. In *Grazing in Temperate Ecosystems Large Herbivores and the Ecology of the New Forest* (pp. 134–164). Springer Netherlands. https://doi.org/10.1007/978-94-011-6081-0_7

Putman, R. J. (1989). The natural history of deer. Cornell University Press.

- Putman, R. J. (1996). Ungulates in temperate forest ecosystems: Perspectives and recommendations for future research. *Forest Ecology and Management*, 88(1–2), 205–214. https://doi.org/10.1016/S0378-1127(96)03878-9
- Putman, R. J., Culpin, S., & Thirgood, S. J. (1993). Dietary differences between male and female fallow deer in sympatry and in allopatry. *Journal of Zoology*, 229(2), 267–275. https://doi.org/10.1111/j.1469-7998.1993.tb02635.x
- Putman, R. J., Edwards, P. J., Mann, J. C. E., How, R. C., & Hill, S. D. (1989). Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. *Biological Conservation*, 47(1), 13–32. https://doi.org/10.1016/0006-3207(89)90017-7

- Putman, R. J., Langbein, J., Green, P., & Watson, P. (2011). Identifying threshold densities for wild deer in the UK above which negative impacts may occur. *Mammal Review*, 41(3), 175–196. https://doi.org/10.1111/j.1365-2907.2010.00173.x
- Putman, R. J., & Moore, N. P. (1998). Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. *Mammal Review*, 28(4), 141–164. https://doi.org/10.1046/j.1365-2907.1998.00031.x
- Putman, R. J., Watson, P., & Langbein, J. (2011). Assessing deer densities and impacts at the appropriate level for management: A review of methodologies for use beyond the site scale. *Mammal Review*, 41(3), 197–219. https://doi.org/10.1111/j.1365-2907.2010.00172.x
- R Core Team. (2021). *R: A language and environment for statistical computing* (4.0.4). R Foundation for Statistical Computing.
- Ramanzin, M., Bailoni, L., & Schiavon, S. (1997). Effect of forage to concentrate ratio on comparative digestion in sheep, goats and fallow deer. *Animal Science*, 64(1), 163–170. https://doi.org/10.1017/S1357729800015678
- Ramirez, J. I. (2021). Uncovering the different scales in deer–forest interactions. *Ecology and Evolution*, *11*(10), 5017–5024. https://doi.org/10.1002/ece3.7439
- Ramirez, J. I., Jansen, P. A., den Ouden, J., Goudzwaard, L., & Poorter, L. (2019). Long-term effects of wild ungulates on the structure, composition and succession of temperate forests. *Forest Ecology* and Management, 432, 478–488. https://doi.org/10.1016/j.foreco.2018.09.049
- Ramirez, J. I., Jansen, P. A., Den Ouden, J., Li, X., Iacobelli, P., Herdoiza, N., & Poorter, L. (2021b). Temperate forests respond in a non-linear way to a population gradient of wild deer. *Forestry*, 94(4), 502–511. https://doi.org/10.1093/forestry/cpaa049
- Ramirez, J. I., Jansen, P. A., den Ouden, J., Moktan, L., Herdoiza, N., & Poorter, L. (2021a). Above- and Below-ground Cascading Effects of Wild Ungulates in Temperate Forests. *Ecosystems*, 24(1), 153– 167. https://doi.org/10.1007/s10021-020-00509-4
- Ramirez, J. I., Jansen, P. A., & Poorter, L. (2018). Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: A semi-quantitative review. *Forest Ecology and Management*, 424(September), 406–419. https://doi.org/10.1016/j.foreco.2018.05.016
- Ramón-Laca, A., Gleeson, D., Yockney, I., Perry, M., Nugent, G., & Forsyth, D. M. (2014). Reliable discrimination of 10 ungulate species using high resolution melting analysis of Faecal DNA. *PLoS ONE*, 9(3), e92043. https://doi.org/10.1371/journal.pone.0092043

- Ramsey, D. S. L., Forsyth, D. M., Veltman, C. J., Richardson, S. J., Allen, R. B., Allen, W. J., Barker, R. J., Bellingham, Peter J. Jacobson, C. L., Nicol, S. J., Robertson, A. W., & Todd, C. R. (2018). A management experiment reveals the difficulty of altering seedling growth and palatable plant biomass by culling invasive deer. *Wildlife Research*, 44(8), 623. https://doi.org/10.1071/wr16206
- Ratikainen, I. I., Panzacchi, M., Mysterud, A., Odden, J., Linnell, J., & Andersen, R. (2007a). Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present. *Journal of Zoology*, 273(2), 192–199. https://doi.org/10.1111/j.1469-7998.2007.00314.x
- Ratikainen, I. I., Panzacchi, M., Mysterud, A., Odden, J., Linnell, J., & Andersen, R. (2007b). Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present. *Journal of Zoology*, 273(2), 192–199. https://doi.org/10.1111/j.1469-7998.2007.00314.x
- Rauchenstein, K., Ecker, K., Bader, E., Ginzler, C., Düggelin, C., Bontadina, F., & Obrist, M. K. (2022). LiDAR metrics predict suitable forest foraging areas of endangered Mouse-eared bats (*Myotis myotis*). Forest Ecology and Management, 515. https://doi.org/10.1016/j.foreco.2022.120210
- Recarte, J. M., Vincent, J. P., & Hewison, A. J. M. (1998). Flight responses of park fallow deer to the human observer. *Behavioural Processes*, 44, 65-72.
- Redick, C. H., & Jacobs, D. F. (2020). Mitigation of deer herbivory in temperate hardwood forest regeneration: A meta-analysis of research literature. *Forests*, *11*(11), 1–16. https://doi.org/10.3390/f11111220
- Reimoser, F. (2003). Steering the impacts of ungulates on temperate forests. *Journal for Nature Conservation*, *10*(4), 243–252. https://doi.org/10.1078/1617-1381-00024
- Reimoser, F., & Putman, R. J. (2011). Impacts of wild ungulates on vegetation: costs and benefits. In *Ungulate Management in Europe* (pp. 144–191). https://doi.org/10.1017/CBO9780511974137.007
- Reimoser, S. (2012). Influence of Anthropogenic Disturbances on Activity, Behavior and Heart Rate of Roe Deer (*Capreolus capreolus*) and Red Deer (*Cervus elaphus*), in Context of their Daily and Yearly Patterns. In A. A. Cahler & J. P. Marsten (Eds.), *Deer: Habitat, Behavior and Conservation* (pp. 1–96). Nova Science Publishers Inc.
- Relva, M. A., Nuñez, M. A., & Simberloff, D. (2010). Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: Evidence for invasional meltdown. *Biological Invasions*, 12(2), 303–311. https://doi.org/10.1007/s10530-009-9623-0
- Relva, M. A., Westerholm, C. L., & Kitzberger, T. (2009). Effects of introduced ungulates on forest understory communities in northern Patagonia are modified by timing and severity of stand mortality. *Plant Ecology*, 201(1), 11–22. https://doi.org/10.1007/s11258-008-9528-5

- Rhodes, A. C., Anderson, V., & St Clair, S. B. (2017). Ungulate herbivory alters leaf functional traits and recruitment of regenerating aspen. *Tree Physiology*, 37(3), 402–413. https://doi.org/10.1093/treephys/tpx015
- Rhodes, A. C., Fitch, C., & St. Clair, S. B. (2019). Ungulate Herbivory Is Correlated with High Aspen Suckering Density but Reductions in Aspen Growth Rates and Recruitment. *Rangeland Ecology* and Management, 72(3), 454–460. https://doi.org/10.1016/j.rama.2018.12.006
- Rhodes, A. C., Larsen, R. T., Maxwell, J. D., & St. Clair, S. B. (2018). Temporal patterns of ungulate herbivory and phenology of aspen regeneration and defense. *Oecologia*, *188*(3), 707–719. https://doi.org/10.1007/s00442-018-4253-9
- Rhodes, A. C., Wan, H. Y., & St. Clair, S. B. (2017). Herbivory impacts of elk, deer and cattle on aspen forest recruitment along gradients of stand composition, topography and climate. *Forest Ecology* and Management, 397, 39–47. https://doi.org/10.1016/j.foreco.2017.04.014
- Richard, E., Morellet, N., Cargnelutti, B., Angibault, J. M., Vanpé, C., & Hewison, A. J. M. (2008). Ranging behaviour and excursions of female roe deer during the rut. *Behavioural Processes*, 79(1), 28–35. https://doi.org/10.1016/j.beproc.2008.04.008
- Richter, L., Balkenhol, N., Raab, C., Reinecke, H., Meißner, M., Herzog, S., Isselstein, J., & Signer, J. (2020). So close and yet so different: The importance of considering temporal dynamics to understand habitat selection. *Basic and Applied Ecology*, 43, 99–109. https://doi.org/10.1016/j.baae.2020.02.002
- Riesch, F., Tonn, B., Stroh, H. G., Meißner, M., Balkenhol, N., & Isselstein, J. (2020). Grazing by wild red deer maintains characteristic vegetation of semi-natural open habitats: Evidence from a threeyear exclusion experiment. *Applied Vegetation Science*, 23(4), 522–538. https://doi.org/10.1111/avsc.12505
- Riganelli, N., Acuti, G., Olivieri, O., Trabalza Marinucci, M., Antonini, C., & Capecci, A. (2010). Dietary preferences and ruminal protozoal populations in roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*) and mouflon (*Ovis musimon*). *Italian Journal of Animal Science*, 4(2s), 401. https://doi.org/10.4081/ijas.2005.2s.401
- Riggs, R. A., Tiedemann, A. R., Cook, J. G., Ballard, T. M., Edgerton, P. J., Vavra, M., Krueger, W. C., Hall, F. C., Bryant, L. D., Irwin, L. L., & Delcurto, T. (2000). Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province. In USDA Forest Service -Research Papers RMRS (Issue PNW-RP-527).
- Ripple, W. J., & Beschta, R. L. (2003). Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*, 184(1–3), 299–313. https://doi.org/10.1016/S0378-1127(03)00154-3

- Ripple, W. J., & Beschta, R. L. (2006). Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management*, 230(1–3), 96– 106. https://doi.org/10.1016/j.foreco.2006.04.023
- Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation*, 145(1), 205–213. https://doi.org/10.1016/j.biocon.2011.11.005
- Ripple, W. J., Beschta, R. L., Fortin, J. K., & Robbins, C. T. (2014). Trophic cascades from wolves to grizzly bears in Yellowstone. *Journal of Animal Ecology*, 83(1), 223–233. https://doi.org/10.1111/1365-2656.12123
- Ripple, W. J., & Larsen, E. J. (2000). Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation*, 95(3), 361–370. https://doi.org/10.1016/S0006-3207(00)00014-8
- Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W.,
 Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., & Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, 1(4). https://doi.org/10.1126/sciadv.1400103
- Rivera, K., Fidino, M., Farris, Z. J., Magle, S. B., Murphy, A., & Gerber, B. D. (2022). Rethinking Habitat Occupancy Modeling and the Role of Diel Activity in an Anthropogenic World. *American Naturalist*, 200(4), 556–570. https://doi.org/10.1086/720714
- Roberson, E. J., Chips, M. J., Carson, W. P., & Rooney, T. P. (2016). Deer herbivory reduces webbuilding spider abundance by simplifying forest vegetation structure. *PeerJ*, 4, e2538. https://doi.org/10.7717/peerj.2538
- Rogan, M. S., Balme, G. A., Distiller, G., Pitman, R. T., Broadfield, J., Mann, G. K. H., Whittington-Jones, G. M., Thomas, L. H., & O'Riain, M. J. (2019). The influence of movement on the occupancy–density relationship at small spatial scales. *Ecosphere*, 10(8). https://doi.org/10.1002/ecs2.2807
- Rogers, G. M., & Leathwick, J. R. (1997). Factors predisposing forests to canopy collapse in the Southern Ruahine Range, New Zealand. *Biological Conservation*, 80(3), 325–338. https://doi.org/10.1016/S0006-3207(96)00043-2
- Rose, J. R., & Cooper, D. J. (2017). The influence of floods and herbivory on cottonwood establishment and growth in Yellowstone National Park. *Ecohydrology*, *10*(1), 1–13. https://doi.org/10.1002/eco.1768
- Roussel, J. R., Auty, D., Coops, N. C., Tompalski, P., Goodbody, T. R. H., Meador, A. S., Bourdon, J. F., de Boissieu, F., & Achim, A. (2020). lidR: An R package for analysis of Airborne Laser

Scanning (ALS) data. *Remote Sensing of Environment*, 251. https://doi.org/10.1016/j.rse.2020.112061

