Ecology of a landscape-scale deer assemblage

Valentina Zini

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University of East Anglia

School of Environmental Sciences

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Abstract

This thesis investigates the ecology of a multi-species ungulate assemblage and their impacts to inform management in commercial forestry (Thetford Forest, eastern England, 195km^2). The aims were to analyse environmental factors influencing deer densities, to identify the species causing the greatest damage to young crop plantings, and to analyse how habitat, landscape context and intra- and inter-specific competition affect roe deer performance. Local roe and muntjac densities (collected in 2018) were related to habitat, landscape context and recreation. Roe deer densities were higher in young (0-5 since planting) stands and lower closer to grasslands and in areas of high recreational activity. Muntjac densities were higher in mature (≥46 years) stands, on calcareous soils, and with high recreation, while being lower closer to grasslands. Effects of local species-specific densities (from 2018 to 2020) of muntjac, roe, fallow deer and large deer (comprising fallow and red deer) on scots pine (*Pinus sylvestris*) leader browsing were assessed while controlling for hares presence and ground vegetation. More pine leaders were browsed in localities with higher densities of fallow or 'large' deer. Using a long-term dataset (2002-2015) we analysed effects of habitat and landscape context on roe deer fertility and body mass. Yearling and adult roe deer were more fertile when heavier; adult body mass was higher closer to arable lands, however, adult fertility was lower closer to arable. Relative importance of intra- and inter-specific competition of fallow deer and muntjac on the condition and fertility of adult roe deer was tested using data from 2011-2016. Densities of muntjac were negatively related to fallow deer densities. Roe deer fertility was lower at higher muntjac densities, while being higher at higher roe deer densities. Roe deer are, therefore, subject to inter-specific competition from muntjac while intra-specific competition wasn't detected. This is among the first studies showing effects of inter-specific competition of introduced species on reproductive output of a native vertebrate. Deer management should focus on reducing large deer and introduced species numbers to reduce impacts on regeneration and alleviate interspecific competition on native roe.

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Chapter One

Introduction

Introduction

Deer are economically and ecologically important (Apollonio et al., 2008); through venison, recreational hunting, and tourism, deer generate income (see example in Skonhoft et al., 2013) and have a key role in the structure and processes of temperate and subtropical terrestrial ecosystems (Côté et al., 2004; Danell, 2006). Deer affect the plant community and the organisms depending on them (Schmitz et al., 2000): at low densities, deer grazing provides a more diverse plant species composition and vegetation structure (Mitchell and Kirby, 1990), while at high densities forest regeneration is prevented and the forest understorey is reduced (Côté et al., 2004). Removal of apex predators (Ripple et al., 2014) and widespread introductions of species outside their native range (Roy et al., 2019) have disrupted ecosystem services worldwide. Apex predators have a key role in shaping ecosystems (Estes et al., 2011; Ripple et al., 2014), and their absence can lead to an overabundance of herbivores (Ripple et al., 2015) leading to cascading effects on the ecosystem (Côté et al., 2004; Fuller and Gill, 2001; Ripple and Beschta, 2012). Vertebrate herbivore abundances have been increasing both as a result of removal of predators and widespread introductions (Dolman and Wäber, 2008). Despite examples of introduced Caprids, such as the Himalayan tahr (*Hemitragus jemlahicus*) introduced in New Zealand and South Africa (Bhatnagar and Lovari, 2008) and the chamois (*Rupicapra rupicapra*) introduced in the south island of New Zealand (Corlatti et al., 2011), Cervids comprise the majority of ungulate introductions (Lever, 1985) and with few exceptions, populations of introduced deer species are growing.

Inter-specific competition of introduced species

Deer have an impact on other ungulate species via inter-specific competition (see examples in Latham, 1999) or facilitation. A study modelling grazing systems shows how small grazers have a competitive advantage on larger grazers as the latter facilitate forage availability for smaller species (Farnsworth, Focardi and Beecham, 2002). It is expected that coevolution of sympatric species would result in resource partitioning, alleviating inter-specific competition (Hutchinson, 1959), however when two species that evolved in different geographical ranges suddenly coexist, interspecific competition can occur (Mooney and Cleland, 2001). Based on the theory of ecological displacement, competition is particularly strong if the species are similar and resources are limited; in this case natural selection will favour individuals of each species that are able to exploit unused (or used to a lesser extent) resources by the other species (Brown and Wilson, 1956). Inter-specific competition can be mediated by consumption of resources when dietary overlap between species occurs, for example between chamois (*Rupicapra pyrenaica*) and red deer (*Cevus elaphus*; Lovari et al., 2014). The Jarman-Bell Principle states that larger herbivores can better tolerate low-quality forage as their ability to extract nutrients from plants is greater compared to smaller herbivores that need to select higher quality food sources (Geist, 1974). A larger body size confers advantages such as lower basal metabolism and longer retention of the food within the digestive tract, allowing better fermentation and consequently increased digestive efficiency (Demment and Soest, 1985). Differences in the ability to digest certain types of resources can give some species a competitive advantage; as an example, the advantage in the digestive ability of sika deer has been suggested to be the cause of the sharp decline in white-tailed deer numbers coexisting with sika within an enclosure in a Texas study (Harmel, 1980). In the case of resource competition, more opportunistic herbivores such as grazers and intermediate-type feeders (red deer, fallow deer *Dama dama*, chamois, muflon *Ovis musimon*) have a competitive advantage over selective browsers such as roe deer *Capreolus capreolus* (Homolka, 1996) that have a more restricted diet (Storms et al., 2008). Reduced access to forage, in turn, affects the performance of the competitive inferior species; for example, it has been shown that high red deer densities correspond to lower fawn body mass in roe deer, and higher chamois kids winter mortality (Ferretti et al., 2015; Richard et al., 2009). Interspecific competition can also occur through behavioural interference as documented for fallow on roe deer (Ferretti, 2011; Ferretti et al., 2011, 2008) that has been shown to affect roe deer spatial behaviour (Focardi et al., 2006). In addition to their potential for competition with native species, introduced species have been shown to differ in their provision of ecosystem services; for example introduced invasive muntjac have been shown to have a lower seed dispersal than native roe deer (Eycott et al., 2007).

Influences of deer on ecosystem structure and function

Through direct and indirect mechanisms, deer have far-reaching effects on other species (Côté et al., 2004; Danell, 2006). The most remarkable effects are achieved through herbivory, that alters the physical environment by limiting forest regeneration (Côté et al., 2004; Gill, 1992a), and changing the understorey layer (Hegland and Rydgren, 2016); terrestrial laser scanning in UK lowland woodlands exemplify this by revealing a dramatic 68% reduction in understorey foliage in areas of high deer density (Eichhorn et al., 2017). In Britain, common Nightingales (*Luscinia megarhynchos*) have decreased in both range and abundance consistent with patterns of deer population expansion (Newson et al., 2012). An exclosure experiment in coppice woodland shows the decrease could be partly related to an increase in deer population as common Nightingales strongly prefer exclosures (with dense vegetation) over browsed areas (Holt et al., 2010). As plants differ in their palatability to deer, heavy grazing changes the composition of the plant community (Arcese et al., 2014; Augustine and McNaughton, 1998; Habeck and Schultz, 2015) with less palatable species like bracken (*Pteridium spp.*) becoming prevalent at high deer densities (Nuttle et al., 2014). These changes in the physical environment, in turn, affect many other species (Foster et al., 2014) of birds (Gill and Fuller, 2007; Holt et al., 2014, 2013, 2011; Newson et al., 2012), small mammals (Flowerdew and Ellwood, 2001) and invertebrates (Allombert et al., 2005b; Lilleeng et al., 2018; Stewart, 2001). In the Boreal forest of Anticosti island (Canada), songbird and rare species of macro *Lepidoptera* (closely linked to vegetation) were higher in richness and diversity at lower deer densities (Côté et al., 2014). In addition, higher deer densities correspond to greater pellet abundance and this has been shown to change the structure of dung beetle communities (Iida et al., 2018). It has also been shown that deer alter soil properties, changing stoichiometry of nutrients (Carline et al., 2005), as well as soil pH, hardness and soil saturation capacity (Kumbasli et al., 2010). A conspicuous body of evidence shows deer greatly reduce natural regeneration (Côté et al., 2004; Gerhardt et al., 2013; Gill, 1992b). Impacts vary greatly depending on tree species palatability (Gill, 2003, 1992b; Kay, 1993; Pépin et al., 2006), species of deer considered (e.g. Palmer and Truscott, 2003) in the study as well as forest management regime (Reimoser and Gossow, 1996) and availability of other forage (Motta, 1996; Partl et al., 2002).

Deer management

Deer impacts can be mitigated by crop impact prevention methods such as diversionary feeding (see example in Arnold et al., 2018), tree guards, growth tubes or fences (Gill, 1996). Using these methods alone is costly and doesn't address some of the other issues related to high deer densities such as the increase in traffic collisions involving deer (Langbein et al., 2011), or the spread of tick-borne diseases (Kilpatrick et al., 2014); for these reasons reducing number of deer has become a necessity (Gordon et al., 2004). While deer may create a substantial economic loss for foresters and farmers, conservationists are more concerned with the biodiversity loss resulting from deer overabundance (Côté et al., 2004). High deer numbers, on the other hand, are welcomed by recreational hunters, that in some instances have reported inflated cull figures to satisfy authorities and let deer population grow (Donaubauer, 1994), showing how deer management is, in some circumstances, disconnected from forestry or conservation.

To solve the conflict between different interest groups, management of ungulates has to be balanced, according to multiple criteria set for conservation, recreational hunting, commercial crops and safety (Reimoser, 2003). Currently, deer management is mostly informed by indicators of body condition and habitat impact, either as proxies for population trends (Morellet et al., 2007; Zannèse et al., 2006), or to achieve a desired habitat outcome (Morellet et al., 2001). Ecological indicators can be hard to apply for populations below ecological thresholds, as the relations between density, habitat and body condition (Pettorelli et al., 2002) and between weight and fertility (Flajšman et al., 2017; Gaillard et al., 1992) are variable and non-linear. Additionally, this approach does not predict the cull levels needed to reduce or stabilise a local population, or whether management that maintains a local population at a 'stable' level (and thus is perceived as appropriate and sustainable) masks situations where this is a 'source' driving regional increase (Wäber *et al*., 2013). Management informed by such indicators may often be unsuitable in solving conflicts between the different interest groups. To address these conflicts, an evidence-based management (Wäber et al., 2013) framework that analyses the demography of the population needs to be adopted, to then set a cull target. A demographic model requires an objective system to assess abundance of the examined ungulate population and age-sex composition, mortality (derived from cull data), as well as neonatal survival and fertility. Fertility can be estimated through carcass inspection by identifying the number of embryos in the uterus. One of the questions that has not yet been answered in this regard is to what extent fertility varies across the landscape according to environmental factors and whether in a demographic model it is still possible to use an average of fertility derived from cull data. Demographic models need to be implemented across large areas to be relevant for the species managed in order to avoid source-sink movements generated by different levels of cull effort between landowners (Wäber et al., 2013) with the objective to reduce densities at the landscape-scale.

Deer management research in the context of landscape-scale dynamics

In order to manage ungulate populations with an evidence-based approach it is important to identify a ‘sustainable’ species-specific herbivore density that the deer populations need to be managed down to. Sustainable densities will vary depending on the level of damage deemed acceptable to certain plant species, therefore this will to some extent, differ between foresters, farmers or conservationists, depending on the value of a given crop or habitat. Expenses for damage mitigation are traded-off with losses arising from damage; for forestry, 20% damage has been proposed to be acceptable (Prien and Müller, 2010), but when mitigating the damage is expensive, even higher levels of damage (>55%) can be accepted (Ward et al., 2004). For a given impact level, critical deer densities will also vary depending on composition of the herbivore guild, palatability of the plant species examined, and will generally be higher with lower forest productivity (Gerhardt et al., 2013). Deer populations should be culled down to sustainable densities. When deer densities are high, landscape-scale reduction of deer numbers to a sustainable density may only be a long-term goal. Some localised reduction of densities (and local impacts mitigation) can still be achieved through the understanding of factors driving deer densities, and in turn, impacts on vegetation (Spake et al., 2020). Among factors affecting habitat suitability (and thus, deer densities) are some aspects of the landscape that can’t be managed such as the proximity to farmlands, grasslands and grass-heaths. Knowledge of these factors can still inform decisions on, for example where to place a new crop and whether to invest in crop protection (Spake et al., 2020). In Thetford Forest, for example, muntjac (*Muntiacus reevesi*) densities were higher in blocks surrounded by open land-use types such as farmland and grassland (Hemami et al., 2005); landscape context has also been shown to be important for roe deer that cause more damage at the edges of coppiced woodlands (Kay, 1993). Other aspects of the environment, such as forest growth stage and recreational access can, instead, be managed. Deer preferentially use some forest growth stages over others (see examples in Hemami et al., 2005; Prokešová et al., 2006) based on their requirements for concealment, thermal shelter and availability of forage; roe deer, for example, have been reported to occur in higher densities in clear-felled areas within the forest (Reimoser and Ellenberg, 1999). Human disturbance is known to be a factor affecting deer behaviour (Stankowich, 2008) and outdoor recreation is increasing. Literature shows deer associate recreationists with potential predatory danger in those areas where they are hunted (Altmann, 1958; Behrend and Lubeck, 1968). Areas of high recreation will then have a lower perceived quality related to the cost of antipredator behaviour and, as a result, a lower density of individuals (Frid and Dill, 2002). Quantifying the effects of recreational disturbance on local deer densities could help inform management to mitigate impacts by managing recreational access to the forest (Mallord *et al.* 2006).

Methodological issues in deer impact studies

Exclosure experiments often show dramatic impacts of deer on vegetation; in the Dinaric mountains for example, red deer significantly affect natural regeneration with silver fir completely failing to establish in the presence of reds (Simončič et al., 2019); long-term exclosure experiments in the upper Midwest (USA), show that white-tailed deer strongly affect the plant community by increasing the abundance of ferns and graminoids, doubling the abundance of exotic plants, reducing tree regeneration, shrub cover (up to 200 fold), abundance of forbs, plant height and reproduction (Frerker et al., 2014). Excluding deer is still the most common experimental approach (Foster et al., 2014), however sustainable densities, can’t be identified through exclosure experiments where densities have not been measured. Even when densities outside the exclosure are estimated, the relationship between impacts and deer abundance cannot be reliably quantified as the nature of the impact of ungulates is complex and the relationship is non-linear with impact rates increasing at higher deer densities, as shown by studies utilising a range of densities (e.g. Gill and Morgan, 2010; Hidding et al., 2012; Tremblay et al., 2007). Some studies used a series of enclosures to test a range of densities (see examples in Hidding et al., 2012; Scott et al., 2000; Tremblay et al., 2007), however enclosures present numerous challenges and may not reflect natural conditions (Allombert et al., 2005a; Diamond, 1983). Enclosures, for example have limits to their size which is problematic for wide-ranging species as this may prevent their social behaviour and habitat selection to fully emerge within a small space. For example, animals with big home-ranges forage in selected patches (Mayor et al., 2009) thus under natural conditions, impacts are spatially and temporally variable; this spatio-temporal variability may not be captured by enclosure studies as the size of enclosure is usually too small to capture landscape-level variations (McShea and Rappole, 2000; Webster et al., 2005). Enclosure experiments also need to reduce the risk of edge effects (Levin, 2009) altering the results. Provided a large enough sized enclosure is available to overcome the aforementioned criticisms, resource limitation may prevent studies from having adequate replication and may still be prone to other experimental artefacts due to placement of the enclosure (Diamond, 1983). To understand landscape-level vegetation effects of deer, free-ranging ungulate populations need to be studied in a natural experiment, in their complex environment where the interaction between habitat selection and herbivory occurs, allowing for direct and indirect effects to be captured. Some studies have implemented this approach (see examples in Gill and Morgan, 2010; Tanentzap et al., 2011), however little study has been conducted in multi-species systems or has been able to discern the species-specific effect on vegetation.

Study system

My study area is Thetford Forest (195km^2), the largest lowland conifer managed forest in the UK, situated in Breckland, Eastern England, a biogeographic region (1000 km^2) characterized by semi-continental climate and sandy soils (Dolman et al., 2012). Established during the 1930-1950s, the forest is managed by rotational clear-felling at economic maturity and replanting of even-aged stands, creating a mosaic of different growth stages (Eycott et al., 2006). Most of the forest (62% of planted crops) is in the second crop rotation. Detailed knowledge of the habitat is available from the Forestry England GIS database , storing for each management sub-compartment (part of a single even-aged planted coupe separated by trackways) information such as tree species, planting year, soil type, thinning and spacing of trees. The forest is dominated by Corsican, *Pinus nigra* (55% of the landscape) and Scots pine *Pinus sylvatica* (17%) while *Larix* spp. and mature deciduous plantings (particularly *Fagus sylvatica*, *Acer pseudoplatanus* and *Betula* spp.) comprise together 10% of the forest. The remaining 18% comprises open habitats including clear-felled areas. Four deer species occur in the forest; re-established native roe and red deer, naturalised fallow, and introduced, invasive Reeves's muntjac. Deer are managed by a team of professional Forestry England wildlife rangers. The forest is subdivided into 12 deer management blocks. The extensive contiguous core of the forest comprises four blocks with primarily acidic soils (podzols and gravelly sands, except for one block that is mainly calcareous) and little access to arable. Seven forest blocks have lower perimeter-area ratio with higher access to arable and grassland; four of these blocks (two in the northern part of the forest and two on the eastern side) are mostly calcareous, while the other three (two on the eastern side of the core and one on the south-western side) are mostly acidic. On the southern side of the contiguous core is located another large mostly calcareous block, surrounded by farmland (Fig. 1.1).

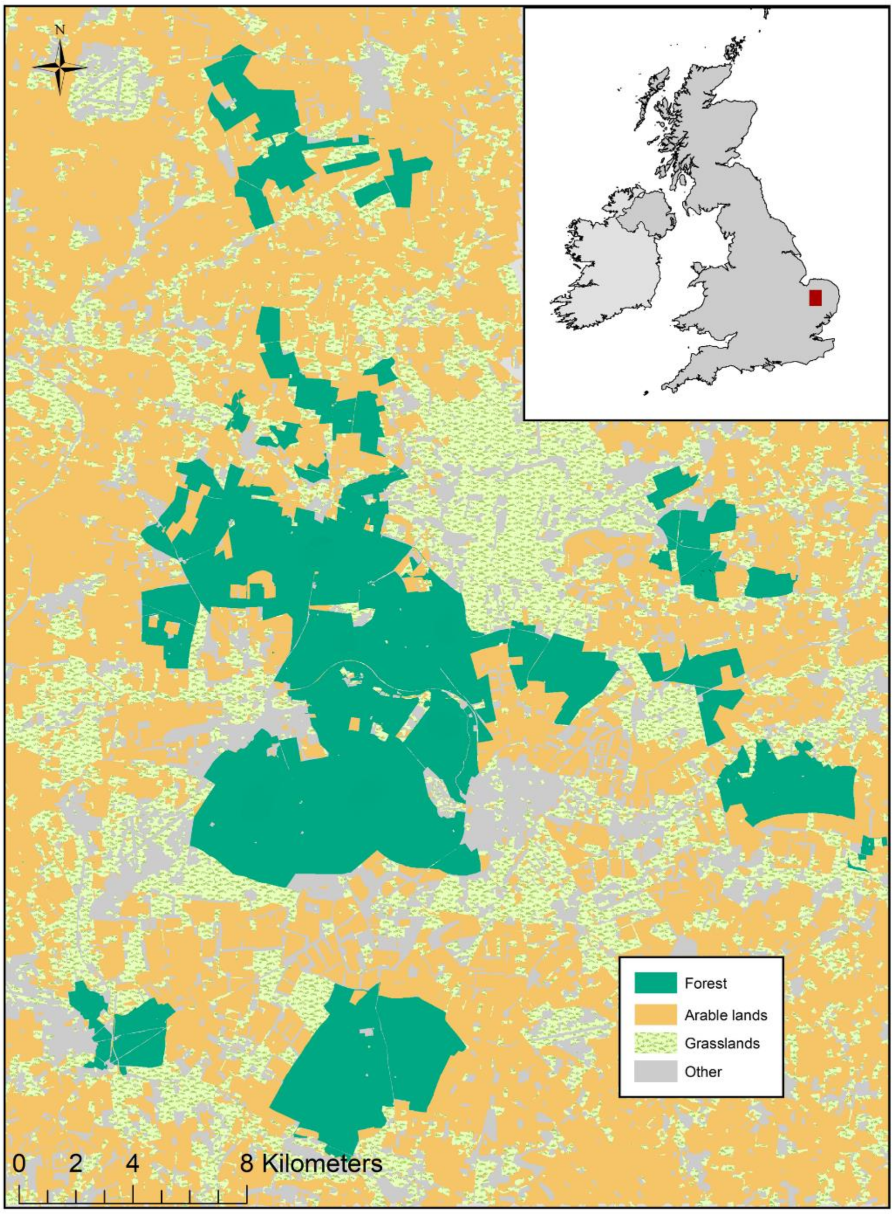


Figure 1.1: Map of Thetford forest showing distribution of forest blocks and access to grasslands and arable lands.

This thesis has a particular focus on roe deer as this species is abundant throughout the study area and has a fixed annual fertility cycle (Raganella-Pelliccioni et al., 2007). These characteristics make this species a model organism to test effects of environment on performance, and being native to the UK the roe deer also represents a model organism to test effects of inter-specific competition with a non-native invasive species such as muntjac (DEFRA, 2018).

Structure of the thesis

In Chapter two I use Density Surface Models to examine variation in relative abundance of roe deer and muntjac to habitat, landscape context features and recreational activity, measured at a local scale. In Chapter three I examine deer impact on commercial forestry; specifically I investigate impacts on Scots Pine measured at a local (forest stand) scale of three of the most widely distributed ungulate species in the UK, roe, muntjac, fallow deer and large deer (including fallow and red deer) while controlling for the presence of rabbits and hares as well as ground vegetation. Deer densities were extracted from species-specific yearly Density Surface Model predictions allowing us to compare local impacts with densities measured at a fine-grained scale. In chapter four I analyse variation in roe deer performance (body mass and fecundity) in relation to habitat and landscape variables. In the context of evidence-based deer management where a demographic model is implemented, I assess whether an average value of fertility for the whole forest is appropriate, or if environmental variables need to be accounted for. In chapter five I test the relative performance of inter- and intra-specific competition of two introduced species on a native species. This is the first attempt at quantifying demographic responses of inter-specific competition of two non-native species (fallow and muntjac) to a native species (roe deer) in a large vertebrate. In chapter six I bring together the findings of the previous chapters, discuss their implications for forest management and highlight research gaps.

References

Allombert, S., Gaston, A.J., Martin, J.L., 2005a. A natural experiment on the impact of overabundant deer on songbird populations. Biol. Conserv. 126, 1–13. https://doi.org/10.1016/j.biocon.2005.04.001

Allombert, S., Stockton, S., Martin, J.L., 2005b. A natural experiment on the impact of overabundant deer on forest invertebrates. Conserv. Biol. 19, 1917–1929. https://doi.org/10.1111/j.1523-1739.2005.00280.x

Altmann, M., 1958. The flight distance in free-ranging big game. J. Wildl. Manage. 22, 207. https://doi.org/10.2307/3797334

Apollonio, M., Andersen, R., Putman, R., 2008. European Ungulates And their Management in The 21st Century. Cambridge University Press, Cambridge.

Arcese, P., Schuster, R., Campbell, L., Barber, A., Martin, T.G., 2014. Deer density and plant palatability predict shrub cover, richness, diversity and aboriginal food value in a North American archipelago. Divers. Distrib. 20, 1368–1378. https://doi.org/10.1111/ddi.12241

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. For. Ecol. Manage. 407, 166–173. https://doi.org/10.1016/j.foreco.2017.10.050

Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. Wildl. Manage. 62, 1165. https://doi.org/10.2307/3801981

Behrend, D.F., Lubeck, R.A., 1968. Summer flight behavior of white-tailed deer in two Adirondack forests. J. Wildl. Manage. 32, 615. https://doi.org/10.2307/3798942

Bhatnagar, Y.V., Lovari, S., 2008. *Hemitragus jemlahicus*. IUCN Red List Threat. Species 2008 e.T9919A13027389.

Brown, W.L., Wilson, E.O., 1956. Character displacement. Syst. Zool. 5, 49–64.

Carline, K.A., Jones, H.E., Bardgett, R.D., Heikki, S., 2005. Large herbivores affect the stoichiometry of nutrients in a regenerating woodland ecosystem. Oikos 110, 453–460.

Corlatti, L., Lorenzini, R., Lovari, S., 2011. The conservation of the chamois *Rupicapra spp.* Mamm. Rev. 41, 163–174. https://doi.org/10.1111/j.1365-2907.2011.00187.x

Côté, S.D., Beguin, J., de Bellefeuille, S., Champagne, E., Thiffault, N., Tremblay, J.-P., 2014. Structuring effects of deer in boreal forest ecosystems. Adv. Ecol. 2014, 1–10. https://doi.org/10.1155/2014/917834

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological Impacts of Deer Overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Danell, K., 2006. Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511617461

DEFRA, 2018. Tackling Invasive Non-Native Species: A New Enforcement Regime.

Demment, M.W., Soest, P.J. Van, 1985. A Nutritional Explanation for Body-Size Patterns of Ruminant and Nonruminant Herbivores. Am. Nat. 125, 641–672. https://doi.org/https://doi.org/10.1086/284369

Diamond, J.M., 1983. Ecology: laboratory, field and natural experiments. Nature.

Dolman, P.M., Panter, C.J., Mossman, H.L., 2012. The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. J. Appl. Ecol. 49, 986–997. https://doi.org/10.1111/j.1365-2664.2012.02174.x

Dolman, P.M., Wäber, K., 2008. Ecosystem and competition impacts of introduced deer. Wildl. Res. 35, 202. https://doi.org/10.1071/WR07114

Donaubauer, E., 1994. Zur Wildschadenssituation in Europa. Prcc. CIC-Tagtmg, Salzbg. 11 pp.

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. J. Appl. Ecol. 54, 1615–1626. https://doi.org/10.1111/1365-2664.12902

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. Science (80-.). 333, 301–306. https://doi.org/10.1126/science.1205106

Eycott, A.E., Watkinson, A.R., Dolman, P.M., 2006. Ecological patterns of plant diversity in a plantation forest managed by clearfelling. J. Appl. Ecol. 43, 1160–1171. https://doi.org/10.1111/j.1365-2664.2006.01235.x

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, 107–118. https://doi.org/10.1007/s00442-007-0812-1

Farnsworth, K.D., Focardi, S., Beecham, J.A., 2002. Grassland-Herbivore Interactions: How Do Grazers Coexist? Am. Nat. 159, 24–39. https://doi.org/10.1086/324114

Ferretti, F., 2011. Interspecific aggression between fallow and roe deer. Ethol. Ecol. Evol. 23, 179–186. https://doi.org/10.1080/03949370.2011.554883

Ferretti, F., Corazza, M., Campana, I., Pietrocini, V., Brunetti, C., Scornavacca, D., Lovari, S., 2015. Competition between wild herbivores: reintroduced red deer and Apennine chamois. Behav. Ecol. 26, 550–559. https://doi.org/10.1093/beheco/aru226

Ferretti, F., Sforzi, A., Lovari, S., 2011. Behavioural interference between ungulate species: roe are not on velvet with fallow deer. Behav. Ecol. Sociobiol. 65, 875–887. https://doi.org/10.1007/s00265-010-1088-8

Ferretti, F., Sforzi, A., Lovari, S., 2008. Intolerance amongst deer species at feeding: roe deer are uneasy banqueters. Behav. Processes 78, 487–491. https://doi.org/10.1016/j.beproc.2008.02.008

Flajšman, K., Jerina, K., Pokorny, B., 2017. Age-related effects of body mass on fertility and litter size in roe deer. PLoS One 12, e0175579. https://doi.org/10.1371/journal.pone.0175579

Flowerdew, J.R., Ellwood, S.A., 2001. Impacts of woodland deer on small mammal ecology. Forestry 74, 277–287. https://doi.org/10.1093/forestry/74.3.277

Focardi, S., Aragno, P., Montanaro, P., Riga, F., 2006. Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. Ecography (Cop.). 29, 407–417. https://doi.org/10.1111/j.2006.0906-7590.04442.x

Foster, C.N., Barton, P.S., Lindenmayer, D.B., 2014. Effects of large native herbivores on other animals. J. Appl. Ecol. 51, 929–938. https://doi.org/10.1111/1365-2664.12268

Frerker, K., Sabo, A., Waller, D., 2014. Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. PLoS One 9, 1–17. https://doi.org/10.1371/journal.pone.0115843

Frid, A., Dill, L.M., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, art11. https://doi.org/10.5751/ES-00404-060111

Fuller, R.J., Gill, R.M.A., 2001. Ecological impacts of increasing numbers of deer in British woodland. Forestry 74, 193–199. https://doi.org/10.1093/forestry/74.3.193

Gaillard, J.M., Sempéré, A.J., Boutin, J.-M., Laere, G. Van, Boisaubert, B., 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (Capreolus capreolus). Can. J. Zool. 70, 1541–1545. https://doi.org/10.1139/z92-212

Geist, V., 1974. On the relationship of social evolution and ecology in ungulates. Am. Zool. 14, 205–220. https://doi.org/10.1093/icb/14.1.205

Gerhardt, P., Arnold, J.M., Hackländer, K., Hochbichler, E., 2013. Determinants of deer impact in European forests – a systematic literature analysis. For. Ecol. Manage. 310, 173–186. https://doi.org/10.1016/j.foreco.2013.08.030

Gill, R.M.A., 2003. The economic implications of deer damage in forests and woodlands, in: Proceedings of the Future for Deer Conference. English Nature Research Report No. 548.

Gill, R.M.A., 1996. Deer Management to Protect Forest Vegetation —A British Perspective, in: The Proceedings of the Cedar Symposium.

Gill, R.M.A., 1992a. A review of damage by mammals in north temperate forests: 1. Deer. Forestry 65, 145–169. https://doi.org/10.1093/forestry/65.2.145

Gill, R.M.A., 1992b. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. Forestry 65, 363–388. https://doi.org/10.1093/forestry/65.4.363-a

Gill, R.M.A., Fuller, R.J., 2007. The effects of deer browsing on woodland structure and songbirds in lowland Britain. Ibis (Lond. 1859). 149, 119–127. https://doi.org/10.1111/j.1474-919X.2007.00731.x

Gill, R.M.A., Morgan, G., 2010. The effects of varying deer density on natural regeneration in woodlands in lowland Britain. Forestry 83, 53–63. https://doi.org/10.1093/forestry/cpp031

Gordon, I.J., Hester, A.J., Festa-Bianchet, M., 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. J. Appl. Ecol. 41, 1021–1031. https://doi.org/10.1111/j.0021-8901.2004.00985.x

Habeck, C.W., Schultz, A.K., 2015. Community-level impacts of white-tailed deer on understorey plants in North American forests: a meta-analysis. AoB Plants 7, plv119. https://doi.org/10.1093/aobpla/plv119

Harmel, D.E., 1980. The influence of exotic artiodactyls on white-tailed deer production and survival. - Performance Report Job Number 20, Federal Aid Project Number W-109- R-3. Austin, Texas, USA.

Hegland, S.J., Rydgren, K., 2016. Eaten but not always beaten: winners and losers along a red deer herbivory gradient in boreal forest. J. Veg. Sci. 27, 111–122. https://doi.org/10.1111/jvs.12339

Hemami, M.R., Watkinson, A.R., Dolman, P.M., 2005. Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* in a lowland pine forest. For. Ecol. Manage. 215, 224–238. https://doi.org/10.1016/j.foreco.2005.05.013

Hidding, B., Tremblay, J.-P., Côté, S.D., 2012. Survival and growth of balsam fir seedlings and saplings under multiple controlled ungulate densities. For. Ecol. Manage. 276, 96–103. https://doi.org/10.1016/j.foreco.2012.03.023

Holt, C.A., Fuller, R.J., Dolman, P.M., 2014. Exclusion of deer affects responses of birds to woodland regeneration in winter and summer. Ibis (Lond. 1859). 156, 116–131. https://doi.org/10.1111/ibi.12096

Holt, C.A., Fuller, R.J., Dolman, P.M., 2013. Deer reduce habitat quality for a woodland songbird: evidence from settlement patterns, demographic parameters, and body condition. Auk 130, 13–20. https://doi.org/10.1525/auk.2012.12090

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. Biol. Conserv. 144, 2151–2162. https://doi.org/10.1016/j.biocon.2011.05.004

Holt, C.A., Fuller, R.J., Dolman, P.M., 2010. Experimental evidence that deer browsing reduces habitat suitability for breeding common nightingales *Luscinia megarhynchos*. Ibis (Lond. 1859). 152, 335–346. https://doi.org/10.1111/j.1474-919X.2010.01012.x

Homolka, M., 1996. Foraging strategy of large herbivores in forest habitats. Folia Zool. 45, 127–136.

Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93, 145–159. https://doi.org/10.1086/282070

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

Kay, S., 1993. Factors affecting severity of deer browsing damage within coppiced woodlands in the south of England. Biol. Conserv. 63, 217–222. https://doi.org/10.1016/0006-3207(93)90715-D

Kilpatrick, H.J., Labonte, A.M., Stafford, K.C., 2014. The relationship between deer density, tick abundance, and human cases of Lyme disease in a residential community. J. Med. Entomol. 51, 777–784. https://doi.org/10.1603/ME13232

Kumbasli, M., Makineci, E., Cakir, M., 2010. Long term effects of red deer (*Cervus elaphus*) grazing on soil in a breeding area. J. Environ. Biol. 31, 185–188.