- Rowcliffe, J. M., Field, J., Turvey, S. T., & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45(4), 1228–1236. https://doi.org/10.1111/j.1365-2664.2008.01473.x
- Rowland, M. M., Averett, J. P., Endress, B. A., Wisdom, M. J., & Naylor, B. J. (2017). Wild ungulate herbivory suppresses deciduous woody plant establishment following salmonid stream restoration. *Forest Ecology and Management*, *391*, 135–144. https://doi.org/10.1016/j.foreco.2017.02.017
- Royo, A. A., Kramer, D. W., Miller, K. V., Nibbelink, N. P., & Stout, S. L. (2017). Spatio-temporal variation in foodscapes modifies deer browsing impact on vegetation. *Landscape Ecology*, 32(12), 2281–2295. https://doi.org/10.1007/s10980-017-0568-x
- Roženbergar, D., Klevišar, R., & Diaci, J. (2019). Topography and deer browsing in a mixed silver firbeech forest. *Acta Silvae et Ligni*, *118*(118), 41–51. https://doi.org/10.20315/asetl.118.4
- Rupprecht, D., Jedrzejek, B., & Hölzel, N. (2022). Fallow deer foraging alone does not preserve the vegetation of traditionally sheep-grazed calcareous grasslands. *Journal of Applied Ecology*, 59(10), 2520–2530. https://doi.org/10.1111/1365-2664.14253
- Ryding, J. (2016). Assessing new methods for measuring forest understorey vegetation using terrestrial *laser scanning* [PhD Thesis]. University of Nottingham.
- Ryding, J., Williams, E., Smith, M. J., & Eichhorn, M. P. (2015). Assessing handheld mobile laser scanners for forest surveys. *Remote Sensing*, 7(1), 1095–1111. https://doi.org/10.3390/rs70101095
- Sabo, A. E., Forrester, J. A., Burton, J. I., Jones, P. D., Mladenoff, D. J., & Kruger, E. L. (2019). Ungulate exclusion accentuates increases in woody species richness and abundance with canopy gap creation in a temperate hardwood forest. *Forest Ecology and Management*, 433, 386–395. https://doi.org/10.1016/j.foreco.2018.11.004
- Sage, R. B., Hollins, K., Gregory, C. L., Woodburn, M. I. A., & Carroll, J. P. (2004). Impact of roe deer Capreolus capreolus browsing on understorey vegetation in small farm woodlands. *Wildlife Biology*, 10(1), 115–120. https://doi.org/10.2981/wlb.2004.016
- Sakai, A., Hirayama, T., Oshioka, S., & Hirata, Y. (2006). Effects of elevation and postharvest disturbance on the composition of vegetation established after the clear-cut harvest of conifer plantations in southern Shikoku, Japan. *Journal of Forest Research*, 11(4), 253–265. https://doi.org/10.1007/s10310-005-0182-7

- Sakai, M., Natuhara, Y., Fukushima, K., Naito, R., Miyashita, H., Kato, M., & Gomi, T. (2013). Responses of macroinvertebrate communities to 4 years of deer exclusion in first-and second-order streams. *Freshwater Science*, 32(2), 563–575. https://doi.org/10.1899/12-116.1
- Sakai, M., Natuhara, Y., Imanishi, A., Imai, K., & Kato, M. (2012). Indirect effects of excessive deer browsing through understory vegetation on stream insect assemblages. *Population Ecology*, 54(1), 65–74. https://doi.org/10.1007/s10144-011-0278-1
- Sakata, Y., Shirahama, N., Uechi, A., & Okano, K. (2021). Variability in deer diet and plant vulnerability to browsing among forests with different establishment years of Sika deer. *PeerJ*, 9. https://doi.org/10.7717/peerj.12165
- Sakata, Y., & Yamasaki, M. (2015). Deer overbrowsing on autumn-flowering plants causes bumblebee decline and impairs pollination service. *Ecosphere*, 6(12), art274. https://doi.org/10.1890/ES15-00401.1
- Salek, L., Harmacek, J., Jerabkova, L., Topacoglu, O., & Machar, I. (2019). Thorny shrubs limit the browsing pressure of large herbivores on tree regeneration in temperate lowland forested landscapes. *Sustainability*, 11(13), 1–14. https://doi.org/10.3390/su11133578
- San José, C., Lovari, S., Ferrari, N., José, S., & Ferrari, L. S. (1997). Grouping in roe deer: an effect of habitat openness or cover distribution? In *Acta Theriologica* (Vol. 42, Issue 2).
- Schippers, P., van Teeffelen, A. J. A., Verboom, J., Vos, C. C., Kramer, K., & Wallis De Vries, M. F. (2014). The impact of large herbivores on woodland-grassland dynamics in fragmented landscapes: The role of spatial configuration and disturbance. *Ecological Complexity*, *17*(1), 20–31. https://doi.org/10.1016/j.ecocom.2013.07.002
- Schmidt, K. (2008). Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability. *Acta Theriologica*, *53*(1), 1–16. https://doi.org/10.1007/BF03194274
- Schoenecker, K. A., Singer, F. J., Zeigenfuss, L. C., Binkley, D., & Menezes, R. S. C. (2004). Effects of Elk Herbivory on Vegetation and Nitrogen Processes. *Journal of Wildlife Management*, 68(4), 837– 849. https://doi.org/10.2193/0022-541x(2004)068[0837:eoehov]2.0.co;2
- Schreiner, E. G., Krueger, K. A., Houston, D. B., & Happe, P. J. (1996). Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. *Canadian Journal of Forest Research*, *26*(2), 255–265.
- Schulze, E. D., Bouriaud, O., Wäldchen, J., Eisenhauer, N., Walentowski, H., Seele, C., Heinze, E., Pruschitzki, U., Dănilă, G., Marin, G., Hessenmöller, D., Bouriaud, L., & Teodosiu, M. (2014). Ungulate browsing causes species loss in deciduous forests independent of community dynamics and silvicultural management in Central and Southeastern Europe. *Annals of Forest Research*, 57(2), 267–288. https://doi.org/10.15287/afr.2014.273

- Schuttler, S. G., Parsons, A. W., Forrester, T. D., Baker, M. C., Mcshea, W. J., Costello, R., & Kays, & R. (2017). Deer on the lookout: how hunting, hiking and coyotes affect white-tailed deer vigilance. *Journal of Zoology*, 301, 320–327. https://doi.org/10.1111/jzo.12416
- Schwegmann, S., Hendel, A. L., Frey, J., Bhardwaj, M., & Storch, I. (2023). Forage, forest structure or landscape: What drives roe deer habitat use in a fragmented multiple-use forest ecosystem? *Forest Ecology and Management*, 532. https://doi.org/10.1016/j.foreco.2023.120830
- Scott, D., Welch, D., & Elston, D. A. (2009). Long-term effects of leader browsing by deer on the growth of Sitka spruce (Picea sitchensis). *Forestry*, 82(4), 387–401. https://doi.org/10.1093/forestry/cpp007
- Šebková, B., Šamonil, P., Janík, D., Adam, D., Král, K., Vrška, T., Hort, L., & Unar, P. (2011). Spatial and volume patterns of an unmanaged submontane mixed forest in Central Europe: 160 years of spontaneous dynamics. *Forest Ecology and Management*, 262(5), 873–885. https://doi.org/10.1016/j.foreco.2011.05.028
- Seki, S. I., Fujiki, D., & Sato, S. (2014). Assessing changes in bird communities along gradients of undergrowth deterioration in deer-browsed hardwood forests of western Japan. *Forest Ecology and Management*, 320, 6–12. https://doi.org/10.1016/j.foreco.2014.02.015
- Sergeyev, M., McMillan, B. R., Hersey, K. R., & Larsen, R. T. (2020). The influence of habitat use on harvest vulnerability of cow elk (*Cervus canadensis*). *PLoS ONE*, 15(11 November), 1–14. https://doi.org/10.1371/journal.pone.0242841
- Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS ONE*, 9(4). https://doi.org/10.1371/journal.pone.0094630
- Shannon, G., Mackey, R. L., & Slotow, R. (2013). Diet selection and seasonal dietary switch of a large sexually dimorphic herbivore. *Acta Oecologica*, *46*, 48–55.
- Shelton, A. L., Henning, J. A., Schultz, P., & Clay, K. (2014). Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. *Forest Ecology and Management*, 320, 39–49. https://doi.org/10.1016/j.foreco.2014.02.026
- Shibata, E. (2007). Effects of deer debarking on masting and trunk radial growth of Hondo spruce, *Picea jezoensis var. hondoensis*, in a subalpine forest of central Japan. *Forest Ecology and Management*, 252(1–3), 159–164. https://doi.org/10.1016/j.foreco.2007.06.028
- Shibata, E., Saito, M., & Tanaka, M. (2008). Deer-proof fence prevents regeneration of *Picea jezoensis* var. hondoensis through seed predation by increased woodmouse populations. Journal of Forest Research, 13(2), 89–95. https://doi.org/10.1007/s10310-007-0056-2

- Shibata, E., & Torazawa, Y. (2008). Effects of bark stripping by sika deer, *Cervus nippon*, on wind damage to coniferous trees in subalpine forest of central Japan. *Journal of Forest Research*, 13(5), 296–301. https://doi.org/10.1007/s10310-008-0080-x
- Shimoda, K., Kimura, K., Kanzaki, M., & Yoda, K. (1994). The regeneration of pioneer tree species under browsing pressure of Sika deer in an evergreen oak forest. *Ecological Research*, *9*(1), 85–92. https://doi.org/10.1007/BF02347245
- Silva, J. S., Catry, F. X., Moreira, F., & Bugalho, M. N. (2015). The effects of deer exclusion on the development of a Mediterranean plant community affected by a wildfire. *Restoration Ecology*, 23(6), 760–767. https://doi.org/10.1111/rec.12242
- Silva, J. S., Catry, F. X., Moreira, F., Lopes, T., Forte, T., & Bugalho, M. N. (2014). Effects of deer on the post-fire recovery of a Mediterranean plant community in Central Portugal. *Journal of Forest Research*, *19*(2), 276–284. https://doi.org/10.1007/s10310-013-0415-0
- Simard, M. A., Dussault, C., Huot, J., & Côté, S. D. (2013). Is hunting an effective tool to control overabundant deer? A test using an experimental approach. *Journal of Wildlife Management*, 77(2), 254–269. https://doi.org/10.1002/jwmg.477
- Singer, F. J., & Schoenecker, K. A. (2003). Do ungulates accelerate or decelerate nitrogen cycling? *Forest Ecology and Management*, 181(1–2), 189–204. https://doi.org/10.1016/S0378-1127(03)00133-6
- Smit, C., den Ouden, J., & Müller-Schärer, H. (2006). Unpalatable plants facilitate tree sapling survival in wooded pastures. *Journal of Applied Ecology*, *43*(2), 305–312. https://doi.org/10.1111/j.1365-2664.2006.01147.x
- Smit, C., Kuijper, D. P. J., Prentice, D., Wassen, M. J., & Cromsigt, J. P. G. M. (2012). Coarse woody debris facilitates oak recruitment in Białowieża Primeval Forest, Poland. *Forest Ecology and Management*, 284, 133–141. https://doi.org/10.1016/j.foreco.2012.07.052
- Smith, A. F., Brock, C., Conteddu, K., Griffin, L. L., Hynes, C., Murphy, K. J., & Ciuti, S. (2022). Camera trap surveys of deer in Ireland. *Mammal Communications*, 8, 6–14. www.wildlifeinsights.org
- Smith, D. S., Lamit, L. J., Lau, M. K., Gehring, C. A., Shuster, S. M., & Whitham, T. G. (2015). Introduced elk alter traits of a native plant and its plant-associated arthropod community. *Acta Oecologica*, 67, 8–16. https://doi.org/10.1016/j.actao.2015.05.005
- Smith, S. L., Senn, H. V, Sílvia Pérez-Espona, Wyman, M. T., Heap, E., & Pemberton, J. M. (2018). Introgression of exotic Cervus (*nippon* and *canadensis*) into red deer (*Cervus elaphus*) populations in Scotland and the English Lake District. *Ecology and Evolution*, 8, 2122–2134. https://doi.org/10.1002/ece3.3767

- Smith, A. & Shandruk, L. (1979) Comparison of Fecal, Rumen and Utilization Methods for Ascertaining Pronghorn Diets. *Journal of Range Management*, 32(4), 275-279
- Soulsbury, C. D. (2019). Income and capital breeding in males: energetic and physiological limitations on male mating strategies. *The Journal of Experimental Biology*, 222(1), jeb184895. https://doi.org/10.1242/jeb.184895
- Spake, R., Bellamy, C., Gill, R., Watts, K., Wilson, T., Ditchburn, B., & Eigenbrod, F. (2020). Forest damage by deer depends on cross-scale interactions between climate, deer density and landscape structure. *Journal of Applied Ecology*, *June 2019*, 1365-2664.13622. https://doi.org/10.1111/1365-2664.13622
- Sparks, T. H., Jeffree, E. P., & Jeffree, C. E. (2000). An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *International Journal of Biometeorology*, 44, 82–87.
- Speed, J. D. M., Meisingset, E. L., Austrheim, G., Hester, A. J., Mysterud, A., Tremblay, J.-P., & Solberg, E. J. (2013). Low intensities of red deer browsing constrain rowan growth in mature boreal forests of western Norway. *Écoscience*, 20(3), 311–318. https://doi.org/10.2980/20-3-3619
- Spitz, D. B., Rowland, M. M., Clark, D. A., Wisdom, M. J., Smith, J. B., Brown, C. L., & Levi, T. (2019). Behavioral changes and nutritional consequences to elk (Cervus canadensis) avoiding perceived risk from human hunters. *Ecosphere*, 10(9). https://doi.org/10.1002/ecs2.2864
- Spitzer, R., Churski, M., Felton, A., Heurich, M., Kuijper, D. P. J., Landman, M., Rodriguez, E., Singh, N. J., Taberlet, P., van Beeck Calkoen, S. T. S., Widemo, F., & Cromsigt, J. P. G. M. (2019). Doubting dung: eDNA reveals high rates of misidentification in diverse European ungulate communities. *European Journal of Wildlife Research*, 65(2). https://doi.org/10.1007/s10344-019-1264-8
- Spitzer, R., Coissac, E., Felton, A., Fohringer, C., Juvany, L., Landman, M., Singh, N. J., Taberlet, P., Widemo, F., & P.G.M. Cromsigt, J. (2021). Small shrubs with large importance? Smaller deer may increase the moose-forestry conflict through feeding competition over Vaccinium shrubs in the field layer. *Forest Ecology and Management*, 480(July 2020), 118768. https://doi.org/10.1016/j.foreco.2020.118768
- Spitzer, R., Felton, A., Landman, M., Singh, N. J., Widemo, F., & Cromsigt, J. P. G. M. (2020). Fifty years of European ungulate dietary studies: a synthesis. *Oikos*, 129(11), 1668–1680. https://doi.org/10.1111/oik.07435
- Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*, 141(9), 2159–2173. https://doi.org/10.1016/j.biocon.2008.06.026

- Stein, R. M., Lecigne, B., Eitel, J. U. H., Johnson, T. R., McGowan, C., & Rachlow, J. L. (2022). Vegetation and vantage point influence visibility across diverse ecosystems: Implications for animal ecology. *Frontiers in Ecology and Evolution*, 10. https://doi.org/10.3389/fevo.2022.911051
- Stephan, J. G., Pourazari, F., Tattersdill, K., Kobayashi, T., Nishizawa, K., & De Long, J. R. (2017). Long-term deer exclosure alters soil properties, plant traits, understory plant community and insect herbivory, but not the functional relationships among them. *Oecologia*, 184(3), 685–699. https://doi.org/10.1007/s00442-017-3895-3
- Stewart, D. G., Gulsby, W. D., Ditchkoff, S. S., & Collier, B. A. (2022). Spatiotemporal patterns of male and female white-tailed deer on a hunted landscape. *Ecology and Evolution*, 12(9). https://doi.org/10.1002/ece3.9277
- Stewart, F. E. C., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2018). Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use: *Ecosphere*, 9(2). https://doi.org/10.1002/ecs2.2112
- Stewart, K. M., Bowyer, R. T., Ruess, R. W., Dick, B. L., Kie, J. G., & Biology, A. (2006). Herbivore Optimization by North American Elk: Consequences for Theory and Management. *Optimization*, 167, 1–24. https://doi.org/10.2193/0084-0173(2006)167
- Stohlgren, T. J., Coughenour, M. B., Chong, G. W., Binkley, D., Kalkhan, M. A., Schell, L. D., Buckley, D. J., & Berry, J. K. (1997). Landscape analysis of plant diversity. *Landscape Ecology*, 12(3), 155– 170. https://doi.org/10.1023/A:1007986502230
- Stokely, T. D., & Betts, M. G. (2020). Deer-mediated ecosystem service versus disservice depends on forest management intensity. *Journal of Applied Ecology*, 57(1), 31–42. https://doi.org/10.1111/1365-2664.13532
- Stokely, T. D., Verschuyl, J., Hagar, J. C., & Betts, M. G. (2018). Herbicides and herbivory interact to drive plant community and crop-tree establishment. *Ecological Applications*, 28(8), 2011–2023. https://doi.org/10.1002/eap.1777
- Storms, D., Aubry, P., Hamann, J.-L., Saı"d, S. S., Herve'fritz, H., Saint-Andrieux, C., Franc, ois, F., Storms, K., Saı"d, S., Fritz, S., Klein, C. &, & Saı"d, S. (2008). Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. *Wildlife Biology*, *14*(2), 237–250. https://doi.org/10.2981/0909-6396(2008)14[237:SVIDCA]2.0.CO;2
- Strand, E. K., Vierling, L. A., Bunting, S. C., & Gessler, P. E. (2009). Quantifying successional rates in western aspen woodlands: Current conditions, future predictions. *Forest Ecology and Management*, 257(8), 1705–1715. https://doi.org/10.1016/j.foreco.2009.01.026

- Strauss, M. K. L., & Packer, C. (2015). Did the elephant and giraffe mediate change in the prevalence of palatable species in an East African Acacia woodland? *Journal of Tropical Ecology*, 31, 1–12. https://doi.org/10.1017/S0266467414000625
- Subalusky, A. L., Dutton, C. L., Rosi, E. J., & Post, D. M. (2017). Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences*, 114(29), 7647–7652. https://doi.org/10.1073/pnas.1614778114
- Sugimoto, T., Ito, T. Y., Taniguchi, T., Lkhagvasuren, B., Oyunsuren, T., Sakamoto, Y., & Yamanaka, N. (2018). Diet of sympatric wild and domestic ungulates in southern Mongolia by DNA barcoding analysis. *Journal of Mammalogy*, 99(2), 450–458. https://doi.org/10.1093/jmammal/gyx182
- Sullivan, J. D., Ditchkoff, S. S., Collier, B. A., Ruth, C. R., & Raglin, J. B. (2018). Recognizing the danger zone: Response of female white-Tailed to discrete hunting events. *Wildlife Biology*, 1. https://doi.org/10.2981/wlb.00455
- Suzuki, M., & Ito, E. (2014). Combined effects of gap creation and deer exclusion on restoration of belowground systems of secondary woodlands: A field experiment in warm-temperate monsoon Asia. Forest Ecology and Management, 329, 227–236. https://doi.org/10.1016/j.foreco.2014.06.028
- Suzuki, M., Karukome, T., Fujihira, K., Mitsugi, M., & Hisamoto, Y. (2021). Clear-cutting triggers regeneration of abandoned secondary forests but risks alternative successional trajectories with high deer density. *Applied Vegetation Science*, 24(3), 1–11. https://doi.org/10.1111/avsc.12596
- Suzuki, M., Miyashita, T., Kabaya, H., Ochiai, K., Asada, M., & Kikvidze, Z. (2013). Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. *Oikos*, *122*(1), 104–110. https://doi.org/10.1111/j.1600-0706.2012.20431.x
- Suzuki, M., Miyashita, T., Kabaya, H., Ochiai, K., Asada, M., & Tange, T. (2008). Deer density affects ground-layer vegetation differently in conifer plantations and hardwood forests on the Boso Peninsula, Japan. *Ecological Research*, 23(1), 151–158. https://doi.org/10.1007/s11284-007-0348-1
- Synnøve Lilleeng, M., Joar Hegland, S., Rydgren, K., & Moe, S. R. (2021). Ungulate herbivory reduces abundance and fluctuations of herbivorous insects in a boreal old-growth forest. *Basic and Applied Ecology*, *56*, 11–21. https://doi.org/10.1016/j.baae.2021.06.006
- Szemethy, L., Mátrai, K., Bíró, Z., & Katona, K. (2003). Seasonal home range shift of red deer in a forest-agriculture area in southern Hungary. *Acta Theriologica*, 48(4), 547–556. https://doi.org/10.1007/BF03192500
- Szukiel, E. (1981). Food Preferences of Deer in Relation to Winter Fodder Including Woody Plants. *ACTA THERIOLOGICA*, *26*, 319–330.

- Takada, H., & Washida, A. (2020). Ecological drivers of group size variation in sika deer: habitat structure, population density, or both? *Mammalian Biology*, *100*(5), 445–452. https://doi.org/10.1007/s42991-020-00041-x
- Takada, M., Asada, M., & Miyashita, T. (2002). Cross-habitat foraging by sika deer influences plant community structure in a forest-grassland landscape. *Oecologia*, *133*(3), 389–394. https://doi.org/10.1007/s00442-002-1037-y
- Takada, M., Baba, Y. G., Yanagi, Y., Terada, S., & Miyashita, T. (2008). Contrasting Responses of Web-Building Spiders to Deer Browsing Among Habitats and Feeding Guilds. *Environmental Entomology*, 37(4), 938–946. https://doi.org/10.1093/ee/37.4.938
- Takagi, S., & Miyashita, T. (2012). Variation in utilization of young leaves by a swallowtail butterfly across a deer density gradient. *Basic and Applied Ecology*, 13(3), 260–267. https://doi.org/10.1016/j.baae.2012.03.003
- Takarabe, K., & Iijima, H. (2020). Abundant artificial grasslands around forests increase the deer impact on forest vegetation. *European Journal of Forest Research*, 139, 473–482. https://doi.org/10.1007/s10342-020-01262-y
- Takatsuki, S. (2009). Effects of sika deer on vegetation in Japan: A review. *Biological Conservation*, 142(9), 1922–1929. https://doi.org/10.1016/j.biocon.2009.02.011
- Takeshita, K., Tanikawa, K., & Kaji, K. (2017). Applicability of a Bayesian state-space model for evaluating the effects of localized culling on subsequent density changes: sika deer as a case study. *European Journal of Wildlife Research*, 63(4), 71. https://doi.org/10.1007/s10344-017-1128-z
- Tamura, A., & Nakajima, K. (2017). Effects of 10 years of fencing under a gap and closed canopy on the regeneration of tree seedlings in an old-growth Japanese fir (*Abies firma*) forest overbrowsed by sika deer. *Journal of Forest Research*, 22(4), 224–232. https://doi.org/10.1080/13416979.2017.1331694
- Tamura, A., & Yamane, M. (2017). Response of understory vegetation over 10 years after thinning in an old-growth cedar and cypress plantation overgrazed by sika deer in eastern Japan. *Forest Ecosystems*, 4(1). https://doi.org/10.1186/s40663-016-0088-1
- Tanentzap, A. J., Bee, J. N., Lee, W. G., Lavers, R. B., Mills, J. A., Mark, A. F., & Coomes, D. A. (2009). The reliability of palatability estimates obtained from rumen contents analysis and a fieldbased index of diet selection. *Journal of Zoology*, 278(3), 243–248. https://doi.org/10.1111/j.1469-7998.2009.00572.x
- Tanentzap, A. J., Burrows, L. E., Lee, W. G., Nugent, G., Maxwell, J. M., & Coomes, D. A. (2009). Landscape-level vegetation recovery from herbivory: Progress after four decades of invasive red

deer control. *Journal of Applied Ecology*, 46(5), 1064–1072. https://doi.org/10.1111/j.1365-2664.2009.01683.x

- Tanentzap, A. J., Mountford, E. P., Cooke, A. S., & Coomes, D. A. (2012). The more stems the merrier: Advantages of multi-stemmed architecture for the demography of understorey trees in a temperate broadleaf woodland. *Journal of Ecology*, 100(1), 171–183. https://doi.org/10.1111/j.1365-2745.2011.01879.x
- Taniwaki, T., Tamura, A., & Watanabe, K. (2020). Species richness, abundance and diversity of ichneumonid wasps in Japanese beech forests impacted by sika deer and sawfly herbivory. *Entomological Science*, 23(4), 393–404. https://doi.org/10.1111/ens.12437
- Taylor, K. (1982). Inorganic Nutrition of *Rubus vestitus* in a Mixed Deciduous Woodland. In *Source: Journal of Ecology* (Vol. 70, Issue 1). https://about.jstor.org/terms
- Theuerkauf, J., & Rouys, S. (2008). Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. *Forest Ecology and Management*, 256(6), 1325–1332. https://doi.org/10.1016/j.foreco.2008.06.030
- Thirgood, S. J. (1990). Alternate mating strategies and reproductive success in fallow deer. *Behaviour*, *116*(1–2), 1–10.
- Thirgood, S. J. (1996). Ecological factors influencing sexual segregation and group size in fallow deer (Dama dama). *Journal of Zoology*, 239(4), 783–797. https://doi.org/10.1111/j.1469-7998.1996.tb05478.x
- Thirgood, S. J., Langbein, J., & Putman, R. J. (1999). Intraspecific variation in ungulate mating strategies: the case of the flexible fallow deer. In P. Slater, J. Rosenblatt, T. Roper, & C. Snowdon (Eds.), Advances in the Study of Behavior (Vol. 28, pp. 333–355). Academic Press.
- Thomas, P. A. (2016). Biological Flora of the British Isles: *Fraxinus excelsior. Journal of Ecology*, *104*(4), 1158–1209. https://doi.org/10.1111/1365-2745.12566
- Tinsley-Marshall, P. J. (2010). *Red deer habitat management in the Highlands: Consequences for invertebrates* [PhD Thesis]. Imperial College London.
- Tixier, H., & Duncan, P. (1996). Are European roe deer browsers? A review of variations in the composition of their diets. *Revue d'Ecologie (La Terre et La Vie)*, 51(1), 3–17. http://documents.irevues.inist.fr/bitstream/handle/2042/54821/RevuedEcologie_1996_51_1_3.pdf?s equence=1
- Tixier, H., Duncan, P., Scehovic, J., Yani, A., Gleizes, M., & Lila, M. (1997). Food selection by European roe deer (Capreolus capreolus): Effects of plant chemistry, and consequences for the

nutritional value of their diets. *Journal of Zoology*, 242(2), 229–245. https://doi.org/10.1111/j.1469-7998.1997.tb05799.x

- Tsuboike, Y., Fujii, M., Yoshida, Y., & Kamata, N. (2021). An Indirect Impact of Sika Deer Overpopulation on Eutrophication of an Aquatic Ecosystem via Understory Vegetation: An Individual-Based Approach Using Nitrate Reductase Activity. *Frontiers in Ecology and Evolution*, 9(March), 1–10. https://doi.org/10.3389/fevo.2021.626905
- Tsujino, R., & Yumoto, T. (2004). Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan. *Ecological Research*, *19*(3), 291–300. https://doi.org/10.1111/j.1440-1703.2004.00638.x
- Ueda, H., Takatsuki, S., & Takahashi, Y. (2002). Bark stripping of hinoki cypress by sika deer in relation to snow cover and food availability on Mt Takahara, central Japan. *Ecological Research*, 17(5), 545–551. https://doi.org/10.1046/j.1440-1703.2002.00513.x
- Ushio, M., Fukuda, H., Inoue, T., Makoto, K., Kishida, O., Sato, K., Murata, K., Nikaido, M., Sado, T., Sato, Y., Takeshita, M., Iwasaki, W., Yamanaka, H., Kondoh, M., & Miya, M. (2017). Environmental DNA enables detection of terrestrial mammals from forest pond water. *Molecular Ecology Resources*, 17(6), e63–e75. https://doi.org/10.1111/1755-0998.12690
- Uzal, A., Walls, S., Stillman, R. A., & Diaz, A. (2013). Sika deer distribution and habitat selection: The influence of the availability and distribution of food, cover, and threats. *European Journal of Wildlife Research*, *59*(4), 563–572. https://doi.org/10.1007/s10344-013-0705-z
- Valdés-Correcher, E., Rodriguez, E., Kemp, Y. J. M., Wassen, M. J., & Cromsigt, J. P. G. M. (2018). Comparing the impact of a grazing regime with European bison versus one with free-ranging cattle on coastal dune vegetation in the Netherlands. *Mammal Research*, 63(4), 455–466. https://doi.org/10.1007/s13364-018-0373-1
- Valente, A. M., Acevedo, P., Figueiredo, A. M., Fonseca, C., & Torres, R. T. (2020). Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. *Mammal Review*, 50(4), 353–366. https://doi.org/10.1111/mam.12202
- van Beeck Calkoen, S. T. S., Deis, M. H., Oeser, J., Kuijper, D. P. J., & Heurich, M. (2022). Humans rather than Eurasian lynx (*Lynx lynx*) shape ungulate browsing patterns in a temperate forest. *Ecosphere*, *13*(2). https://doi.org/10.1002/ecs2.3931
- van Doormaal, N., Ohashi, H., Koike, S., & Kaji, K. (2015). Influence of human activities on the activity patterns of Japanese sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*) in Central Japan. *European Journal of Wildlife Research*, 61(4), 517–527. https://doi.org/10.1007/s10344-015-0922-8