Langbein, J., Putman, R.J., Pokorny, B., 2011. Traffic collisions involving deer and other ungulates in Europe and available measures for mitigation, in: Putman, R., Apollonio, M., Andersen, R. (Eds.), Ungulate Management in Europe. Cambridge University Press, Cambridge, pp. 215–259. https://doi.org/10.1017/CBO9780511974137.009

Latham, J., 1999. Interspecific interactions of ungulates in European forests: an overview. For. Ecol. Manage. 120, 13–21. https://doi.org/10.1016/S0378-1127(98)00539-8

Lever, C., 1985. Naturalised Mammals of the World. Longman, London.

Levin, S.A., 2009. The Princeton Guide to Ecology. Princeton University Press.

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. Biodivers. Conserv. 27, 2507–2525. https://doi.org/10.1007/s10531-018-1550-x

Lovari, S., Ferretti, F., Corazza, M., Minder, I., Troiani, N., Ferrari, C., Saddi, A., 2014. Unexpected consequences of reintroductions: competition between reintroduced red deer and Apennine chamois. Anim. Conserv. 17, 359–370. https://doi.org/10.1111/acv.12103

Mallord, J.W., Dolman, P.M., Brown, A.F., Sutherland, W.J., 2006. Linking recreational disturbance to population size in a ground-nesting passerine. J. Appl. Ecol. 44, 185–195. https://doi.org/10.1111/j.1365-2664.2006.01242.x

Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat selection at multiple scales. Écoscience 16, 238–247. https://doi.org/10.2980/16-2-3238

McShea, W.J., Rappole, J.H., 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conserv. Biol. 14, 1161–1170. https://doi.org/10.1046/j.1523-1739.2000.99210.x

Mitchell, F.J.G., Kirby, K.J., 1990. The impact of large herbivores on the conservation of semi-natural woods in the british uplands. Forestry 63, 333–353. https://doi.org/10.1093/forestry/63.4.333

Mooney, H.A., Cleland, E.E., 2001. The evolutionary impact of invasive species. Proc. Natl. Acad. Sci. U. S. A. 98, 5446–5451. https://doi.org/10.1073/pnas.091093398

Morellet, N., Champely, Stéphane, Gaillard, J., Ballon, P., Boscardin, Y., Morellet, N., Champely, Stephane, Gaillard, J., Ballon, P., Boscardin, Y., 2001. The browsing index: new tool uses browsing pressure to monitor deer populations. Wildl. Soc. Bull. 29, 1243–1252. https://doi.org/10.2307/3784150

Morellet, N., Gaillard, J.-M., Hewison, A.J.M., Ballon, P., Boscardin, Y., Duncan, P., Klein, F., Maillard, D., 2007. Indicators of ecological change: new tools for managing populations of large herbivores. J. Appl. Ecol. 44, 634–643. https://doi.org/10.1111/j.1365-2664.2007.01307.x

Motta, R., 1996. Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the western Italian Alps. For. Ecol. Manage. 88, 93–98. https://doi.org/10.1016/S0378-1127(96)03814-5

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. J. Appl. Ecol. 49, 278–286. https://doi.org/10.1111/j.1365-2664.2011.02077.x

Nuttle, T., Ristau, T.E., Royo, A.A., 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. J. Ecol. 102, 221–228. https://doi.org/10.1111/1365-2745.12175

Palmer, S.C., Truscott, A.., 2003. Browsing by deer on naturally regenerating scots pine (*Pinus sylvestris L.*) and its effects on sapling growth. For. Ecol. Manage. 182, 31–47. https://doi.org/10.1016/S0378-1127(03)00026-4

Partl, E., Szinovatz, V., Reimoser, F., Schweiger-Adler, J., 2002. Forest restoration and browsing impact by roe deer. For. Ecol. Manage. 159, 87–100. https://doi.org/10.1016/S0378-1127(01)00712-5

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. For. Ecol. Manage. 222, 302–313. https://doi.org/10.1016/j.foreco.2005.10.034

Pettorelli, N., Gaillard, J.-M., Van Laere, G., Duncan, P., Kjellander, P., Liberg, O., Delorme, D., Maillard, D., 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. Proc. R. Soc. London. Ser. B Biol. Sci. 269, 747–753. https://doi.org/10.1098/rspb.2001.1791

Prien, S., Müller, M., 2010. Wildschäden im Wald. Ökologische Grundlagen und integrierte Schutzmaßnahmen. Neumann-Newdamm.

Prokešová, J., Barančeková, M., Homolka, M., 2006. Density of red and roe deer and their distribution in relation to different habitat characteristics in a floodplain forest. Folia Zool. 55, 1–14.

Raganella-Pelliccioni, E., Scremin, M., Toso, S., 2007. Phenology and synchrony of roe deer breeding in northern Italy. Acta Theriol. (Warsz). 52, 95–100. https://doi.org/10.1007/BF03194204

Reimoser, F., 2003. Steering the impacts of ungulates on temperate forests. J. Nat. Conserv. 10, 243–252. https://doi.org/http://dx.doi.org/10.1078/1617-1381-00024

Reimoser, F., Ellenberg, H., 1999. Forest management systems as a component of ungulate-game pest management with special reference to roe deer and edge effects, in: Advances in Vertebrate Pest Management. pp. 219–238.

Reimoser, F., Gossow, H., 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. For. Ecol. Manage. 88, 107–119. https://doi.org/10.1016/S0378-1127(96)03816-9

Richard, E., Gaillard, J.M., Saïd, S., Hamann, J.L., Klein, F., 2009. High red deer density depresses body mass of roe deer fawns. Oecologia 163, 91–97. https://doi.org/10.1007/s00442-009-1538-z

Ripple, W.J., Beschta, R.L., 2012. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. Biol. Conserv. 145, 205–213. https://doi.org/10.1016/j.biocon.2011.11.005

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science (80-.). 343. https://doi.org/10.1126/science.1241484

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. Sci. Adv. 1, e1400103. https://doi.org/10.1126/sciadv.1400103

Roy, D., Alderman, D., Anastasiu, P., Arianoutsou, M., Augustin, S., Bacher, S., Başnou, C., Beisel, J., Bertolino, S., Bonesi, L., Bretagnolle, F., Chapuis, J.L., Chauvel, B., Chiron, F., Clergeau, P., Cooper, J., Cunha, T., Delipetrou, P., Desprez-Loustau, M., Détaint, M., Devin, S., Didžiulis, V., Essl, F., Galil, B.S., Genovesi, P., Gherardi, F., Gollasch, S., Hejda, M., Hulme, P.E., Josefsson, M., Kark, S., Kauhala, K., Kenis, M., Klotz, S., Kobelt, M., Kühn, I., Lambdon, P.W., Larsson, T., Lopez-Vaamonde, C., Lorvelec, O., Marchante, H., Minchin, D., Nentwig, W., Occhipinti-Ambrogi, A., Olenin, S., Olenina, I., Ovcharenko, I., Panov, V.E., Pascal, M., Pergl, J., Perglová, I., Pino, J., Pyšek, P., Rabitsch, W., Rasplus, J., Rathod, B., Roques, A., Roy, H., Sauvard, D., Scalera, R., Shiganova, T.A., Shirley, S., Shwartz, A., Solarz, W., Vilà, M., Winter, M., Yésou, P., Zaiko, A., Adriaens, T., Desmet, P., Reyserhove, L., 2019. DAISIE - Inventory of Alien Invasive Species in Europe. Version 1.6. https://doi.org/doi.org/10.15468/ybwd3x

Schmitz, O.J., Hambäck, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. Am. Nat. 155, 141–153. https://doi.org/10.1086/303311

Scott, D., Welch, D., Thurlow, M., Elston, D.A., 2000. Regeneration of *Pinus sylvestris* in a natural pinewood in NE Scotland following reduction in grazing by *Cervus elaphus*. For. Ecol. Manage. 130, 199–211. https://doi.org/10.1016/S0378-1127(99)00191-7

Simončič, T., Bončina, A., Jarni, K., Klopčič, M., 2019. Assessment of the long-term impact of deer on understory vegetation in mixed temperate forests. J. Veg. Sci. 108–120. https://doi.org/10.1111/jvs.12702

Skonhoft, A., Veiberg, V., Gauteplass, A., Olaussen, J.O., Meisingset, E.L., Mysterud, A., 2013.

Balancing income and cost in red deer management. J. Environ. Manage. 115, 179–188. https://doi.org/10.1016/j.jenvman.2012.11.006

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. J. Appl. Ecol. 57, 1376–1390. https://doi.org/10.1111/1365-2664.13622

Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141, 2159–2173. https://doi.org/10.1016/j.biocon.2008.06.026

Stewart, A.J.A., 2001. The impact of deer on lowland woodland invertebrates: A review of the evidence and priorities for future research. Forestry 74, 259–270. https://doi.org/10.1093/forestry/74.3.259

Storms, D., Aubry, P., Hamann, J.-L., Saïd, S., Fritz, H., Saint-Andrieux, C., Klein, F., 2008. Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. Wildlife Biol. 14, 237–250. https://doi.org/10.2981/0909-6396(2008)14[237:SVIDCA]2.0.CO;2

Tanentzap, A.J., Bazely, D.R., Koh, S., Timciska, M., Haggith, E.G., Carleton, T.J., Coomes, D.A., 2011. Seeing the forest for the deer: do reductions in deer-disturbance lead to forest recovery? Biol. Conserv. 144, 376–382. https://doi.org/10.1016/j.biocon.2010.09.015

Tremblay, J.P., Huot, J., Potvin, F., 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. J. Appl. Ecol. 44, 552–562. https://doi.org/10.1111/j.1365-2664.2007.01290.x

Wäber, K., Spencer, J., Dolman, P.M., 2013. Achieving landscape-scale deer management for biodiversity conservation: the need to consider sources and sinks. J. Wildl. Manage. 77, 726–736. https://doi.org/10.1002/jwmg.530

Ward, A.I., White, P.C.., Smith, A., Critchley, C.H., 2004. Modelling the cost of roe deer browsing damage to forestry. For. Ecol. Manage. 191, 301–310.

https://doi.org/10.1016/j.foreco.2003.12.018

Webster, C.R., Jenkins, M.A., Rock, J.H., 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. Biol. Conserv. 125, 297–307. https://doi.org/10.1016/j.biocon.2005.03.027

Zannèse, A., Baïsse, A., Gaillard, J.M., Hewison, A.J.M., Saint-Hilaire, K., Toïgo, C., Laere, G. Van, Morellet, N., 2006. Hind foot length: an indicator for monitoring roe deer populations at a landscape scale. Wildl. Soc. Bull. 34, 351–358. https://doi.org/10.2193/0091-7648(2006)34[351:HFLAIF]2.0.CO;2

Chapter Two

Human and environmental drivers of spatial variation in deer densities

Abstract

Better understanding of how local habitat, landscape context, and human disturbance influence local deer density supports strategic management to mitigate biodiversity impacts, forest crop damage, disease spread and vehicle collisions. I quantified densities of reintroduced native roe deer *Capreolus capreolus* and invasive introduced muntjac *Muntiacus reevesi* across a heterogeneous forest landscape (187 km^2, in eastern England) using thermal imaging distance sampling. Spatially-explicit density surface models, incorporating geographical coordinates (to account for spatial autocorrelation), related local deer density to local (within a radius of 250m and 300m of the transect segment, for muntjac and roe respectively) habitat composition and human recreational intensity (resampled from a model incorporating forest path-network distance from access points, and household density around these, calibrated by field survey data).Roe deer density (mean=7 km^{-2}, SD=6) was higher in localities with greater extent of young (0-5 years since planting) stands (inter-quartile, IQ, effect size +1.3 deer/km^2) and lower with greater extent of grasslands (-2.9 deer/km^2) and more recreational activity (-1.1 deer/km^2). Muntjac density (mean=21 km^{-2}, SD=10) was higher in localities with a greater intensity of recreational activity (IQ effect size, +2.4 deer/km^2) and with greater extent of mature (≥ 46 years) stands (+1.5 deer/km^2), or calcareous soil (+7.1 deer/km^2) and lower with greater extent of grasslands (-2.9 deer/km^2). Adapting forest management to affect habitat and recreational access may subtly influence local deer densities, but to mitigate impacts in landscapes with abundant deer effective culling programs likely remain the most viable option.

Introduction

Increasing deer abundance across Europe and North America has important consequences for humans and ecosystems. Deer contribute to rising incidence of tick-borne encephalitis (Jaenson et al., 2018) and Lyme borreliosis (Kilpatrick et al., 2014); although also mediated by rodents and hares (Delahay et al., 2002; Tälleklint and Jaenson, 1997) the abundance of ticks has decreased after control measures reduced deer numbers (Gilbert et al., 2012). Increasing deer populations alter forest ecosystem structure, nutrient cycling and biodiversity (Ramirez et al., 2018; Trdan and Vidrih, 2008). At high density, deer can limit forest regeneration (Côté et al., 2004; Gill, 1992), but complete regeneration failure is rare (though see examples in (Miller et al., 1998) with implications for strategies to mitigate climate change by enhancing carbon sequestration. Globally, carbon capture by trees is the most effective, available climate change solution (Bastin et al., 2019) while in the UK, the Committee on Climate Change has recommended tree planting to increase UK woodland from 13 to 15% by 2025 to meet UK's carbon reduction targets (UK Climate Change Committee, 2020). Deer management has primarily utilised culling and harvest to control deer abundance and impacts (Department for Environment, 2010). However, ethical wildlife control principles, state that before implementing lethal measures to reduce numbers, it is important to assess wether the problem could be mitigated by altering human practices (Dubois et al., 2017) and environmental management organisations, particularly charities deriving their influence from a broad memebership, have a responsibility to their members and the wider public to demonstrate that non-lethal methods of deer impact mitigation have been explored. Immunocontraception in wild deer has been approved and tested as a method for population control on white-tailed deer (Gionfriddo et al., 2009), however the high cost, as well as the increased length of time to achieve the desired population target compared to the removal of the individual make this method ineffective for wildlife management (IUCN, 2017). Fencing to exclude deer is expensive and requires regular inspections and maintenance; costs can be reduced by increasing the size of the fence, but while making sure all the deer are excluded from big fences on open habitats is possible, it is impractical within existing woodlands. Fences also limit access to people and cause mortality in other species (e.g. black grouse *Tetrao tetrix*, red grouse *Lagopus lagopus scoticus* and capercaille *Tetrao urugallus*, Moss 2001; Baines & Andrew 2003). Management of deer populations by culling is assisted by quantifying landscape-scale abundance and productivity across sources and sinks (Wäber et al., 2013), but the severity of deer impacts does not just depend on their overall abundance. The local distribution and aggregation of deer, and the severity of their impacts, are both influenced by habitat and landscape attributes (Hurley et al., 2012; Jarnemo et al., 2014; Royo et al., 2017; Spake et al., 2020), and by forest management (Redick and Jacobs, 2020; Reimoser and Gossow, 1996; Reimoser et al., 2009; Vospernik and Reimoser, 2008). Here I examine the extent to which local habitat quality and landscape context influence local deer density to assess the efficacy of manipulating these features to reduce the need for lethal control in areas where vulnerable crops are grown, as well as creating high deer density areas for cost-effective culling.

Although local habitat preferences are well-understood for many deer species (Chapman et al., 1994; Palmer et al., 2007), landscape context effects are less well studied (though see Saïd & Servanty 2005; Lamberti *et al.* 2006; Coulon *et al.* 2008). Importantly, the potential influence of recreational activity on deer distribution (Stankowich, 2008) has often been overlooked. Countryside recreation is encouraged for benefits to health and human wellbeing, and levels are increasing (Johna et al., 2010), while in the UK the Countryside and Rights of Way Act 2000 (CROW Act) designated large areas as open access including much of the national forest (Edward and Kazushige, 2015). Recreational access constrains deer management through safety concerns over shooting in popular areas. However, manipulating the distribution of recreational activity through changing the location of car-parks, access points and pathways (Mallord et al., 2006) could potentially facilitate deer management – by creating hotspots with higher deer density and few public recreationists were culling can be more cost-effective. Studies are currently encouraging the implementation of 'hunting for fear' as a management strategy, such that where the reduction of densities is harder to achieve in the short term, areas requiring protection from deer impacts are managed to become perceived high predation risk zones for deer (Cromsigt et al., 2013). Cromsigt et al. (2013) suggest that hunting on foot could increase deer perception or risk when they encounter recreationists, and this effect could be amplified if recreationists are accompanied by dogs (Miller et al., 2001). Deer increase vigilance (Ciuti et al., 2012) and flush away from recreationists (Miller et al., 2001; Taylor and Knight, 2003) and human disturbance can affect deer habitat use and ranging behaviour (Bonnot et al., 2013; Coulon et al., 2008). But it is unclear whether individuals in hunted populations consistently perceive recreationists as a predatory threat (Altmann, 1958; Behrend and Lubeck, 1968; Frid and Dill, 2002), as deer in some hunted populations may differentiate, avoiding the characteristic behaviour of stalkers but being habituated to, and relatively tolerant of, recreational walkers or other tourists (Laundre et al., 2010).

In an extensive study across a large heterogeneous landscape, I quantified the local abundance (at scales of c0.25 km^2, representing aggregation or settlement) of individuals within a re-introduced population of native roe deer (*Capreolus capreolus,* Ward 2005) and introduced invasive non-native muntjac (*Muntjacus reevesi,* DEFRA 2018), by thermal imaging on 567 km of distance sampling transects. Local abundance was related to fine-grained habitat suitability (local extent of forest growth stages, arable and grassland, and soil composition), using spatially-explicit modelling that accounts for spatial intercorrelation (Miller et al., 2013). I tested *a priori* habitat and landscape context features previously shown, or considered likely, to be correlated with abundances of roe deer and or muntjac (Putman and Moore, 1998; Sinclair, 1997). In addition, I examined whether local deer distribution was affected by levels of recreational activity, using a spatially-explicit interpolation of recreational frequency from a model relating intensively-sampled recreational data to trackway network distance from access points, and the parking capacity at and distance-weighted household density around, each access point. I *a priori* considered that roe would respond more strongly to recreation, as they are considered sensitive to disturbance (Bonnot et al., 2013; Coulon et al., 2008; Hewison et al., 2001); in contrast muntjac appear tolerant of human contact at least in their introduced UK range. Last, I compared the change in the spatial variation in local deer density produced by a model including the fine-grained variables examined to a simpler model ignoring these variables, to assess their effectiveness as tools for impact mitigation.

Methods

Study area

The study was conducted in Thetford Forest, a 187 km^2 conifer-dominated lowland plantation landscape in eastern England, characterized by a semi-continental climate and sandy soils that vary from acidic podsols to calcareous redzinas. Four deer species occurred in the forest during the study period (Zini et al., 2019): roe deer, muntjac, red (*Cervus elaphus*) and fallow (*Dama dama*) deer. These are managed by a professional ranger team to mitigate deer impacts, particularly on vulnerable tree species. Most (75%) of the forest is designated as open access and is visited by approximately 1 million people per year (1,064 visitors/km^2, Armour-Chelu, Brooke & Riley 2014). Planted in the 1930-1950s, and managed by rotational clear-felling at maturity and replanting (Eycott et al., 2006), approximately two-thirds (63%) of the forest is now in the second crop rotation, providing a fine-grained mosaic of even-aged planting 'stands' (mean area = 0.045km^2 SD= 0.065), each comprised of sub-compartments (individual management polygons: mean area = 0.03 km^2) separated by an extensive trackway network (Eycott et al., 2006) that permeated the forest. Deer management consider 12 forest 'blocks' that vary in relative tree species composition, predominant soil type and configuration — ranging from contiguous core blocks in a largely forest-dominated landscape (on predominantly acidic soils), to outlying fragments (some with greater representation of calcareous soils) providing easier access to surrounding arable fields and grasslands (Appendix A).

Survey method

I used distance sampling thermal imaging as this gives greater precision than dung-based assessments of distribution and abundance (Smart et al., 2004) that are vulnerable to uncertainty in sex-, diet- and season-dependent defecation rates, habitat-specific and date-dependent faecal decay rates, and species identification where more than one ungulate species coexist (Hemami and Dolman, 2005; Swanson and Armstrong, 2008). Nocturnal distance sampling was conducted from the forest trackways during late winter (January to March 2018) as low temperatures enhance thermal contrast and detection is greater following leaf-drop of deciduous under-canopy and collapse of tall herbaceous vegetation and bracken *Pteridium aquilinum* (Wäber and Dolman, 2015). One-sided (from passenger-window) vehicle-based distance-transect surveys were conducted using a thermal imager

(Pulsar Helion XP50), while driving at ≤16 km/hr with headlights off, between 20.00-02.00 hrs. Each deer detected was briefly illuminated by a roof-mounted spotlight ('lamped') allowing distance ($\text{distance}_{\text{sighting}}$) to be measured accurately, using Leica Geovid 10x42 laser rangefinder binoculars. Lamped animals remained stationary or slowly walked away; this lack of urgent escape behaviour is explained by a lack of night hunting; professional rangers do not operate at night and illegal poaching gangs have not been detected in the study landscape despite extensive multi-annual fieldwork. The angle of the observed animal relative to the transect line ($\text{angle}_{\text{sighting}}$) was estimated to 5° using an angle board, allowing perpendicular distance (from the transect line) to be calculated as

$$\text{Distance}_{\text{perpendicular}} = \cos(\text{angle}_{\text{sighting}}) \,.\, \text{distance}_{\text{sighting}} \quad (1)$$

Each transect was driven twice, totalling 567 km, overall sampling intensity was 3.02 km/km^2 across the forest, and was similar in each of the 12 blocks (mean per block = 3.3 km/km^2 SD=0.8, see Appendix A for transect routes). As forest trackways vary in width, I reduced the perpendicular distance according to the mean verge width of the trackway class (forest roads=8m, SD=6; fire routes= 3.8m, SD=2.1; forest rides=0.60m, SD=0.2) following (Wäber and Dolman, 2015). Deer detectability during thermal imaging varies between forest growth stages (Hemami et al., 2007; Wäber and Dolman, 2015); stands were categorised into three visibility classes (open, dense, mature) depending on crop age and whether they had been thinned (see Appendix B for details of classification). Data was recorded from 2414 single-sided transect 'sections' (each defined by the age-class and identity of the surveyed adjacent stand, mean length=225 m, SD=128), but these were not suitable for density surface modelling because of zero inflation (making it difficult to find a suitable error structure, with potential for biased parameter estimates due to overdispersion, Tu 2006). Consequently, sections of the same visibility class lying in close proximity (on one or both sides of the transect centre-line, but spanning <600m along the transect) were combined as 1162 composite 'segments' (mean length=462m, SD=297) for analysis, irrespective of whether they were contiguous or interrupted by sections of another visibility class (see Appendix B for criteria on combined sections). Thus segments may partially overlap, or be nested within, other segments that differed in detectability class but sample similar neighbourhood characteristics (in terms of growth stage composition, soil and arable access); their lack of spatial independence was accounted for by spatially-explicit analysis (see below).

Candidate variables

I related the local abundance of muntjac and of roe deer to measures of: the local intensity of recreational activity, and four environmental variables that characterise habitat and landscape context (Table 2.1), extracted from buffers around each sampled transect-segment (hereafter ’localities’; for details of buffer radii, see below). Selection of environmental variables was informed by the ecology of the two deer species modelled. Both muntjac and roe are small- to medium-sized deer (10-18kg and 17-23kg respectively, Macdonald 2009) that, as concentrate selectors (Tixier et al., 1997), require relatively nutritious forage. This, combined with a requirement for thermal and security shelter (Mysterud and Østbye, 1995), determines much of the habitat selection preferences of both species (Hemami et al., 2005). Roe deer density is greater in recently re-planted and also in mature forest stands; muntjac density is greatest in mature stands, and both species occur at low densities in closed-canopy (pole-stage) stands (Hemami et al., 2004) in which ground vegetation is supressed (Eycott et al., 2006). I extracted the proportion of forest habitat in each locality comprising young (aged 0-5 years since planting; Table 2.1) and mature (> 45 years, following Hemami, Watkinson & Dolman 2004) stands from the Forestry England (FE) sub-compartment database (mean polygon area =2.9ha SD=3.0) and, for surrounding areas, from the Centre for Ecology and Hydrology Land Cover Map 2015, hereafter LCM2015 (Rowland et al., 2017).

Table 2.1: Candidate variables examined in density-surface models of local roe and muntjac deer abundance. For each variable the mean, standard deviation (SD) and coefficient of variation (CV, SD:mean) across n=1162 sampled transect segments are shown.

Candidate Variable	**Description**	**Roe deer mean ± SD (CV)**	**Muntjac mean ± SD (CV)**
Calcareous	Percentage of calcareous soil in localities.	36.7 ± 31.3 (0.8)	36.7 ± 31.3 (0.8)
Recreational intensity	Interpolated modelled disturbance events of dog walkers, across spring and summer in localities.	0.4 ± 0.2 (0.5)	0.4 ± 0.2 (0.5)
Grassland	Percentage of grassland in localities.	9.1 ± 10.8 (1.2)	9.1 ± 10.8 (1.2)
Arable land	Percentage of arable (crops and freshly ploughed) land in localities extracted from CROME 2018.	26.9 ± 20.7 (0.7)	26.9 ± 20.7 (0.7)
Young stands	Percentage of FC 1 to 5 year-old tree crop in localities.	5.7 ± 8.5 (1.5)	5.7 ± 8.5 (1. 5)
Mature stands	Percentage of FC tree crop aged > 45 years-old in the localities.	31.8 ± 18.2 (0.6)	31.8 ± 18.2 (0.6)

Forest extracted from LCM2015 was classified as mature forest after ground-truthing. LCM2015 land cover is classified from composite summer-winter satellite images (pixel resolution 20-30 m), spatially referenced to digital cartography (Ordnance Survey MasterMap topographic layer) with a minimum polygon resolution >0.5 ha. Arable fields can provide high-quality food (Putman and Moore, 1998) and fragmented forest with access to arable is believed to enhance landscape suitability for deer (Sinclair, 1997), while adult female roe deer in forest stands closer to arable have greater body mass (Zini et al., 2019). I extracted the proportionate cover of arable lands from the 2018 Crop Map of England, hereafter CROME2018, that maps crop types using supervised classification of Sentinel-1 Radar and Sentinel-2 Optical Satellite images. As outdoor pig units were not entered by either deer specie (confirmed through extensive thermal imaging survey), fields holding pigs were mapped manually using satellite data derived from Sentinel-2 (Copernicus Sentinel data 2018) and excluded from the arable extent mapped by CROME2018. All other crop types classified by CROME2018 are considered to provide forage for deer, and were therefore pooled in the single landcover class 'arable'. Within forest habitats, calcareous soils support mineral-rich and palatable forage (important during gestation and lactation Brown 1990) and greater plant species richness (Dolman et al., 2012; Eycott et al., 2006); while acidic soils are often dominated by less-palatable *Deschampsia flexuosa* (Scurfield, 1954), or bracken (Marrs and Watt, 2006). Soil classification for the forest was extracted from high-resolution data (Corbett, 1973) comprising 18 soil series, and for surrounding areas from coarser (9 series) Cranfield NATMAP data; following Zini, Wäber & Dolman (2019) these were reconciled to a common classification. I calculated the percentage of calcareous soil in each locality, across the combined extent of forest and grassland, excluding arable lands that provide nutrition irrespective of underlying soils that are modified by marling and fertiliser application. I extracted the proportion of grassland from each locality, combining all permanent open habitat within the forest (extracted from the FE management database) and all grassland in the surrounding landscape (from LCM2015). For the surrounding landscape, I pooled LCM2015 classes of: improved grassland; rough grassland; neutral grassland; calcareous grassland; acidic grassland and heather, as ground-truthing showed unreliable classification to finer ecological resolution (Zini et al., 2019), and furthermore as dwarf-shrub heathland, calcareous grassland and acid grassland are often intimately mixed in Breckland (Dolman et al., 2012). Within the forest open areas may include areas of bracken or scattered scrub (particularly hawthorn, *Crataegus monogyna* or common gorse *Ulex europaea*). The local intensity of recreational activity in each locality was extracted from an empirical model extrapolated across the forest-wide trackway network (Hornigold, 2016). Calibration data comprised 1536 observations (single recreational disturbance events) collected during 1713 one-hour survey visits (controlling for time of day, day of week, and season), across 180 locations (intersection nodes in the pathway network) over five years (138 points surveyed in 2007, 180 points in 2008 and 2009, and 26 in 2013-2014, for further details of methodology and recreational modelling see Appendix C). The model related the observed frequency of dog walkers for each footpath element using a GIS-based Network Analysis considering: path element class (forestry road, fire route, ride), path network-distance from the lowest impedance access point (considering behavioural impedance accounting for path classes, as a weighted distance, following Oh & Jeong 2007), car parking capacity at this access point, and population density in concentric buffers around the access point, controlling for hour of day and day of week. Mean marginal and conditional R^2 of the model from 10-fold cross validation were 0.13 and 0.41, respectively. The extrapolated model predicted the mean frequency of disturbance events (DE) for all footpath elements across the forest. A locality may span multiple footpath elements while deer were counted from a neighbourhood that may encompass other nearby footpath elements, and local deer density may reflect disturbance across a wider buffer. Therefore, an index of the intensity of recreational activity for the locality j, was calculated as:

$$\sum_{i=1}^{n}\frac{pde\ i*length\ i}{area\,j} \qquad (2)$$

where pde_i is the predicted mean frequency of DE (per hour) on element *i*, $length_i$ is the length (m) of footpath element *i* intersected by the locality, and *area j* the area (m^2) of the locality surrounding element *i*.

Statistical analysis

I built separate Density Surface Models (DSMs) for muntjac and roe deer, following (Miller et al., 2013) as a two stage process. First, a detection function (that accounts for the decline in detection probability with increasing perpendicular distance from the transect line) was fitted to the distance observations. Detection functions were fitted, using package “Distance” (Miller, 2016), accounting for segment detectability class (three categories: open, dense, mature), after right-truncating data excluding the 5% most distal observations, following Buckland *et al.* (2001). The most appropriate function (among uniform, half-normal and hazard-rate) and selection of: adjustments (hermite, cosine, polynomial), coefficients of the detectability class covariate and whether group size was related to perpendicular distance (to account for lower probability of detecting smaller groups at further distances) were selected by comparing model AIC. The selected detection function, provided detection probabilities per segment from which density per segment was calculated. Then, a generalized additive model (GAM) was fitted relating density per segment to geographical coordinates (as non-parametric smoothing parameters) and the

set of candidate environmental variables (habitat, landscape, recreation extracted from each locality) as linear predictors, using package “dsm” (Marshall et al., 2017). I fitted latitude and longitude as ‘smoothing parameters’, to provide a smooth curve that best fits the data, using a penalised thin plate regression spline that accounted for spatial autocorrelation. Candidate a *priori* variables were incorporated assuming a linear response and Gaussian error structure. Environmental variables were extracted from each locality, with buffer radii selected to define the locality’s size informed both by home-range size reported in the literature and statistical analysis of the dataset. For roe deer, winter home-ranges measuring 75ha were reported in literature in the study area (Chapman et al., 1993), corresponding to a circular home-range of 500m radius. A 500m radius represented a coarser grain than the scale of individual stands within the forest landscape (mean forest stand width = 355m, SD=60), thus I inspected a series of full DSMs (including all candidate environmental variables, geographical coordinates as smoothing parameters, and the random effect of forest block, n=12) across a range of buffer radii (100-650m, maximum roe deer home-range reported (Morellet et al., 2013) that showed a clear AIC minima at 300m that was selected for subsequent modelling. For muntjac, the winter home-range reported in the literature measured 18ha (Chapman *et al.* 1993; corresponding to a circular home-range of 250m radius). A similar inspection to the one conducted for roe deer, of AIC values across DSMs built with incremental buffers, revealed an inflexion at 250m that was selected for subsequent modelling (for more detail see Appendix D). Analyses were conducted in R software (R core Team, 2018). Variables were non-colinear (r≤0.7, Freckleton 2002).
Whether candidate environmental variables contribute to explaining local deer density, was assessed using multi-model inference in an information theoretic framework (Burnham and Anderson, 2002) using ‘MuMIn’ package (Bartoń, 2018), applied across the set of alternative models comprising all possible combinations of candidate variables (geographical coordinates were included in all models as soothing parameters). A variable was considered supported if included in the 95% model confidence set (the sub-set of candidate models for which cumulative Akaike weights amount to 95% of the total) with a model-averaged CI that didn’t span zero (Boughey et al., 2011). I report model-averaged coefficients of the variables tested, and quantify effect sizes in terms of the magnitude of change in local deer density resulting from an increase in the candidate variable from the lower to the upper distribution quartile. As a measure of explanatory power I report the adjusted R^2 of a model constructed

comprising geographical coordinates and supported environmental variables, as well R^2 of the model comprising geographical coordinates only. Geographical coordinates are included in our model to capture spatial variation that is not modelled by the candidate variables. When the model only consists of geographical coordinates, thin plate regression splines will model spatial variation in deer density, thus coordinates will indirectly, capture the effects of the candidate variables (if these significantly affect deer density) as well as other variance in deer density due to unexplained effects. I expect that a model specifying the candidate variables directly, would have a greater R^2 than a model using geographical coordinates only if these variables greatly affect deer density. Lastly, I predicted muntjac and roe deer densities using the supported variables and geographical coordinates in a raster of 100 x 100m and compared it to the prediction of the simpler model, comprising geographical coordinates only. To compare the change in the spatial prediction of deer numbers generated by the supported environmental variables and the model including geographical coordinates only I calculated the correlation coefficient between the two raster predictions.