- van Ginkel, H. A. L., Churski, M., Kuijper, D. P. J., & Smit, C. (2021). Impediments affect deer foraging decisions and sapling performance. *Forest Ecology and Management*, 482. https://doi.org/10.1016/j.foreco.2020.118838
- van Klink, R., van der Plas, F., van Noordwijk, C. G. E. T., Wallisdevries, M. F., & Olff, H. (2015). Effects of large herbivores on grassland arthropod diversity. *Biological Reviews*, 90(2), 347–366. https://doi.org/10.1111/brv.12113
- van Moorter, B., Gaillard, J. M., McLoughlin, P. D., Delorme, D., Klein, F., & Boyce, M. S. (2009). Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. *Oecologia*, *159*(3), 669–678. https://doi.org/10.1007/s00442-008-1245-1
- Vasiliauskas, R., & Stenlid, J. (1998). Discoloration following bark stripping wounds on *Fraxinus* excelsior. European Journal of Forest Pathology, 28(6), 383–390. https://doi.org/10.1111/j.1439-0329.1998.tb01192.x
- Vaughan, I. P., Gotelli, N. J., Memmott, J., Pearson, C. E., Woodward, G., & Symondson, W. O. C. (2018). econullnetr: An r package using null models to analyse the structure of ecological networks and identify resource selection. *Methods in Ecology and Evolution*, 9(3), 728–733. https://doi.org/10.1111/2041-210X.12907
- Veblen, T. T., Mermoz, M., Martin, C., Kitzberger, T., Biology, S. C., & Mar, N. (2010). Ecological Impacts of Introduced Animals in Nahuel Huapi National Park, Argentina. *Conservation Biology*, 6(1), 71–83.
- Veblen, T. T., Mermoz, M., Martin, C., & Ramilo, E. (2006). Effects of Exotic Deer on Forest Regeneration and Composition in Northern Patagonia. *The Journal of Applied Ecology*, 26(2), 711. https://doi.org/10.2307/2404095
- Veblen, T. T., & Stewart, G. H. (1982). The Effects of Introduced Wild Animals on New Zealand Forests. Annals of the Association of American Geographers, 72(3), 372–397. https://doi.org/10.1111/j.1467-8306.1982.tb01832.x
- Vera, F. W. M., Bakker, E. S., & Olff, H. (2008). Large herbivores: missing partners of western European light-demanding tree and shrub species? *Austral Ecology*, 33(5), 702–702. https://doi.org/10.1111/j.1442-9993.2008.01861.x
- VerCauteren, K. C., Seward, N. W., Lavelle, M. J., Fischer, J. W., & Philips, G. E. (2010). A Fence Design for Excluding Elk Without Impeding Other Wildlife. *Rangeland Ecology & Management*, 60, 529–532. https://doi.org/10.2111/1551-5028(2007)60
- Verheyden-Tixier, H., Renaud, P. C., Morellet, N., Jamot, J., Besle, J. M., & Dumont, B. (2008). Selection for nutrients by red deer hinds feeding on a mixed forest edge. *Oecologia*, 156(3), 715–726. https://doi.org/10.1007/s00442-008-1020-3

- Vierling, K. T., Vierling, L. A., Gould, W. A., Martinuzzi, S., & Clawges, R. M. (2008). Lidar: Shedding new light on habitat characterization and modeling. *Frontiers in Ecology and the Environment*, 6(2), 90–98. https://doi.org/10.1890/070001
- Vila, B., Torre, F., Martin, J. L., & Guibal, F. (2003). Response of young *Tsuga heterophylla* to deer browsing: Developing tools to assess deer impact on forest dynamics. *Trees - Structure and Function*, 17(6), 547–553. https://doi.org/10.1007/s00468-003-0272-0
- Vild, O., Hédl, R., Kopecký, M., Szabó, P., Suchánková, S., & Zouhar, V. (2017). The paradox of longterm ungulate impact: increase of plant species richness in a temperate forest. *Applied Vegetation Science*, 20(2), 282–292. https://doi.org/10.1111/avsc.12289
- Vourc'h, G., Martin, J. L., Duncan, P., Escarré, J., & Clausen, T. P. (2001). Defensive adaptations of Thuja plicata to ungulate browsing: A comparative study between mainland and island populations. *Oecologia*, 126(1), 84–93. https://doi.org/10.1007/s004420000491
- Vuorinen, K. E. M., Rao, S. J., Hester, A. J., & Speed, J. D. M. (2020). Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming? *Ecological Applications*, 30(6), 1–13. https://doi.org/10.1002/eap.2119
- Walker, S. C., Anderson, V. J., & Fugal, R. A. (2015). Big Game and Cattle Influence on Aspen Community Regeneration Following Prescribed Fire. *Rangeland Ecology and Management*, 68(4), 354–358. https://doi.org/10.1016/j.rama.2015.05.005
- Walton, Z., Mattisson, J., Linnell, J. D. C., Stien, A., & Odden, J. (2017). The cost of migratory prey: seasonal changes in semi-domestic reindeer distribution influences breeding success of Eurasian lynx in northern Norway. *Oikos*, 126(5), 642–650. https://doi.org/10.1111/oik.03374
- Wam, H. K., & Hjeljord, O. (2010). Moose summer and winter diets along a large scale gradient of forage availability in southern Norway. *European Journal of Wildlife Research*, 56(5), 745–755. https://doi.org/10.1007/s10344-010-0370-4
- Wang, L., Wang, D., Bai, Y., Jiang, G., Liu, J., Huang, Y., & Li, Y. (2010). Spatial distributions of multiple plant species affect herbivore foraging selectivity. *Oikos*, 119(2), 401–408. https://doi.org/10.1111/j.1600-0706.2009.17774.x
- Wang, Y., & Fang, H. (2020). Estimation of LAI with the LiDAR technology: A review. *Remote Sensing*, *12*(20), 1–28. https://doi.org/10.3390/rs12203457
- Ward, A. I. (2005). Expanding ranges of wild and feral deer in Great Britain. *Mammal Review*, 35(2), 165–173. https://doi.org/10.1111/j.1365-2907.2005.00060.x

- Ward, A. I., Richardson, S., & Mergeay, J. (2021). Reeves' muntjac populations continue to grow and spread across Great Britain and are invading continental Europe. *European Journal of Wildlife Research*, 67(34). https://doi.org/10.1007/s10344-021-01478-2/Published
- Ward, A. I., White, P. C. L., Walker, N. J., & Critchley, C. H. (2008). Conifer leader browsing by roe deer in English upland forests: Effects of deer density and understorey vegetation. *Forest Ecology* and Management, 256(6), 1333–1338. https://doi.org/10.1016/j.foreco.2008.06.034
- Ward, D. (2016). Clipping frequency but not nutrients affect the architecture and non-structural carbohydrates of a browsing lawn. *Plant Ecology*, 217(1), 21–29. https://doi.org/10.1007/s11258-015-0555-8
- Ward-Jones, J., Pulsford, I., Thackway, R., Bishwokarma, D., & Freudenberger, D. (2019). Impacts of feral horses and deer on an endangered woodland of Kosciuszko National Park. *Ecological Management and Restoration*, 20(1), 37–46. https://doi.org/10.1111/emr.12353
- Watt, P. J., & Donoghue, D. N. M. (2005). Measuring forest structure with terrestrial laser scanning. *International Journal of Remote Sensing*, 26(7), 1437–1446. https://doi.org/10.1080/01431160512331337961
- Wedding, L. M., Jorgensen, S., Lepczyk, C. A., & Friedlander, A. M. (2019). Remote sensing of threedimensional coral reef structure enhances predictive modeling of fish assemblages. *Remote Sensing in Ecology and Conservation*, 5(2), 150–159. https://doi.org/10.1002/rse2.115
- Wei, S., Yin, T., Dissegna, M. A., Whittle, A. J., Ow, G. L. F., Yusof, M. L. M., Lauret, N., & Gastellu-Etchegorry, J. P. (2020). An assessment study of three indirect methods for estimating leaf area density and leaf area index of individual trees. *Agricultural and Forest Meteorology*, 292– 293(June), 108101. https://doi.org/10.1016/j.agrformet.2020.108101
- Weisberg, P. J., & Bugmann, H. (2003). Forest dynamics and ungulate herbivory: From leaf to landscape. *Forest Ecology and Management*, *181*(1–2), 1–12. https://doi.org/10.1016/S0378-1127(03)00123-3
- Weiss, F., Michler, F. U., Gillich, B., Tillmann, J., Ciuti, S., Heurich, M., & Rieger, S. (2022). Displacement Effects of Conservation Grazing on Red Deer (*Cervus elaphus*) Spatial Behaviour. *Environmental Management*. https://doi.org/10.1007/s00267-022-01697-6
- Welch, D., & Scott, D. (1998). Bark-stripping damage by red deer in a Sitka spruce forest in western Scotland: IV. Survival and performance of wounded trees. *Forestry*, 71(3), 225–235. https://doi.org/10.1093/forestry/71.3.225
- Welch, D., & Scott, D. (2008). An estimate of timber degrade in Sitka spruce due to bark stripping by deer in a Scottish plantation. *Forestry*, 81(4), 489–497. https://doi.org/10.1093/forestry/cpn016

- Welch, D., & Scott, D. (2017). Observations on bark-stripping by red deer in a *Picea sitchensis* forest in Western Scotland over a 35-year period. *Scandinavian Journal of Forest Research*, 32(6), 473–480. https://doi.org/10.1080/02827581.2016.1247464
- Welch, D., Scott, D., & Elston, D. A. (2013). Declining incidence of multi-trunking over time in a Scottish plantation of *Picea sitchensis*. *Scandinavian Journal of Forest Research*, 28(1), 17–27. https://doi.org/10.1080/02827581.2012.683039
- Welch, D., Scott, D., & Staines, B. W. (1997). Bark stripping damage by red deer in a Sitka spruce forest in western Scotland III. Trends in wound condition. *Forestry*, *70*(2), 113–120.
- Welch, D., Staines, B. W., Scott, D., & French, D. D. (1992). Leader browsing by red and roe deer on young sitka spruce trees in Western Scotland. II. Effects on growth and tree form. *Forestry*, 65(3), 309–330. https://doi.org/10.1093/forestry/65.3.309
- Welsh Government. (2018). Woodlands for Wales. The Welsh Assembly Government's Strategy for Woodlands and Trees. Available at: https://www.gov.wales/sites/default/files/publications/2018-06/woodlands-for-wales-strategy_0.pdf
- White, C. A., Feller, M. C., & Bayley, S. (2003). Predation risk and the functional response of elk-aspen herbivory. *Forest Ecology and Management*, 181(1–2), 77–97. https://doi.org/10.1016/S0378-1127(03)00119-1
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org
- Widenmaier, K. J., & Strong, W. L. (2010). Tree and forest encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada. *Forest Ecology and Management*, 259(10), 1870– 1879. https://doi.org/10.1016/j.foreco.2010.01.049
- Wiemers, D. W., Fulbright, T. E., Wester, D. B., Alfonso Ortega-S, J., Allen Rasmussen, G., Hewitt, D. G., & Hellickson, M. W. (2014). Role of thermal environment in habitat selection by male white-tailed deer during summer in Texas, USA. *Wildlife Biology*, 20(1), 47–56. https://doi.org/10.2981/wlb.13029
- Wilson, D. J., Ruscoe, W. A., Burrows, L. E., McElrea, L. M., & Choquenot, D. (2006). An experimental study of the impacts of understorey forest vegetation and herbivory by red deer and rodents on seedling establishment and species composition in Waitutu Forest, New Zealand. *New Zealand Journal of Ecology*, 30(2), 191–207.
- Wisdom, M. J., Preisler, H. K., Naylor, L. M., Anthony, R. G., Johnson, B. K., & Rowland, M. M. (2018). Elk responses to trail-based recreation on public forests. *Forest Ecology and Management*, 411, 223–233. https://doi.org/10.1016/j.foreco.2018.01.032

- Wisdom, M. J., Vavra, M., Boyd, J. M., Hemstrom, M. A., Ager, A. A., & Johnson, B. K. (2006). Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. *Wildlife Society Bulletin*, 34(2), 283–292. https://doi.org/10.2193/0091-7648(2006)34[283:uuhdeo]2.0.co;2
- Wiskirchen, K. H., Jacobsen, T. C., Ditchkoff, S. S., Demarais, S., & Gitzen, R. A. (2022). Behaviour of a large ungulate reflects temporal patterns of predation risk. *Wildlife Research*, 49(6), 500–512. https://doi.org/10.1071/WR21047
- Worrall, J. J., Rehfeldt, G. E., Hamann, A., Hogg, E. H., Marchetti, S. B., Michaelian, M., & Gray, L. K. (2013). Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology* and Management, 299, 35–51. https://doi.org/10.1016/j.foreco.2012.12.033
- Xu, H., Zheng, X., & Lu, H. (1998). Impact of Human Activities and habitat changes on distribution of Chinese water deer along the coast arsa in northern Jiangsu. *Acta Theriologica Sinica*, *18*, 161–167.
- Yamaguchi, S., Takeshita, K. M., Tanikawa, K., & Kaji, K. (2020). Relationship Between Hunting Time Schedule and Sika Deer Spatial Displacement in Hunting with and Without Driving. *Wildlife Society Bulletin*, 44(4), 724–731. https://doi.org/10.1002/wsb.1136
- Yamauchi, K., Mori, Y., Hamasaki, S., Miyazaki, K., Kikusui, T., & Takeuchi, Y. (2000). Sex determination based on fecal DNA analysis of the amelogenin gene in sika deer (*Cervus nippon*). *Journal of Veterinary Medical Science*, 62(6), 669–671.
- Yellowstone National Park Service (US). 2022. *Elk*. Available from: https://www.nps.gov/yell/learn/nature/elk.htm
- Yokoyama, S., Maeji, I., Ueda, T., Ando, M., & Shibata, E. (2001). Impact of bark stripping by sika deer, *Cervus nippon*, on subalpine coniferous forests in central Japan. *Forest Ecology and Management*, 140(2–3), 93–99. https://doi.org/10.1016/S0378-1127(00)00279-6
- Zamora, R., Gómez, J. M., Hódar, J. A., Castro, J., & García, D. (2001). Effect of browsing by ungulates on sapling growth of Scots pine in a mediterranean environment: Consequences for forest regeneration. *Forest Ecology and Management*, *144*(1–3), 33–42. https://doi.org/10.1016/S0378-1127(00)00362-5
- Zegler, T. J., Moore, M. M., Fairweather, M. L., Ireland, K. B., & Fulé, P. Z. (2012). Populus tremuloides mortality near the southwestern edge of its range. Forest Ecology and Management, 282, 196–207. https://doi.org/10.1016/j.foreco.2012.07.004
- Zeigenfuss, L. C., Schoenecker, K. A., & Amburg, L. K. van. (2011). Ungulate Herbivory on Alpine Willow in the Sangre De Cristo Mountains of Colorado. Western North American Naturalist, 71(1), 86–96. https://doi.org/10.3398/064.071.0112

- Zerbe, S., & Kreyer, D. (2007). Influence of different forest conversion strategies on ground vegetation and tree regeneration in pine (*Pinus sylvestris L.*) stands: A case study in NE Germany. *European Journal of Forest Research*, 126(2), 291–301. https://doi.org/10.1007/s10342-006-0148-0
- Zhang, C., Zhang, M., & Stott, P. (2014). Does prey density limit Amur tiger *Panthera tigris altaica* recovery in northeastern China? *Wildlife Biology*, *19*(4), 452–461. https://doi.org/10.2981/12-090
- Zhang, E., Teng, L., & Wu, Y. (2006). Habitat selection of the Chinese water deer (*Hydropotes inermis*) in Yancheng Reserve, Jiangsu Province. *Acta Theriologica Sinica*, 26(1), 49–53.
- Zhao, K., García, M., Liu, S., Guo, Q., Chen, G., Zhang, X., Zhou, Y., & Meng, X. (2015). Terrestrial lidar remote sensing of forests: Maximum likelihood estimates of canopy profile, leaf area index, and leaf angle distribution. *Agricultural and Forest Meteorology*, 209–210, 100–113. https://doi.org/10.1016/j.agrformet.2015.03.008
- Zong, X., Wang, T., Skidmore, A. K., & Heurich, M. (2022). LiDAR reveals a preference for intermediate visibility by a forest-dwelling ungulate species. *Journal of Animal Ecology*, 00, 1–14. https://doi.org/10.1111/1365-2656.13847
- Zweifel-Schielly, B., Leuenberger, Y., Kreuzer, M., & Suter, W. (2012). A herbivore's food landscape: Seasonal dynamics and nutritional implications of diet selection by a red deer population in contrasting Alpine habitats. *Journal of Zoology*, 286(1), 68–80. https://doi.org/10.1111/j.1469-7998.2011.00853.x
- Żywiec, M., Fedriani, J. M., Kurek, P., & Holeksa, J. (2019). Non-trophic plant–animal interactions mediate positive density dependence among conspecific saplings. *Oikos*, *128*(7), 1041–1050. https://doi.org/10.1111/oik.06071

Supporting information

S2.1. Database of the 404 sources identified for inclusion in the systematic map, provided as an accompanying Excel file <u>S2.1.systematic.map.database.xlsx</u>.

S2.2. Search terms entered into the UK Government website and the Opengrey thesis database. These searches yielded two PhD theses for inclusion. One PhD thesis had published data as peer reviewed journal articles; therefore, those articles were included instead of the thesis. Relevant theses were also excluded when no electronic download was available.

Search terms	Search engine	Date	Number of hits	Number of relevant articles	Number of articles selected for inclusion
"red deer"	Gov.UK	21/04/2020	4	0	0
"muntjac"	Gov.UK	21/04/2020	14	1	0
"roe deer"	Gov.UK	21/04/2020	7	0	0
"fallow deer"	Gov.UK	21/04/2020	1	0	0
"sika deer"	Gov.UK	21/04/2020	2	0	0
"chinese water deer"	Gov.UK	21/04/2020	4	1	0
"deer" AND "damage"	Gov.UK	21/04/2020	61	1	0
"cervus elaphus" OR "red deer"	Opengrey	21/04/2020	74	7	1
"muntiacus reevesi" OR "muntjac"	Opengrey	21/04/2020	10	2	1
"cervus nippon" OR "sika deer"	Opengrey	21/04/2020	8	0	0
"dama dama OR "fallow deer"	Opengrey	22/04/2020	18	2	1
"hydropotes inermis" OR "chinese water deer"	Opengrey	22/04/2020	2	0	0

S4.1. Woody plant taxa identified in the medium, large or very large stem diameter categories with their corresponding shade-casting categories (Ellenberg, 1988) (p. 50).

Taxon	Shade casting category
Abies spp	High
Acer campestre	Medium
Acer pseudoplatanus	High
Acer spp	Medium
Alnus rubra	Medium
<i>Betula</i> spp	Very low
Carpinus betulus	Very high
Castanea sativa	Medium
Corylus avellana	Medium
Cotoneaster sp	Very high
Crataegus spp	Low
Dead	Extremely low
Euonymus europaeus	Low
Fagus sylvatica	Very high
Fraxinus excelsior	Medium
llex aquifolium	Very high
Larix decidua	Very low
Malus spp	Low
Picea sitchensis	Very low
Pinus sylvestris	Very low
Prunus avium	Medium
Prunus laurocerasus	Very high
Prunus spinosa	Low
Pseudotsuga menziesii	High
<i>Pyrus</i> spp	Low
Quercus rubra	Medium
Quercus spp	Medium
Salix caprea	Low
Salix spp	Low
Sambucus nigra	Low
Sorbus aucuparia	Low
Thuja occidentalis	High
Thuja plicata	High
Tillia cordata	High
Ulnus glabra	High

S4.2. Stem density per hectare per sample plot, split by site and coloured by woody plant size category. Woody plant size categories were defined as follows: Sapling (> 0.3 m, < 1.3 m height); Small (> = 1.3 m height, < 10 cm DBH); Medium (10 - 20 cm DBH); Large (21 - 30 cm DBH) and Very large (> = 31 cm DBH).



S4.3. Average percentage cover of bramble across the ten woodland sites. Error bars represent the standard error of the mean.



S4.4. Average resting height of survey quadrats during summer bramble cover surveys across the ten study sites. This provides an indication of the height of the field layer vegetation including bramble. Caution is advised when interpreting these data however, for two reasons: 1) there was an effect of the quadrat squashing down vegetation, and 2) it is likely there was surveyor bias of avoiding areas where the field vegetation was so dense that safe access was not possible. For these reasons, these data are likely to underestimate the height of the field layer vegetation, including bramble. The error bars represent the standard error of the means.



S4.5. Understory Leaf Area Index (LAI) of the ten study sites. The LAI is derived from point clouds from between four and ten plots at each of the woodland sites at 0.75 - 1.5 metres above the ground. The error bars represent the standard error of the means.



S5.1. Average Horizontal Visibility Coefficient at 1 metre from the ground across each of the ten woodland sites. Error bars represent the standard error of the mean.



S5.2. Candidate models for assessing effects of covariates on occupancy probability (Ψ). Detection probability (p) was modelled alongside Ψ using single covariates.

Ψ~1	p~1
Ψ~VIS	p~1
Ψ ~ Bramble	p~1
Ψ ~ Rec	p~1
Ψ ~ Hunt	p~1
Ψ~VIS+Rec	p~1
$\Psi \sim \text{Bramble+Rec}$	p~1
Ψ ~ VIS+Hunt	p~1
$\Psi \sim \text{Bramble+Hunt}$	p~1
$\Psi \sim VIS+Bramble$	p~1
$\Psi \sim \text{Rec+Hunt}$	p~1
Ψ~1	p~VIS
Ψ~VIS	p~VIS
Ψ ~ Bramble	p~VIS
Ψ ~ Rec	p~VIS
Ψ ~ Hunt	p~VIS
Ψ~VIS+Rec	p~VIS
$\Psi \sim \text{Bramble+Rec}$	p~VIS
Ψ ~ VIS+Hunt	p~VIS
$\Psi \sim \text{Bramble+Hunt}$	p~VIS
$\Psi \sim VIS+Bramble$	p~VIS
Ψ ~ Rec+Hunt	p~VIS
Ψ~1	p~Bramble
Ψ~VIS	p~Bramble
Ψ ~ Bramble	p~Bramble
Ψ ~ Rec	p~Bramble
Ψ ~ Hunt	p~Bramble
Ψ ~ VIS+Rec	p~Bramble
$\Psi \sim \text{Bramble+Rec}$	p~Bramble
Ψ ~ VIS+Hunt	p~Bramble
$\Psi \sim \text{Bramble+Hunt}$	p~Bramble
Ψ ~ VIS+Bramble	p~Bramble
Ψ ~ Rec+Hunt	p~Bramble
Ψ~1	p~Rec
Ψ~VIS	p~Rec
Ψ ~ Bramble	p~Rec
Ψ ~ Rec	p~Rec
Ψ ~ Hunt	p~Rec
Ψ ~ VIS+Rec	p~Rec
$\Psi \sim \text{Bramble+Rec}$	p~Rec
Ψ ~ VIS+Hunt	p~Rec
$\Psi \sim \text{Bramble+Hunt}$	p~Rec
$\Psi \sim VIS+Bramble$	p~Rec
$\Psi \sim \text{Rec+Hunt}$	p~Rec
Ψ~1	p~Hunt
Ψ~VIS	p~Hunt
Ψ ~ Bramble	p~Hunt
Ψ ~ Rec	p~Hunt
Ψ ~ Hunt	p~Hunt
$\Psi \sim VIS+Rec$	p~Hunt
$\Psi \sim \text{Bramble+Rec}$	p~Hunt
Ψ ~ VIS+Hunt	p~Hunt
$\Psi \sim \text{Bramble+Hunt}$	p~Hunt
$\Psi \sim VIS+Bramble$	p~Hunt
$\Psi \sim \text{Rec+Hunt}$	p~Hunt
Ψ~1	p~Bioseason
$\Psi \sim VIS$	p~Bioseason

Ψ ~ Bramble	p~Bioseason
Ψ ~ Rec	p~Bioseason
Ψ ~ Hunt	p~Bioseason
Ψ ~ VIS+Rec	p~Bioseason
$\Psi \sim \text{Bramble+Rec}$	p~Bioseason
Ψ ~ VIS+Hunt	p~Bioseason
$\Psi \sim \text{Bramble+Hunt}$	p~Bioseason
$\Psi \sim VIS+Bramble$	p~Bioseason
Ψ~Rec+Hunt	p~Bioseason

S5.3. Candidate models for assessing effects of covariates on detection probability (p). Occupancy probability (Ψ) was modelled alongside p using single covariates.

p~1	Ψ~1
p ~ VIS	Ψ~1
p ~ Bramble	Ψ~1
p ~ Rec	Ψ~1
p ~ Hunt	Ψ~1
p ~ Bioseason	Ψ~1
p ~ VIS+Rec	Ψ~1
p ~ Bramble+Rec	Ψ~1
p ~ VIS+Hunt	Ψ~1
p ~ Bramble+Hunt	Ψ~1
p ~ VIS+Bramble	Ψ~1
p ~ Rec+Hunt	Ψ~1
, p ~ Bioseason+Rec	Ψ~1
, p ~ Bioseason+Hunt	Ψ~1
p ~ Bioseason+Bramble	Ψ~1
p ~ Bioseason+VIS	Ψ~1
p~1	Ψ~VIS
n ~ VIS	Ψ~VIS
n ~ Bramble	Ψ~VIS
n ~ Rec	Ψ~VIS
n ~ Hunt	Ψ~VIS
n ~ Bioseason	W~VIS
n ~ VIS+Bec	Ψ~VIS
$p \sim \text{Bramble+Rec}$	Ψ~VIS
$p \sim VIS+Hunt$	₩~\/IS
n ~ Bramble+Hunt	₩~\/IS
n ~ VIS+Bramble	Ψ~VIS
n ~ Rec+Hunt	₩~\/IS
$n \sim Bioseason+Bec$	₩~\/IS
n ~ Bioseason+Hunt	₩~\/IS
$p \sim Bioseason+Bramble$	₩~\/IS
p ~ Bioseason+VIS	₩~\/IS
p~1	Ψ VIS W∼Bramble
p + n ~ MS	♥ Bramble
p vis n ~ Bramble	
$p \approx V/S + Boc$	
$p = v_{13} + kec$	
p ^{ro} VIS+Hunt	Ψ [~] Bramble
p ~ Bramble+Hunt	Ψ~Bramble
p ^{···} vIS+Bramble	Ψ~Bramble
p ~ Rec+Hunt	Ψ~Bramble
p ~ Bioseason+Rec	Ψ~Bramble
p ~ Bioseason+Hunt	Ψ~Bramble

p ~ Bioseason+Bramble	Ψ~Bramble
p ~ Bioseason+VIS	Ψ~Bramble
p~1	Ψ~Rec
p ~ VIS	Ψ~Rec
p ~ Bramble	Ψ~Rec
p ~ Rec	Ψ~Rec
p ~ Hunt	Ψ~Rec
p ~ Bioseason	Ψ~Rec
p ~ VIS+Rec	Ψ~Rec
p ~ Bramble+Rec	Ψ~Rec
p ~ VIS+Hunt	Ψ~Rec
p ~ Bramble+Hunt	Ψ~Rec
p ~ VIS+Bramble	Ψ~Rec
p ~ Rec+Hunt	Ψ~Rec
p ~ Bioseason+Rec	Ψ~Rec
p ~ Bioseason+Hunt	Ψ~Rec
p ~ Bioseason+Bramble	Ψ~Rec
p ~ Bioseason+VIS	Ψ~Rec
p~1	Ψ~Hunt
p ~ VIS	Ψ~Hunt
p ~ Bramble	Ψ~Hunt
p ~ Rec	Ψ~Hunt
p ~ Hunt	Ψ~Hunt
p ~ Bioseason	Ψ~Hunt
p ~ VIS+Rec	Ψ~Hunt
p ~ Bramble+Rec	Ψ~Hunt
p ~ VIS+Hunt	Ψ~Hunt
p ~ Bramble+Hunt	Ψ~Hunt
p ~ VIS+Bramble	Ψ~Hunt
p ~ Rec+Hunt	Ψ~Hunt
p ~ Bioseason+Rec	Ψ~Hunt
p ~ Bioseason+Hunt	Ψ~Hunt
p ~ Bioseason+Bramble	Ψ~Hunt
p ~ Bioseason+VIS	Ψ~Hunt

S5.4. Corrected AIC table for models assessing effects of covariates on diurnal occupancy probability (Ψ) where model weight > 0. Detection probability (p) was modelled alongside Ψ using single covariates.