Results

Roe deer

For roe deer, a hazard-rate detection function, incorporating segment-specific detectability class, best explained the decline in detectability with distance. A model that incorporated a decline in observed group size (mean =1.7 SD=0.8) at greater detection distance, received similar support (ΔAIC=0.14, Appendix B) and was therefore excluded by parsimony, so that no group size adjustment was made in subsequent density estimation. Effective strip (half) width averaged across the three detectability classes was 90m (SE=4m). Of the 1162 segments 894 (77%) had zero deer detected on either visits, while 268 (23%) had one or more deer detections on both visits. Roe density across the forest (estimated for 100x100m raster cells) ranged from a 0.9 km^{-2} to 55.4 km^{-2} (Fig. 2.1). DSM averaging across candidate environmental variables showed that roe deer density was lower in 'localities' (segment-buffers of mean length=475m, SD=298, width=300m) containing a greater intensity of recreational activity (Figs 2.2-2.3A), or a greater cover of grassland (Figs 2.2-2.3B) and was higher in localities with a greater cover of young stands (Figs 2.2-2.3C). Roe deer density was not affected by the extent of mature stands, arable lands or calcareous soil (Fig. 2.2).

Adjusted R^2 of the DSM including supported candidate variables was 0.17, compared to 0.13 for the model including geographical coordinates only. The roe deer density raster predicted by the DSM comprising geographical coordinates and supported environmental variables was strongly related to that predicted using geographical coordinates only (R^2 =0.74).

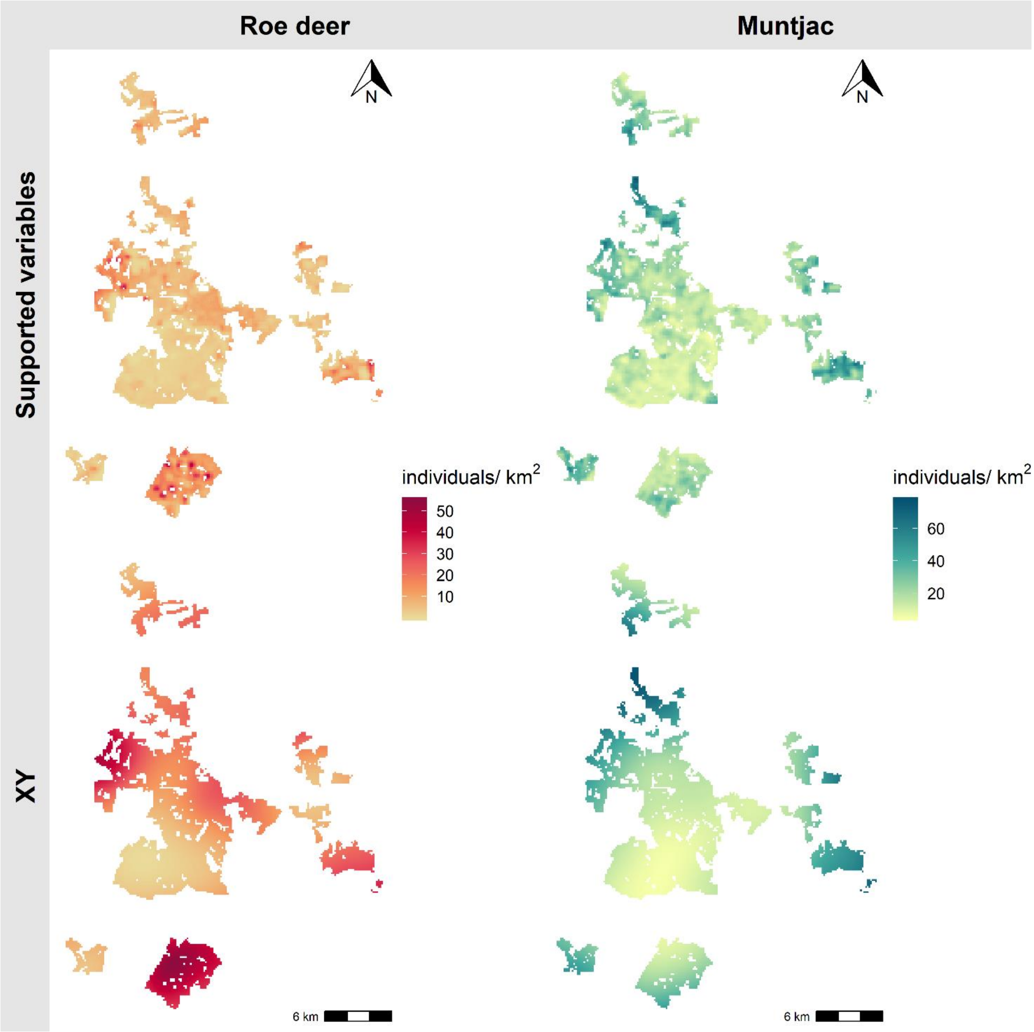


Figure 2.1: Muntjac and roe deer density (individuals km^{-2}) predicted for a 100m x100m raster. Predictions are from models including supported candidate variables and geographical coordinates or by models including geographical coordinates only. All models included random effects of forest block (n=12).

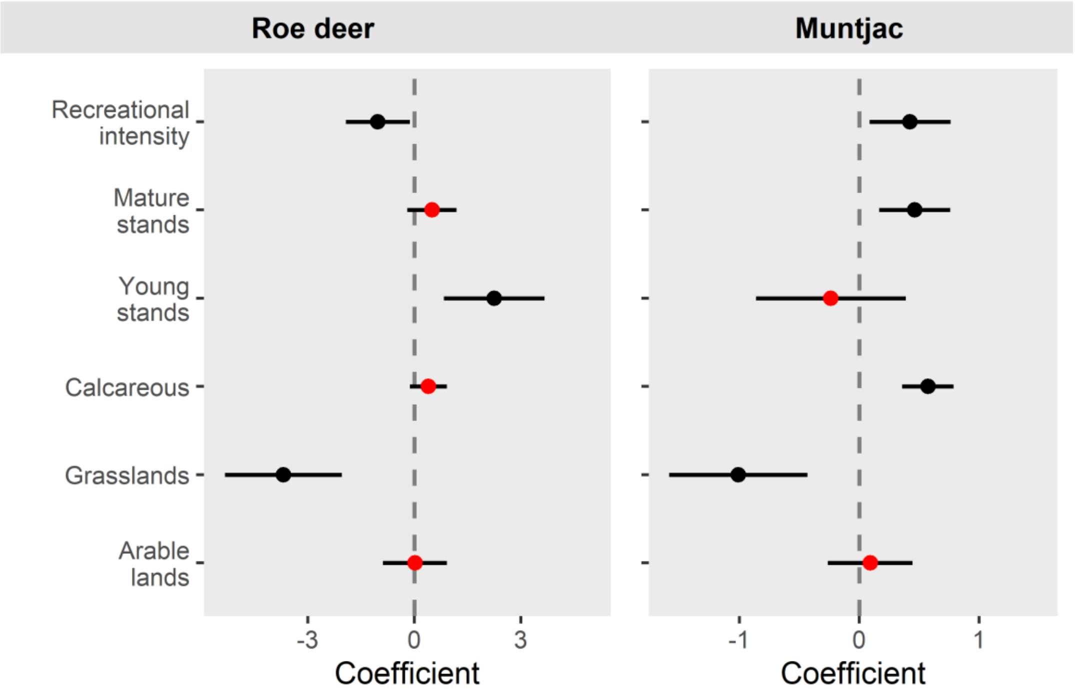


Figure 2.2: Models of local roe deer and muntjac density showing effects of candidate variables. For each variable, model-averaged coefficients following multi-model inference (red filled symbols non-supported variables, black filled symbols supported variables) with 95% Confidence Intervals (bars) are shown, calculated across the 95% model confidence set. All models included the random effect of forest block (n=12).

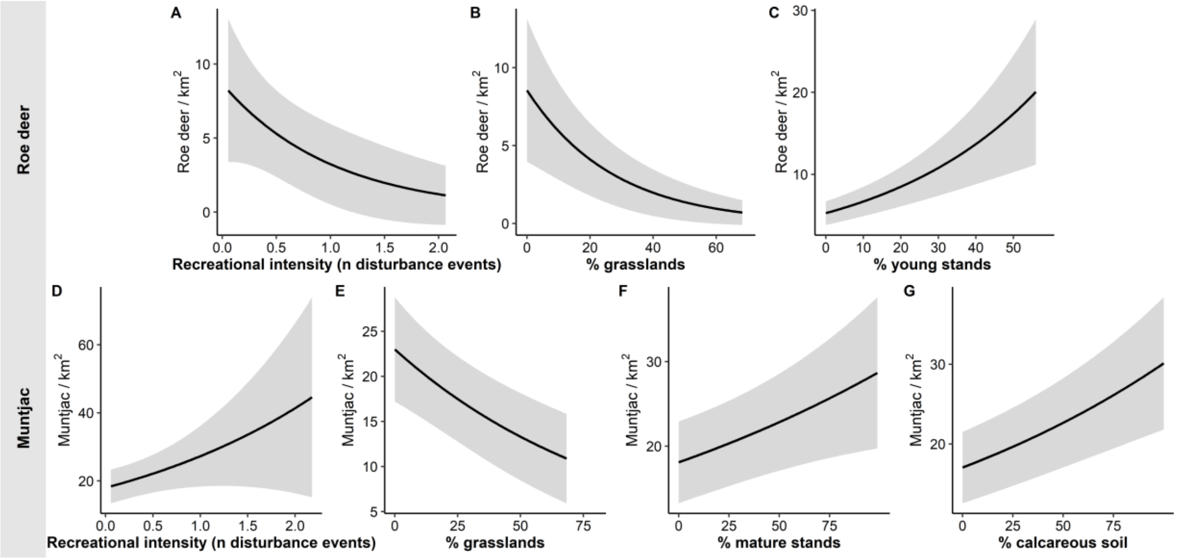


Figure 2.3: Relation of local roe deer and muntjac density to supported variables. Roe deer and muntjac density were predicted from density surface models including geographical coordinates and those variables supported by multi-model inference. Shown are: local

density of roe (A-C) and muntjac (D-G) deer in relation to: recreational intensity (A, D): sum of disturbance events per hour across trackways per buffer weighted by buffer area; percentage of cover of grasslands (B, E); young stands (C); mature stands (F); and calcareous soil (G) within localities.

Muntjac deer

For muntjac, a hazard-rate detection function, incorporating segment-specific detectability class, best explained the decline in detectability with distance. Greater group size (mean =1.16 SD=0.4), increased the probability of detection at greater distance (ΔAIC=+10.75 on removal of group-size term, Appendix B), an adjustment for group size was therefore made in subsequent density estimation. Effective strip (half) width averaged across detectability classes was 75m (SE=3m). Of the 1162 segments, 481 (41%) had zero deer detected on either visits, while 681 (59%) had one or more deer detections on both visits. Muntjac density across the forest (at 100x100m) ranged from 4.7 km^{-2} to 77.5 km^{-2} (Fig. 2.1). DSM averaging across candidate environmental variables showed that muntjac density was greater in localities containing greater intensity of recreational activity (Figs 2.2-2.3D) and with greater cover of mature stands (Figs 2.2-2.3F) or of calcareous soil (Figs 2.2-2.3G), but was lower in localities with a greater cover of grassland (Figs 2.2-2.3E). Muntjac density was not affected by the extent of young stands or arable lands (Fig. 2.2). Adjusted R^2 of the DSM including supported candidate variables was 0.33, compared to 0.30 for the model including geographical coordinates. The muntjac density raster predicted by the DSM comprising geographical coordinates and the supported variables was strongly related to that predicted using the DSM comprising geographical coordinates only (R =0.81).

Discussion

This study was conducted across an extensive forest landscape (187km^2), with a large sample size (1590 and 400 groups observed of muntjac and roe deer, respectively, across 567km of driven transects) that allowed analyses to control for known factors affecting deer distribution. I investigated fine-scale responses of local deer densities at 1150 localities to a fine-grained measure of recreational intensity (calibrated from 1536 observations over 1713 survey hours at 180 survey points). Importantly, roe deer had lower abundance in the most disturbed areas, while the reverse was true for muntjac. The fine-scale deer density estimates predicted from the DSMs show densities varied greatly across the forest (coefficient of variation, SD:mean = 0.8 and 0.5 for roe and muntjac, respectively), though were broadly comparable to coarser-scale densities (per forest block) reported previously in this study area: 3.5 km^{-2} to 40.2 km^{-2} for muntjac and 10.8 km^{-2} to 71.2 km^{-2} for roe deer, during 2008-2010 (Wäber et al., 2013). Roe deer and muntjac were both less abundant in localities containing a greater extent of grassland, and muntjac were more abundant in localities with a greater percentage of calcareous soil. The two species differed in their responses to forest habitat: roe were more abundant in localities with greater percentage of young stands, while muntjac, as previously reported (Hemami et al., 2005, 2004), were more abundant in areas with greater percentage of mature stands and calcareous soil. Although ecologically interesting, the effects of each of these variables on local deer density were relatively small and thus unsuitable to be used as tools for deer impact mitigation.

Local habitat effects

Roe deer local abundances were higher (inter-quartile, IQ, effect size, +1.3 deer/km^2) in localities with a greater percentage of young stands. Younger stands have previously been shown to be important for roe deer populations, with increased recruitment after extensive (75%) conifer re-planting of a woodland in Dorset, and subsequent population declines as the forest matured (Gill et al., 1996). In contrast, local muntjac abundance was higher (IQ effect size, +2.4 deer/km^2) in localities comprising greater cover of mature forest. These results are consistent with previous research in the study landscape, based on faecal pellet density, that similarly found roe deer density was higher in young stands, and muntjac density was higher in mature stands (Hemami et al., 2004). In a forest managed by clear felling and replanting, young stands offer the greatest amount of ground forage (Smolko et al., 2018), but mature stands (with open canopy) offer both ground vegetation and cover (Hemami et al., 2005). Within Britain, bramble (*Rubus fruticosa* agg.) is widely exploited by deer (Holt et al., 2010; Wäber, 2010) including roe and muntjac (Chapman et al., 1985) that both occur in higher densities where more bramble is available (Hemami et al., 2005, 2004); bramble is restricted to early and late forest growth stages by shading (Battles et al., 2001; Hemami et al., 2004). Furthermore, there is a harsh, clearly identifiable boundary between the young stands and the surrounding forest; this has been shown to provide a settling stimulus for roe deer, irrespective of the forage supply available (Reimoser and Ellenberg, 1999). Differences in habitat use between these two species may be further explained by physiology and predator escape mode: while roe deer use open habitats to forage (Putman, 1986) muntjac have shorter legs and more curved backs, adaptations that do not favour sustained running as an escape response but facilitate sheltering in dense low cover. The association of the smaller sub-tropical muntjac with dense shrub may be further explained by a greater requirement for thermal cover, relative to the temperate-boreal distribution of roe deer (Dolman and Wäber, 2008).

Muntjac abundance was higher in localities with a greater percentage (IQ effect size, 7.1 deer/km^2) of calcareous soil. Muntjac are smaller-bodied than roe, potentially placing them at the extreme of the browser-grazer continuum (Bodmer, 1990) compared to roe, further increasing the need to select nutritious food (sensu Gordon & Illius 1994). As their need for cover constrains them in mature stands that have less ground vegetation cover than young stands exploited by roe, this may explain the stronger preference for calcareous soils - that have more diverse forage (Eycott *et al.*, 2006).

Roe deer and muntjac abundance were both lower in localities with a greater percentage of grassland (IQ effect size, -2.9 and -2.6 deer/km^2, respectively). This may be a direct consequence of habitat suitability, as both species have a concentrate-selector diet in contrast to larger grazing deer such as fallow and red deer (Gordon and Illius, 1994; Obidziński et al., 2013). It is also possible that grassland extent may be a proxy for higher local abundance of these larger and potentially competitively dominant (Dolman and Wäber, 2008) species that congregate around and graze within grassland areas (Thirgood, 1995; Trdan and Vidrih, 2008).

Recreational intensity

Roe deer local abundance was negatively affected by the local frequency of dog walkers (IQ effect size, -1.1 deer/km^2). According to the 'human-caused predation risk' hypothesis, animals perceive disturbance from recreational activities as a predation risk (Frid and Dill, 2002). This can ultimately result in avoidance of disturbed areas and increased energetic costs of antipredator behaviour reducing effective habitat quality (Gill et al., 2001). Animals may trade-off the degree of perceived risk against the resource value of a patch (Charnov, 1976): in a hunted population in southwestern France observational studies showed roe deer adjust their vigilance behaviour trading-off risk avoidance against forage availability (Benhaiem et al., 2008; Bonnot et al., 2017). GPS data from roe deer in south-western France showed their ranging behaviour was influenced by human disturbance (Bonnot et al., 2013); similarly, avoidance of buildings and roads have been shown to be the most important factors in roe deer habitat use (Coulon et al., 2008). Across three study sites in northern and one in southwestern France, roe deer occurred more frequently in areas with less human infrastructure (Hewison *et al.* 2001). Red deer and fallow deer have also been shown to be affected by recreation (Boer et al., 2004; Sibbald et al., 2011; Westekemper et al., 2018) and in Germany, red deer used zones with lower recreational activity (Coppes et al., 2017), however differences in recreational access were applied across a bigger scale than the one examined here.

Local abundance of muntjac was positively related to the local frequency of dog walkers (IQ effect size, +1.5 deer/km^2); their smaller size makes it easier for them to hide in dense shrubs and avoid recreationists. Rangers in Thetford Forest avoid culling deer in areas popular with recreationists over safety concern; animals more tolerant of recreation can therefore reduce the risk of being culled by establishing their home-range in these parts of the forest. While comparison of flight distances in different environments is not an accurate method for inferring behavioural differences it is notable that in a high-throughput ‘safari-park’, in southern England, muntjac flight distances were only 8m in non-public areas, and 11m in public areas (Champion, 1997), significantly less than those reported for roe deer in the Netherlands (64m when walking down wind, 41m upwind, 44m in calm wind (Boer et al., 2004). This short flight distance, combined with the difficulty of culling deer in areas of high recreational pressure suggests the trade-off of occupying areas with high number of recreationists is positive for muntjac. Numerous records report muntjac in urban gardens (Harris et al., 1994), suggesting muntjac to be tolerant of proximity to humans. When comparing results of surveys of muntjac and roe deer numbers in urban environments and rural areas muntjac seems to outnumber roe deer in urban environments. Data from the BTO UK-wide Breeding Bird Survey (covering 3295 and 3941 1km^2 grid cells in 2006 and 2017 respectively) provide observations of some mammal species including both deer, this shows that both roe and muntjac increased in rural areas by 81% and 117% respectively between 2006 and 2017 (Harris *et al.* 2018).

Models incorporating geographical coordinates and supported candidate variables performed better than simpler models including solely geographical coordinates, however the increase in variance explained was small, and the majority of the variance is to be attributed to unexplained spatial variation. It is possible that the influence of variables reported here, relating to local deer distribution (aggregative response, Sutherland 1983), may not affect underlying demographic processes (driven by fertility or neo-natal survival) and therefore overall numbers across the landscape. Regarding forest management, this study showed that felling and restocking tree crops may increase local roe deer abundance (as they tend to congregate more in young stands) while decreasing local muntjac abundance. As recreation appears to negatively affect roe deer local distribution, it may be possible to manage recreation (changing the spatial distribution of access points and paths accessibility) and change and local density of roe deer to create 'safe refuges' favouring greater local abundance. Culling in these areas would then be simultaneously safer and more cost-effective (in terms of the effort required to achieve a given harvest, Hatter 2001). Managing recreation however, would only slightly improve forest management if roe was the only deer species present, or the species having the greatest impact. This solution is not suitable for managing muntjac, for which the opposite response to recreational intensity was found. Managing recreation at a fine-scale doesn't appear to provide a useful tool for muntjac and roe deer management.

Conclusions

The results show that forest management affects local deer density, but the effects found here were not strong enough to justify adapting forest managemet to mitigate impacts and would not allow the removal of lethal control by shooting. The variance explained by the models including the variables supported as well as the effect sizes of each variable were relatively low, showing little effect on local deer aggregation. My conclusion is that culling deer continues to offer the most effective tool for local density and impact reduction. An ethical and effective culling program should start from an assessment of deer numbers to build a demographic model, as well as a continuous evaluation of impacts and population size to monitor its effecteness (Dubois et al., 2017).

References

Altmann, M., 1958. The flight distance in free-ranging big game. J. Wildl. Manage. 22, 207. https://doi.org/10.2307/3797334

Armour-Chelu, N., Brooke, R., Riley, R., 2014. Open Habitats Implementation Plan for The Forestry Commission, Thetford Public Forest Estate, 2014 Onward, FC England. Bristol.

Baines, D., Andrew, M., 2003. Marking of deer fences to reduce frequency of collisions by woodland grouse. Biol. Conserv. 110, 169–176. https://doi.org/10.1016/S0006-3207(02)00185-4

Bartoń, K., 2018. MuMIn: Multi-Model Inference. R package version 1.42.1.

Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C.M., Crowther, T.W., 2019. The global tree restoration potential. Science (80-.). 365, 76–79. https://doi.org/10.1126/science.aax0848

Battles, J.J., Shlisky, A.J., Barrett, R.H., Heald, R.C., Allen-Diaz, B.H., 2001. The effects of forest management on plant species diversity in a Sierran conifer forest. For. Ecol. Manage. 146, 211–222. https://doi.org/10.1016/S0378-1127(00)00463-1

Behrend, D.F., Lubeck, R.A., 1968. Summer flight behavior of white-tailed deer in two Adirondack forests. J. Wildl. Manage. 32, 615. https://doi.org/10.2307/3798942

Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.J.M., Morellet, N., Verheyden, H., 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Anim. Behav. 76, 611–618. https://doi.org/10.1016/j.anbehav.2008.03.012

Bodmer, R.E., 1990. Ungulate frugivores and the browser-grazer continuum. Oikos 57, 319. https://doi.org/10.2307/3565960

Boer, H.Y. de, Breukelen, L. van, Hootsmans, M.J.M., Wieren, S.E. van, 2004. Flight distance in roe deer, *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. Wildlife Biol. 10, 35–41. https://doi.org/10.2981/wlb.2004.007

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. Eur. J. Wildl. Res. 59, 185–193. https://doi.org/10.1007/s10344-012-0665-8

Bonnot, N.C., Hewison, A.J.M., Morellet, N., Gaillard, J.M., Debeffe, L., Couriot, O., Cargnelutti, B., Chaval, Y., Lourtet, B., Kjellander, P., Vanpé, C., 2017. Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. Anim. Behav. 124, 35–46. https://doi.org/10.1016/j.anbehav.2016.11.031

Boughey, K.L., Lake, I.R., Haysom, K.A., Dolman, P.M., 2011. Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. Biol. Conserv. 144, 2300–2310. https://doi.org/10.1016/j.biocon.2011.06.008

Brown, R.D., 1990. Nutrition and antler development, in: Horns, Proghorns and Antlers. New York, pp. 426–442.

Buckland, S.T., Anderson, D.R., Thomas, L., Burnham, K.P., Laake, J.L., Borchers, D.L., 2001. Line transects, in: Introduction To Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, pp. 104–14.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference. A Practical Information—Theoretic Approach, 2nd ed. New York.

Champion, R., 1997. A Behavioural and Ecological study on the Impact of Disturbance on a Free Roaming population of Chinese Water (Hydropotes inermis). Royal Holloway, University of London, London.

Chapman, N.G., Claydon, K., Claydon, M., Forde, P.G., Harris, S., 1993. Sympatric populations of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*): a comparative analysis of their ranging behaviour, social organization and activity. J. Zool. 229, 623–640. https://doi.org/10.1111/j.1469-7998.1993.tb02660.x

Chapman, N.G., Claydon, K., Claydon, M., Harris, S., 1985. Distribution and habitat selection by muntjac and other species of deer in a coniferous forest. Acta Theriol. (Warsz). 30, 287–303.

Chapman, N.G., Harris, S., Stanford, A., 1994. Reeves' muntjac *Muntiacus reevesi* in Britain: their history, spread, habitat selection, and the role of human intervention in accelerating their dispersal. Mamm. Rev. 24, 113–160. https://doi.org/10.1111/j.1365-2907.1994.tb00139.x

Charnov, E.L., 1976. Optimal foraging theory: the marginal value theorem. Theor. Popul. Biol. 9, 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

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, e50611. https://doi.org/10.1371/journal.pone.0050611

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, e0175134. https://doi.org/10.1371/journal.pone.0175134

Corbett, W.M., 1973. Breckland Forest Soils Special Survey 7, Soil Survey of England and Wales. Harpenden, UK.

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J.-M., Hewison, A.J.M., 2008. Inferring the effects of landscape structure on roe deer (*Capreolus capreolus*) movements using a step selection function. Landsc. Ecol. 23, 603–614. https://doi.org/10.1007/s10980-008-9220-0

Cromsigt, J.P.G.M., Kuijper, D.P.J., Adam, M., Beschta, R.L., Churski, M., Eycott, A., Kerley, G.I.H., Mysterud, A., Schmidt, K., West, K., 2013. Hunting for fear: innovating management of human-wildlife conflicts. J. Appl. Ecol. 50, 544–549. https://doi.org/10.1111/1365-2664.12076

Crop Map of England (CROME), 2018.

DEFRA, 2018. Tackling Invasive Non-Native Species: A New Enforcement Regime.

Delahay, R.J., De Leeuw, A.N.S., Barlow, A.M., Clifton-Hadley, R.S., Cheeseman, C.L., 2002.

The status of *Mycobacterium bovis* infection in UK wild mammals: a review. Vet. J. 164, 90–105. https://doi.org/10.1053/tvjl.2001.0667

Department for Environment, F.& R.A. [DEFRA], 2010. The sustainable management of wild deer populations in England: a review of 2005–2008 and summary ofaction to March 2011. Wrexham, United Kingdom.

Dolman, P.M., Panter, C.J., Mossman, H.L., 2012. The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. J. Appl. Ecol. 49, 986–997. https://doi.org/10.1111/j.1365-2664.2012.02174.x

Dolman, P.M., Wäber, K., 2008. Ecosystem and competition impacts of introduced deer. Wildl. Res. 35, 202. https://doi.org/10.1071/WR07114

Dubois, S., Fenwick, N., Ryan, E.A., Baker, L., Baker, S.E., Beausoleil, N.J., Carter, S., Cartwright, B., Costa, F., Draper, C., Griffin, J., Grogan, A., Howald, G., Jones, B., Littin, K.E., Lombard, A.T., Mellor, D.J., Ramp, D., Schuppli, C.A., Fraser, D., 2017. International consensus principles for ethical wildlife control. Conserv. Biol. 31, 753–760. https://doi.org/10.1111/cobi.12896

Edward, T., Kazushige, Y., 2015. Changing access and conservation mechanisms in the parks of England and Wales: a review of five policy milestones. J. For. Econ. 61.

Eycott, A.E., Watkinson, A.R., Dolman, P.M., 2006. Ecological patterns of plant diversity in a plantation forest managed by clearfelling. J. Appl. Ecol. 43, 1160–1171. https://doi.org/10.1111/j.1365-2664.2006.01235.x

Freckleton, R.P., 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. J. Anim. Ecol. 71, 542–545. https://doi.org/10.1046/j.1365-2656.2002.00618.x

Frid, A., Dill, L.M., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, art11. https://doi.org/10.5751/ES-00404-060111

Gilbert, L., Maffey, G.L., Ramsay, S.L., Hester, A.J., 2012. The effect of deer management on the abundance of *Ixodes ricinus* in Scotland. Ecol. Appl. 22, 658–667. https://doi.org/10.1890/11-0458.1

Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biol. Conserv. 97, 265–268. https://doi.org/10.1016/S0006-3207(00)00002-1

Gill, R.M.A., 1992. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. Forestry 65, 363–388. https://doi.org/10.1093/forestry/65.4.363-a

Gill, R.M.A., Johnson, A.L., Francis, A., Hiscocks, K., Peace, A.J., 1996. Changes in roe deer (*Capreolus capreolus L.*) population density in response to forest habitat succession. For. Ecol. Manage. 88, 31–41. https://doi.org/10.1016/S0378-1127(96)03807-8

Gionfriddo, J.P., Eisemann, J.D., Sullivan, K.J., Healey, R.S., Miller, L.A., Fagerstone, K.A., Engeman, R.M., Yoder, C.A., 2009. Field test of a single-injection gonadotrophin-releasing hormone immunocontraceptive vaccine in female white-tailed deer. Wildl. Res. 36, 177. https://doi.org/10.1071/WR08061

Gordon, I.J., Illius, A.W., 1994. The functional significance of the browser-grazer dichotomy in African ruminants. Oecologia 98, 167–175. https://doi.org/10.1007/BF00341469

Harris, S., Chapman, N.G., Harris, A., 1994. What gardeners say about muntjac., in: Deer. pp. 302–306.

Harris, S.J., Massimino, D., Gillings, S., Eaton, M.A., Noble, D.G., Balmer, D.E., Procter, D., Pearce-Higgins, J.W., Woodcock, P., 2018. The 2017 BBS Report.

Hatter, I., 2001. An assessment of catch-per-unit effort to estimate rate of change in deer and moose populations. Alces 37, 71–77.

Hemami, M.R., Dolman, P.M., 2005. The disappearance of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) pellet groups in a pine forest of lowland England. Eur. J. Wildl. Res. 51, 19–24. https://doi.org/10.1007/s10344-004-0067-7

Hemami, M.R., Watkinson, A.R., Dolman, P.M., 2005. Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* in a lowland pine forest. For. Ecol. Manage. 215, 224–238. https://doi.org/10.1016/j.foreco.2005.05.013

Hemami, M.R., Watkinson, A.R., Dolman, P.M., 2004. Habitat selection by sympatric muntjac

(*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a lowland commercial pine forest. For. Ecol. Manage. 194, 49–60. https://doi.org/10.1016/j.foreco.2004.01.049

Hemami, M.R., Watkinson, A.R., Gill, R.M.A., Dolman, P.M., 2007. Estimating abundance of introduced chinese muntjac /*Muntiacus reevesi* and native roe deer *Capreolus capreolus* using portable thermal imaging equipment. Mamm. Rev. 37, 246–254. https://doi.org/10.1111/j.1365-2907.2007.00110.x

Hewison, A.J.M., Vincent, J.P., Joachim, J., Angibault, J.M., Cargnelutti, B., Cibien, C., 2001. The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. Can. J. Zool. 79, 679–689. https://doi.org/10.1139/z01-032

Holt, C.A., Fuller, R.J., Dolman, P.M., 2010. Experimental evidence that deer browsing reduces habitat suitability for breeding common nightingales *Luscinia megarhynchos*. Ibis (Lond. 1859). 152, 335–346. https://doi.org/10.1111/j.1474-919X.2010.01012.x

Hornigold, K., 2016. Modelling nature-based recreation to inform land management. PhD thesis. University of East Anglia.

Hurley, P.M., Webster, C.R., Flaspohler, D.J., Parker, G.R., 2012. Untangling the landscape of deer overabundance: reserve size versus landscape context in the agricultural Midwest. Biol. Conserv. 146, 62–71. https://doi.org/10.1016/j.biocon.2011.10.034

IUCN, 2017. Technical Note on Non-Lethal Measures to Eradicate or Manage Vertebrates Included on the List of IAS of Union Concern.

Jaenson, T.G.T., Petersson, E.H., Jaenson, D.G.E., Kindberg, J., Pettersson, J.H.O., Hjertqvist, M., Medlock, J.M., Bengtsson, H., 2018. The importance of wildlife in the ecology and epidemiology of the TBE virus in Sweden: incidence of human TBE correlates with abundance of deer and hares. Parasit. Vectors 11, 477. https://doi.org/10.1186/s13071-018-3057-4

Jarnemo, A., Minderman, J., Bunnefeld, N., Zidar, J., Mansson, J., 2014. Managing landscapes for multiple objectives: alternative forage can reduce the conflict between deer and forestry. Ecosphere 5, 97. https://doi.org/10.1890/ES14-00106.1

Johna, N., Annerstedt, M., Boman, M., Mattsson, L., 2010. Influence of outdoor recreation on self-rated human health: comparing three categories of Swedish recreationists.

Scand. J. For. Res. 234–244.

Kilpatrick, H.J., Labonte, A.M., Stafford, K.C., 2014. The relationship between deer density, tick abundance, and human cases of Lyme disease in a residential community. J. Med. Entomol. 51, 777–784. https://doi.org/10.1603/ME13232

Lamberti, P., Mauri, L., Merli, E., Dusi, S., Apollonio, M., 2006. Use of space and habitat selection by roe deer *Capreolus capreolus* in a Mediterranean coastal area: how does woods landscape affect home range? J. Ethol. 24, 181–188. https://doi.org/10.1007/s10164-005-0179-x

Laundre, J.W., Hernandez, L., Ripple, W.J., 2010. The landscape of fear: ecological implications of being afraid. Open Ecol. J. 3, 1–7. https://doi.org/10.2174/1874213001003030001

Macdonald, D.W., 2009. The Princeton Encyclopedia of Mammals, 1st ed. Windmill Books (Andromeda International).

Mallord, J.W., Dolman, P.M., Brown, A.F., Sutherland, W.J., 2006. Linking recreational disturbance to population size in a ground-nesting passerine. J. Appl. Ecol. 44, 185–195. https://doi.org/10.1111/j.1365-2664.2006.01242.x

Marrs, R.H., Watt, A.S., 2006. Biological flora of the British isles: *Pteridium aquilinum (L.) Kuhn*. J. Ecol. 94, 1272–1321. https://doi.org/10.1111/j.1365-2745.2006.01177.x

Marshall, L., Miller, D.L., Rexstad, E., Burt, L., Bravington, M. V, Hedley, S., 2017. Package ‘ dsm .’

Miller, D.L., 2016. Package ‘Distance.’