ID	Model	AIC	npar	warn.conv	warn.VC	DAIC	Model weight
44	Ψ(VIS+Hunt)p(Bramble)	3715.086	5	7	0	0	0.5543
45	Ψ(Bramble+Hunt)p(Bramble)	3715.592	5	7	0	0.5055	0.4305
34	Ψ(.)p(Bramble)	3725.002	3	7	0	9.9155	0.0039
37	Ψ(Bramble)p(Bramble)	3726.267	4	7	0	11.1804	0.0021
36	Ψ(VIS)p(Bramble)	3726.659	4	7	0	11.5726	0.0017
46	Ψ(VIS+Bramble)p(Bramble)	3726.709	5	7	0	11.6228	0.0017
38	Ψ(Rec)p(Bramble)	3726.891	4	7	0	11.8052	0.0015
35	Ψ(Bioseason)p(Bramble)	3727.349	5	7	0	12.2629	0.0012
43	Ψ(Bramble P Rec)p(Bramble)	3727.963	5	7	0	12.8768	9.00E-04
40	Ψ(Bioseason P Bramble)p(Bramble)	3728.594	6	7	0	13.5078	6.00E-04
42	Ψ(VIS P Rec)p(Bramble)	3728.608	5	7	0	13.5221	6.00E-04
39	Ψ(Bioseason P VIS)p(Bramble)	3728.998	6	7	0	13.9121	5.00E-04
41	Ψ(Bioseason P Rec)p(Bramble)	3729.235	6	7	0	14.1493	5.00E-04

S5.5. Summed Akaike weights for covariates modelled against diurnal occupancy probability (Ψ) for models where model weight > 0

Covariate	Ψ AIC weight
Hunt	0.98
VIS	0.56
Bramble	0.44
Rec	0
Bioseason	0

S5.6. Corrected AIC table for models assessing effects of covariates on diurnal detection probability (p) where model weight > 0. Occupancy probability (Ψ) was modelled alongside Ψ using single covariates.

ID	Model	AIC	npar	warn.conv	warn.VC	DAIC	Model weight
78	Ψ(Hunt)p(Bramble+Hunt)	3512.927	5	7	0	0	0.9896
14	Ψ(.)p(Bramble+Hunt)	3523.683	4	7	0	10.7563	0.0046
62	Ψ(Bramble)p(Bramble+ Hunt)	3524.953	5	7	0	12.0264	0.0024
46	Ψ(VIS)p(Bramble+Hunt)	3525.29	5	7	0	12.3638	0.002
30	Ψ(Bioseason)p(Bramble+Hunt)	3526.09	6	7	0	13.1631	0.0014

S5.7. Summed Akaike weights for covariates modelled against diurnal detection probability (p) for models where model weight > 0

Covariate	p AIC weight
Bramble	1
Hunt	1
Bioseason	0
VIS	0
Rec	0

S5.8. Corrected AIC table for models assessing effects of covariates on crepuscular occupancy probability (Ψ) where model weight > 0. Detection probability (p) was modelled alongside Ψ using single covariates.

ID	Model	AIC	neg2ll	npar	warn.conv	warn.VC	DAIC	Model weight
16	$\Psi(.)p(Bioseason)$	2942	2934	4	7	0	0	0.2123
19	$\Psi(Bramble)p(Bioseason)$	2942.937	2932.937	5	7	0	0.9369	0.1329
18	$\Psi(VIS)p(Bioseason)$	2943.011	2933.011	5	7	0	1.0111	0.1281
20	Ψ(Rec)p(Bioseason)	2943.681	2933.681	5	7	0	1.6802	0.0917
29	Ψ (VIS P Bramble)p(Bioseason)	2944.583	2932.583	6	7	0	2.5825	0.0584
28	$\Psi(Bramble P Hunt)p(Bioseason)$	2944.624	2932.624	6	7	0	2.6233	0.0572
26	Ψ(Bramble+Rec)p(Bioseason)	2944.828	2932.828	6	7	0	2.8272	0.0517
25	Ψ(VIS+Rec)p(Bioseason)	2944.835	2932.835	6	7	0	2.8343	0.0515
27	Ψ(VIS+Hunt)p(Bioseason)	2945.005	2933.005	6	7	0	3.0046	0.0473
17	Ψ(Bioseason)p(Bioseason)	2945.439	2933.439	6	7	0	3.4384	0.0381
22	Ψ(Bioseason+	2946 199	2932 199	7	7	0	4 1985	0.026
~~~	Bramble)p(Bioseason)	2340.133	2552.155	,	,	Ū	4.1505	0.020
21	Ψ(Bioseason+VIS)p(Bioseason)	2946.288	2932.288	7	7	0	4.2878	0.0249
23	Ψ(Bioseason+Rec)p(Bioseason)	2947.051	2933.051	7	7	0	5.0507	0.017
24	Ψ(Bioseason+Hunt)p(Bioseason)	2947.439	2933.439	7	7	0	5.4384	0.014
69	Ψ(.)p(Hunt)	2947.736	2941.736	3	7	0	5.7359	0.0121
71	Ψ(Bramble)p(Hunt)	2948.784	2940.784	4	7	0	6.7837	0.0071
70	Ψ(VIS)p(Hunt)	2948.84	2940.84	4	7	0	6.8392	0.0069
72	Ψ(Rec)p(Hunt)	2949.47	2941.47	4	7	0	7.4696	0.0051
76	Ψ(Bramble+Hunt)p(Hunt)	2950.45	2940.45	5	7	0	8.4499	0.0031
77	Ψ(VIS+Bramble)p(Hunt)	2950.463	2940.463	5	7	0	8.4626	0.0031
75	Ψ(VIS+Rec)p(Hunt)	2950.7	2940.7	5	7	0	8.6995	0.0027
30	Ψ(.)p(VIS)	2951.927	2945.927	3	7	0	9.9263	0.0015
73	Ψ(Bioseason+Bramble)p(Hunt)	2952.203	2940.203	6	7	0	10.2027	0.0013
32	Ψ(Bramble)p(VIS)	2952.725	2944.725	4	7	0	10.7246	0.001
31	Ψ(VIS)p(VIS)	2952.791	2944.791	4	7	0	10.7905	0.001
74	Ψ(Bioseason+Rec)p(Hunt)	2952.971	2940.971	6	7	0	10.9705	9.00E-04
33	Ψ(Rec)p(VIS)	2953.569	2945.569	4	7	0	11.5691	7.00E-04
40	Ψ(VIS+Bramble)p(VIS)	2954.317	2944.317	5	7	0	12.3165	4.00E-04
39	Ψ(Bramble+Hunt)p(VIS)	2954.429	2944.429	5	7	0	12.4288	4.00E-04
37	Ψ(VIS+Rec)p(VIS)	2954.6	2944.6	5	7	0	12.5994	4.00E-04
38	Ψ(Bramble+Rec)p(VIS)	2954.606	2944.606	5	7	0	12.6053	4.00E-04
35	Ψ(Bioseason+Bramble)p(VIS)	2955.933	2943.933	6	7	0	13.9323	2.00E-04
34	Ψ(BIOSEASO+VIS)p(VIS)	2956.013	2944.013	6	7	0	14.0129	2.00E-04
36	Ψ(Bioseason+Rec)p(VIS)	2956.894	2944.894	6	7	0	14.8932	1.00E-04
41	Ψ(.)p(Bramble)	2957.067	2951.067	3	7	0	15.0671	1.00E-04
43	Ψ(Bramble)p(Bramble)	2958.074	2950.074	4	7	0	16.0739	1.00E-04
42	Ψ(VIS)p(Bramble)	2958.133	2950.133	4	7	0	16.1329	1.00E-04

S5.9.	Summed	Akaike	weights for	covariates	s modelled	against	crepuscular	occupancy	probability
(Ψ) f	or models	where r	nodel weig	ht > 0					

Covariate	Ψ AIC weight
Bramble	0.34
VIS	0.32
Rec	0.22
Bioseason	0.12

**S5.10.** Corrected AIC table for models assessing effects of covariates on crepuscular detection probability (*p*) where model weight > 0. Occupancy probability ( $\Psi$ ) was modelled alongside  $\Psi$  using single covariates.

ID	Model	AIC	npar	warn.conv	warn.VC	DAIC	Model weight
10	Ψ(.) <i>p</i> (Bioseason+Hunt)	2931.399	5	7	0	0	0.3429
50	Ψ(Bramble)p(Bioseason+Hunt)	2932.452	6	7	0	1.0528	0.2026
34	Ψ(VIS)p(Bioseason+Hunt)	2932.515	6	7	0	1.1163	0.1962
65	Ψ(Rec)p(Bioseason+Hunt)	2933.124	6	7	0	1.7255	0.1447
22	Ψ(Bioseason)p(Bioseason+Hunt)	2934.913	7	7	0	3.5138	0.0592
7	Ψ(.)p(Bioseason+VIS)	2938.447	5	7	0	7.0481	0.0101
47	Ψ(Bramble)p(Bioseason+VIS)	2939.257	6	7	0	7.858	0.0067
31	Ψ(VIS)p(Bioseason+VIS)	2939.335	6	7	0	7.9357	0.0065
62	Ψ(Rec)p(Bioseason+VIS)	2940.08	6	7	0	8.6815	0.0045
74	Ψ(Hunt)p(Bioseason+VIS)	2940.447	6	7	0	9.0481	0.0037
8	Ψ(.)p(Bioseason+Bramble)	2940.667	5	7	0	9.2683	0.0033
48	Ψ(Bramble)p(Bioseason+Bramble)	2941.688	6	7	0	10.2888	0.002
32	Ψ(VIS)p(Bioseason+Bramble)	2941.756	6	7	0	10.3575	0.0019
20	Ψ(Bioseason)p(Bioseason+VIS)	2941.808	7	7	0	10.4096	0.0019
2	Ψ(.)p(Bioseason)	2942	4	7	0	10.6015	0.0017
63	Ψ(Rec)p(Bioseason+Bramble)	2942.379	6	7	0	10.9804	0.0014
75	Ψ(Hunt)p(Bioseason+Bramble)	2942.662	6	7	0	11.2631	0.0012
42	Ψ(Bramble)p(Bioseason)	2942.937	5	7	0	11.5384	0.0011
26	Ψ(VIS)p(Bioseason)	2943.011	5	7	0	11.6126	0.001
13	Ψ(.)p(VIS+Hunt)	2943.352	4	7	0	11.9536	9.00E-04
9	Ψ(.)p(Bioseason+Rec)	2943.411	5	7	0	12.0118	8.00E-04
57	Ψ(Rec)p(Bioseason)	2943.681	5	7	0	12.2817	7.00E-04
53	Ψ(Bramble)p(VIS+Hunt)	2944.287	5	7	0	12.8878	5.00E-04
49	Ψ(Bramble)p(Bioseason+Rec)	2944.32	6	7	0	12.9207	5.00E-04
37	Ψ(VIS)p(VIS+Hunt)	2944.346	5	7	0	12.9467	5.00E-04
33	Ψ(VIS)p(Bioseason+Rec)	2944.396	6	7	0	12.9973	5.00E-04
68	Ψ(Rec)p(VIS+Hunt)	2945.046	5	7	0	13.6471	4.00E-04
64	Ψ(Rec)p(Bioseason+Rec)	2945.079	6	7	0	13.6802	4.00E-04
78	Ψ(Hunt)p(VIS+Hunt)	2945.351	5	7	0	13.9517	3.00E-04
18	Ψ(Bioseason)p(Bioseason)	2945.439	6	7	0	14.0399	3.00E-04
15	Ψ(.)p(VIS+Bramble)	2946.176	4	7	0	14.7773	2.00E-04
21	Ψ(Bioseason)p(Bioseason+Rec)	2946.829	7	7	0	15.4297	2.00E-04
55	Ψ(Bramble)p(VIS+Bramble)	2947.079	5	7	0	15.68	1.00E-04
39	Ψ(VIS)p(VIS+Bramble)	2947.138	5	7	0	15.7394	1.00E-04
6	Ψ(.)p(Hunt)	2947.736	3	7	0	16.3374	1.00E-04
70	$\Psi(\text{Rec})p(\text{VIS+Bramble})$	2947.857	5	7	0	16.4584	1.00E-04
16	Ψ(.)p(Rec+Hunt)	2948.622	4	7	0	17.2236	1.00E-04
46	Ψ(Bramble)p(Hunt)	2948.784	4	7	0	17.3852	1.00E-04
30	Ψ(VIS)p(Hunt)	2948.84	4	7	0	17.4407	1.00E-04

**S5.11.** Summed Akaike weights for covariates modelled against crepuscular detection probability (p) for models where model weight > 0.

Covariate	p AIC weight
Bioseason	1
Hunt	0.95
VIS	0.04
Bramble	0.01
Rec	0

**S5.12.** Corrected AIC table for models assessing effects of covariates on nocturnal occupancy probability ( $\Psi$ ) where model weight > 0. Detection probability (p) was modelled alongside  $\Psi$  using single covariates.

ID	Model	AIC	npar	warn.conv	warn.VC	DAIC	wgt
17	Ψ(.)p(Bioseason)	2119.343	4	7	0	0	0.116
58	Ψ(.)p(Rec)	2120.289	3	7	0	0.9463	0.0723
19	Ψ(VIS)p(Bioseason)	2120.366	5	7	0	1.0229	0.0696
21	Ψ(Rec)p(Bioseason)	2120.431	5	7	0	1.0882	0.0673
22	Ψ(Hunt)p(Bioseason)	2120.936	5	7	0	1.5932	0.0523
24	Ψ(VIS+Rec)p(Bioseason)	2121.069	6	7	0	1.7257	0.0489
59	Ψ(VIS)p(Rec)	2121.193	4	7	0	1.85	0.046
20	Ψ(Bramble)p(Bioseason)	2121.276	5	7	0	1.9336	0.0441
18	Ψ(Bioseason)p(Bioseason)	2121.344	6	7	0	2.0016	0.0426
61	Ψ(Rec)p(Rec)	2121.481	4	7	0	2.1385	0.0398
26	Ψ(VIS+Hunt)p(Bioseason)	2121.898	6	7	0	2.5553	0.0323
62	Ψ(Hunt)p(Rec)	2121.932	4	7	0	2.5889	0.0318
29	Ψ(Rec+Hunt)p(Bioseason)	2121.963	6	7	0	2.6199	0.0313
66	Ψ(VIS+Rec)p(Rec)	2121.999	5	7	0	2.6565	0.0307
25	Ψ(Bramble+Rec)p(Bioseason)	2122.181	6	7	0	2.8384	0.0281
60	Ψ(Bramble)p(Rec)	2122.188	4	7	0	2.8451	0.028
28	Ψ(VIS+Bramble)p(Bioseason)	2122.312	6	7	0	2.9692	0.0263
27	Ψ(Bramble+Hunt)p(Bioseason)	2122.6	6	7	0	3.257	0.0228
68	Ψ(VIS+Hunt)p(Rec)	2122.775	5	7	0	3.4322	0.0209
23	Ψ(Bioseason+Hunt)p(Bioseason)	2122.856	7	7	0	3.5133	0.02
71	Ψ(Rec+Hunt)p(Rec)	2123.069	5	7	0	3.7265	0.018
70	Ψ(VIS+Bramble)p(Rec)	2123.155	5	7	0	3.8119	0.0172
67	Ψ(Bramble+Rec)p(Rec)	2123.179	5	7	0	3.8366	0.017
63	Ψ(Bioseason+VIS)p(Rec)	2123.359	6	7	0	4.0166	0.0156
64	Ψ(Bioseason+Rec)p(Rec)	2123.408	6	7	0	4.0656	0.0152
69	Ψ(Bramble+Hunt)p(Rec)	2123.534	5	7	0	4.1912	0.0143
65	Ψ(Bioseason+Hunt)p(Rec)	2123.939	6	7	0	4.5961	0.0117
45	Ψ(.)p(Bramble)	2127.341	3	7	0	7.9977	0.0021
48	Ψ(Rec)p(Bramble)	2128.342	4	7	0	8.9996	0.0013
46	Ψ(VIS)p(Bramble)	2128.445	4	7	0	9.1024	0.0012
49	Ψ(Hunt)p(Bramble)	2128.892	4	7	0	9.5495	0.001
72	Ψ(.)p(Hunt)	2128.936	3	7	0	9.5936	0.001
52	$\Psi(VIS+Rec)p(Bramble)$	2129.064	5	7	0	9.7207	9.00E-04
47	Ψ(Bramble)p(Bramble)	2129.296	4	7	0	9.9533	8.00E-04
30	Ψ(.)p(VIS)	2129.354	3	7	0	10.0116	8.00E-04
57	Ψ(Rec+Hunt)p(Bramble)	2129.828	5	7	0	10.485	6.00E-04
54	Ψ(VIS+Hunt)p(Bramble)	2129.934	5	7	0	10.5913	6.00E-04
75	Ψ(Rec)p(Hunt)	2129.967	4	7	0	10.6239	6.00E-04
73	Ψ(VIS)p(Hunt)	2130.008	4	7	0	10.6649	6.00E-04

51	Ψ(Bioseason+Rec)p(Bramble)	2130.05	6	7	0	10.7072	5.00E-04
53	Ψ(Bramble+Rec)p(Bramble)	2130.128	5	7	0	10.785	5.00E-04
31	Ψ(VIS)p(VIS)	2130.265	4	7	0	10.9219	5.00E-04
56	$\Psi$ (VIS+Bramble)p(Bramble)	2130.376	5	7	0	11.0328	5.00E-04
50	Ψ(Bioseason+VIS)p(Bramble)	2130.379	6	7	0	11.0362	5.00E-04
33	Ψ(Rec)p(VIS)	2130.474	4	7	0	11.1313	4.00E-04
76	Ψ(Hunt)p(Hunt)	2130.491	4	7	0	11.1482	4.00E-04
55	Ψ(Bramble+Hunt)p(Bramble)	2130.598	5	7	0	11.2556	4.00E-04
78	Ψ(VIS+Rec)p(Hunt)	2130.648	5	7	0	11.3055	4.00E-04
74	Ψ(Bramble)p(Hunt)	2130.881	4	7	0	11.5378	4.00E-04
39	Ψ(VIS+Rec)p(VIS)	2130.976	5	7	0	11.6332	3.00E-04
34	Ψ(Hunt)p(VIS)	2131.001	4	7	0	11.6578	3.00E-04
32	Ψ(Bramble)p(VIS)	2131.254	4	7	0	11.9115	3.00E-04
83	Ψ(Rec+Hunt)p(Hunt)	2131.463	5	7	0	12.1197	3.00E-04
80	Ψ(VIS+Hunt)p(Hunt)	2131.497	5	7	0	12.1542	3.00E-04
79	Ψ(Bramble+Rec)p(Hunt)	2131.73	5	7	0	12.3873	2.00E-04
41	Ψ(VIS+Hunt)p(VIS)	2131.849	5	7	0	12.5058	2.00E-04
82	Ψ(VIS+Bramble)p(Hunt)	2131.948	5	7	0	12.6055	2.00E-04
44	Ψ(Rec+Hunt)p(VIS)	2132.064	5	7	0	12.7207	2.00E-04
40	Ψ(Bramble+Rec)p(VIS)	2132.163	5	7	0	12.8202	2.00E-04
81	Ψ(Bramble+Hunt)p(Hunt)	2132.166	5	7	0	12.8235	2.00E-04
43	Ψ(VIS+Bramble)p(VIS)	2132.226	5	7	0	12.8836	2.00E-04
37	Ψ(Bioseason+Rec)p(VIS)	2132.315	6	7	0	12.9718	2.00E-04
35	Ψ(Bioseason+VIS)p(VIS)	2132.334	6	7	0	12.9915	2.00E-04
42	Ψ(Bramble+Hunt)p(VIS)	2132.61	5	7	0	13.2673	2.00E-04
77	Ψ(Bioseason+Bramble)p(Hunt)	2132.779	6	7	0	13.4363	1.00E-04
38	Ψ(Bioseason+Hunt)p(VIS)	2132.907	6	7	0	13.5645	1.00E-04
3	Ψ(VIS)p(.)	2133.141	3	7	0	13.7984	1.00E-04
36	Ψ(Bioseason+Bramble)p(VIS)	2133.27	6	7	0	13.9267	1.00E-04
11	Ψ(VIS+Rec)p(.)	2133.811	4	7	0	14.4685	1.00E-04
Covariate	Ψ AlC weight						
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VIS	0.31						
Rec	0.3						
Hunt	0.26						
Bramble	0.2						
Bioseason	0.11						

**S5.13.** Summed Akaike weights for covariates modelled against nocturnal occupancy probability  $(\Psi)$  for models where model weight > 0.

**S5.14.** Corrected AIC table for models assessing effects of covariates on nocturnal detection probability (*p*) where model weight > 0. Occupancy probability ( $\Psi$ ) was modelled alongside  $\Psi$  using single covariates.

ID	Model	AIC	npar	warn.conv	warn.VC	DAIC	wgt
9	Ψ(.)p(Bioseason+Rec)	2108.832	5	7	0	0	0.2083
32	Ψ(VIS)p(Bioseason+Rec)	2109.764	6	7	0	0.9323	0.1307
61	Ψ(Rec)p(Bioseason+Rec)	2110.079	6	7	0	1.2478	0.1116
77	Ψ(Hunt)p(Bioseason+Rec)	2110.466	6	7	0	1.6339	0.092
8	Ψ(.)p(Bioseason+Bramble)	2110.69	5	7	0	1.8586	0.0823
60	Ψ(Rec)p(Bioseason+Bramble)	2111.665	6	7	0	2.8332	0.0505
31	Ψ(VIS)p(Bioseason+Bramble)	2111.853	6	7	0	3.021	0.046
12	Ψ(.)p(Bramble+Rec)	2112.068	4	7	0	3.2363	0.0413
76	Ψ(Hunt)p(Bioseason+Bramble)	2112.178	6	7	0	3.3459	0.0391
20	Ψ(Bioseason)p(Bioseason+Bramble)	2112.628	7	7	0	3.7959	0.0312
47	Ψ(Bramble)p(Bioseason+Bramble)	2112.668	6	7	0	3.8367	0.0306
35	Ψ(VIS)p(Bramble+Rec)	2113.084	5	7	0	4.2523	0.0249
64	Ψ(Rec)p(Bramble+Rec)	2113.221	5	7	0	4.3889	0.0232
80	Ψ(Hunt)p(Bramble+Rec)	2113.656	5	7	0	4.824	0.0187
50	Ψ(Bramble)p(Bramble+Rec)	2114.009	5	7	0	5.1773	0.0157
10	Ψ(.)p(Bioseason+Hunt)	2115.916	5	7	0	7.0846	0.006
15	Ψ(.)p(VIS+Bramble)	2116.48	4	7	0	7.6486	0.0045
62	Ψ(Rec)p(Bioseason+Hunt)	2116.949	6	7	0	8.1173	0.0036
33	Ψ(VIS)p(Bioseason+Hunt)	2117.011	6	7	0	8.1792	0.0035
78	Ψ(Hunt)p(Bioseason+Hunt)	2117.434	6	7	0	8.6028	0.0028
38	Ψ(VIS)p(VIS+Bramble)	2117.474	5	7	0	8.6423	0.0028
67	Ψ(Rec)p(VIS+Bramble)	2117.532	5	7	0	8.7006	0.0027
21	Ψ(Bioseason)p(Bioseason+Hunt)	2117.852	7	7	0	9.02	0.0023
48	Ψ(Bramble)p(Bioseason+Hunt)	2117.871	6	7	0	9.0391	0.0023
83	Ψ(Hunt)p(VIS+Bramble)	2118.069	5	7	0	9.2371	0.0021
23	Ψ(Bioseason)p(VIS+Bramble)	2118.4	6	7	0	9.5681	0.0017
7	Ψ(.)p(Bioseason+VIS)	2118.498	5	7	0	9.6661	0.0017
16	Ψ(.)p(Rec+Hunt)	2118.975	4	7	0	10.1432	0.0013
11	Ψ(.)p(VIS+Rec)	2119.177	4	7	0	10.3451	0.0012

2	Ψ(.)p(Bioseason)	2119.343	4	7	0	10.5112	0.0011
30	Ψ(VIS)p(Bioseason+VIS)	2119.445	6	7	0	10.6134	0.001
59	Ψ(Rec)p(Bioseason+VIS)	2119.617	6	7	0	10.7855	9.00E-04
39	Ψ(VIS)p(Rec+Hunt)	2119.944	5	7	0	11.1126	8.00E-04
34	Ψ(VIS)p(VIS+Rec)	2119.997	5	7	0	11.165	8.00E-04
75	Ψ(Hunt)p(Bioseason+VIS)	2120.121	6	7	0	11.289	7.00E-04
68	Ψ(Rec)p(Rec+Hunt)	2120.131	5	7	0	11.2993	7.00E-04