Miller, D.L., Burt, M.L., Rexstad, E.A., Thomas, L., 2013. Spatial models for distance sampling data: recent developments and future directions. Methods Ecol. Evol. 4, 1001–1010. https://doi.org/10.1111/2041-210X.12105

Miller, G.R., Cummins, R.P., Hester, A., 1998. Red deer and woodland regeneration in the Cairngorms. Scottish For. 52.

Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. Wildl. Soc. Bull. 29, 124–132.

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J.D.C., Nicoloso, S., Sustr, P., Urbano, F., Mysterud, A., 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. J. Anim. Ecol. 82, 1326–1339. https://doi.org/10.1111/1365-2656.12105

Moss, R., 2001. Second extinction of capercaillie (*Tetrao urugallus*) in Scotland? Biol. Conserv. 101, 255–257. https://doi.org/10.1016/S0006-3207(01)00066-0

Mysterud, A., Østbye, E., 1995. Bed-site selection by European roe deer (*Capreolus capreolus*) in southern Norway during winter. Can. J. Zool. 73, 924–932. https://doi.org/10.1139/z95-108

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. Open Life Sci. 8, 8–17. https://doi.org/10.2478/s11535-012-0108-2

Oh, K., Jeong, S., 2007. Assessing the spatial distribution of urban parks using GIS. Landsc. Urban Plan. 82, 25–32. https://doi.org/10.1016/j.landurbplan.2007.01.014

Palmer, S.C.F., Broadhead, J.E., Ross, I., Smith, D.E., 2007. Long-term habitat use and browsing by deer in a Caledonian pinewood. For. Ecol. Manage. 242, 273–280. https://doi.org/10.1016/j.foreco.2007.01.061

Putman, R.J., 1986. Foraging by roe deer in agricultural areas and impact on arable crops. J. Appl. Ecol. 23, 91. https://doi.org/10.2307/2403083

Putman, R.J., Moore, N.P., 1998. Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. Mamm. Rev. 28, 141–164. https://doi.org/10.1046/j.1365-2907.1998.00031.x

R core Team, 2018. R: A Language and Environment for Statistical Computing.

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. For. Ecol. Manage. 424, 406–419. https://doi.org/10.1016/j.foreco.2018.05.016

Redick, C.H., Jacobs, D.F., 2020. Mitigation of deer herbivory in temperate hardwood forest regeneration: a meta-analysis of research literature. Forests 11, 1220. https://doi.org/10.3390/f11111220

Reimoser, F., Ellenberg, H., 1999. Forest management systems as a component of ungulate-game pest management with special reference to roe deer and edge effects, in: Advances in Vertebrate Pest Management. pp. 219–238.

Reimoser, F., Gossow, H., 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. For. Ecol. Manage. 88, 107–119. https://doi.org/10.1016/S0378-1127(96)03816-9

Reimoser, S., Partl, E., Reimoser, F., Vospernik, S., 2009. Roe-deer habitat suitability and predisposition of forest to browsing damage in its dependence on forest growth-Model sensitivity in an alpine forest region. Ecol. Modell. 220, 2231–2243. https://doi.org/10.1016/j.ecolmodel.2009.05.022

Rowland, C.S., Morton, R.D., Carrasco, L., McShane, G., O’Neil, A.W., Wood, C.M., 2017. Land Cover Map 2015 (vector, GB). https://doi.org/https://doi.org/10.5285/6c6c9203-7333-4d96-88ab-78925e7a4e73

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. Landsc. Ecol. 32, 2281–2295. https://doi.org/10.1007/s10980-017-0568-x

Saïd, S., Servanty, S., 2005. The influence of landscape structure on female roe deer home-range size. Landsc. Ecol. 20, 1003–1012. https://doi.org/10.1007/s10980-005-7518-8

Scurfield, G., 1954. *Deschampsia flexuosa (L.) Trin*. J. Ecol. 42, 225. https://doi.org/10.2307/2256995

Sibbald, A.M., Hooper, R.J., McLeod, J.E., Gordon, I.J., 2011. Responses of red deer (*Cervus elaphus*) to regular disturbance by hill walkers. Eur. J. Wildl. Res. 57, 817–825. https://doi.org/10.1007/s10344-011-0493-2

Sinclair, A.R.E., 1997. Carrying capacity and the overabundance of deer, in: The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Institution, Washington, pp. 380–394.

Smart, J.C.R., Ward, A.I., White, P.C.L., 2004. Monitoring woodland deer populations in the UK: an imprecise science. Mamm. Rev. 34, 99–114. https://doi.org/10.1046/j.0305-1838.2003.00026.x

Smolko, P., Veselovská, A., Kropil, R., 2018. Seasonal dynamics of forage for red deer in temperate forests: importance of the habitat properties, stand development stage and overstorey dynamics. Wildlife Biol. 2018, wlb.00366. https://doi.org/10.2981/wlb.00366

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. J. Appl. Ecol. 57, 1376–1390. https://doi.org/10.1111/1365-2664.13622

Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141, 2159–2173. https://doi.org/10.1016/j.biocon.2008.06.026

Sutherland, W.J., 1983. Aggregation and the `Ideal Free' Distribution. J. Anim. Ecol. 52, 821. https://doi.org/10.2307/4456

Swanson, G., Armstrong, H., 2008. Estimating deer abundance in woodlands: the combination plot technique. For. Comm. Bull. 128.

Tälleklint, L., Jaenson, T.G.T., 1997. Infestation of mammals by *Ixodes ricinus* ticks (Acari: Ixodidae) in south-central Sweden. Exp. Appl. Acarol. 21, 755–771. https://doi.org/10.1023/A:1018473122070

Taylor, A.R., Knight, R.L., 2003. Wildlife responses to recreation and associated visitor perceptions. Ecol. Appl. 13, 951–963. https://doi.org/10.1890/1051-0761(2003)13[951:WRTRAA]2.0.CO;2

Thirgood, S.J., 1995. The effects of sex, season and habitat availability on patterns of habitat use by fallow deer (*Dama dama*). J. Zool. 235, 645–659. https://doi.org/10.1111/j.1469-7998.1995.tb01775.x

Tixier, H., Duncan, P., Scehovic, J., Yant, A., Gleizes, M., Lila, M., Yani, A., 1997. Food selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional value of their diets. J. Zool. 242, 229–245.

https://doi.org/10.1111/j.1469-7998.1997.tb05799.x

Trdan, S., Vidrih, M., 2008. Quantifying the damage of red deer (*Cervus elaphus*) grazing on grassland production in southeastern Slovenia. Eur. J. Wildl. Res. 54, 138–141. https://doi.org/10.1007/s10344-007-0106-2

Tu, W., 2006. Zero-Inflated Data, in: Encyclopedia of Environmetrics. John Wiley & Sons, Ltd, Chichester, UK. https://doi.org/10.1002/9780470057339.vaz000g

UK Climate Change Committee, 2020. The Sixth Carbon Budget. The UK's Path to Net Zero.

Vospernik, S., Reimoser, S., 2008. Modelling changes in roe deer habitat in response to forest management. For. Ecol. Manage. 255, 530–545. https://doi.org/10.1016/j.foreco.2007.09.036

Wäber, K., 2010. Landscape scale deer management. PhD Thesis. PhD Thesis. University of East Anglia.

Wäber, K., Dolman, P.M., 2015. Deer abundance estimation at landscape-scales in heterogeneous forests. Basic Appl. Ecol. 16, 610–620. https://doi.org/10.1016/j.baae.2015.06.005

Wäber, K., Spencer, J., Dolman, P.M., 2013. Achieving landscape-scale deer management for biodiversity conservation: the need to consider sources and sinks. J. Wildl. Manage. 77, 726–736. https://doi.org/10.1002/jwmg.530

Ward, A.I., 2005. Expanding ranges of wild and feral deer in Great Britain. Mamm. Rev. 35, 165–173. https://doi.org/10.1111/j.1365-2907.2005.00060.x

Westekemper, K., Reinecke, H., Signer, J., Meißner, M., Herzog, S., Balkenhol, N., 2018. Stay on trails – effects of human recreation on the spatiotemporal behavior of red deer *Cervus elaphus* in a German national park. Wildlife Biol. 2018. https://doi.org/10.2981/wlb.00403

Zini, V., Wäber, K., Dolman, P.M., 2019. Habitat quality, configuration and context effects on roe deer fecundity across a forested landscape mosaic. PLoS One 14, e0226666. https://doi.org/10.1371/journal.pone.0226666

Appendices

Appendix A. Composition and configuration of forest blocks

Table A2.1: Thetford Forest blocks, for each showing total area (ha), and percentages of: calcareous soil; grassland; mature tree crops (>45 years old); restocked tree crops (0-5 years from planting); and, the percentage of the block perimeter that abuts arable.

Forest Block	Area (ha)	% calcareous	% grassland	% mature	% restock	% arable perimeter
1	1337	22	19	11	2	82
2	918	22	28	17	1	87
3	2401	51	16	3	3	68
4	3025	31	27	36	3	52
5	714	17	19	24	4	60
6	833	2	28	31	1	48
7	545	14	34	16	4	68
8	908	26	28	27	4	63
9	3464	32	13	36	3	39
10	1656	18	16	29	4	12
11	2333	27	17	27	5	60
12	592	18	32	34	2	51

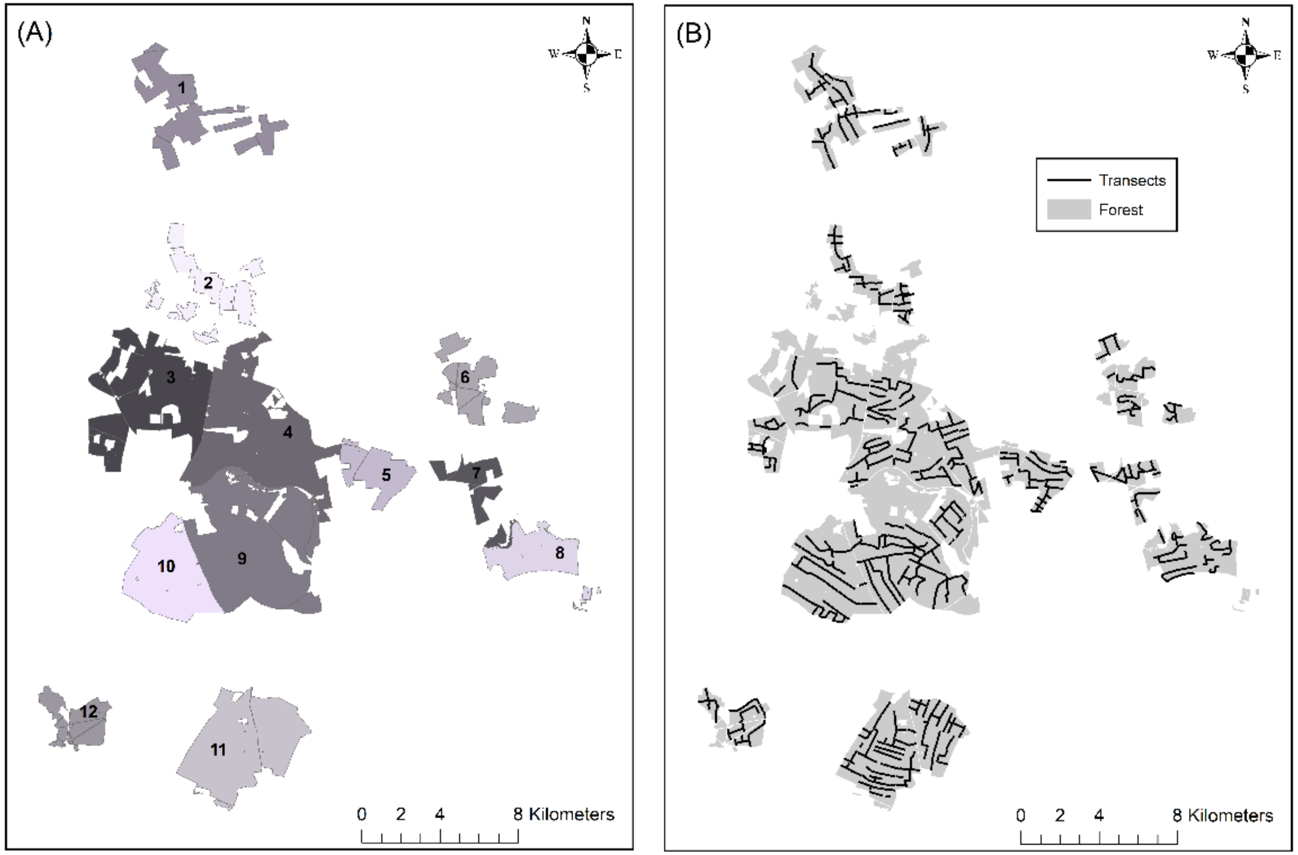


Figure A2.1: Thetford Forest blocks layout and sampling intensity pattern. In A: Forest blocks labelled as identified in table A2.1. In B: Transects driven to sample deer abundance across Thetford Forest. Each transect was driven in both directions, with one-sided nocturnal distance sampling of deer by thermal imaging.

Appendix B. Detectability class covariate and detection function analysis

Criteria for combined sections

An observers ability to detect an individual deer (‘detectability’) during nocturnal thermal imaging distance sampling, reduces with perpendicular distance of the deer (or group) but also systematically differs between forest growth stages, according to structural closure (Hemami et al., 2007; Wäber and Dolman, 2015). Detection functions in models of detectability, therefore, included an *a priori* 3-level categorical variable, at the scale of the stand in each transect section, as either:

‘open’ (comprising permanent open areas, clearfelled unplanted stands, and recently restocked stands 0-3 years since planting); ‘dense’ (comprising restocked stands 4-5 years old, pre-thicket stands 6-10 years old and thicket stands 11-20 years old, and those pole stage stands, between 21-40 years old, that had not yet received a first thinning cut, when rows are removed), or ‘mature’ (comprising thinned pole stage stands 20-40 years old and mature stands >40 years old).

Individual forest stands defined by growth stage and potentially by visibility class, surveyed as contiguous or sequential single-sided driven transects, generating a series of short (n=2414, mean length 225m, SD=128) transect ‘sections’ (with the start and end defined for each individual forest stand). Large numbers of sections with zero observations caused zero-inflation in the density surface model (DSM) and generated inflated high values of local density in those sections with one or more deer observed. To improve model precision and avoid zero-inflation, sections were combined into fewer, longer composite ‘segments’, each comprising a single visibility class, either contiguous or interrupted (interspersed with sections of another detectability class, lying on either side of the transect centre-line) but extending for no more than 600m between start and end point, by an algorithm. In a few instances (n=29) where longer individual sections (max length=944m, mean =700m, SD=102) ran through or alongside a single large stand (of uniform visibility class), these were retained in their entirety despite being >600m in length. Figure A2.2 shows three examples of this process, whereby the initial 2414 sections were merged and reduced to 1162 segments (mean length=462m, SD=297). Candidate variables were extracted from a series of buffers (sequentially sampling radii from 100m to 650 for roe and 100m to 700m for muntjac) around each combined segment (segment buffered are referred to as 'localities'); therefore, individual localities sampled similar environmental attributes to neighbouring, overlapping or interspersed localities that differed in detectability class.

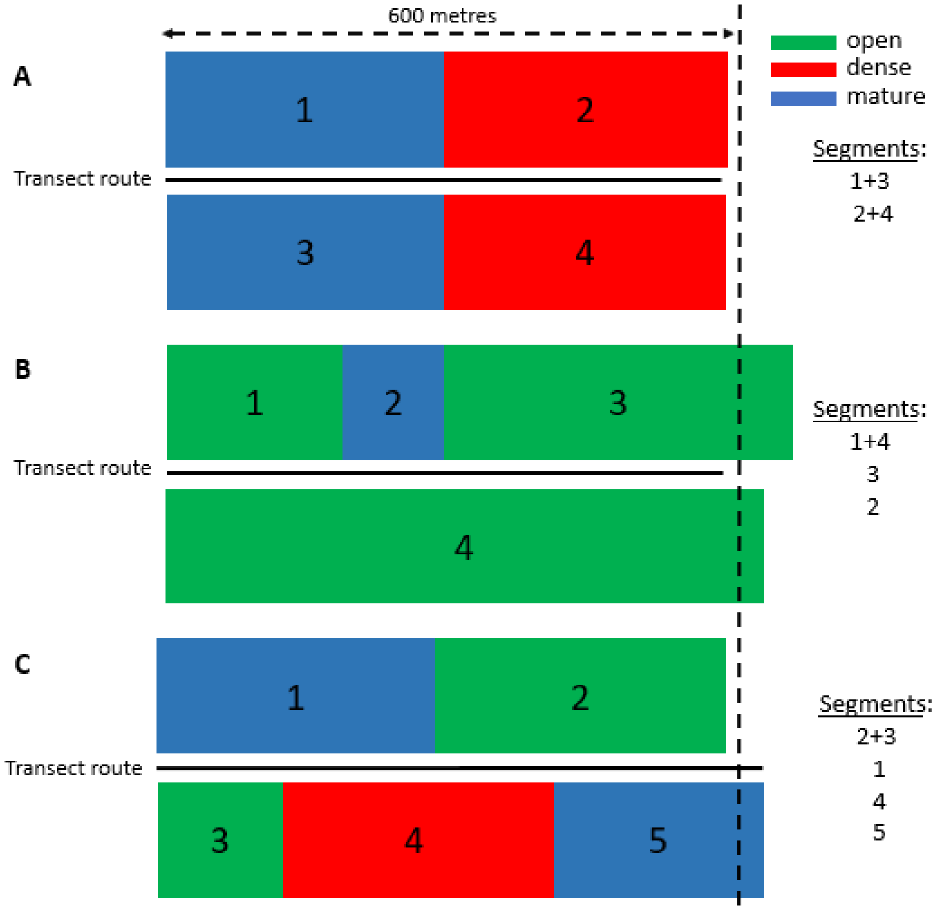


Figure A2.2: Schematic illustrating combination of proximal distance transect 'sections' (defined by stands) into fewer, longer, 'segments' of common detectability class (denoted by colours). In A: one segment comprised two single-sided sections that sampled mature stands (1 and 3) on opposite sides of the transect centre-line (spatially linked, but separated by transect timing, first and second pass), and a second segment comprising two sections that each sampled dense stands (2 and 4). In B: one long section (4) exceeded 600m but was not subdivided (as it sampled a single stand), this was combined with a short section (1) on the opposite side of the transect centre-line, that also sampled a stand of the same visibility class (open). Although the remaining section also sampled a stand of this visibility class (open), this section was not combined in the same segment as it projected further beyond section (4); section (2) sampled a different visibility class (mature) and was not combined with either of these segments (though would be a candidate for combination with other nearby section(s) further along the centre line if they also sampled a mature stand and lay within 600m). In C: we combined two sections (2 and 3) on opposite sides of the transect centre-line as both sampled stands of the same visibility class (open) and lay within 600m, while two sections (1 and 5) that sampled mature stands were not combined as they exceeded 600m from start to finish, section (4) sampled a different visibility class (dense) and was therefore not combined with any of these segments; again sections 1, 5, 4 would be candidates for combination with other nearby sections lying within 600m along the transect centre-line if theye sampled the same visibility class.

References

Buckland, S.T., Anderson, D.R., Thomas, L., Burnham, K.P., Laake, J.L., Borchers, D.L., 2001. Line transects, in: Introduction To Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, pp. 104–14.

Hemami, M.R., Watkinson, A.R., Gill, R.M.A., Dolman, P.M., 2007. Estimating abundance of introduced chinese muntjac /*Muntiacus reevesi* and native roe deer *Capreolus capreolus* using portable thermal imaging equipment. Mamm. Rev. 37, 246–254. https://doi.org/10.1111/j.1365-2907.2007.00110.x

Miller, D.L., 2016. Package 'Distance.'

R core Team, 2018. R: A Language and Environment for Statistical Computing.

Wäber, K., Dolman, P.M., 2015. Deer abundance estimation at landscape-scales in heterogeneous forests. Basic Appl. Ecol. 16, 610–620. https://doi.org/10.1016/j.baae.2015.06.005

Appendix C. Spatially-explicit model of recreational forest use

A spatially-explicit layer of relative recreational intensity was constructed (Hornigold, 2016) calibrated by data from field-based surveys of recreational activity. The spatially-explicit recreational model (Hornigold, 2016) related observed recreational disturbance events (DE) per path element, to measures of the path network distance from the lowest impendence access point, path characteristics, and housing density (in a buffer around the lowest impendence access point), controlling for day in week and time of day. The model was then used to extrapolate predictions of recreational intensity across the pathway network, allowing resampling within each deer distance-transect segment-buffer.

Methods

Visitor surveys

Visitor surveys were collected from April to October of 2007 (number of sampling points = 138), 2008 (n = 174), 2009 (n = 174); with further data collected in 2013 and 2014 to record the numbers of people at popular sites (n = 15, as these have greater car park capacity but were omitted from the original surveys) while re-sampling 11 of the original survey points to control for potential effects of year. Points were randomly selected throughout the forest pathway network, constrained to be placed at intersections (junctions) of paths allowing data to be collected simultaneously from each converging pathway element (between consecutive junctions). In each year, each point was surveyed 3 times on different days at different times (between 06:00 – 18:00 hrs) to incorporate variability in the number of recreationists. At each visit, the number of DE in each path segment over a period of 1 hour was recorded, and for each DE, the number of recreationists, their activity (dog walking, walking or cycling) and the path element used to approach and leave the intersection were recorded. Additional methodological details can be found in (Dolman, 2009; Dolman et al., 2008).

Explanatory variables

Pathway elements were classified using to Forestry England GIS data as forest roads (median verge width = 6 m, Wäber & Dolman 2015), fire routes (median verge width = 3 m) and narrow tracks (median verge width = 0.6 m, that may be grassy or muddy). Tracks were further classified based on the vegetation cutting regime as cut and uncut. As the forest is intersected by roads, links joining paths across the roads were classified according to the road crossed with links crossing ‘A’ roads (major arterial roads comprising the top tier of the UK roads classification system) excluded as too dangerous to cross, while links crossing ‘B’ roads (connecting A roads and smaller roads, comprising the second tier of the UK roads classification) and minor roads were retained for analysis with links crossing ‘B’ roads considered as a greater barrier than links crossing minor roads).

It was hypothesised that path type in combination with distance to nearest access point, and car capacity at access points may also affect number of DE. Access points were defined as either formal or informal car parks (gateways where fire routes or tracks meet roads) and car capacity at every potential access point (defined on GIS from the pathway network) was visually estimated from Google Earth following calibration during field visits. As it is unlikely that larger car parks are completely filled, car capacity was square-root transformed prior to modelling.

The larger the residential population in the vicinity of access points, the more disturbance events are recorded (Dolman et al., 2008), thus the number of households (taken from the 2011 census of households; Office for National Statistics 2011 and linked to coordinates using the UK Postcode Directory UKDS, 2013) was initially extracted from a sequence of 15 concentric buffers built around access points (from 0 m to 5,000 m with 500 m radius increments, then from 5,000 m to 10,000 m using wider 1,000 m radius increments). Because of adjoining buffers being co-linear, buffers were merged based on Spearman correlation coefficient > 0.6 producing 9 distance ‘bands’, used as independent predictor variables to be used in subsequent modelling of DE. If the absolute or relative numbers of households in the vicinity of access points had changed between 2014 and 2018 (when deer distance sampling data were collected) this may have altered the overall number and relative spatial distribution of recreational DE. I therefore obtained data on areas designated for new housing and number of houses per development from Site Allocation Plans of relevant District Councils. Using Google Earth imagery, I verified that none of the ne proposed housing (within a buffer of 2000 m from access points) had been built in 2018.

Modelling disturbance events

The dependent variables were the number of walkers and the number of dog walkers per pathway element, modelled separately. Cyclists only made up 6% of observations and, as cyclists are more mobile than walkers I considered network distance from the nearest access point was unlikely to predict their frequency, therefore these were excluded from subsequent modelling. For walkers and dog walker, the frequency of observations on each network element were modelled separately using a Generalised Linear Mixed Effects Model, with Poisson error incorporating point ID to control for spatial autocorrelation.

First, models of dog walkers and walkers were modelled in relation to day and time. Based on a process of model selection and parsimony, the final model incorporated day of week (categorical, Mon (reference level), Tue/Fri, Wed/Thu, Sat, Sun/national holiday), time of day (dog walkers: 6 (reference level), 8, 9, 11/13/14/16, 12/17, 7/10/15, walkers: 6 (reference level), 7/8/18, 11/14/15/17, 13, 9/10/12/16), month (dog walkers: April (reference), May/June, July/October, August, September); walkers: (April (reference), May, June-September, October) and a dummy variable indicating school holidays.

Local source population was extracted from the number of households around access points. First, the Closest Facility tool in ArcGIS 10.3 (Copyright © ESRI, USA) was used to find the nearest access point (measured along the path network) to the sampling point. Then, the local source population variables extracted from the 9 bands were added to models of walkers and dog walkers with the best fitting combination of time, day and month. Based on changes in AIC and coefficients similarity distance bands were further simplified to 3 distance bands (of 0-2000m, 2000-6000m and 6000-10000m) both for dog walkers and walkers models used in subsequent modelling.

A weighted network distance between sampling points and access points was calculated using the Closest Facility tool in ArcGIS 10.3 (Copyright © ESRI, USA). Different combinations of weightings (corresponding to distance 'modified for the effect of landscape and behaviour' Adriaensen *et al.* 2003, 'effective distance') were tested for car park capacity, road crossings and path type while controlling for source population, time, day and month. As with different weightings the lowest impedance access point to a given sampling point can vary, household data were re-assigned accordingly each time. The weighting giving the lowest model AIC was selected.

Results

Weighted network analysis

The best-fitting model considered ‘B’ roads as barriers, while minor roads were classed as of no impedance for both walkers and dog walkers. Car park capacity differed in their impedance for walkers and dog walkers with car parks with lower capacity being of less impedance to dog walkers. As concerns path types, dogs preferred wider paths (impedance weightings; forest road = 1, fire route = 0.9, track = 2) than walkers (forest road = 1, fire route = 0.5, track = 1). Verges cutting regime didn’t affect the impedance of paths.

Models of recreational disturbance

DE of dog walkers and walkers were both higher in weekends and school holidays but differed in time of day with DE of dog walkers being highest at 9:00 while walkers DE being highest at 13:00. A lower car park capacity and a route crossing the tracks instead of a fire route or forest road increased the effective distance for both walkers and dog walkers. Of the three distance bands used to extract number of households only the 2km buffer had a positive significant effect on DE. DE were lower in paths sections further (in terms of effective distance) away from access points.

Predictions

In order to analyse the response of deer densities to recreational activity I, a priori, selected dog walkers as the index of recreational activity as dog walkers are less subject to seasonal variation than walkers and deer have been reported to be more affected by dog walkers than walkers (e.g. Miller, Knight & Miller 2001). Dog walkers were predicted for all combination of time, day and month. All the combinations were created for school holiday and non-school holiday and predictions were multiplied by the ratio of school holiday or non school holidays in each month (to control for relative abundance of DE) and then averaged over spring summer and autumn (1st of April- 31st of October). Distance sampling thermal imaging data were collected over the winter months, unlike the recreational data, however the spatial pattern of disturbance events is the same across seasons as it is determined by the distribution of access points and housing density.

References

Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., Matthysen, E., 2003. The application of 'least-cost' modelling as a functional landscape model. Landsc. Urban Plan. 64, 233–247. https://doi.org/10.1016/S0169-2046(02)00242-6

Dolman, P.M., 2009. Woodlark and Nightjar Recreational Disturbance and Nest Predator Study 2008 and 2009 Final Report to Breckland District Council. University of East Anglia, Norwich.

Dolman, P.M., Lake, I.R., Bertoncelj, I., 2008. Visitor flow rate and recreational modelling in Breckland. Report to Breckland District Council. Norwich. University of East Anglia.

Hornigold, K., 2016. Modelling nature-based recreation to inform land management. PhD thesis. University of East Anglia.

Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. Wildl. Soc. Bull. 29, 124–132.

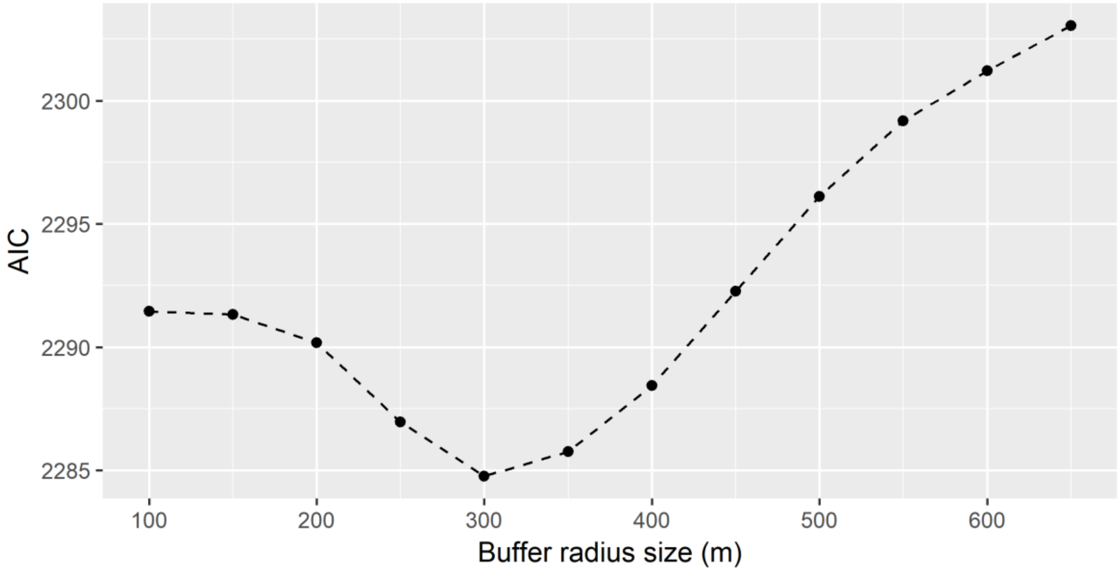
UKDS, 2013. Postcode Directory. http://borders.edina.ac.uk/html/pcluts_main.html, n.d.

Wäber, K., Dolman, P.M., 2015. Deer abundance estimation at landscape-scales in heterogeneous forests. Basic Appl. Ecol. 16, 610–620. https://doi.org/10.1016/j.baae.2015.06.005

Appendix D. Transect segment’s buffer radius selection

Local candidate variables were extracted from a symmetrical (two-sided) buffer around the transect centre-line of each segment (locality). Winter home-ranges of roe deer and muntjac (averaged across males and females individuals) based on earlier radio-telemetry in the study area (Chapman et al., 1993) measured 75ha and 18ha, respectively; these home-range areas correspond to a circular home-range radius of 500 and 250m. As concerns roe deer, the 500m radius was of similar scale, but slightly greater than the landscape grain (mean stand width = 355m, SD=60), and would result in bigger localities compared to the home-ranges (mean segment length = 462m, SD=297; corresponding localities built using a 500m buffer radius of mean area = 113ha SD = 18). I examined a series of full Density-Surface Models (DSMs), that included all candidate variables, geographical coordinates (as smoothing parameters), and the random effect of forest block, n=12) with variables extracted at buffer radii between a minimum of 100m to a maximum 650m (corresponding to the maximum roe deer monthly home-range reported of 136ha, southern Norway, Morellet *et al.* 2013) and examined the most informative radius at which to inform variable extraction. For roe deer, exploratory modelling showed a clear AIC minima at 300m (Fig A2.3 A, corresponding in localities with mean area = 48ha SD= 11.4), lower than the home-range based on historic VHF telemetry (that might overestimate the home-range, corresponding to a 500m circular home-range), therefore 300m was used in modelling. A similar inspection of muntjac full DSMs across buffer radii from a minimum of 100m to a maximum of 700m (with 700m corresponding to a 153ha circular home-range, maximum home-range reported in Taiwan McCullough, Pei & Wang 2000), provided an AIC inflexion at 250m (Fig A2.3 B, corresponding in localities with mean area = 37ha SD= 9) that was used for subsequent modelling.

(A) Roe deer density surface model AIC plot



(B) Muntjac density surface model AIC plot

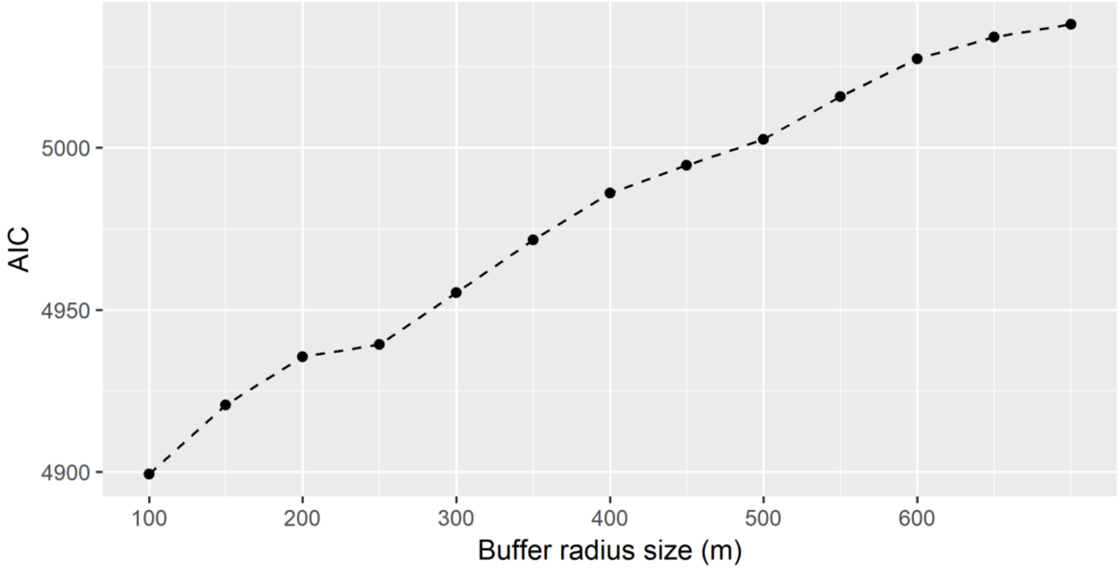


Figure A2.3: Selection of buffer radii for which candidate variables were extracted to model local density surfaces (DSMs) of roe deer (A) and muntjac (B). The AIC of a full model (including all candidate variables, geographic coordinates as smoothing parameters and the random effect of forest block) is shown across sequential buffer radii, from 100 to 650 for roe deer and from 100m to 700m for muntjac with increments of 50m, buffering distance transect segments (n=1162, mean length=462m, SD=297).

References

Chapman, N.G., Claydon, K., Claydon, M., Forde, P.G., Harris, S., 1993. Sympatric populations of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*): a comparative analysis of their ranging behaviour, social organization and activity. J. Zool. 229, 623–640. https://doi.org/10.1111/j.1469-7998.1993.tb02660.x

McCullough, D.R., Pei, K.C.J., Wang, Y., 2000. Home range, activity patterns, and habitat relations of Reeves' muntjacs in Taiwan. J. Wildl. Manage. 64, 430. https://doi.org/10.2307/3803241

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J.D.C., Nicoloso, S., Sustr, P., Urbano, F., Mysterud, A., 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. J. Anim. Ecol. 82, 1326–1339. https://doi.org/10.1111/1365-2656.12105

Chapter Three

Relation of forest crop damage to species-specific density in a multi-ungulate assemblage

Abstract

Effective deer management in forest ecosystems is strengthened where information on deer densities and impacts inform culling decisions, with a known target density at which damage levels are acceptable. In multi-ungulate assemblages, managers also need knowledge of relative impacts by different species or guilds, that in western Europe remain poorly understood. In an extensive (195 km^2) lowland conifer forest in eastern England, I related intensity of Scots pine (*Pinus sylvestris*) leader damage (% dominant shoots browsed) in 48 restocked stands (1-3 years of growth) over multiple years (29 in 2018, 23 in 2019, 27 in 2020, total n=79 observations) to species-specific annual local densities of introduced muntjac (*Muntiacus reevesi*), native roe deer (*Capreolus capreolus*), non-native fallow deer (*Dama dama*) and ‘large deer’ (composite of annual fallow and multi-year mean red deer *Cervus elaphus* density) using generalized mixed effects models (GLMMs). Forest-wide deer Density-Surface Models were calibrated through intensive annual thermal imaging distance transects, and local densities around stands sampled for crop impact were extracted, resampled within confidence bounds. GLMMs also examined effects of ground vegetation composition, or presence of European (brown) hare (*Lepus europaeus*). A greater proportion of pine leaders were browsed at higher fallow or large deer densities (respective effect sizes: 22% and 18% increase in leader damage intensity across inter-quartile density range). Leader damage intensity was not influenced by ground vegetation, presence of hares, density of muntjac (across the range 8.3 – 41.6 individuals km^{-2}) or roe deer (1.7 – 19.4 individuals km^{-2}). To reduce damage on newly-planted pine crops to economically acceptable levels (defined as 20% yr^{-1}), managers would need to remove fallow deer (acceptable density of 0.6 CI=0.06-1.44 individuals km^{-2}) – considered impractical and potentially culturally unacceptable – or reduce combined density of large deer to a low level of 2.3 (CI=1.18-3.46) individuals km^{-2}. Reducing muntjac or roe abundance would have negligible effect on leader damage in this system, but may be important for other tree species. Management of multi-species deer assemblages requires species-specific understanding of impacts and robust density estimates.

Introduction

Increasing forest extent is key to meeting carbon targets and limiting global climate change (Bastin et al., 2019; Griscom et al., 2017; Lewis et al., 2019; UK Committee on Climate Change, 2019). However, across much of temperate Europe, North America, Japan and New Zealand, high deer abundance threatens successful tree establishment (Latham et al., 2020; Lesser et al., 2019; Ramirez et al., 2018; Takatsuki, 2009) as well as profoundly altering forest structure and ecosystem function (Carline et al., 2005; Côté et al., 2004; Gill, 1992a). Controlling such impacts in the absence of natural predators requires deer to be managed (Crete, 1999; Hothorn and Müller, 2010); ensuring such management is effective and justifying it to a wider public requires an appropriate evidence base (Reimoser, 2003). Identifying species-specific deer density thresholds below which forest crop damage is either acceptable, or where marginal costs of culling at such low numbers outweigh benefits of further reducing damage, supports deer managers by defining a sustainable density (Welch *et al.* 1992; Welch, Scott & Staines 1995) allowing appropriate cull targets to be set. A complicating issue is that deer species have been introduced beyond their natural range (Carden et al., 2011; Champagnon et al., 2012; Dolman and Wäber, 2008). Evidence-based management of natural and modified multi-species ungulate assemblages requires understanding of which species cause the greatest impacts and of the species-specific relation of damage to density.

Although exclosure experiments, that contrast controls exposed to deer and experimental plots lacking deer, can usefully demonstrate the dramatic nature of vegetation impacts (see for example, Simončič, Bončina, Jarni, & Klopčič, 2019), they cannot identify what target density of deer is sustainable or desirable. To achieve this, local impact intensity should be examined across a range of known local deer densities, ideally in for free-ranging deer at landscape-scale not in small or poorly replicated exclosures. Heinze *et al.* (2011) related browsing damage on tree saplings to local densities of free-ranging fallow (*Dama dama*) and roe deer (*Capreolus capreolus*); but with estimates of plot-specific density estimates having wide uncertainty through faecal pellet counts (Campbell et al., 2004; Gill et al., 1997; Hemami et al., 2007). In England combined impacts of muntjac (*Muntiacuus reevesi*), roe, fallow, red (*Cervus elaphus*) and sika (*C. nippon*) deer on tree regeneration were examined across multiple lowland coniferous and deciduous woodland blocks, but without separating species-specific contributions (Gill and Morgan, 2010). There remains a need for studies that evaluate species-specific forest crop impacts across a range of deer densities using reliable methods of density estimation.

I examined impacts of three deer species: muntjac, roe and fallow deer, in 48 forest stands re-sampled in multiple years, across an extensive forest landscape in eastern England, to predict species-specific densities for successful regeneration of replanted Scots pine *Pinus sylvestris*. Annual thermal imaging distance sampling, that reliably quantifies deer densities (Gill et al., 1997; Morelle et al., 2012; Wäber and Dolman, 2015), allowed us to relate local impacts to species-specific densities of each species extracted from fine-grained density surface models. I tested an explicit *a priori* expectation that damage intensity would be more strongly predicted by the density of fallow or the combined density of large deer (annual fallow and multi-year mean red density), rather than either of the two smaller concentrate selectors, roe and muntjac. Crop impacts may be modified by the local availability and relative palatability of other forage and ground-layer vegetation (Augustine and Jordan, 1998; Gill, 1992a; Harmer et al., 2010; Palmer and Truscott, 2003; Welch et al., 1991), therefore, I also tested whether damage intensity was reduced with greater availability of preferred browse and forage within stands, as well as the presence of European (brown) hares (*Lepus europaeus*; hereafter 'hare').

Methods

Study system

The study was conducted in Thetford Forest, an extensive (195 km^2) lowland conifer-dominated forest landscape in eastern England managed by rotational clear-felling and replanting of even-aged stands (mean stand area=8.1ha, SD=9.1). Four deer species occur (Wäber et al., 2013): muntjac and roe are the most abundant, both are relatively sedentary (Chapman et al., 1993) and their density varies within and between 12 forest 'blocks' (Hemami et al., 2005; Wäber et al., 2013), that vary from contiguous core to outlying areas with greater access to the surrounding arable crops and grass-heath. Fallow deer occur at lower densities and are concentrated in the southern forest blocks; although having a larger home range than the two smaller species (Borkowski and Pudełko, 2007) fallow deer tend to be hefted (Apollonio et al., 2003), further contributing to local variance in density. For each of these three species it was possible to map local densities annually and examine their independent contribution to impact levels. In contrast, red deer occur at a low density across the landscape (mean =1.4 individuals km^{-2}, SE=0.26), and are wide-ranging (Reinecke et al., 2014) resulting in low spatial variance (see Fig. A3.1 in Appendix A) so that stand-level crop impacts could not be analysed in relation to local red deer density. However, I combined the local density of red deer and fallow deer (with greater spatial variance) in an aggregate measure of 'large deer' density, to assess whether this better predicted damage than the influence of fallow deer alone.

The forest landscape is dominated by Corsican pine (*Pinus nigra var. maritima*, 59% of forest area), Scots pine (15%), and other conifers (5%); and limited deciduous tree crops (10%). Despite dominating second rotation planting during the last decades of the 20th century, re-planting of Corsican pine ceased from 2006 due to increased prevalence of red-banded needle blight (*Dothistroma septosporum*), most likely owing to milder and wetter recent winters (Dolman et al., 2010). Subsequent replanting has used a variety of tree species, with sufficient restocked stands of Scots pine available for impacts to be related to species-specific deer density.

Crop impact data

I assessed leader (dominant shoot) damage as this commonly causes the greatest effect on forest crop harvest values (Motta, 1996). Young conifers are particularly vulnerable while deer are still able to reach the leader (Welch et al., 1992), with greatest browsing damage in winter (Miller et al., 1982; Welch et al., 1992).

I collected impact data in 2018, 2019 and 2020, from restocked Scots pine stands aged 1-3 years, as Scots pine is most vulnerable to leader browsing within three years of planting (Holloway, 1967). In 2018, 29 suitably-aged stands were sampled, these were resurveyed in subsequent years unless they exceeded 3 years age, and additional newly planted stands were added (sampling 23 in 2019 of which 17 had been sampled in 2018, and 27 in 2020 of which 12 were sampled in 2019), providing 79 observations across 48 unique stands. Between March and April I recorded winter browsing that removed leader buds from the previous growing season, and recorded major fraying damage sufficient to cause leader death. In each replicate stand a transect was walked on the longest diagonal, assessing the nearest tree every five paces, sampling at least 60 saplings per stand.

It was not possible to consistently distinguish deer browsing damage from possible contributions from hares or rabbits, *Oryctolagus cuniculus*, however, most damage is likely attributable to relatively abundant deer; nevertheless I controlled for the local presence of hares in analyses, but rabbits were excluded as they are unlikely to browse pine (see Appendix B). Other small mammals were considered unlikely to have contributed to leader damage as, although bank vole *Myodes glareolus* may consume coniferous buds (see review in Lyly *et al.* 2014), they did not consume *Pinus sylvestris* foliage in cafeteria experiments (Hjältén et al., 2004), the number of branches or height of *Pinus sylvestris* seedlings were not reduced by exposure to both bank and field vole *Microtus agrestis* in the field (Lyly et al., 2014) and small mammals most commonly damage bark rather than browsing pine foliage (Gill, 1992b).

In order to measure alternative sources of food, at each transect point ground cover was classified as: bramble *Rubus fruticosa* agg., other shrubs (mainly silver birch, *Betula pendula*), grass, herbaceous vegetation (hereafter 'herbs') or non-forage (e.g. bare ground, brash, or bracken *Pteridium aquilinum* litter), with the proportionate contribution of each class considered in analyses. Herbs and grasses may divert browsing impacts in early winter before dying back, in contrast bramble is semi-evergreen, offers forage all year round and is an important predictor of roe and muntjac winter distribution (Hemami et al., 2005, 2004). As calcareous soils support greater plant species richness (Eycott et al., 2006) and more palatable grass species (Rodwell, 1992), I calculated the percentage of calcareous soil in each restock stand (extracted from Corbett, 1973) as a proxy for palatability of forage.

Deer density and hare presence

Annual species-specific winter deer density-surfaces were generated in 2018, 2019 and 2020 from distance sampling data, obtained in late winter immediately before sampling tree crops. Intensive nocturnal thermal imaging transects (Fig. A3.3 in Appendix C) were conducted by thermal imaging (Pulsar Helion XP50) between January and March at the end of the cull season when vegetation concealment is minimal. Methodology followed Wäber and Dolman (2015), but with distances to detected deer measured using laser rangefinder binoculars (Leica Geovid 10x42). Each one-sided transect section was surveyed twice in both 2018 and 2019 (mean annual effort: 567 km, or 3.02 km km^{-2} across the forest), and once in 2020 owing to resource limitations (mean effort 1.5 km km^{-2}). Across the three years, the mean number of observations (single or groups of deer) was 1193 (SD=415) for muntjac, 312 (SD=110) for roe, 73 (SD=12) for fallow and 30 (SD=18) for red deer.

Species-specific detection functions that account for the reduced probability of detection of individuals at greater distances (Buckland et al., 2001) were fitted pooling data from the three years (using the R package 'Distance', Miller, 2016), excluding 5% of most distal observations (following Buckland *et al.* 2001) and controlling for three structural visibility classes *a priori* defined by crop age (Appendix D). The best-fitting key detection function was selected and adjustments for group size (to account for lower probability of detecting smaller groups at further distances) evaluated, by comparing model AIC (see Appendix D for details). I then fitted the selected detection functions separately for each survey year to obtain annual density estimates for muntjac, roe and, fallow deer for each of 1162 surveyed composite transect 'segments' (mean length=462m, SD=297; for details on segment demarcation see Appendix D). These were used to calibrate landscape-wide DSMs, using a GAM (package "dsm" Marshall et al., 2017) that related abundance per segment to geographical coordinates, using penalised thin-plate regression splines to produce a the best-fitting smoothed surface at a broad scale, greater than that of fine-scale stand structure. Thus the DSM implicitly accounts for a range of factors affecting local deer density, including local habitat, neighbouring deer management regimes, and ease of access to surrounding arable crops. The GAM was interpolated to predict densities for the entire study area as 100x100 m rasters using packages "raster" and "sp" (Bivand et al., 2013; Hijmans, 2017; Pebesma and Bivand, 2005), allowing resampling for the stands in which crop impacts were measured. Uncertainty around deer density estimates comes from both the detection function and the GAM. Assuming the detection function and GAM are independent, I calculated estimates of variance of predicted deer density per raster cell following Miller et al., (2013). In Appendix D (Table A3.4) I report the yearly, species-specific coefficient of variation (CV) associated with the detection function, the CV associated with the GAM and the total CV (comprising both detection function and GAM CV). Red deer are a wide-ranging species (Reinecke et al., 2014), and the limited number of observations didn't allow annual density surfaces to be modelled. Therefore, red deer observations from 2018-2020 were pooled and modelled with a single detection function (again incorporating the visibility class detectability covariate) to fit a single GAM, generating a multi-year average DSM (Appendix A). The proportion of deviance explained by DSMs was 0.13 for muntjac, 0.14 for roe, 0.40 for fallow (multi-annual means) and 0.70 for red deer (single pooled DSM).

For each sampled stand in each year, species-specific deer densities (and pooled 'large deer' density) were resampled from the annual density-surfaces using packages "rgeos" and "raster" (Bivand and Rundel, 2018; Hijmans, 2017) within a buffer around the centroid of each stand at a scale relevant to the species winter home range. For muntjac and roe deer buffer radii of 250 m (18 ha) 500 m (75 ha), respectively, were based on the mean of sex-specific home ranges measured in Thetford Forest using radio-telemetry in November-December and January-February (Chapman et al., 1993). For fallow deer (and for large deer), a buffer radius of 850 m (219 ha) was based on home ranges of radio-collared male and female fallow deer in southern Poland (Borkowski and Pudełko, 2007). Fallow and large deer densities were square-rooted to avoid leverage during modelling.

During thermal imaging sampling, hare and rabbit were also recorded when seen but without distance measurement owing to time constraints; hare were considered in analysis on the basis of presence/absence. Hares are long-lived sedentary animals (Hulbert et al., 1996; Macdonald, 2009) and their home ranges (11.8ha in agricultural areas in Austria, 22.2ha in Scotland, Hulbert *et al.* 1996; Schai-Braun & Hackländer 2014) are two- to three-times the area of a stand. For modelling, I considered presence of hares (as a dummy variable, zero=absent, 1=present) if they were recorded (either during nocturnal distance sampling or during impact assessment fieldwork) from the focal stand sampled for tree impacts, or a directly adjacent stand, in any of the three years.

Analysis

I examined the percentage of sampled leaders recorded as damaged, hereafter 'damage intensity' and incorporated stand identity to control for lack of spatial independence of stands resampled more than one year. I examined two model sets: one including fallow deer density, the second including large deer density, as correlation between these (r=0.9) precluded combining them within the same models (Freckleton, 2002). All remaining candidate explanatory variables were non-colinear (r≤0.7, Freckleton, 2002). Given the relatively large number of candidate variables (Table 3.1) I conducted analysis of each model set in three phases. In each phase, model-averaged variable coefficients and CIs were averaged across 1000 iterative models calibrated by resampling (independently for each stand-year) the 95% CI of species-specific deer density (derived from the maps of the coefficient of variation), to incorporate uncertainty in deer local deer estimates. I included a random effect of stand ID (n=48) in all models to account for pseudoreplication of stands sampled in multiple years.

Table 3.1: Candidate explanatory variables examined in models of Scots pine leader damage intensity. Table is showing their mean and coefficient of variation (CV, proportion of SD relative to mean) across the study and separately for stands aged 1, 2 or 3 years since planting. Densities of each deer species were resampled from species-specific buffer radii around each replicate stand.

	Total (n=79)		1 yo (n=29)		2 yo (n=23)		3 yo (n=27)	
Variable	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Muntjac (individuals km^{-2})	23.1	0.4	23.4	0.4	22.1	0.3	23.4	0.4
Roe deer (individuals km^{-2})	7.4	0.6	6.8	0.5	8.5	0.5	7.1	0.7
Fallow deer (individuals km^{-2})	1.4	1.1	1.0	1.1	1.7	1.0	1.4	1.3
Large deer (individuals km^{-2})	3.3	0.6	2.8	0.5	3.9	0.5	3.4	0.7
Hare (n presence, absence)	38, 43		13, 16		16, 7		14, 15	
% shrubs	4.2	2.1	2.0	3.0	4.2	1.9	6.4	1.8
% bramble	8.0	1.2	8.1	1.3	8.7	1.2	7.4	1.1
% herbs	8.4	1.0	9.9	1.0	8.0	1.1	7.2	1.0
% grass	46.1	0.4	41.2	0.4	48.6	0.3	48.5	0.4
% calcareous soil	57.5	0.6	59.6	0.6	60.1	0.5	53.5	0.69

First, I related damage intensity (as % per stand) to all combinations of species-specific deer densities, presence of hares and tree crop age using generalized mixed effects models with random intercept and negative binomial error distribution, using MMI (Burnham & Anderson, 2002) in package "MuMIn" (Bartoń, 2018). Candidate variables were considered supported if included in the 95% confidence subset of models and their model-averaged coefficient didn't span zero, following (Boughey et al., 2011); any lacking support in this initial MMI were excluded from subsequent analyses. Second, for each set (fallow or large deer), I built a series of further models each comprising the base herbivore model (incorporating species variables supported at phase one) and one of the vegetation modifiers. For each model set, I then subjected the provisionally supported variables (base herbivore model plus any supported vegetation modifier) to MMI. Last, for each model set, a final model comprising the supported herbivore and vegetation variables was used to predict the threshold deer density above which pine leader damage exceeded 20% intensity per annuum (that has been proposed as economically acceptable, Prien and Müller, 2010), and the damage intensity expected at deer densities of 1, 5 or 10 individuals km^{-2}. The explanatory power of the two final model sets was compared in terms of their conditional (proportion of total variance explained through both fixed and random effects) and marginal (proportion of total variance explained through fixed effects) R^{2}. All analyses were performed in R (R core Team, 2018).

Results

Deer density

Deer density in buffers around the crop impact stands was highly variable: ranging 8.2-42.0 individuals km^{-2} for muntjac, 1.8-19.3 km^{-2} for roe, 0-28.1 for fallow km^{-2}, 0.9-2.0 km^{-2} for red deer, and 0.9-29.9 km^{-2} for large deer (see Table 3.1) – but with large deer overwhelmingly comprising fallow. Across the crop impact stands, muntjac were the most evenly distributed deer species, while spatial variance in density was greatest for fallow deer (Table 3.1). Relative spatial distribution of deer was broadly consistent between years, the mean of the correlation coefficient between density in stand buffers in 2018 *versus* 2019 and 2019 *versus* 2020 was 0.77 for muntjac, 0.92 for roe, 0.96 for fallow deer and 0.75 for large deer.

Models of crop damage

The mean leader damage per stand per annuum was 32.1% (SD=25.9). The spatial distribution of leader damage intensity and species-specific density of fallow, large, roe deer and muntjac are shown in Fig. 3.1. MMI showed that the intensity of leader damage was greater in restocked stands with younger trees and with greater fallow deer density in the surrounding buffer, or with greater density of large deer (Figs 3.2, 3.3). In contrast, no support was found for any effects of muntjac density, roe deer density or presence of hares in either model set (Fig. 3.2), these herbivores were therefore excluded from subsequent modelling.

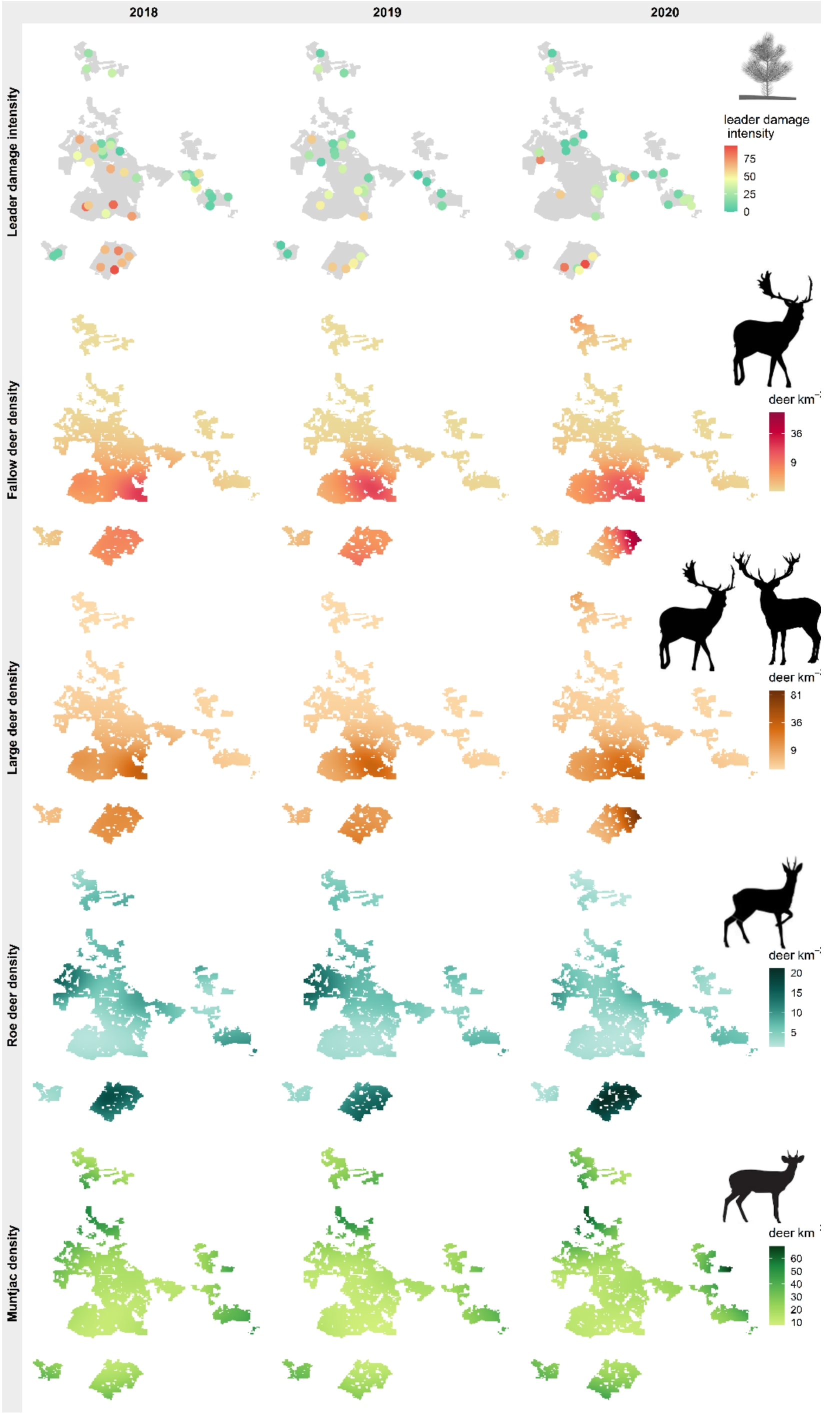


Figure 3.1. The distribution within the forest landscape of the intensity of Scots pine leader damage and densities of fallow deer, combined large (fallow and red) deer, roe and muntjac. Densities were (predicted at 100x100 m grid from DSMs including latitude and longitude) shown separately for each of three study years.

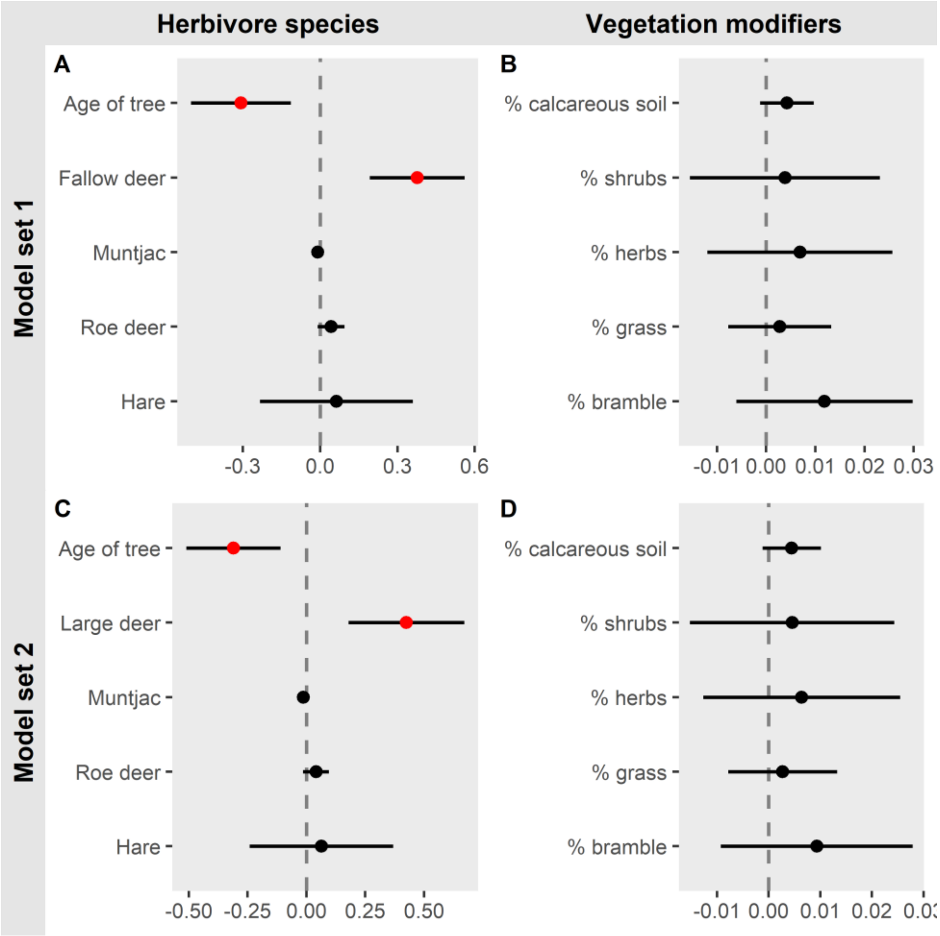


Figure 3.2: Relation of Scots pine leader damage to candidate explanatory variables of herbivore abundance and ground vegetation composition. Shown are model-averaged coefficients (filled symbol: supported variables in red, variables lacking support in black; bars represent 95% CI) from 1000 MMI iterations, each randomly resampling deer densities across the CI of density surfaces generated from intensive thermal imaging distance sampling. Model coefficients of herbivore species and crop age MMI are shown in A and C. Variables retained in the herbivore base model (fallow deer or large deer density; tree crop age) were also supported in MMI analysis of models incorporating each ground vegetation variable in turn, therefore, for each of presentation only the ground vegetation coefficients are reported (B and D). All models controlled for the random effect of forest stand identity (n=48).

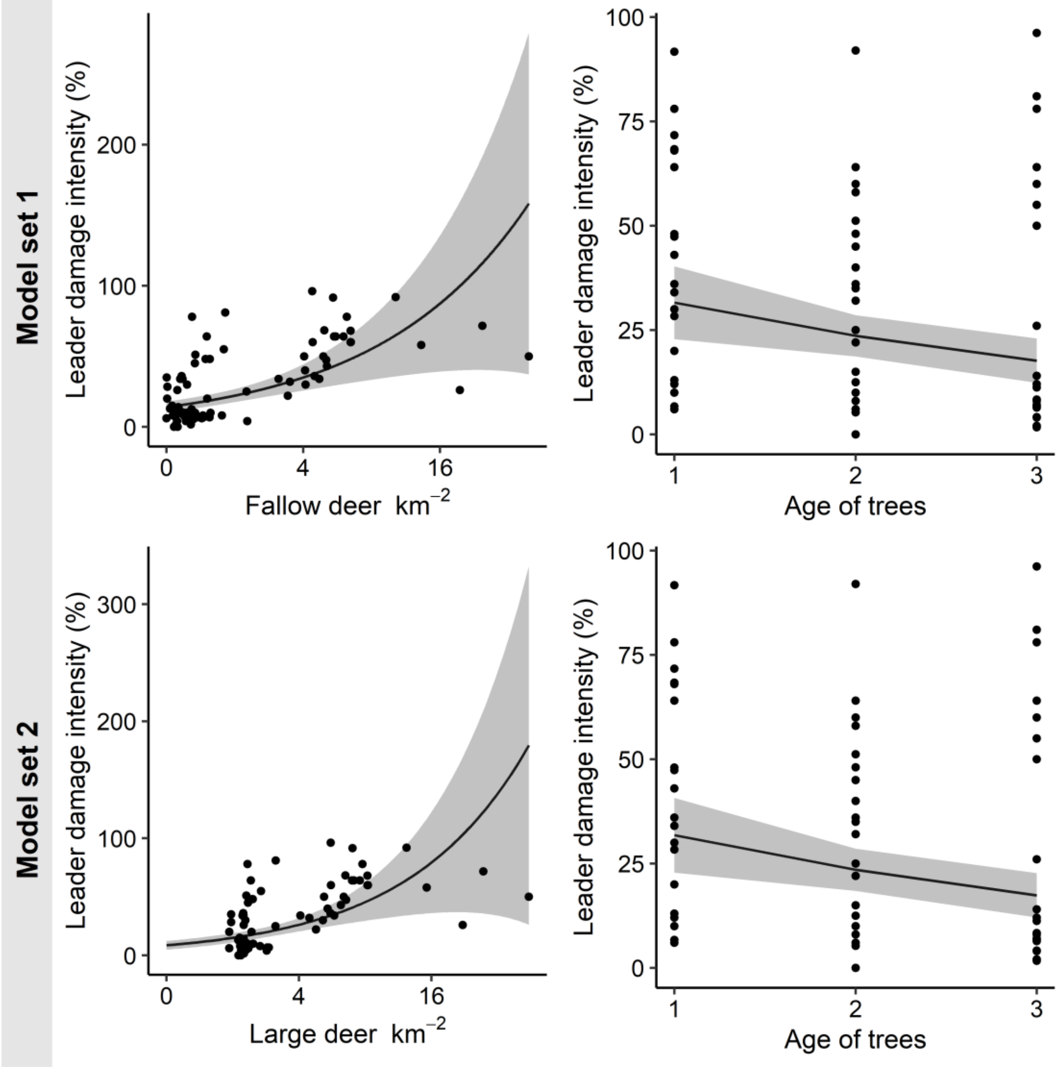


Figure 3.3: Intensity of Scots pine leader damage related to the density of fallow deer, density of large deer and tree age (separately for each model set). Shown are predictions (continuous line) from a model including supported variables only (fallow or large deer density and crop age), incorporating the random effect of forest stand identity (n=48). Shading represents (95% CI).

No support was found for an effect of any ground vegetation variable, in the subsequent series of models that included the supported variables from either of the herbivore base models (fallow deer or large deer density; tree crop age) and each vegetation variable in turn (Fig. 3.2). Final models therefore comprised effects of tree crop age and the density of fallow deer plus or density of large deer; these provided similar explanatory power (for fallow deer conditional R^2 = 0.37, marginal R^2 = 0.65, for large deer 0.35 and 0.65 respectively; delta AIC for large deer relative to fallow =1.8).

Deer densities above which impacts exceed 20% leader damage per annuum were 0.6 (CI=0.06-1.4) fallow km^{-2}, or 2.3 (CI=1.2-3.5) large deer km^{-2}. At deer densities of 1 individual km^{-2}, 5 km^{-2} and 10 km^{-2}, predicted damage intensity for fallow deer alone was 22% (CI=17-27%), 39% (CI=27-50%), and 59% (CI=34-84%) leader damage per annum, respectively, but may be slightly less for equivalent combined densities of large deer, 15% (CI=11-19%), 30% (CI=23-37%), and 50% (CI=31-69%), respectively.