5	Ψ(.)p(Rec)	2120.289	3	7	0	11.4575	7.00E-04
25	Ψ(VIS)p(Bioseason)	2120.366	5	7	0	11.5341	7.00E-04
63	Ψ(Rec)p(VIS+Rec)	2120.404	5	7	0	11.5725	6.00E-04
46	Ψ(Bramble)p(Bioseason+VIS)	2120.414	6	7	0	11.5822	6.00E-04
54	Ψ(Rec)p(Bioseason)	2120.431	5	7	0	11.5994	6.00E-04
19	Ψ(Bioseason)p(Bioseason+VIS)	2120.533	7	7	0	11.7013	6.00E-04
84	Ψ(Hunt)p(Rec+Hunt)	2120.561	5	7	0	11.7291	6.00E-04
79	Ψ(Hunt)p(VIS+Rec)	2120.853	5	7	0	12.0211	5.00E-04
52	$\Psi(Bramble)p(Rec+Hunt)$	2120.893	5	7	0	12.0612	5.00E-04
70	Ψ(Hunt)p(Bioseason)	2120.936	5	7	0	12.1044	5.00E-04
49	Ψ(Bramble)p(VIS+Rec)	2121.051	5	7	0	12.219	5.00E-04
28	Ψ(VIS)p(Rec)	2121.193	4	7	0	12.3612	4.00E-04
41	Ψ(Bramble)p(Bioseason)	2121.276	5	7	0	12.4448	4.00E-04
22	Ψ(Bioseason)p(VIS+Rec)	2121.286	6	7	0	12.454	4.00E-04
18	Ψ(Bioseason)p(Bioseason)	2121.344	6	7	0	12.5128	4.00E-04
57	Ψ(Rec)p(Rec)	2121.481	4	7	0	12.6497	4.00E-04
73	Ψ(Hunt)p(Rec)	2121.932	4	7	0	13.1001	3.00E-04
44	Ψ(Bramble)p(Rec)	2122.188	4	7	0	13.3563	3.00E-04

**S5.15.** Summed Akaike weights for covariates modelled against nocturnal detection probability (p) for models where model weight > 0.

Covariate	p AIC weight
Bioseason	0.85
Rec	0.68
Bramble	0.42
Hunt	0.02
VIS	0.02

### S6.1. Faecal sample preparation

Prior to starting work, the workbench was cleaned with 10% bleach solution and all pipettes, racks and pipette tips were exposed to UV light in a hood for at least 20 minutes. Faecal samples were defrosted at room temperature. A scalpel and tweezers were dipped in 70% ethanol and held in a Bunsen burner flame after each sample, and periodically cleaned with 10% bleach. At first, faecal pellets were placed on a clean glass tile and the external part of the pellet was cut off, the centre extracted using the tweezers and the external parts discarded. This was to minimise any contamination from exterior sources such as aerial pollen or soil. However, this process was deemed inefficient as it greatly lengthened the amount of time spent processing each sample. Therefore, the final method involved removing any obvious contaminants such as pieces of vegetation using the tweezers and scalpel but retaining whole pellets. Each sample was then homogenised using a mortar and pestle. Each mortar and pestle set were cleaned with 10% bleach between samples. A portion of 0.04 - 0.08 g of crushed faecal material was weighed out in a plastic weigh boat. The remaining faecal material was then returned to storage at -20 °C in their original containers, unless the container was particularly soiled by invertebrates which has emerged from the sample when it was first frozen, in which case the remaining material was frozen in a new falcon tube.

Where there was no time to perform DNA extractions following sample preparation, samples were refrozen in 1.5 millilitre microcentrifuge tubes at -20 °C.

## S6.2. DNA extraction protocol

- UV racks, tips, tubes etc.
- UV ethanol
- Soak steel beads in bleach, rinse in water then soak in ethanol. Rinse in water before use.
- Warm buffer AP1 to 65°C on heat block
- Remember to include a tube for negative control!
- Make lysis solution:
  - Buffer AP1 @ 400 ul per sample
  - RNase A (100mg/ml) @ 1ul per sample *spin down RNase A
  - Protenaise K (20mg/ml) @ 4ul per sample *defrost & vortex to mix

### Protocol:

- 1. Place a steel bead inside the tube with the sample
- 2. Add 405 µl lysis solution to sample
- 3. Place lid locks on all samples / tape lids if no lid locks
- 4. Bead beat sample for 4 mins / 30hz / 1800 rpm
- 5. Remove lid locks / tape
- 6. Incubate samples @ 65°C for 30 mins
- 7. Cool tubes to RT (can store samples overnight)
- 8. Micro centrifuge tubes (few secs)
- 9. Add Buffer P3 @ 130 ul per sample *Change tip each time
- 10. Shake all samples up and down for 15 secs
- 11. Micro centrifuge for a few seconds
- 12. Incubate sample in  $-20^{\circ}$ C for 10 mins
- 13. Centrifuge @ 14,000 rpm for 5 mins
- 14. Transfer liquid from each sample into new 1.5ml micro centrifuge tube
- 15. Centrifuge again @ 14,000 rpm for 5 mins
- 16. Transfer liquid from each sample into new 1.5ml micro centrifuge tube
- 17. Add 600 ul Buffer AW1 to each sample (this should be ~1.5 x volume therefore 600 ul)
- 18. Shake vigorously up and down for 15 secs
- 19. Centrifuge @ 3000rpm
- 20. Transfer 650 ul of this mixture into a labelled DNeasy mini spin column placed in a 2 ml collection tube
- 21. Centrifuge for 1 min @ **14,000** rpm
- 22. Discard the flowthrough
- 23. Repeat steps (21-22) until samples are empty
- 24. Place spin column into new 2ml collection tube
- 25. Add 500 ul Buffer AW2
- 26. Centrifuge for 1 min @ 14,000 rpm
- 27. Discard the flow through
- 28. Add another 500 ul Buffer AW2
- 29. Centrifuge for 2 mins @ 14,000 rpm
- 30. Discard the flow through
- 31. Add 500 ul ethanol (96-100%)
- 32. Centrifuge for 2 mins @ 14,000 rpm
- 33. Remove spin column carefully so it doesn't come into contact with flow through
- 34. Transfer the spin column into a new 1.5ml micro centrifuge tube *SNIP LIDS!
- 35. Elution step: Add 60 ul Buffer AE
- 36. Incubate @ RT for 10 mins
- 37. Centrifuge for 1 min @ 8000 rpm
- 38. Transfer the elution back into the spin column on to the membrane
- 39. Incubate @ RT for 10 mins
- 40. Centrifuge for 1 min @ 8000 rpm
- 41. Discard the spin column
- 42. Aliquot DNA from snipped 1.5ml tubes into a new 1.5ml tube
- 43. If using Q-BIT aliquot out accordingly
- 44. Store samples at -20°C
- 45. Remove steel beads from original tubes and soak in 50% bleach

# S6.3. Bead clean-up protocol for 25 ul volume

### Reagents required:

80% freshly prepared Ethanol

e.g for a final volume of 10 ml, add 8 ml of 100% ethanol to 2 ml of distilled water, Or can make up 40 ml of ethanol with 10 ml ultrapure water

- Agencourt[®] AMPure[®] XP (Beckman Coulter)

Preparation: UV following equipment for 20 minutes:

- New storage plate + strip caps (if needed)
- PCR water storage plate
- 8 tube strip and strip caps
- Rack + 1.5ml tube for bead aliquot
- Pipette tips
- Multichannel + single channel pipettes

### **Protocol** :

- 1. Leave the Agencourt AMPure XP bottle at room temperature for 30 minutes.
- 2. Gently shake the AMPure XP bottle to re-suspend any magnetic particles that may have settled. Check the bottom of the bottle to see if the beads are stuck to it. Can vortex a little and tap to "spin down".
- 3. Aliquot out some to prevent future contamination (number of samples + extra for pipetting error + extra again for pipetting into strip).
- 4. Split the beads into an 8-tube strip for the multi-channel pipette according to the number of rows you are doing.
- 5. Add **17.5** µl of Agencourt AMPure XP to **25** µl of Round 1 PCR product (0.7x)
- 6. Mix reagent and PCR product thoroughly by pipette mixing 15 times. Let the mixed samples incubate for **5 minutes** at room temperature for maximum recovery.
- 7. Quick spin (optional < 500rpm) and place the 96-well plate onto an Agencourt SPRIPlate 96 Super Magnet Plate for **5 minutes** to separate beads from the solution.
- Using 200ul or 100ul tips, remove very slowly the cleared solution (around 43 μl) from the 96 well PCR plate, making sure not to disturb the ring of separated magnetic beads (or remove from one side if using a strip). Discard the cleared solution.
- 9. With the PCR plate still on the magnetic plate, add **200 μl** of freshly prepared 80% ethanol (made fresh each day, in a 15ml falcon tube 8ml 100% etoh and 2ml distilled water) to each well and incubate for 30 seconds at room temperature.
- 10. Using 200 ul tips, very slowly remove the ethanol and discard.
- 11. Add **200 µl** of freshly prepared 80% ethanol to each well and incubate for 30 seconds at room temperature.
- 12. Using 200 ul tips, very slowly remove the ethanol and discard. For the second ethanol wash, be sure to remove all the ethanol from the bottom of the well as it is a known PCR inhibitor. Use 10ul tips to remove any final drops.
- 13. Still on the magnetic plate, dry for 3 minutes at room temperature to ensure all traces of ethanol are removed. Watch for ethanol droplets and make sure they have evaporated before proceeding. Don't leave for much longer than 4 mins as the beads will dry out (but this is variable).
- 14. Take the PCR plate off the magnetic plate, then add **26ul µl of PCR water** to each well of the 96-well plate and pipette mix 10 times. Make sure that the beads are put back in suspension and well mixed.
- 15. Incubate on bench for 5 minutes, spin down (optional: incubate at 37°C in PCR machine if beads are not well mixed, make sure lid is at 37°C).
- 16. Place the PCR plate onto an Agencourt SPRIPlate 96 Super Magnet Plate for 5 minute to separate beads from the solution.
- 17. Using 200 ul tips, transfer 25 μl of the eluent to individual PCR tubes, leaving a few microlitres behind if necessary, to ensure no beads are in the final elution. If beads are drawn out, leave a few microliters behind. If beads are present in the pipette tip, resuspend the beads and try again.

**S6.4.** List of final pools for ITS2 and rbcL. Number of samples includes positive controls (one per plate), first and second round PCR controls (one each per plate) and negative controls for DNA extractions (2-3 per plate). The peak size indicates the average base pair length for the PCR amplicons in each pool. The peak size and concentration were recorded on the 4150 TapeStation System (Agilent).

Marker	Pool ID	Pool contents	Number of samples	Peak size	Peak conc ng/ul
ITS2	Pool 1	No band plate 1 + 2	31	494	0.60
ITS2	Pool 2	No band plate 3 + 4	25	509	3.70
ITS2	Pool 3	Weak plate 1 + 4	43	510	4.94
ITS2	Pool 4	Weak plate 2 + 3	24	505	1.85
ITS2	Pool 5	Medium plate 1 + 4	38	507	6.32
ITS2	Pool 6	Medium plate 2 + 3	40	508	2.90
ITS2	Pool 7	Strong plate 1	33	501	9.99
ITS2	Pool 8	Strong plate 2	31	518	2.49
ITS2	Pool 9	Strong plate 3 A	36	515	18.10
ITS2	Pool 10	Strong plate 3 B	35	508	11.70
ITS2	Pool 11	Strong plate 4	27	509	12.00
rbcL	Pool 12	No band plate 1 + 2	33	666	0.33
rbcL	Pool 13	No band plate 3 + 4	34	666	1.44
rbcL	Pool 14	Weak plate 1 + 2	35	669	2.42
rbcL	Pool 15	Weak plate 3 + 4	32	664	5.42
rbcL	Pool 16	Medium plate 1 + 3	26	670	9.08
rbcL	Pool 17	Medium plate 2 + 4	31	675	9.78
rbcL	Pool 18	Strong plate 1	29	667	15.60
rbcL	Pool 19	Strong plate 2 A	26	679	6.21
rbcL	Pool 20	Strong plate 2 B	27	688	6.05
rbcL	Pool 21	Strong plate 3	40	666	19.60
rbcL	Pool 22	Strong plate 4	38	672	24.70

Marker	Pool ID	Pool	ng/ul	n Samples	ng per sample	Volume	ng in pool
ITS2	Pool 1	No band plate 1 + 2	0.60	31	1.10	57.4	34.21
ITS2	Pool 4	Weak plate 2 + 3	1.85	24	3.43	44.4	82.22
ITS2	Pool 8	Strong plate 2	2.49	31	1.82	22.6	56.39
ITS2	Pool 6	Medium plate 2 + 3	2.90	40	2.12	29.2	84.74
ITS2	Pool 2	No band plate 3 + 4	3.70	25	2.70	18.3	67.57
ITS2	Pool 3	Weak plate 1 + 4	4.94	43	3.61	31.4	155.18
ITS2	Pool 5	Medium plate 1 + 4	6.32	38	4.62	27.8	175.44
ITS2	Pool 7	Strong plate 1	9.99	33	7.30	24.1	240.83
ITS2	Pool 10	Strong plate 3 B	11.70	35	8.55	25.6	299.15
ITS2	Pool 11	Strong plate 4	12.00	27	8.77	19.7	236.69
ITS2	Pool 9	Strong plate 3 A	18.10	36	13.22	26.3	476.01
rbcL	Pool 12	No band plate 1 + 2	0.33	33	0.43	42.9	14.14
rbcL	Pool 13	No band plate 3 + 4	1.44	34	1.87	44.2	63.58
rbcL	Pool 14	Weak plate 1 + 2	2.42	35	1.92	27.7	67.10
rbcL	Pool 15	Weak plate 3 + 4	5.42	32	4.29	25.4	137.41
rbcL	Pool 16	Medium plate 1 + 3	9.08	26	7.19	20.6	187.04
rbcL	Pool 17	Medium plate 2 + 4	9.78	31	7.75	24.6	240.20
rbcL	Pool 18	Strong plate 1	15.60	29	12.36	23.0	358.42
rbcL	Pool 19	Strong plate 2 A	6.21	26	4.92	20.6	127.92
rbcL	Pool 20	Strong plate 2 B	6.05	27	4.79	21.4	129.41
rbcL	Pool 21	Strong plate 3	19.60	40	15.53	31.7	621.13
rbcL	Pool 22	Strong plate 4	24.70	38	19.57	30.1	743.61

**S6.5.** Details of the volume of each plate pool added to the two final pools for ITS2 and rbcL for sequencing