Discussion

Scots pine leader damage was primarily attributed to fallow deer or the combined effect of large deer (primarily comprising fallow), with interquartile effect sizes, +22% and 18%, respectively, but I found no evidence of any effect of introduced muntjac or native roe deer. Although fallow deer are bulk feeders with their diet mostly comprising grass and graminoids, conifer leaves comprised up to 20% of winter rumen content in southern England (Jackson, 1980) and pine foliage comprised 6% or 10% of winter diet in southern or northern Poland, respectively (Borkowski and Obidziński, 2003). Despite pine not being a major component of fallow deer diet, their herding behaviour (Apollonio et al., 1998) means many individuals can simultaneously aggregate in a restocked stand. Red deer have a similar herding behaviour and dietary strategy (Clutton-Brock et al., 1982) and have been shown to browse on Scots pine (Krojerová-Prokešová et al., 2010; Palmer and Truscott, 2003; Pépin et al., 2006), however their overall density in Thetford Forest is low. Models predicted moderate residual levels of damage even at very low density (e.g. 1 km^{-2}) of fallow or combined large deer, that suggests additional impacts not being captured by this analysis, potentially due to other deer species or hares, or early-winter presence of fallow in areas where they were not detected by late-winter thermal imaging survey.

Pine leader damage intensity was not affected by muntjac or roe deer density in this landscape. For roe this is consistent with evidence from both highland Scotland, were winter browsing incidence on Scots pine was unrelated to roe density (Palmer and Truscott, 2003), and northeastern Germany, where browsing on pine trees also was not related to roe density, across a similar range as observed in the current study (approximately 1-15 individuals km^{-2}) (Heinze et al., 2011). A previous study in north-east England, however, showed a positive association between conifer leader browsing and an index of roe deer occupancy (Ward et al., 2008). Roe deer have high nutrient demands (Gordon and Illius,

1994) and fibrous, tannin-rich conifer foliage does not represent optimal browse (Gonzalez-Hernandez and Silva-Pando, 1999) and only forms a negligible part of roe deer diet (Duncan et al., 1998; Storms et al., 2008; Tixier et al., 1997). The lack of any relation of leader damage to muntjac density is notable, as elsewhere pine has been found to be browsed by this species. For muntjac in south-east England, rumen analysis showed Scots pine was mostly browsed in late winter when alternative forage was scarce (33% of individuals culled in March and April had Scots pine in their rumen, declining to 8% in May and June; Chapman and Tutchener, 2017). Given muntjac's small size (for which I can assume a similar dietary strategy to the roe deer; Bodmer, 1990) and the evidence showing Scots pine is only browsed when food is scarce, it is plausible that muntjac could also have fed on Scots pine but not enough to be detected by this analysis. The lower spatial variance in muntjac density may have reduced the power to detect any additive impact if this was subtle relative to that of the larger fallow.

Leader damage was also unrelated to presence of hares though these were only sparsely distributed weakening the ability to detect any contribution. In the Scottish Highlands browsing impact of mountain hare on saplings (mostly birch) was only detectable at high densities (45 hares km^{-2}), while below one hare km^{-2} no effect was found (Miller et al., 1982). Although hares are capable of browsing pine, grasses comprise the majority of their diet (Schai-Braun et al., 2015) and their impact on Scots pine is likely negligible where alternative forage is widely available.

Effects of ground vegetation composition

After accounting for the density of fallow or large deer, the intensity of leader damage was not modified by ground vegetation composition, availability of alternative browse, or percentage of calcareous soil, contrary to the 'neighbour contrast defence' hypothesis (Bergvall et al., 2006). In contrast, in highland Scotland, damage to Scots pine by red deer was less when high quality graminoid forage was available but greater when ground vegetation predominantly comprised heather (Palmer and Truscott, 2003). It is possible that in the current study ground vegetation composition may not have influenced crop damage due to the generally low availability of bramble in restocked stands (that could shield Scots pine and offer alternative forage), in contrast to local bramble dominance in pre-thicket and mature stands. But fallow, being generalist feeders (Obidziński et al., 2013) may not be diverted from browsing on Scots pine saplings. In contrast, more specialist browsers such as roe and white-tailed deer, are more likely to be diverted by the presence of palatable species in the understorey (Augustine and Jordan, 1998; Hjältén et al., 1993; Tuomi and Augner, 1993; Ward et al., 2008).

Deer density thresholds to alleviate crop damage

To reduce leader damage intensity on restocked Scots pine to only 20% per annuum would require substantial control effort supressing fallow density towards zero (0.6 individuals km^{-2}) or the combined large deer density to a low level (2.3 individuals km^{-2}). Tolerable levels of damage depend on crop value relative to management costs; damage can be tolerated at higher levels (>55%) if further reducing impacts (through culling) is expensive (Ward et al., 2004). Deer density thresholds required for successful regeneration in this landscape may not apply to some other systems. Successful regeneration of lowland mixed woodland in England exposed to varying mixtures of sika, red, fallow, roe deer and muntjac occurred with a combined overall density of 10 individuals km^{-2}, higher than in this study (Gill and Morgan, 2010). However, for lower productivity upland or moorland areas, impact density thresholds are around 4-5 large deer or 25 roe deer km^{-2} for native woodland regeneration (Putman et al., 2011), while for regeneration of Scots pine in highland Scotland, red deer density should not exceed 3-4 km^{-2} (Scott et al., 2000), similar to the large deer threshold of this study. For deciduous forest in northwestern Pennsylvania regeneration occurred at a density of 7-9 white-tailed deer (*Odocoileus virginianus*) km^{-2} (Horsley et al., 2003), for balsam fir (*Abies balsamea*) in Canadian boreal forest with white-tailed deer 15 km^{-2} (Hidding, Tremblay & Côté 2012). However, all of these studies consider natural regeneration; in contrast browsing predisposition may be greater with clear-felling and replanting (Partl et al., 2002; Reimoser and Gossow, 1996), particularly as herding species can aggregate and feed for a prolonged period in a large restocked stand offering concentrated food with reduced travel cost. In contrast, higher fallow deer density may potentially be tolerated in forest management by small-gap creation and natural regeneration (Peterken, 1996).

Conclusions

In the forest landscape I investigated, cultural preferences have led to an emphasis on controlling muntjac, that is regarded as un undesirable and damaging invasive species. However, this analysis instead shows large numbers of fallow deer are causing most crop damage. Fallow have increased to high abundance since colonising the study area in the late 19th century (Wäber, 2010), partly due to a tolerance due to their aesthetic appeal and economic value for recreational stalking, and have similarly increased to high density in many other parts of the UK. Achieving the low density required to supress impacts to an acceptable level would be a considerable challenge for deer management. Fallow and red deer are wider-ranging than roe or muntjac and, if heavily culled, can move to areas where they perceive a lower risk of predation (Proffitt et al., 2009; Tolon et al., 2009). Although fallow and red deer management must therefore operate at a landscape-scale, requiring coordination across landowners (POST, 2009), reductions to a negligible level may still be impracticable. In the forest landscape considered here, forest managers should also consider alternative approaches to mitigation, including planting tree species whose commercial value is more resilient to deer damage, greater reliance on natural regeneration instead of planting, or use of fencing in areas where crop impacts are unavoidable and crop value offsets this expense. More generally, these findings emphasise the crucial importance of taking an evidence-based approach when managing deer in a multi-species system, and of understanding which deer species are responsible for impacts.

References

Apollonio, M., Focardi, S., Toso, S., Nacci, L., 1998. Habitat selection and group formation pattern of fallow deer *Dama dama* in a submediterranean environment. Ecography (Cop.). 21, 225–234. https://doi.org/10.1111/j.1600-0587.1998.tb00560.x

Apollonio, M., Scotti, M., Gosling, L.M., 2003. Mating success and fidelity to territories in a fallow deer lek: a female removal experiment. Naturwissenschaften 90, 553–557. https://doi.org/10.1007/s00114-003-0475-7

Augustine, D.J., Jordan, P.A., 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. J. Wildl. Manage. 62, 1076.

https://doi.org/10.2307/3802560

Bartoń, K., 2018. MuMIn: Multi-Model Inference. R package version 1.42.1.

Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C.M., Crowther, T.W., 2019. The global tree restoration potential. Science (80-.). 365, 76–79. https://doi.org/10.1126/science.aax0848

Bergvall, U.A., Rautio, P., Kesti, K., Tuomi, J., Leimar, O., 2006. Associational effects of plant defences in relation to within- and between-patch food choice by a mammalian herbivore: neighbour contrast susceptibility and defence. Oecologia 147, 253–260. https://doi.org/10.1007/s00442-005-0260-8

Bivand, R., Rundel, C., 2018. rgeos: Interface to Geometry Engine - Open Source ('GEOS’). R package version 0.3-28.

Bivand, R.S., Pebesma, E., Gomez-Rubio, V., 2013. Applied Spatial Data Analysis with R, Second. ed. New York.

Bodmer, R.E., 1990. Ungulate frugivores and the browser-grazer continuum. Oikos 57, 319. https://doi.org/10.2307/3565960

Borkowski, J., Obidziński, A., 2003. The composition of the autumn and winter diets in two Polish populations of fallow deer. Acta Theriol. (Warsz). 48, 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.

Boughey, K.L., Lake, I.R., Haysom, K.A., Dolman, P.M., 2011. Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. Biol. Conserv. 144, 2300–2310. https://doi.org/10.1016/j.biocon.2011.06.008

Buckland, S.T., Anderson, D.R., Thomas, L., Burnham, K.P., Laake, J.L., Borchers, D.L., 2001. Line transects, in: Introduction To Distance Sampling: Estimating Abundance of

Biological Populations. Oxford University Press, Oxford, pp. 104–14.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference. A Practical Information—Theoretic Approach, 2nd ed. New York.

Campbell, A.D., Swanson, G.M., Sales, J., 2004. Comparing the precision and cost-effectiveness of faecal pellet group count methods. J. Appl. Ecol. 41, 1185–1196. https://doi.org/https://www.jstor.org/stable/3505793

Carden, R.F., Carlin, C.M., Marnell, F., Mcelholm, D., Hetherington, J., Gammell, M.P., 2011. Distribution and range expansion of deer in Ireland. Mamm. Rev. 41, 313–325. https://doi.org/10.1111/j.1365-2907.2010.00170.x

Carline, K.A., Jones, H.E., Bardgett, R.D., Heikki, S., 2005. Large herbivores affect the stoichiometry of nutrients in a regenerating woodland ecosystem. Oikos 110, 453–460.

Champagnon, J., Elmberg, J., Guillemain, M., Gauthier-Clerc, M., Lebreton, J.D., 2012. Conspecifics can be aliens too: a review of effects of restocking practices in vertebrates. J. Nat. Conserv. 20, 231–241. https://doi.org/10.1016/j.jnc.2012.02.002

Chapman, N.G., Claydon, K., Claydon, M., Forde, P.G., Harris, S., 1993. Sympatric populations of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*): a comparative analysis of their ranging behaviour, social organization and activity. J. Zool. 229, 623–640. https://doi.org/10.1111/j.1469-7998.1993.tb02660.x

Chapman, N.G., Tutchener, J., 2017. The diversity of diet of muntjac *Muntiacuus reevesi* in woodlands in the Hitchin area. Hertfordsh. Nat. 49.

Clutton-Brock, T.H., Guinness, F.E., Albon, S.D., 1982. Red deer: behaviour and ecology of two sexes. University of Chicago Press.

Corbett, W.M., 1973. Breckland Forest Soils Special Survey 7, Soil Survey of England and Wales. Harpenden, UK.

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological Impacts of Deer Overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147.

https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Crete, M., 1999. The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems. Ecol. Lett. 2, 223–227. https://doi.org/10.1046/j.1461-0248.1999.00076.x

Dolman, P., Panter, C., Mossman, H., 2010. Securing biodiversity in Breckland: guidance for conservation and research., First Report of the Breckland Biodiversity Audit. Norwich. University of East Anglia.

Dolman, P.M., Wäber, K., 2008. Ecosystem and competition impacts of introduced deer. Wildl. Res. 35, 202. https://doi.org/10.1071/WR07114

Duncan, P., Tixier, H., Hofman, R., Lechner-Doll, M., 1998. Feeding strategies and the physiology of digestion in roe deer, in: The European Roe Deer: The Biology Of Success. Scandinavian University Press, Oslo, pp. 91–116.

Eycott, A.E., Watkinson, A.R., Dolman, P.M., 2006. Ecological patterns of plant diversity in a plantation forest managed by clearfelling. J. Appl. Ecol. 43, 1160–1171. https://doi.org/10.1111/j.1365-2664.2006.01235.x

Freckleton, R.P., 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. J. Anim. Ecol. 71, 542–545. https://doi.org/10.1046/j.1365-2656.2002.00618.x

Gill, R.M.A., 2003. The economic implications of deer damage in forests and woodlands, in: Proceedings of the Future for Deer Conference. English Nature Research Report No. 548.

Gill, R.M.A., 1992a. A review of damage by mammals in north temperate forests: 1. Deer. Forestry 65, 145–169. https://doi.org/10.1093/forestry/65.2.145

Gill, R.M.A., 1992b. A Review of damage by mammals in north temperate forests. 2. Small mammals. Forestry 65, 281–308. https://doi.org/10.1093/forestry/65.3.281

Gill, R.M.A., Morgan, G., 2010. The effects of varying deer density on natural regeneration in woodlands in lowland Britain. Forestry 83, 53–63. https://doi.org/10.1093/forestry/cpp031

Gill, R.M.A., Thomas, M.L., Stocker, D., 1997. The use of portable thermal imaging for estimating deer population density in forest habitats. J. Appl. Ecol. 34, 1273–1286. https://doi.org/10.2307/2405237

Gonzalez-Hernandez, M.P., Silva-Pando, F.J., 1999. Nutritional attributes of understory plants known as components of deer diets. J. Range Manag. 52, 132. https://doi.org/10.2307/4003506

Gordon, I.J., Illius, A.W., 1994. The functional significance of the browser-grazer dichotomy in African ruminants. Oecologia 98, 167–175. https://doi.org/10.1007/BF00341469

Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., Schlesinger, W.H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R.T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M.R., Herrero, M., Kiesecker, J., Landis, E., Laestadius, L., Leavitt, S.M., Minnemeyer, S., Polasky, S., Potapov, P., Putz, F.E., Sanderman, J., Silvius, M., Wollenberg, E., Fargione, J., 2017. Natural climate solutions. Proc. Natl. Acad. Sci. 114, 11645–11650. https://doi.org/10.1073/pnas.1710465114

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, 93–102. https://doi.org/10.1093/forestry/cpp032

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. For. Ecol. Manage. 261, 288–296. https://doi.org/10.1016/j.foreco.2010.10.022

Hemami, M.R., Watkinson, A.R., Dolman, P.M., 2005. Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* in a lowland pine forest. For. Ecol. Manage. 215, 224–238.

https://doi.org/10.1016/j.foreco.2005.05.013

Hemami, M.R., Watkinson, A.R., Dolman, P.M., 2004. Habitat selection by sympatric muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a lowland commercial pine forest. For. Ecol. Manage. 194, 49–60. https://doi.org/10.1016/j.foreco.2004.01.049

Hemami, M.R., Watkinson, A.R., Gill, R.M.A., Dolman, P.M., 2007. Estimating abundance of introduced chinese muntjac /*Muntiacus reevesi* and native roe deer *Capreolus capreolus* using portable thermal imaging equipment. Mamm. Rev. 37, 246–254. https://doi.org/10.1111/j.1365-2907.2007.00110.x

Hidding, B., Tremblay, J.-P., Côté, S.D., 2012. Survival and growth of balsam fir seedlings and saplings under multiple controlled ungulate densities. For. Ecol. Manage. 276, 96–103. https://doi.org/10.1016/j.foreco.2012.03.023

Hijmans, R.J., 2017. raster: Geographic data analysis and modeling.

Hjältén, J., Danell, K., Ericson, L., 2004. Hare and vole browsing preferences during winter. Acta Theriol. (Warsz). 49, 53–62. https://doi.org/10.1007/BF03192508

Hjältén, J., Danell, K., Lundberg, P., 1993. Herbivore avoidance by association: vole and hare utilization of woody plants. Oikos 68, 125–131.

Holloway, C.W., 1967. The Effect of Red Deer and Other Animals on Naturally Regenerated Scots Pine. Ph.D. Thesis. University of Aberdeen.

Horsley, S.B., Stout, S.L., De Calesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13, 98–118. https://doi.org/10.1890/1051-0761(2003)013[0098:wtdiot]2.0.co;2

Hothorn, T., Müller, J., 2010. Large-scale reduction of ungulate browsing by managed sport hunting. For. Ecol. Manage. 260, 1416–1423. https://doi.org/10.1016/j.foreco.2010.07.019

Hulbert, I.A.R., Iason, G.R., Elston, D.A., Racey, P.A., 1996. Home-range sizes in a stratified upland landscape of two lagomorphs with different feeding strategies. J. Appl. Ecol. 33,

1479. https://doi.org/10.2307/2404786

Jackson, J., 1980. The annual diet of the fallow deer (*Dama dama*) in the New Forest, Hampshire, as determined by rumen content analysis. J. Zool. 192, 71–83. https://doi.org/10.1111/j.1469-7998.1980.tb04220.x

Krojerová-Prokešová, J., Barančeková, M., Šustr, P., Heurich, M., 2010. Feeding patterns of red deer *Cervus elaphus* along an altitudinal gradient in the Bohemian Forest: effect of habitat and season. Wildlife Biol. 16, 173–184. https://doi.org/10.2981/09-004

Latham, A.D.M., Latham, M.C., Norbury, G.L., Forsyth, D.M., Warburton, B., 2020. A review of the damage caused by invasive wild mammalian herbivores to primary production in New Zealand. New Zeal. J. Zool. 47, 20–52. https://doi.org/10.1080/03014223.2019.1689147

Lesser, M.R., Dovciak, M., Wheat, R., Curtis, P., Smallidge, P., Hurst, J., Kramer, D., Roberts, M., Frair, J., 2019. Modelling white-tailed deer impacts on forest regeneration to inform deer management options at landscape scales. For. Ecol. Manage. 448, 395–408. https://doi.org/10.1016/j.foreco.2019.06.013

Lewis, S.L., Wheeler, C.E., Mitchard, E.T.A., Koch, A., 2019. Restoring natural forests is the best way to remove atmospheric carbon. Nature 568, 25–28. https://doi.org/10.1038/d41586-019-01026-8

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, 271–281. https://doi.org/10.1007/s00442-013-2761-1

Macdonald, D.W., 2009. The Princeton Encyclopedia of Mammals, 1st ed. Windmill Books (Andromeda International).

Marshall, L., Miller, D.L., Rexstad, E., Burt, L., Bravington, M. V, Hedley, S., 2017. Package ‘ dsm .’

Miller, D.L., 2016. Package ‘Distance.’

Miller, D.L., Burt, M.L., Rexstad, E.A., Thomas, L., 2013. Spatial models for distance sampling data: recent developments and future directions. Methods Ecol. Evol. 4, 1001–1010. https://doi.org/10.1111/2041-210X.12105

Miller, G.R., Kinnaird, J.W., Cummins, R.P., 1982. Liability of saplings to browsing on a red deer range in the Scottish Highlands. J. Appl. Ecol. 19, 941–951.

Morelle, K., Bouché, P., Lehaire, F., Leeman, V., Lejeune, P., 2012. Game species monitoring using road-based distance sampling in association with thermal imagers: A covariate analysis. Anim. Biodivers. Conserv. 35, 253–265.

Motta, R., 1996. Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the western Italian Alps. For. Ecol. Manage. 88, 93–98. https://doi.org/10.1016/S0378-1127(96)03814-5

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. Open Life Sci. 8, 8–17. https://doi.org/10.2478/s11535-012-0108-2

Palmer, S.C., Truscott, A.., 2003. Browsing by deer on naturally regenerating scots pine (*Pinus sylvestris L.*) and its effects on sapling growth. For. Ecol. Manage. 182, 31–47. https://doi.org/10.1016/S0378-1127(03)00026-4

Partl, E., Szinovatz, V., Reimoser, F., Schweiger-Adler, J., 2002. Forest restoration and browsing impact by roe deer. For. Ecol. Manage. 159, 87–100. https://doi.org/10.1016/S0378-1127(01)00712-5

Pebesma, E.J., Bivand, R.S., 2005. Classes and methods for spatial data in R. R News 5 2, 9–13.

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. For. Ecol. Manage. 222, 302–313. https://doi.org/10.1016/j.foreco.2005.10.034

Peterken, G.F., 1996. Natural Woodland: Ecology and Conservation in Northern Temperate

Regions. Cambridge University Press, Cambridge.

POST, 2009. Note number 325 Wild Deer in the UK: Impacts of rising deer populations. The Parliamentary Office of Science and Technology, London.

Prien, S., Müller, M., 2010. Wildschäden im Wald. Ökologische Grundlagen und integrierte Schutzmaßnahmen. Neumann-Newdamm.

Proffitt, K.M., Grigg, J.L., Hamlin, K.L., Garrott, R.A., 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. J. Wildl. Manage. 73, 345–356. https://doi.org/10.2193/2008-210

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. Mamm. Rev. 41, 175–196. https://doi.org/10.1111/j.1365-2907.2010.00173.x

R core Team, 2018. R: A Language and Environment for Statistical Computing.

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. For. Ecol. Manage. 424, 406–419. https://doi.org/10.1016/j.foreco.2018.05.016

Reimoser, F., 2003. Steering the impacts of ungulates on temperate forests. J. Nat. Conserv. 10, 243–252. https://doi.org/http://dx.doi.org/10.1078/1617-1381-00024

Reimoser, F., Gossow, H., 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. For. Ecol. Manage. 88, 107–119. https://doi.org/10.1016/S0378-1127(96)03816-9

Reinecke, H., Leinen, L., Thißen, I., Meißner, M., Herzog, S., Schütz, S., Kiffner, C., 2014. Home range size estimates of red deer in Germany: environmental, individual and methodological correlates. Eur. J. Wildl. Res. 60, 237–247. https://doi.org/10.1007/s10344-013-0772-1

Rodwell, J.S., 1992. British Plant Communities. Volume 3: Grasslands and Montane Vegetation. Cambridge University Press, Cambridge.

Schai-Braun, S.C., Hackländer, K., 2014. Home range use by the European hare (*Lepus europaeus*) in a structurally diverse agricultural landscape analysed at a fine temporal scale. Acta Theriol. (Warsz). 59, 277–287. https://doi.org/10.1007/s13364-013-0162-9

Schai-Braun, S.C., Reichlin, T.S., Ruf, T., Klansek, E., Tataruch, F., Arnold, W., Hackländer, K., 2015. The European hare (*Lepus europaeus*): a picky herbivore searching for plant parts rich in fat. PLoS One 10. https://doi.org/10.1371/journal.pone.0134278

Scott, D., Welch, D., Thurlow, M., Elston, D.A., 2000. Regeneration of *Pinus sylvestris* in a natural pinewood in NE Scotland following reduction in grazing by *Cervus elaphus*. For. Ecol. Manage. 130, 199–211. https://doi.org/10.1016/S0378-1127(99)00191-7

Simončič, T., Bončina, A., Jarni, K., Klopčič, M., 2019. Assessment of the long-term impact of deer on understory vegetation in mixed temperate forests. J. Veg. Sci. 108–120. https://doi.org/10.1111/jvs.12702

Storms, D., Aubry, P., Hamann, J.-L., Saïd, S., Fritz, H., Saint-Andrieux, C., Klein, F., 2008. Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. Wildlife Biol. 14, 237–250. https://doi.org/10.2981/0909-6396(2008)14[237:SVIDCA]2.0.CO;2

Takatsuki, S., 2009. Effects of sika deer on vegetation in Japan: a review. Biol. Conserv. 142, 1922–1929. https://doi.org/10.1016/j.biocon.2009.02.011

Tixier, H., Duncan, P., Scehovic, J., Yant, A., Gleizes, M., Lila, M., Yani, A., 1997. Food selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional value of their diets. J. Zool. 242, 229–245. https://doi.org/10.1111/j.1469-7998.1997.tb05799.x

Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C., Baubet, E., 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. Can. J. Zool. 87, 1129–1137. https://doi.org/10.1139/Z09-101

Tuomi, J., Augner, M., 1993. Synergistic selection of unpalatability in plants. Evolution (N. Y). 47, 668. https://doi.org/10.2307/2410078

UK Committee on Climate Change, 2019. Net Zero: The UK's Contribution to Stopping Global Warming.

Wäber, K., 2010. Landscape scale deer management. PhD Thesis. PhD Thesis. University of East Anglia.

Wäber, K., Dolman, P.M., 2015. Deer abundance estimation at landscape-scales in heterogeneous forests. Basic Appl. Ecol. 16, 610–620. https://doi.org/10.1016/j.baae.2015.06.005

Wäber, K., Spencer, J., Dolman, P.M., 2013. Achieving landscape-scale deer management for biodiversity conservation: the need to consider sources and sinks. J. Wildl. Manage. 77, 726–736. https://doi.org/10.1002/jwmg.530

Ward, A.I., White, P.C.., Smith, A., Critchley, C.H., 2004. Modelling the cost of roe deer browsing damage to forestry. For. Ecol. Manage. 191, 301–310. https://doi.org/10.1016/j.foreco.2003.12.018

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. For. Ecol. Manage. 256, 1333–1338. https://doi.org/10.1016/j.foreco.2008.06.034

Welch, D., Scott, D., Staines, B.W., 1995. Survival rates and performance of multi-trunked trees in even-aged stands of sitka spruce in western Scotland. Forestry 68, 245–254. https://doi.org/10.1093/forestry/68.3.245

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, 309–330. https://doi.org/10.1093/forestry/65.3.309

Welch, D., Staines, B.W., Scott, D., French, D.D., Catt, D.C., 1991. Leader browsing by red and roe deer on young sitka spruce trees in western Scotland I. Damage rates and the influence of habitat factors. Forestry 64, 61–82. https://doi.org/10.1093/forestry/64.1.61

Appendices

Appendix A. Red deer density pooled across 2018, 2019, 2020.

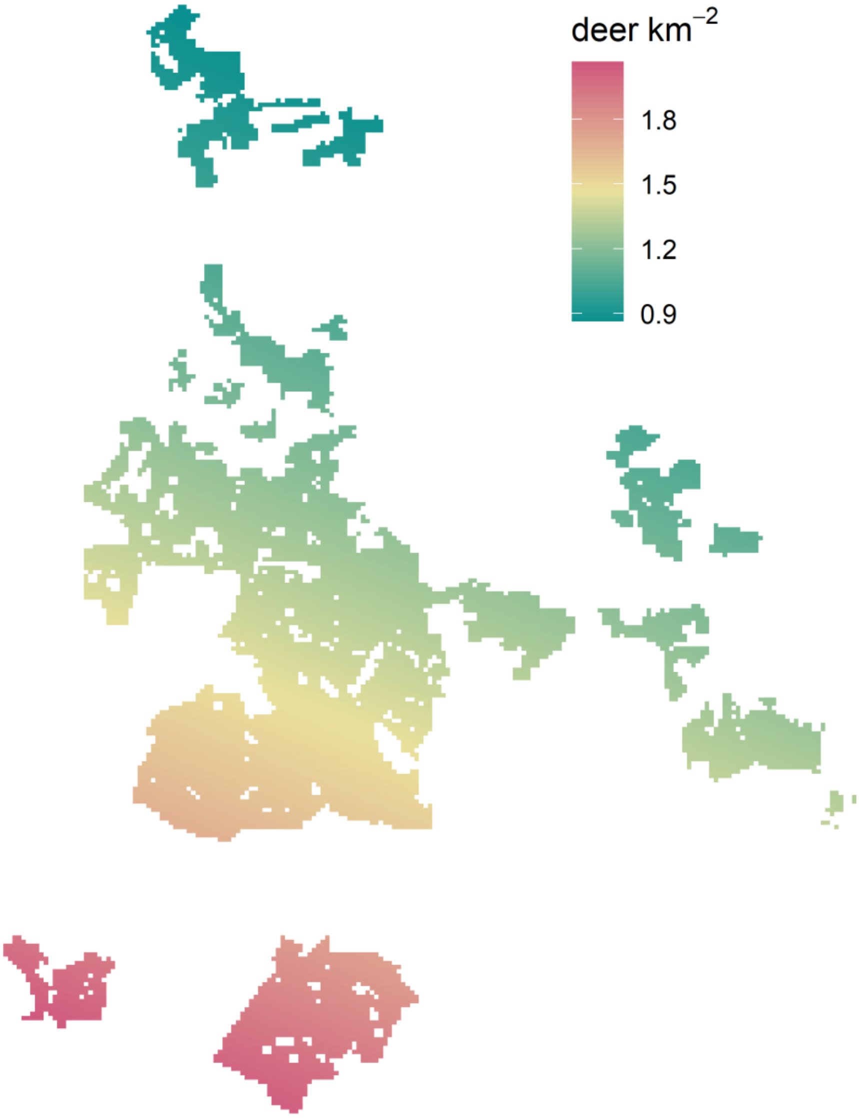


Figure A3.1. The spatial distribution of red deer density predicted at 100x100 m grid from a density surface model using data pooled across 2018, 2019 and 2020.

Across the forest, red deer density (mean pooled over the three years, 1.4 individuals km^{-2} CV=0.21) contributed little to the combined total density of large deer in areas with abundant fallow (minimum 6%, at 29 large deer km^{-2}), but dominated total large deer density where fallow were scarce (maximum of 100%, but with only 0.8 large deer km^{-2}).

Appendix B. Rabbits and hares in Thetford forest

Hare can utilise young conifer forest plantations (Hulbert, Iason and Racey, 1996) and regularly occur in restocked stands in Thetford forest (Fig A3.2) while only low numbers of rabbits were observed during distance sampling thermal imaging. Although hare mostly eat herbaceous vegetation (Schai-Braun *et al.*, 2015) they can use woody species in the winter (Homolka and Heroldová, 2003; Hjältén, Danell and Ericson, 2004) and can browse young pine (Gill, 1992; Lyly *et al.*, 2014). Rabbits also feed mainly on graminoid and herbaceous vegetation, but consume some shrub browse, particularly *Cistus* spp., Ericaceae spp, *Ulex*, *Olea*, evergreen *Quercus* spp. and deciduous browse (Marques and Mathias, 2001; Martins, Milne and Rego, 2002; Ferreira and Alves, 2009; Kontsiotis *et al.*, 2015); however, I am not aware of evidence that rabbit also browse pine foliage. I therefore considered the potential influence of hare but excluded rabbits from modelling of crop impacts.

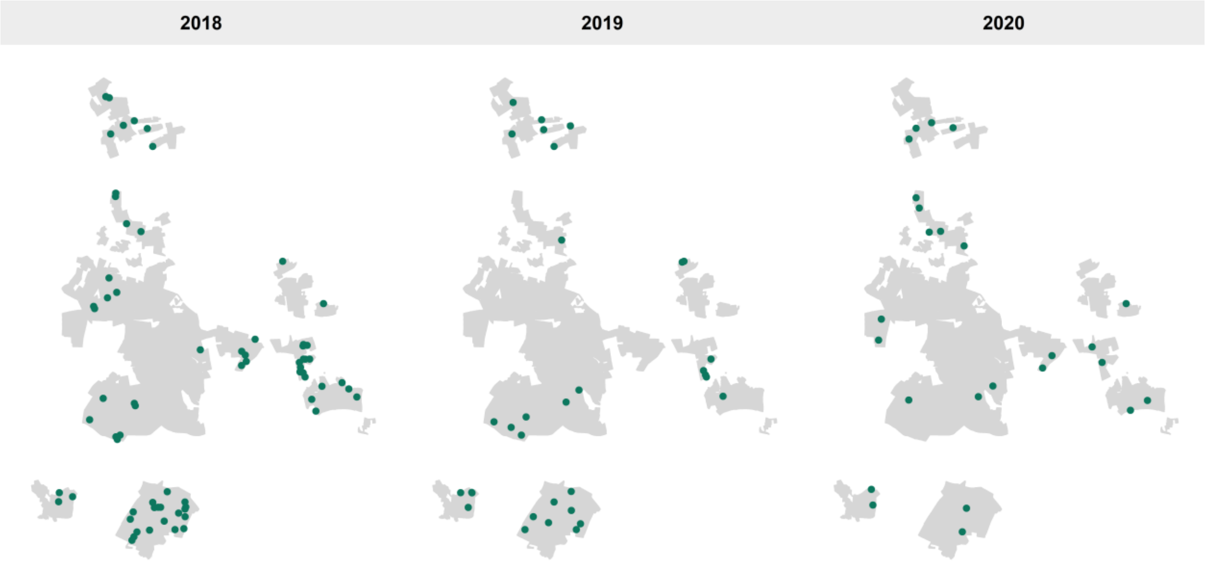


Figure A3.2. The distribution of hare *Lepus europaeus* presence recorded during thermal imaging surveys conducted across Thetford Forest in each year (2018, 2019 and 2020).

References

Ferreira, C. and Alves, P. C. (2009) ‘Influence of habitat management on the abundance and diet of wild rabbit (*Oryctolagus cuniculus algirus*) populations in Mediterranean ecosystems’, *European Journal of Wildlife Research*, 55(5), pp. 487–496. doi: 10.1007/s10344-009-0257-4.

Gill, R. M. A. (1992) ‘A Review of damage by mammals in north temperate forests. 2. Small mammals’, *Forestry*. Oxford University Press, 65(3), pp. 281–308. doi: 10.1093/forestry/65.3.281.

Hjältén, J., Danell, K. and Ericson, L. (2004) ‘Hare and vole browsing preferences during winter’, *Acta Theriologica*, 49(1), pp. 53–62. doi: 10.1007/BF03192508.

Homolka, M. and Heroldová, M. (2003) ‘Impact of large herbivores on mountain forest stands in the Beskydy Mountains’, *Forest Ecology and Management*, 181(1–2), pp. 119–129. doi: 10.1016/S0378-1127(03)00121-X.

Hulbert, I. A. R., Iason, G. R. and Racey, P. A. (1996) ‘Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding strategies’, *The Journal of Applied Ecology*, 33(2), p. 315. doi: 10.2307/2404753.

Kontsiotis, V. J. *et al.* (2015) ‘Trophic ecology of the European wild rabbit *Oryctolagus cuniculus* on the Mediterranean island of Lemnos, Greece’, *Ecological Research*. Springer Japan, 30(4), pp. 683–691. doi: 10.1007/s11284-015-1269-z.

Lyly, M. *et al.* (2014) ‘Varying impacts of cervid, hare and vole browsing on growth and survival of boreal tree seedlings’, *Oecologia*, 174(1), pp. 271–281. doi: 10.1007/s00442-013-2761-1.

Marques, C. and Mathias, M. L. (2001) ‘The diet of the European wild rabbit, *Oryctolagus cuniculus (L.)*, on different coastal habitats of central Portugal’, *Mammalia*, 65(4). doi: 10.1515/mamm.2001.65.4.437.

Martins, H., Milne, J. A. and Rego, F. (2002) ‘Seasonal and spatial variation in the diet of the wild rabbit (*Oryctolagus cuniculus L.*) in Portugal’, *Journal of Zoology*, 258(3), pp. 395–404. doi: 10.1017/S0952836902001541.

Schai-Braun, S. C. *et al.* (2015) ‘The European hare (*Lepus europaeus*): a picky herbivore searching for plant parts rich in fat’, *PLOS ONE*, 10(7). doi: 10.1371/journal.pone.0134278.

Appendix C. Thermal imaging distance transects used to sample deer density and lagomorph presence.

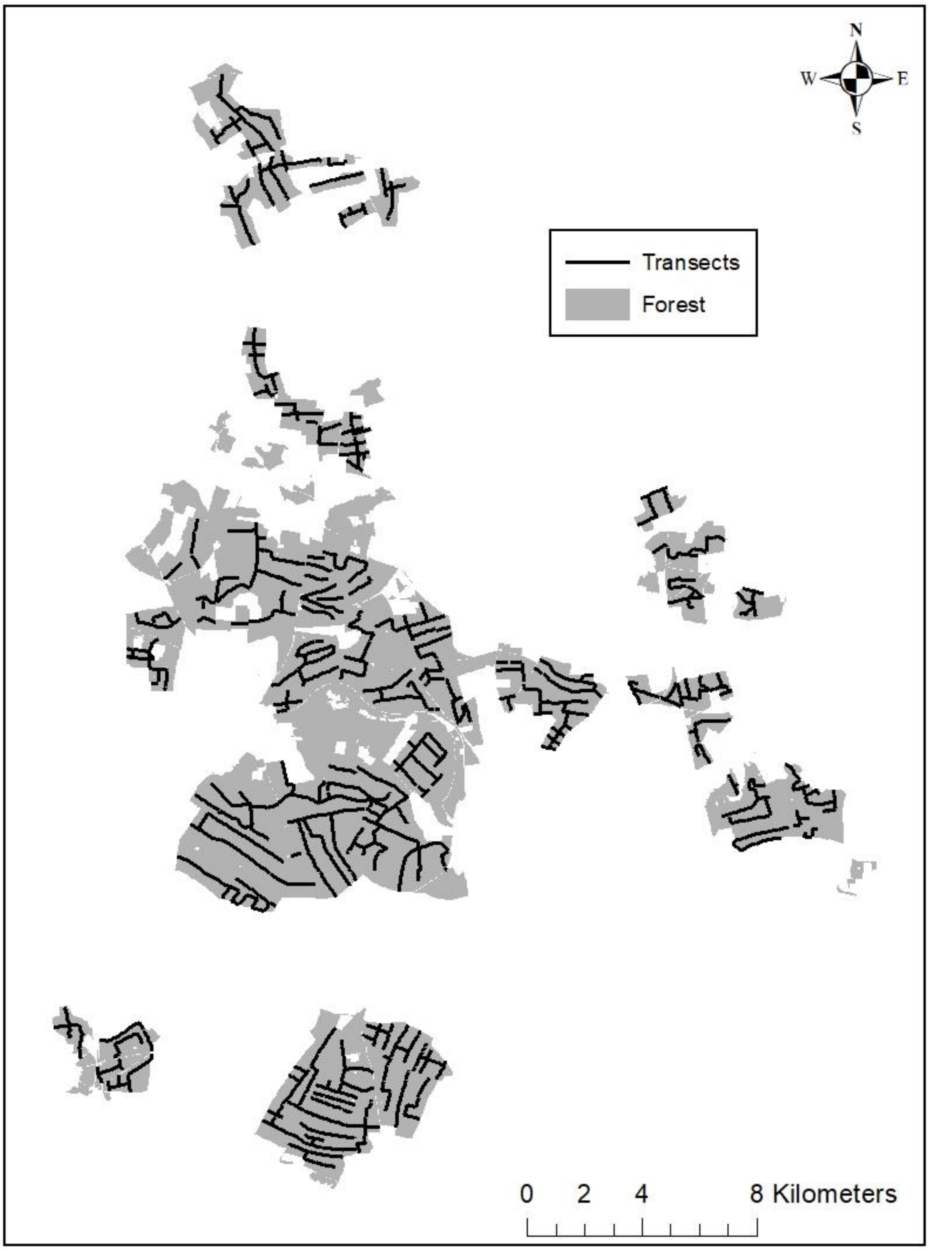


Figure A3.3: Thermal imaging distance sampling transects driven to sample deer abundance and hare *Lepus europaeus* presence across Thetford Forest.

Appendix D. Thermal imaging distance sampling methodological detail

Detectability class covariate and criteria for combining sections

Deer detectability during nocturnal thermal imaging distance sampling changes with forest growth stage (Hemami et al., 2007; Wäber and Dolman, 2015). For this reason, I included a categorical variable in the detection function to model differences in detectability due to the tree crop age of the forest stand sampled by each transect section. Following (Hemami, 2003), detectability classes of stands were classified *a priori* between three categories according to growth stage and management, as: ‘open’ (comprising permanent open areas, clear-felled unplanted stands, and recently restocked stands 0-3 years since planting); ‘dense’ (comprising restocked stands 4-5 years old, pre-thicket stands 6-10 years old and thicket stands 11-20 years old, and those pole stage stands, between 21-40 years old, that had not yet received a first thinning cut, when one in four tree rows are removed) and ‘mature’ (comprising those pole stage stands 21-40 years old that had received at least one thinning cut and all mature stands >40 years old).

Single-sided driven transects sequentially surveyed individual forest stands that differed in growth stage and potentially in visibility class, generating a series of short (n=2414, mean length 225 m, SD=128) transect ‘sections’ (with the start and end defined for each individual forest stand). Large numbers of sections with zero observations caused zero-inflation in the density surface model (DSM) and also generated inflated high values of local density in those sections with one or more deer recorded. Therefore, to improve model precision and avoid zero-inflation, sections were combined into fewer, longer, composite ‘segments’ that were constrained to have a consistent visibility class. In a few instances (n=29) where longer individual sections (max length=944m, mean =700 m, SD=102) ran through or alongside a single large stand (of uniform visibility class), these were retained in their entirety. Remaining segments were created by running an algorithm structured such that the full extent of the combined segment was no greater than 600 m between the most distal points (combined start and end). As long as the constraints of overall length ≤600 m and common visibility class were met, a composite segment could comprise contiguous (end-to-end) sections, and/or non-contiguous sections interrupted by other sections differing in detectability class (that were kept unique, or combined in a different segment), with sections lying on the same or on alternative sides of the transect centre-line. Figure A3.4 shows three examples of this process, whereby the initial 2414 sections were merged and reduced to 1162 composite segments (mean length=462 m, SD=297).

Nearby or overlapping segments allowed models to control for detectability when estimating local density estimates that were then used to calibrate the density surface map.

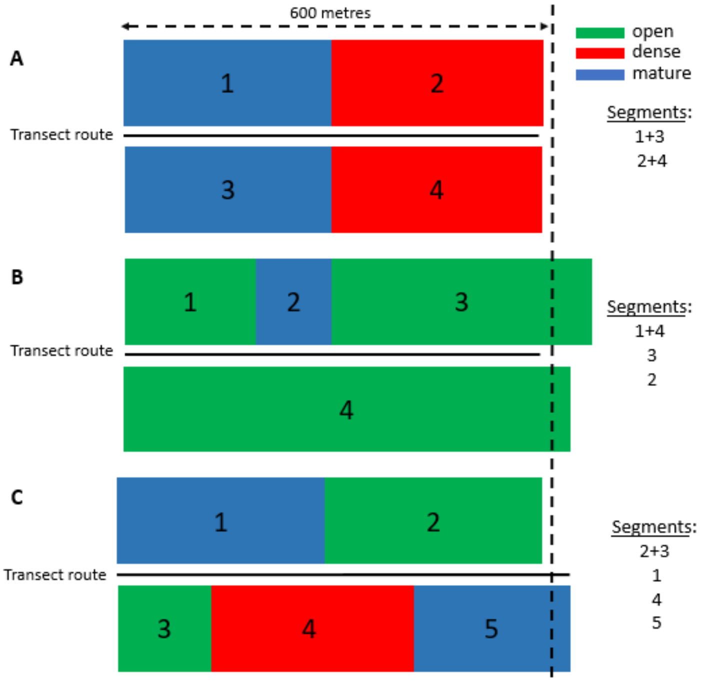


Figure A3.4: Schematic illustrating showing how nearby distance transect sections were combined into fewer longer segments of common detectability class (denoted by colours). In A: one segment comprised two single-sided sections that each sampled mature stands (1 and 3) on opposite sides of the transect centre-line, a second segment comprised two sections that each sampled dense stands (2 and 4). In B: one long section (4) exceeded 600 m but was not subdivided (as it sampled a single stand), this was combined with a short section (1) on the opposite side of the transect centre-line, that also sampled a stand of the same visibility class (open). Although the remaining section also sampled a stand of this visibility class (open), this section was not combined in the same segment as it projected further beyond section (4); section (2) sampled a different visibility class (mature) and was not combined with either of these segments (though would be a candidate for combination with other nearby section(s) further along the centre line if they also sampled a mature stand and lay within 600 m). In C: I combined two sections (2 and 3) on opposite sides of the transect centre-line as both sampled stands of the same visibility class (open) and lay within 600 m, while two sections (1 and 5) that sampled mature stands were not combined as they exceeded 600 m from start to finish, section (4) sampled a different visibility class (dense) and was therefore not combined with any of these segments; again sections 1, 5, 4 would be candidates for combination with other nearby sections lying within 600 m along the transect centre-line if these sampled the same visibility class.

Detection function, covariate and adjustments selection.

In order to correctly model the decreasing probability of detecting an animal with increasing perpendicular distance from the transect line, I evaluated alternative models fitting each of the available key detection functions: half-normal and hazard-rate with adjustments (cosine, hermite, polynomial), with and without a term relating group size to perpendicular distance (to account for potential lower detectability of distant smaller groups) and with and without detectability class (categorical covariate with three levels: open, dense, mature). Detection function analyses were conducted separately for each species, using data pooled across 2018, 2019 and 2020, excluding the 5% most distal observation, following (Buckland et al., 2001). For each species, the model with the lowest value of Akaike's information criterion (AIC) was selected; when alternative models differed by less than 2 units then the most parsimonious model was chosen. Analyses were performed in R (R core Team, 2018) using package "Distance" (Miller, 2016).

For muntjac and roe deer a hazard-rate detection function with detectability class and group size covariates provided models that were clearly superior to alternative formulations (Table A3.1, Fig A3.5). For fallow and red deer, a hazard-rate detection function with detectability class covariate was selected as the most parsimonious model, with no support for group size adjustment that was, therefore, excluded from the model (Table A3.1, Fig A3.5).

Table A3.1: Detection function, covariate and adjustment selection of muntjac, roe, fallow and red deer distance sampling data. For each model AIC and the difference in AIC value relative to the best supported model (ΔAIC) are shown.

Muntjac			
Key function	**Covariate or adjustment**	**AIC**	**ΔAIC**
Hazard-rate	~detectability class + group size	31058.07	0
Hazard-rate	~detectability class	31068.03	9.963024
Hazard-rate	~hermite	31136.7	78.63347
Hazard-rate	~cosine	31136.7	78.63347
Hazard-rate	~polynomial	31136.7	78.63347
Hazard-rate	~1	31136.7	78.63347
Half-normal	~cosine	31178.84	120.7681

Half-normal	~detectability class + group size	31180.22	122.1471
Half-normal	~detectability class	31189.38	131.3079
Half-normal	~polynomial	31191.24	133.1713
Half-normal	~hermite	31232.3	174.2305
Half-normal	~1	31240.73	182.6609
	Roe deer		
Key function	**Covariate or adjustment**	**AIC**	**ΔAIC**
Hazard-rate	~detectability class + group size	8334.087	0
Hazard-rate	~detectability class	8338.743	4.656428
Hazard-rate	~hermite	8356.379	22.29201
Hazard-rate	~cosine	8356.379	22.29201
Hazard-rate	~polynomial	8356.379	22.29201
Hazard-rate	~1	8356.379	22.29201
Half-normal	~cosine	8365.747	31.65991
Half-normal	~polynomial	8377.352	43.26561
Half-normal	~detectability class + group size	8400.034	65.94728
Half-normal	~detectability class	8402.753	68.66656
Half-normal	~hermite	8409.915	75.82834
Half-normal	~1	8418.583	84.49674
	Fallow deer		
Key function	**Covariate or adjustment**	**AIC**	**ΔAIC**
Hazard-rate	~detectability class	2149.46	0
Hazard-rate	~hermite	2151.522	2.062082
Hazard-rate	~cosine	2151.522	2.062082
Hazard-rate	~polynomial	2151.522	2.062082
Hazard-rate	~1	2151.522	2.062082
Hazard-rate	~detectability class + group size	2152.451	2.991193
Half-normal	~hermite	2153.387	3.927129
Half-normal	~cosine	2153.992	4.532285
Half-normal	~polynomial	2156.637	7.176894
Half-normal	~detectability class	2156.65	7.190524

Half-normal	~1	2157.453	7.992853
Half-normal	~detectability class + group size	2158.584	9.12391
Red deer			
Key function	**Covariate or adjustment**	**AIC**	**ΔAIC**
Hazard-rate	~detectability class	921.5031	0
Half-normal	~detectability class	921.902	0.398813
Hazard-rate	~detectability class + group size	922.5826	1.079487
Half-normal	~detectability class + group size	923.0191	1.515968
Half-normal	~hermite	927.8669	6.363763
Half-normal	~cosine	927.8669	6.363763
Half-normal	~polynomial	927.8669	6.363763
Half-normal	~1	927.8669	6.363763
Hazard-rate	~hermite	928.7859	7.282798
Hazard-rate	~cosine	928.7859	7.282798
Hazard-rate	~polynomial	928.7859	7.282798
Hazard-rate	~1	928.7859	7.282798

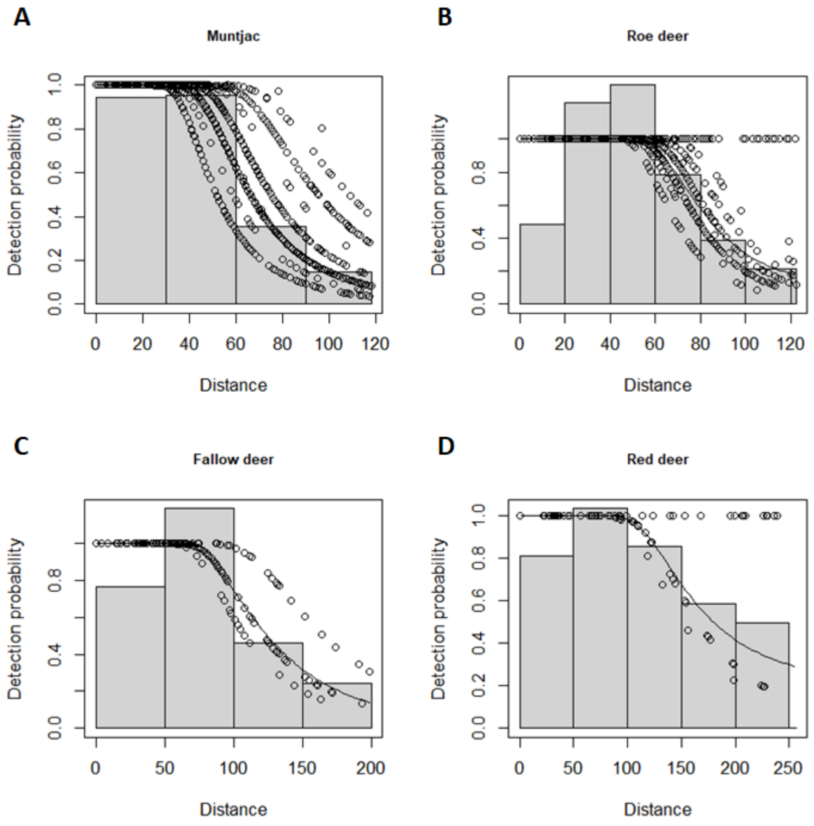


Figure A3.5: Species-specific detection functions. Selected species-specific detection functions of muntjac (A), roe deer (B), fallow deer (C) and red deer (D) of distance sampling data pooled across 2018, 2019 and 2020. Continuous line represents the average detection function, while hollow points represent observations along the categories of the covariate adjustments: for muntjac and roe deer these consider detectability class and group size covariates; for fallow and red deer, detectability class.

The distance sampling thermal imaging data were recorded from one sided transects, from the passenger side of a vehicle. As the opposing side of the transect was then driven within the same night, I have to acknowledge the possibility that animals might already have moved away from the transect if the vehicle disturbed them during the first visit, thereby resulting in under-estimation of deer density. If this was the case, I would expect the detection function to differ between the first and second side visited (within that night); specifically, I would expect significantly greater detection distances for the latter side, inflating the effective strip width of the second side. Furthermore, I would expect that the inclusion of the variable indicating whether each transect section was a first or second visit (within the same night) would significantly increase the explanatory power of the detection function. I evaluated whether inclusion of visitation order (categorical covariate, first or second) affected the detection function in this way, using data from the 2018 survey (where most of the observations have accurate timestamps reported). Inclusion of visitation order in the selected detection functions of muntjac, roe deer and fallow deer did not increase the explanatory power of any of these detection functions (delta AIC relative to the selected detection function < 2 in all cases, see table A3.2).

Table A3.2: Detection function, covariate and adjustment selection of muntjac, roe and fallow deer distance sampling data. For each model AIC and the difference in AIC value relative to the best supported model (ΔAIC) are shown

Muntjac			
Key function	**Covariate or adjustment**	**AIC**	**ΔAIC**
Hazard-rate	~detectability class + group size	-6801.925	0
Hazard-rate	~detectability class + group size + visitation order	-6801.063	0.862
Roe deer			
Key function	**Covariate or adjustment**	**AIC**	**ΔAIC**
Hazard-rate	~detectability class + group size	-1620.335	0
Hazard-rate	~detectability class + group size + visitation order	-1617.725	2.609
Fallow deer			
Key function	**Covariate or adjustment**	**AIC**	**ΔAIC**
Hazard-rate	~detectability class	-235.704	0
Hazard-rate	~detectability class + visitation order	-232.345	3.359

Comparison of detection functions separately built, using data from transect sections surveyed first or second showed that effective strip width did not differ significantly with visitation order (see Table A3.3). The comparison was not possible for red deer, as too few observations were available for a similar analysis.

Table A3.3: Comparison of Effective strip width (ESW) of muntjac, roe deer and fallow deer detection function analysed with data from the sections visited as first and as second, separately.

Muntjac		
	Visitation order: first	**Visitation order: second**
ESW	73m	78m
ESW CI	68-78m	73-83m
Roe deer		
ESW	88m	90m
ESW CI	80-96m	80-100m
Fallow deer		
ESW	114m	108m
ESW CI	95-133m	65-154m

Variance in species-specific density surface models.

Table A3.4: Species-specific coefficients of Variation (CV) of detection functions, GAM and total CV.

	CV Detection function	CV from GAM	Total CV
Muntjac 2018	0.02	0.03	0.04
Muntjac 2019	0.02	0.04	0.04
Muntjac 2020	0.03	0.04	0.05
Roe deer 2018	0.04	0.06	0.07
Roe deer 2019	0.04	0.07	0.08
Roe deer 2020	0.04	0.09	0.1
Fallow deer 2018	0.08	0.16	0.18
Fallow deer 2019	0.09	0.16	0.18
Fallow deer 2020	0.09	0.16	0.19
Red deer (single, pooled density surface model)	0.11	0.15	0.19

References

Buckland, S.T., Anderson, D.R., Thomas, L., Burnham, K.P., Laake, J.L., Borchers, D.L., 2001. Line transects, in: Introduction To Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, pp. 104–14.

Hemami, M.R., 2003. The ecology of roe deer (Capreolus capreolus) and muntjac (Muntiacus reevesi) in a forested landscape in eastern England. University of East Anglia.

Hemami, M.R., Watkinson, A.R., Gill, R.M.A., Dolman, P.M., 2007. Estimating abundance of introduced chinese muntjac /*Muntiacus reevesi* and native roe deer *Capreolus capreolus* using portable thermal imaging equipment. Mamm. Rev. 37, 246–254. https://doi.org/10.1111/j.1365-2907.2007.00110.x

Miller, D.L., 2016. Package ‘Distance.’

R core Team, 2018. R: A Language and Environment for Statistical Computing.

Wäber, K., Dolman, P.M., 2015. Deer abundance estimation at landscape-scales in heterogeneous forests. Basic Appl. Ecol. 16, 610–620. https://doi.org/10.1016/j.baae.2015.06.005

Chapter Four

Habitat quality, configuration and context effects on roe deer fecundity across a forested landscape mosaic

Abstract

Effective landscape-scale management of source-sink deer populations will be strengthened by understanding whether local variation in habitat quality drives heterogeneity in productivity. I related female roe deer *Capreolus capreolus* fecundity and body mass to habitat composition and landscape context, separately for adults and yearlings, using multi-model inference (MMI) applied to a large sample of individuals (yearlings: fecundity=202, body mass=395; adults: fecundity=908, body mass=1669) culled during 2002-2015 from an extensive (195 km^2) heterogeneous forest landscape. Adults were heavier (inter-quartile, IQ, effect size=+0.5kg) when culled in buffers comprising more arable lands while contrary to my prediction no effects on body mass of grassland, young forest or access to vegetation on calcareous soil were found. Heavier adults were more fertile (IQ effect size, +12% probability of having two embryos instead of one or zero). Counter-intuitively, adults with greater access to arable lands were less fecund (IQ effect of arable: -7% probability of having two embryos, instead of one or zero), and even accounting for greater body mass of adults with access to arable, their modelled fecundity was similar to or lower than that of adults in the forest interior. In contrast, effects of grassland, young forest and calcareous soil did not receive support. Yearling body mass had an effect on fecundity twice that found in adults (+23% probability of having one additional embryo), but yearling body mass and fecundity were not affected by any candidate habitat or landscape variables. Effect of arable lands on body mass and fecundity were small, with little variance explained (Coefficient of Variation of predicted fecundity across forest sub-regions=0.03 for adults). More variance in fecundity was attributed to other differences between forest management sub-regions (modelled as random effects), suggesting other factors might be important. When analysing source-sink population dynamics to support management, an average value of fecundity can be appropriate across a heterogeneous forest landscape.

Introduction

Deer populations are increasing in both North America and Europe (Côté *et al.* 2004; Ward 2005; Dolman & Wäber 2008), with important consequences for biodiversity, human health and traffic collisions (Fuller & Gill 2001; Langbein, Putman & Pokorny 2011; Kilpatrick, Labonte & Stafford 2014). Management effectiveness is improved by landscape-scale analysis of source-sink demography (Wäber, Spencer & Dolman 2013); however, measuring the required parameters of density, fecundity, neonatal and adult mortality can be time consuming and challenging (Wäber, Spencer & Dolman 2013; Wäber & Dolman 2015). Local, context-specific, measures are required as deer fecundity can vary with both density (Albon, Mitchell & Staines 1983; Focardi *et al.* 2002) and landscape suitability (Nilsen, Linnell & Andersen 2004; McLoughlin *et al.* 2007; Miyashita *et al.* 2008). Although fecundity can be assessed where culled carcasses are available (Wäber, Spencer & Dolman 2013), it is important to understand the degree to which fecundity varies across a heterogeneous landscape and the scale at which management can be simplified by spatially-averaging data.

Roe deer *Capreolus capreolus* fecundity and its relation with body mass vary substantially between populations. Rates of implantation failure vary across Britain, in relation to climatic severity, whilst within populations there is no consistent effect of weather on female fecundity (Hewison & Gaillard 2001). Similarly, fertility (the percentage of pregnant 2-year-old females) was lower in a Norwegian than in a French roe population of similar density, despite greater body mass (Andersen & Linnell 2000). In Britain, although fertility was positively related to body mass overall, the asymptote at which fertility became maximal differed among 15 populations (Hewison 1996). Fertility also varies within a population in relation to local landscape heterogeneity. Female roe deer with greater availability of preferred habitat within their winter home-range had larger litters in the subsequent spring (Nilsen, Linnell & Andersen 2004). In an enclosed roe deer population in Northern France, female lifetime reproductive success was positively associated with presence of open habitat edges within the home range and negatively associated with mature open forest (McLoughlin *et al.* 2007). Similarly, in central Japan (Miyashita *et al.* 2008) GPS-collared sika deer (*Cervus nippon*) with greater access to forest edges had higher probability of pregnancy. Climate, density and food availability also influence red deer (*Cervus elaphus*) fertility (Clutton-Brock & Albon 1989).

I examined the degree to which forest habitat (stand structure and soil type) and landscape context (access to preferred non-forest habitats) affect body mass and fecundity of roe deer. I used extensive cull data collected from 2064 individuals, in a landscape-scale (195 km^2 forest mosaic in eastern England), long-term (14 year) study. Tree crop, forest growth stage and soil composition vary locally and across the extensive forest landscape; while the progression of annual felling-replanting activity across forest sub-regions further de-coupled growth stage composition from local soil, forest configuration and landscape context. Together, this provided an unusual degree of landscape replication allowing powerful analysis.

I predicted that individuals with better quality habitat would have greater body mass and fecundity. Roe deer prefer early-successional relative to mature forest habitats (Gill *et al.* 1996; Tufto, Andersen & Linnell 1996), likely as these provide both concealment and high quality forage (Saïd & Servanty 2005; Kramer, Groot Bruinderink & Prins 2006; Freschi *et al.* 2017). Similarly, roe in the study area preferentially utilise young stands (0-10 years) prior to canopy closure, where ground vegetation, particularly bramble *Rubus fruticosa* agg., are available (Hemami, Watkinson & Dolman 2004, 2005). Calcareous soil supports greater understory plant species richness (Eycott, Watkinson & Dolman 2006), thus I hypothesized better quality home ranges to have greater local availability of young forests, calcareous soils, grasslands, and arable lands. Furthermore, I predicted that habitat effects would differ between yearling and adult females due to greater sensitivity of yearling fecundity to both habitat and body mass (Flajšman, Jerina & Pokorny 2017).

Material and Methods

Study area

The study was conducted in Thetford Forest (Fig 4.1),

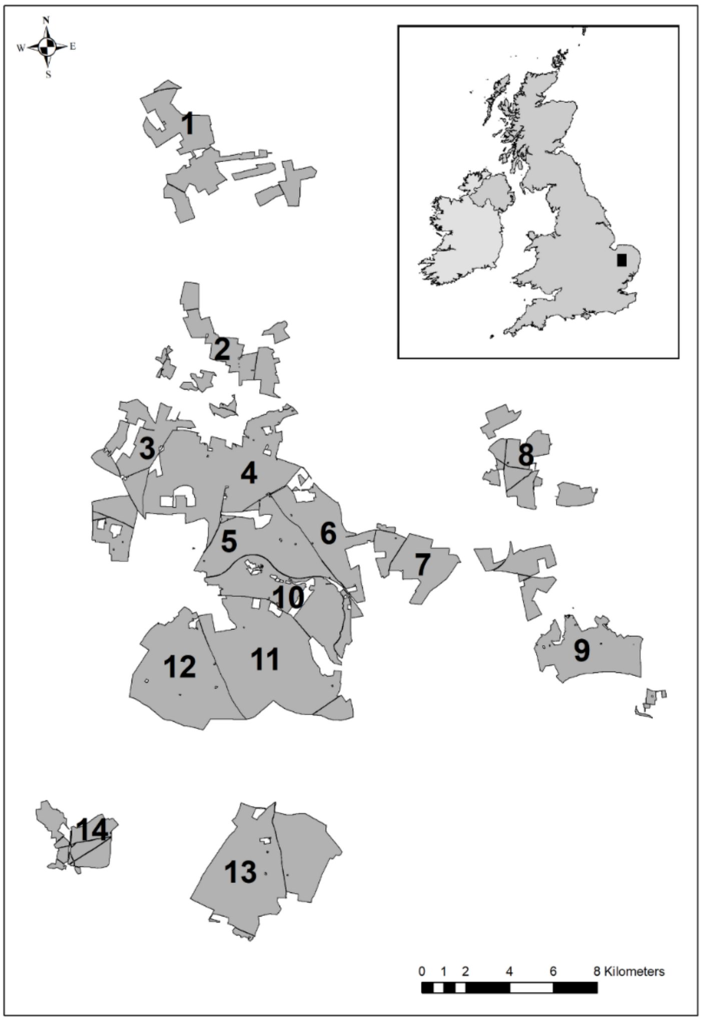


Figure 4.1: Study area map. Thetford Forest showing management sub-regions (see Appendix A).

a conifer-dominated lowland plantation, established during the 1930-1950s on sandy soils in eastern England. Conifer crops (see Appendix A for composition) managed by clear-felling and replanting at economic maturity comprised a mosaic of discrete even-aged plantings (hereafter 'coupes'; mean area = 9.0 ha ± 8.6 SD). I sub-divided the forest landscape into 14 'sub-regions' (mean area= 13.2 km^2, SD= 5.6, Fig 1), that varied in their proportionate representation of deciduous plantings, soil types ('acidic' podsols and gravelly sands; 'calcareous' chalky sands and rendzinas) and configuration (Appendix A). Sub-region's area, perimeter, perimeter-area ratio, and percentage of calcareous soil were independent, with replicates for each relative combination of factors (Appendix A). This permitted effects of habitat and landscape composition to be estimated without confounding geographical effects.

Four deer species were present in the study area (Wäber, Spencer & Dolman 2013): re-established native roe and red, naturalised fallow *Dama dama*, and introduced Reeves's muntjac *Muntiacus reevesi*. In the absence of large predators, deer populations are managed by wildlife rangers employed by Forestry Commission England (FC) to mitigate their impacts on forest crop establishment, biodiversity and road collisions. Forest-wide density of roe deer (estimated using nocturnal distance-sampling by thermal imaging (Wäber & Dolman 2015)) remained low throughout the study period, fluctuating between ca. 2.6 to 4.7 deer/km^2 (Zini et al., unpublished data).

Fecundity and body mass data

Female roe body mass and fecundity data for 2002-2015 were obtained through a long-term research collaboration with FC. For each individual, the cull location (recorded using handheld GPS), date, sex, 'body mass' (measured to the nearest 0.1 kg, after removal of head, feet and viscera, hung with blood drained), number of embryos and remarks (e.g. if shot damage affected body mass) were recorded. Age was estimated by tooth eruption (Aitken 1975) a method that reliably classes individuals as juvenile (born the preceding summer), yearling (in their second winter) or adult; it is however worth noting that a small error may occur when classifying yearlings (Hewison *et al.* 1999). Carcasses recorded in the database as damaged (i.e. incomplete) or considered likely to be damaged as they weighed less than a threshold of 6 kg for yearlings and 8 kg for adults (see Appendix B), were excluded from analysis.

Roe deer exhibit delayed implantation (Sempere, Mauget & Mauget 1998) and in Britain embryos are not visible on opening the uterus before early January (Hewison 1996). I used data from 1st January to 31st of March and included week in models as a fixed effect to account for the seasonal increase in embryo detectability (for further detail, see Appendix C). I couldn't account for any senescence effects, however it is likely that my heavily hunted, low density population comprised only a small fraction of senescent-aged roe deer. I therefore assumed effects of ageing (Hewison & Gaillard 2001) to be negligible and non-confounding.

Environmental variables

I selected four *a priori* habitat variables considered likely to affect roe deer performance: calcareous soil, young forest, arable lands and grasslands (Table 4.1).

Table 4.1: Candidate environmental variables. Variables examined in models of adult and yearling female roe deer fecundity and body mass, showing their mean and coefficient of variation (CV, proportion of SD relative to mean extracted at the Akaike-weighted mean buffer radius).

Variable		**Adult**		**Yearling**	
		body mass	fecundity	body mass	fecundity
%Young forest	Mean	19	16	15	16
	CV	1.1	1.2	1.2	1.2
%Arable	Mean	19	14	15	14
	CV	1.0	1.3	1.3	1.3
%Grassland	Mean	10	8	7.8	8
	CV	1.1	1.5	1.4	1.5
%Calcareous soil	Mean	38	40	41	40
	CV	0.7	0.8	0.8	0.8

Land cover within Thetford forest was extracted from the FC GIS management database that provided spatially-explicit information on the area, crop species and planting year of each management polygon (mean=0.029 km^2 SD=0.03 km^2). Surrounding grasslands and arable lands were extracted from the Land Cover Map 2007 (hereafter LCM 2007; Morton *et al.* 2014) that maps 23 classes to 0.5 ha resolution. All LCM 2007 grassland and heathland classes were combined as ‘grassland’ as finer ecological categories were not reliably classified (Appendix D). Permanent unplanted open space within Thetford forest was also classified as grassland. I considered the percentage of young forest combining felled and unplanted, recently restocked and pre-thicket growth stages aged 0-10 years) in each culling year. The percentage of calcareous soil was calculated for the forest and grassland area, excluding arable that provides high-quality food (in this region comprising wheat, barley, oilseed rape, potatoes and maize) irrespective of underlying soil class. See Appendix D for details of soil classification and data. Variables were extracted from GIS layers using R statistical software (R core Team 2018) and the packages "sp" (Pebesma & Bivand 2005), "rgeos" and "rgdal" (Roger *et al.* 2017).

Extracting environmental data at scales relevant to roe deer home range

Separately, I sought to relate individual body mass and fecundity, to habitat quality in the area readily available to that individual. Adult roe deer have been shown to be sedentary within a defined home-range (Linnell & Andersen 1998), particularly in autumn and winter (e.g. (Bideau *et al.* 1993)). As deer were managed by stalking rather than drive hunting, I assumed each individual was shot somewhere within its home-range. Given uncertainty in home-range extent (and in the absence of telemetry data for culled individuals), rather than assuming a single *a priori* home-range size I ran a series of models that related fecundity and body mass to habitat variables extracted from biologically-plausible buffer radii around the individual's cull location. Based on the monthly home-range extent reported in a previous study in Thetford Forest (Chapman *et al.* 1993) and other western European study sites with similar temperate climate (northern Italy, France and Germany, see Morellet *et al.* 2013), my buffer radii ranged from 400m to 600m (59ha to 113ha) with 50m increments. Models at different radii were subsequently weighted by their predictive ability (see below).

Analyses

Body mass was analysed by Generalised Linear Mixed Models (GLMMs) with random intercept and normal error distribution. Body mass models incorporated random effects of forest sub-region, to account for reduced spatial independence of individuals culled from nearby areas and variation between subregions in roe density, human recreational density and other factors. However subregions were larger than finer-grained variation in local density or recreation so only partly account for these effects. Models also incorporated random effects of cull year (to control for severity of the winter in which the individual was culled, plus any potential lagged weather-related effects of variation in forage availability from the previous growing season) and calendar week (as a continuous variable to control for seasonal body mass fluctuations).

Adult fecundity examined whether the female carried twins (two embryos), versus zero or one embryos (combined as the reference level), given the high frequency of twins (63%) and low frequency of non-pregnant females (8.5%), in GLMMs with binomial error. Fecundity of yearlings (that were born two summers before the winter in which culled, aged 20-22 months at culling, and approximately 15 months when first impregnated), was analysed by ordinal logistic models, as 20% were non-pregnant, 54% carried one embryo and 26% carried twins, using R package "ordinal". Fecundity was modelled incorporating landscape and environmental variables and the individual's body mass, to interpret direct environmental effects from indirect effects acting via body mass. All fecundity models included a fixed effect of calendar week to account for embryo detectability (coded as a categorical dummy variable, adults: 0=weeks 1-3, 1=weeks 4-12; yearlings: 0=weeks 1-2, 1=weeks 3-12; see Appendix C) and random effects of forest sub-region and cull year.

Model selection and parameter estimation were performed using Multi-Model Inference (MMI) in an information theoretic framework (Burnham & Anderson 2002) using 'MuMIn' package in R (Bartoń 2018). For each incremental buffer radius I built candidate models comprising all possible variable combinations, I then examined the relative performance of the full complement of candidate models across the range of radii, with parameters averaged across the 95% model confidence set, weighting models by their Akaike weight. Environmental variables were considered supported if included in the 95% model confidence set and their model-averaged parameter CI did not span zero. Explanatory power was assessed as the R^2 of models comprising supported variables only at the Akaike-weighted mean buffer radius.

Correlation between explanatory variables was lower (maximum r from pairwise comparisons between all explanatory variables: 0.27) than the threshold (r>0.78) of confounding intercorrelation (Freckleton 2002). Spatial autocorrelation of residuals of reduced models incorporating supported variables only was examined using Moran's I

(Package “spdep”, (Bivand 2017)), defining neighbour objects as the GPS points occurring inside the Akaike-weighted mean buffer radii and assigning spatial weights to the neighbouring GPS points using row standardization (see Bivand, Pebesma & Gómez-Rubio 2013). Consequences of environmental variables for fecundity were examined from model-averaging with variables extracted at the Akaike-weighted mean buffer radius, first by solely considering the direct effect of environment on fecundity (not including body mass in the model), second by holding body mass at the forest-wide mean, and third also accounting for the indirect effect of environment on fecundity as mediated by body mass (with body mass resampled from the body mass - environment model, according to model mean and standard error, and incorporated in the fecundity – environment model, to predict the overall distribution of fecundity with environment).

Last, I examined the degree to which variation in habitat and landscape context caused fecundity to vary between the 14 forest sub-regions. The spatial distribution of adult and yearling body mass was predicted for each cell of a raster of 100m resolution across the study area, using a reduced model including supported variables only, extracted from the Akaike-weighted mean buffer radius built around the centroid of each 100m x 100m raster cell and then averaged across cells in each forest sub-region. Mean fecundity of each forest sub-region and the variance between them was then predicted from the raster of predicted body mass, together with supported environment and landscape variables.

All analyses were performed in R 3.2.5 (R core Team 2018).

Results

Body mass

Mean body mass of adults was 13.7 kg (SD=1.65) and of yearlings 12.1 kg (SD=1.71), with little variation observed between forest sub-regions (CV_{adults}=0.05 $CV_{yearlings}$=0.06, S7). Only a small subset of models comprised the 95% confidence set (13% of all candidate models). The Akaike-weighted mean buffer radii across the 95% confidence set of adult body mass models was 578m (SD=27m). Adult female roe deer were heavier when culled in localities comprising a greater percentage of arable lands (Fig 2, Fig 3).

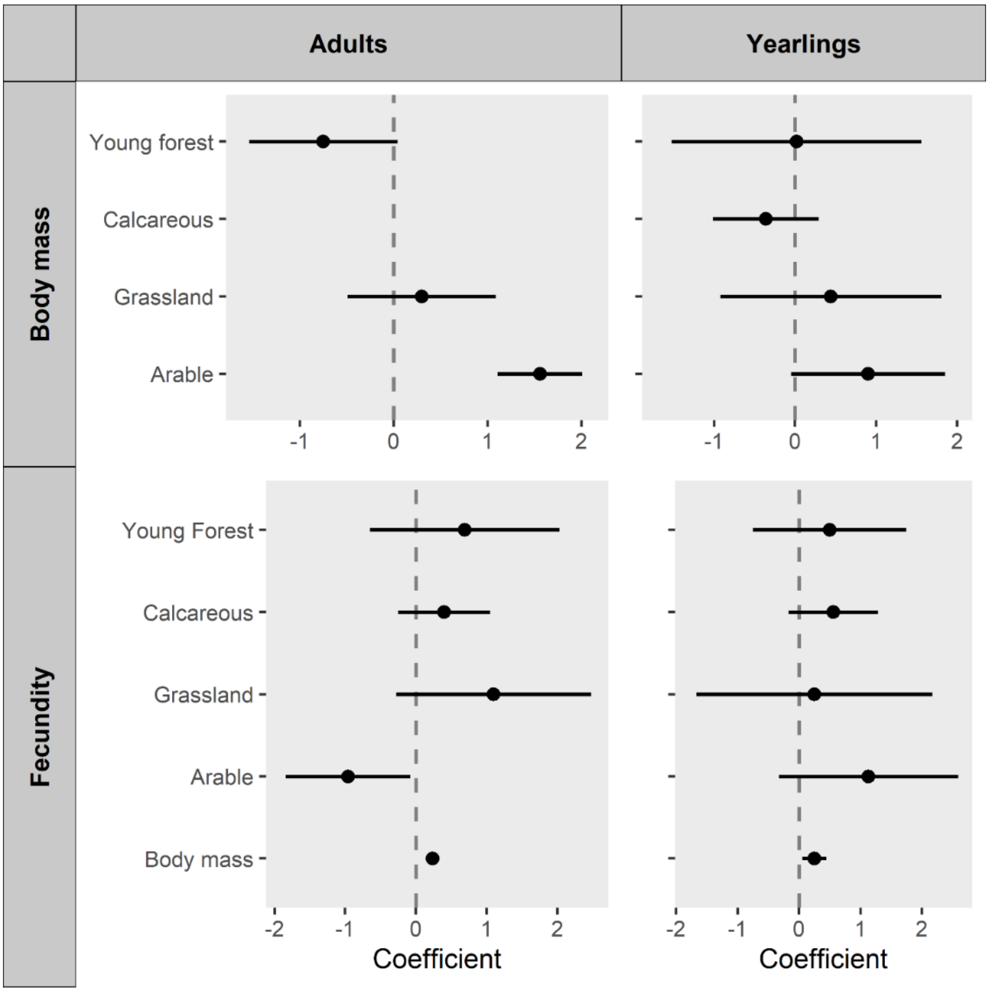


Figure 4.2: Models relating adult and yearling roe deer body mass and fecundity to landscape and environment. Coefficients of environmental variables, model-averaged across buffer radii (filled symbol) and their 95% Confidence Interval (CI, bars), are presented. All models controlled for random effects of calendar week (as a continuous variable in body mass models, as a dummy categorical variable in fecundity models), forest sub-region and culling year.

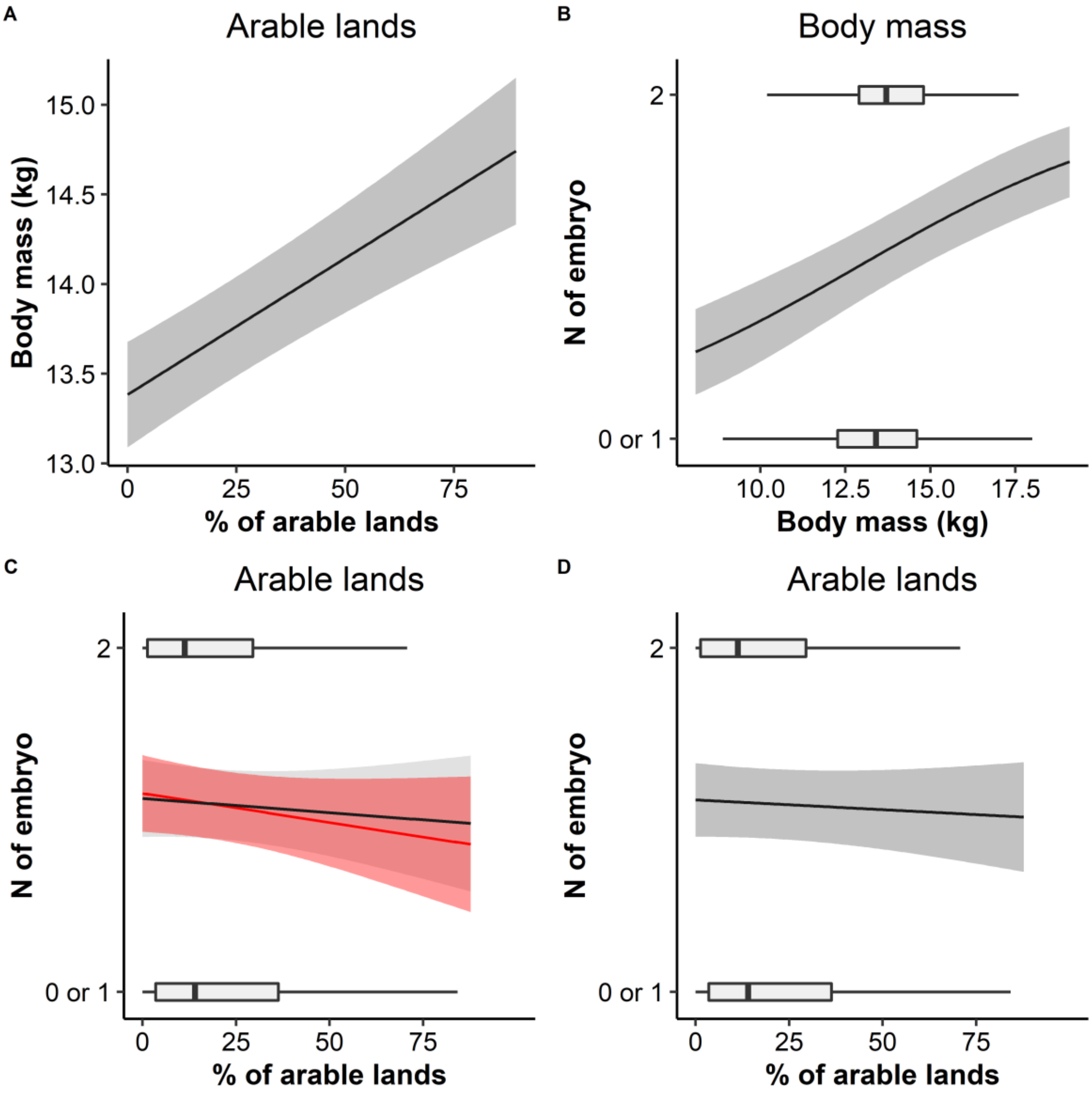


Figure 4.3: Predicted adult roe deer body mass and fecundity in relation to percentage of arable lands. (A) Body mass is predicted from model-averaging the body mass-environment model, with variables measured at the Akaike-weighted mean buffer radius, controlling for random effect of calendar week, cull year and forest sub-region. Fecundity is predicted from model-averaging the fecundity-environment model, with variables measured at the Akaike-weighted mean buffer radius, incorporating calendar week (to account for embryo detectability) and random effects of cull year and forest sub-region. (B) shows the relation of fecundity to body mass, holding other variables at their mean; (C) shows the relation of fecundity to % arable, predicted when holding body mass at the forest-wide mean (red line) and accounting for greater body mass of adults with more arable (with body mass resampled according to arable extent, from the body mass – environment model) (black line); (D) shows

the direct relation of fecundity to % arable predicted from a model including % of arable lands only.

Adult body mass model had a conditional R^2 (weighted-average by Akaike weights across radii) of 0.13 and marginal R^2 of 0.03. No residual spatial autocorrelation was found in my models.

In contrast to adults, no effect of any of my environmental variables was supported for yearlings' body mass (Fig 2). The subset of candidate models comprising the 95% confidence set was 80% of all candidate yearlings body mass models. The Akaike-weighted mean buffer radii, across the 95% confidence set, was 500m (SD=76m).

Fecundity

Mean fecundity calculated from models controlling for calendar week was 1.6 (SD=0.5) embryos per adult female (mean fecundity at maximum embryo detectability weeks 4-12=1.55) and 0.9 (SD=0.7) embryos per yearling female (mean fecundity at maximum embryo detectability, week 3-12=1.0).

The subset of candidate models comprising the 95% confidence set was 38% of all candidate adult fecundity models. The Akaike-weighted mean buffer radii, across the 95% confidence set, was 500m (SD=72m). Adults were more fecund when heavier (Fig 2, Fig 3B). The response of adult fecundity to the farmland boundary was complex and counter-intuitive. Model-averaging showed fecundity was reduced by a greater percentage of arable lands (fixed additive effect Fig 2 and Fig 3C) and holding body mass at the forest-wide mean, adults were less fecund close to the arable boundary (Fig 3C, red line). However, fecundity was more strongly affected by body mass than arable lands (Fig 2) and body mass was greater at the arable boundary (Fig 3A). Accounting for both the direct effect of arable on fecundity, and indirect effect mediated by the relation of body mass to arable, overall fecundity of adult females close to farmland was similar to or lower than that of females in the forest interior (Fig 3C black line). No support was found for an effect of grassland, young forest or calcareous soils on adult fecundity. Adult fecundity models had a mean conditional R^2 (weighted-average by Akaike weights across radii) of 0.17 and marginal R^2 of 0.07.

The subset of candidate models comprising the 95% confidence set was 64% of all candidate yearling fecundity models. The Akaike-weighted mean buffer radii, across the 95% confidence set, was 500m (SD=102m). Yearlings also were more fertile when heavier (Fig 2, Fig 4), but no effect of any environmental variable was supported (Fig 2).

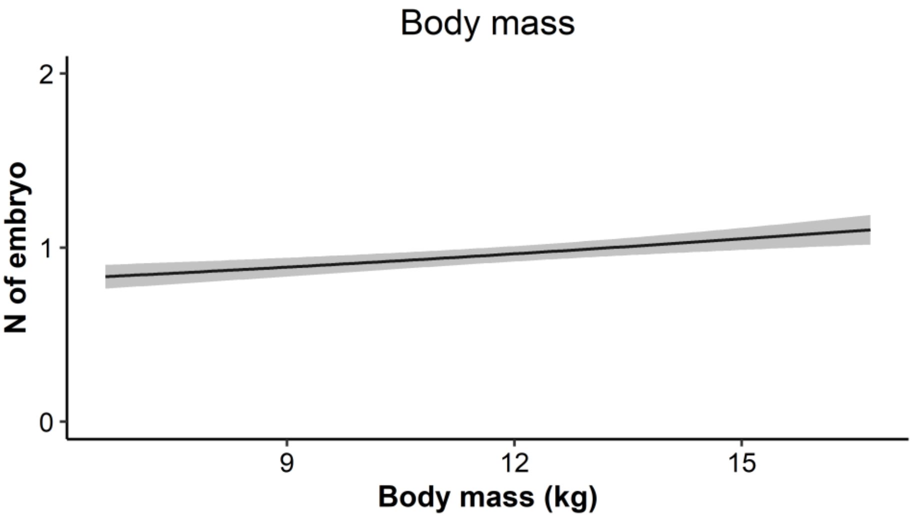


Figure 4.4: Predicted yearling fecundity in relation to body mass. Fecundity predicted from the averaged-model incorporating body mass and calendar week to account for embryo detectability, and random effects of cull year and forest sub-region.

Average adult fecundity calculated from predictions (including predicted spatial distribution of body mass) was 1.5 (SD=0.1) embryos, similar to the raw means. Mean predicted fecundity per sub-region ranged from 1.5 to 1.6 for adults, with low variance between sub-regions (CV_{Adults}=0.03; Appendix E).

Discussion

This study utilised a large sample of individuals collected across an extensive landscape mosaic over 14 years. Only arable lands contributed to observed variation in fecundity and body mass, but with both expected and counter-intuitive effects.

Roe is a medium-sized deer with a 'concentrate-selector' feeding strategy (Gordon & Illius 1994), depending on relatively high quality foods (Duncan *et al.* 1998; Freschi *et al.* 2017); their weight is expected to increase with better habitat quality. Adult roe deer were slightly heavier (inter-quartile, effect size=+0.5kg) when culled in areas with a greater percentage of arable lands. Consistent with my findings, a previous study (Hewison *et al.* 2009) showed that roe deer in fragmented woodlands in an arable landscape were heavier and fecal samples in these areas had higher levels of nitrogen and phosphorous compared to roe in a forest environment, implicating higher nutritional content of arable forage as contributing to weight. Contrary to my predictions, no effects of calcareous soil, grasslands or young forest was found on roe body mass. This is possibly due to the average body mass being high already so food limitation may be negligible.

Adult female roe deer culled in localities buffered by a greater percentage of arable lands were heavier, conferring reproductive advantage. However, this was offset by a negative effect of arable area on fecundity (inter-quartile effect size of arable: -7% probability of having two embryos, instead of one or zero), so that fecundity of adult females at the farmland boundary was similar to or less than those in the forest interior, even accounting for the positive indirect effect of arable on fecundity mediated by body mass. Fecundity data were collected during late winter, when shortage of food determines fecundity. Roe deer graze on arable lands particularly during winter (Putman 1986) when young crops or weedy stubbles are widespread; so the lower than expected fecundity of individuals with greater access to arable was counter-intuitive, and contradicted the 'fragmentation nutrition hypothesis' (Sinclair 1997), that proposes fragmented woodlands in a matrix of nutritious farmland favour deer population growth. Within the forest, muntjac and roe deer densities are greater closer (<350 m) to arable lands (Zini et al unpublished data). It is possible that fecundity, and apparent habitat 'suitability', may be reduced by intra and inter-specific agonistic interference and stress (Dolman & Wäber 2008) close to the forest-arable margin. Fecundity wasn't related to the percentage of young forest, grasslands or calcareous soil.

Yearling body mass and fecundity were not related to any environmental variables tested. Yearling performance is likely to be influenced by their natal (i.e. their mother's) home range, where most growth takes place within the first year (Andersen *et al.* 1998). However depending on body condition, some individual are philopatric while approximately a third undertake natal dispersal away from the maternal home-range at 10-12 months of age (Debeffe *et al.* 2012), making it more difficult to detect a relationship between the newly established home range (where they were culled at 20-23 months of age) and their performance. In contrast adults are more likely to be occupying an established home range when culled.

In this study, heavier adult females were slightly more fertile (inter-quartile effect size of weight: +12% probability of having two embryos, instead of one or zero), as widely documented by previous studies (Hewison & Gaillard 2001; Flajšman, Jerina & Pokorny 2017). Interestingly, for adult fecundity the effect of body mass was greater, but with the same order of magnitude to that of arable lands, while the effect of body mass on yearling fecundity was twice (+23% probability of having one additional embryo) that found for adults. In roe deer, body mass plays a predominant role in determining potential litter size at the conception stage (Flajšman, Jerina & Pokorny 2017), determining the maximum reproductive output for a given body size; therefore having a greater influence on yearlings that – in contrast to adults – haven't yet reached their maximum body size (Andersen *et al.* 1998).

Although ecologically interesting, the small overall effect size of landscape context (proximity to arable lands) resulted in little variation in predicted (or observed) fecundity among forest sub-regions, while none of the other factors considered in this study affected roe deer performance. This study suggests it will be sufficient to base estimates of population fecundity on forest-wide measures.

References

Aitken, R.J. (1975) Cementum layers and tooth wear as criteria for ageing roe deer (Capreolus capreolus). *Journal of Zoology*, **175**, 15–28.

Albon, S.D., Mitchell, B. & Staines, B.W. (1983) Fertility and body weight in female red deer: a density-dependent relationship. *Journal of Animal Ecology*, **52**, 969–980.

Andersen, R., Gaillard, J.-M., Liberg, O. & Jose´, C.S. (1998) Variation in life-history parameters. *The European Roe Deer: The Biology of Success*, pp. 285–307. Scandinavian University Press, Oslo.

Andersen, R. & Linnell, J.D.C. (2000) Irruptive potential in roe deer: density-dependent effects on body mass and fertility. *The Journal of Wildlife Management*, **64**, 698.

Bartoń, K. (2018) MuMIn: Multi-Model Inference. R package version 1.42.1.

Bideau, E., Gerard, J.F., Vincent, J.P. & Maublanc, M.L. (1993) Effects of age and sex on space occupation by European roe deer. *Journal of Mammalogy*, **74**, 745–751.

Bivand, R. (2017) Package ‘ spdep ’.

Bivand, R., Pebesma, E. & Gómez-Rubio, V. (2013) Spatial neighbours and spatial weights. *Applied Spatial Data Analysis With R*, 2nd ed, pp. 266–274. Springer, New York.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multi-Model Inference. A Practical Information—Theoretic Approach*, 2nd ed (ed Springer Verlag). New York.

Chapman, N.G., Claydon, K., Claydon, M., Forde, P.G. & Harris, S. (1993) Sympatric populations of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*): a comparative analysis of their ranging behaviour, social organization and activity. *Journal of Zoology*, **229**, 623–640.

Clutton-Brock, T.H. & Albon, S.D. (1989) *Red Deer In The Highlands*. Blackwell scientific publications, Oxford.

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.

Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Bon, R., Gaillard, J.-M. & Mark Hewison, A.J. (2012) Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. *Journal of Animal Ecology*, **81**, 1327–1327.

Dolman, P.M. & Wäber, K. (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research*, **35**, 202.

Duncan, P., Tixier, H., Hofman, R. & Lechner-Doll, M. (1998) Feeding strategies and the physiology of digestion in roe deer. *The European Roe Deer: The Biology Of Success*, pp. 91–116. Scandinavian University Press, Oslo.

Eycott, A.E., Watkinson, A.R. & Dolman, P.M. (2006) Ecological patterns of plant diversity in a plantation forest managed by clearfelling. *Journal of Applied Ecology*, **43**, 1160–1171.

Flajšman, K., Jerina, K. & Pokorny, B. (2017) Age-related effects of body mass on fertility and litter size in roe deer. *PLOS ONE*, **12**, e0175579.

Focardi, S., Pelliccioni, E., Petrucco, R. & Toso, S. (2002) Spatial patterns and density dependence in the dynamics of a roe deer (*Capreolus capreolus*) population in central Italy. *Oecologia*, **130**, 411–419.

Freckleton, R.P. (2002) On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *Journal of Animal Ecology*, **71**, 542–545.

Freschi, P., Fascetti, S., Riga, F., Cosentino, C., Rizzardini, G. & Musto, M. (2017) Diet composition of the Italian roe deer (*Capreolus capreolus italicus*) (Mammalia: Cervidae) from two protected areas. *The European Zoological Journal*, **84**, 34–42.

Fuller, R.J. & Gill, R.M.A. (2001) Ecological impacts of increasing numbers of deer in British woodland. *Forestry*, **74**, 193–199.

Gill, R.M.A., Johnson, A.L., Francis, A., Hiscocks, K. & Peace, A.J. (1996) Changes in roe deer

(*Capreolus capreolus L.*) population density in response to forest habitat succession. *Forest Ecology and Management*, **88**, 31–41.

Gordon, I.J. & Illius, A.W. (1994) The functional significance of the browser-grazer dichotomy in African ruminants. *Oecologia*, **98**, 167–175.

Hemami, M.R., Watkinson, A.R. & Dolman, P.M. (2004) Habitat selection by sympatric muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a lowland commercial pine forest. *Forest Ecology and Management*, **194**, 49–60.

Hemami, M.R., Watkinson, A.R. & Dolman, P.M. (2005) Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* in a lowland pine forest. *Forest Ecology and Management*, **215**, 224–238.

Hewison, A.J.M. (1996) Variation in the fecundity of roe deer in Britain: effects of age and body weight. *Acta Theriologica*, **41**, 187–198.

Hewison, A.J.M. & Gaillard, J.M. (2001) Phenotypic quality and senescence affect different components of reproductive output in roe deer. *Journal of Animal Ecology*, **70**, 600–608.

Hewison, A.J.M., Morellet, N., Verheyden, H., Daufresne, T., Angibault, J.-M., Cargnelutti, B., Merlet, J., Picot, D., Rames, J.-L., Joachim, J., Lourtet, B., Serrano, E., Bideau, E. & Cebe, N. (2009) Landscape fragmentation influences winter body mass of roe deer. *Ecography*, **32**, 1062–1070.

Hewison, A., Vincent, J.P., Angibault, J.M., Delorme, D., Laere, G. Van & Gaillard, J.M. (1999) Tests of estimation of age from tooth wear on roe deer of known age: variation within and among populations. *Canadian Journal of Zoology*, **77**, 58–67.

Kilpatrick, H.J., Labonte, A.M. & Stafford, K.C. (2014) The relationship between deer density, tick abundance, and human cases of Lyme disease in a residential community. *Journal of Medical Entomology*, **51**, 777–784.

Kramer, K., Groot Bruinderink, G.W.T.A. & Prins, H.H.T. (2006) Spatial interactions between ungulate herbivory and forest management. *Forest Ecology and Management*, **226**, 238–247.

Langbein, J., Putman, R.J. & Pokorny, B. (2011) Traffic collisions involving deer and other ungulates in Europe and available measures for mitigation. *Ungulate Management in Europe* (eds R. Putman, M. Apollonio, & R. Andersen), pp. 215–259. Cambridge University Press, Cambridge.

Linnell, J.D.C. & Andersen, R. (1998) Territorial fidelity and tenure in roe deer bucks. *Acta Theriologica*, **43**, 67–75.

McLoughlin, P.D., Gaillard, J., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Van Moorter, B., Said, S. & Klein, F. (2007) Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, **88**, 3192–3201.

Miyashita, T., Suzuki, M., Ando, D., Fujita, G., Ochiai, K. & Asada, M. (2008) Forest edge creates small-scale variation in reproductive rate of sika deer. *Population Ecology*, **50**, 111–120.

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J.D.C., Nicoloso, S., Sustr, P., Urbano, F. & Mysterud, A. (2013) Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, **82**, 1326–1339.

Morton, R.D., Rowland, C.S., Wood, C.M., Meek, L., Marston, C.G. & Smith, G.M. (2014) Land Cover Map 2007 (25m raster, GB) v1.2. *NERC Environmental Information Data Centre*.

Nilsen, E.B., Linnell, J.D.C. & Andersen, R. (2004) Individual access to preferred habitat affects fitness components in female roe deer *Capreolus capreolus*. *Journal of Animal Ecology*, **73**, 44–50.

Pebesma, E.J. & Bivand, R.S. (2005) Classes and methods for spatial data in R. *R News 5*, **2**, 9–13.

Putman, R.J. (1986) Foraging by roe deer in agricultural areas and impact on arable crops. *The Journal of Applied Ecology*, **23**, 91.

R core Team. (2018) R: A Language and Environment for Statistical Computing.

Roger, A., Rowlingson, B., Sumner, M., Hijmans, R. & Rouault, E. (2017) Package ‘ rgdal ’.

Saïd, S. & Servanty, S. (2005) The influence of landscape structure on female roe deer home-range size. *Landscape Ecology*, **20**, 1003–1012.

Sempere, A.J., Mauget, R. & Mauget, C. (1998) Reproductive physiology of roe deer. *The European Roe Deer: The Biology of Success*, pp. 161–188. Scandinavian University Press, Oslo.

Sinclair, A.R.E. (1997) Carrying capacity and the overabundance of deer. *The Science of Overabundance: Deer Ecology and Population Management*, pp. 380–394. Smithsonian Institution, Washington.

Tufto, J., Andersen, R. & Linnell, J. (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *The Journal of Animal Ecology*, **65**, 715.

Wäber, K. & Dolman, P.M. (2015) Deer abundance estimation at landscape-scales in heterogeneous forests. *Basic and Applied Ecology*, **16**, 610–620.

Wäber, K., Spencer, J. & Dolman, P.M. (2013) Achieving landscape-scale deer management for biodiversity conservation: the need to consider sources and sinks. *Journal of Wildlife Management*, **77**, 726–736.

Ward, A.I. (2005) Expanding ranges of wild and feral deer in Great Britain. *Mammal Review*, **35**, 165–173.

Appendices

Appendix A. Study landscape.

Thetford Forest is a pine-dominated plantation landscape; during the study period it comprised Corsican, *Pinus nigra* (55% of the landscape), and Scots *Pinus sylvatica* (17%) pines, *Larix* spp., open habitats including clearfelled areas (18%) and some mature deciduous plantings (particularly *Fagus sylvatica*, *Acer pseudoplatanus* and *Betula* spp.) (together 10%). Most of the forest (62% of planted crops) was in the second crop rotation.

For spatial analysis, the twelve forest 'blocks' recognised as management units by the Forestry Commission (that differed greatly in size and included heterogeneous blocks) were further divided into 14 'subregions' (mean area= 13.2 km^2, SD= 5.6), that differed in landuse character, particularly the representation of soil types and configuration. These subregions were included as *a priori* random effects in roe deer fecundity and body mass models in order to account for unmeasured variance between locations. A number of conifer-dominated subregions on primarily acidic soils (podsols and gravelly sands) formed an extensive contiguous core, while smaller outlying subregions on more diverse soils (including sandy calcareous rendzinas or limited areas of wetter gleys or peats) had greater perimeter (defined as subregion boundary adjoining arable or grasslands) to area ratio and greater tree crop diversity. Extent of calcareous soil, subregion area, perimeter, and perimeter-area ratio metrics of these 14 subregions were independent, while having some replication of multiple subregions within each class (Table A4.1). Unsupervised cluster analysis (hierarchical clustering and average agglomeration method in R (R core Team 2018) using "stats" package) of perimeter-area ratio and percentage of calcareous soil resolved one group comprising four larger subregions (Kings, Mundford, Elveden and High Lodge), two of which are more calcareous while the other two are more acidic); and three groups of smaller subregions; of which two had greater perimeter-area ratio (one more calcareous group: Harling, Swaffham, Didlington and Hockwold; one more acidic group: Croxton, Mildenhall, Hockham) and one comprised subregions with moderate or low perimeter-area ratio (Santon Downham, West Tofts, Lynford) (Fig. 4.1). These groupings of subregions confirm independent replicates (located in different parts of the forested landscape) for each combination of variables.

Table A4.1: Thetford forest's subregions. Subregions of Thetford Forest, showing area, perimeter, perimeter area ratio and percentage of calcareous soil. Shading indicates deviation of the subregion-specific measure from the mean value (as % of the mean: 0-25%, 26-50%, 51-75%, 76-100%, >100%), red positive (> mean) green negative (< mean), lighter shades indicated smaller deviation while darker indicated larger deviation.

Cluster ID	Subregion number	Subregion name	Area (km^2)	Perimeter (km)	Perimeter-Area ratio	% calcareous soil
1	5	Lynford	11.8	6.1	0.5	30.4
	6	West Tofts	8.9	13.8	1.5	29.7
	10	Santon Downham	11.9	1.2	0.1	34.8
2	11	High Lodge	22.7	8.4	0.3	24.8
	12	Elveden	16.5	6.0	0.3	18.9
	13	Kings	23.3	26.0	1.1	42.5
	4	Mundford	21.2	32.1	1.5	45.7
3	7	Croxton	10.2	26.2	2.7	19.9
	8	Hockham	8.3	28.7	3.4	4.5
	14	Mildenhall	5.9	15.7	2.6	15.9
4	1	Swaffham	13.3	50.9	3.8	42.8
	2	Didlington	9.1	42.0	4.5	43.3
	3	Hockwold	12.1	34.7	2.8	64.7
	9	Harling	11.4	35.1	3.0	45.8
		Mean	13.3	23.3	2.0	33.1

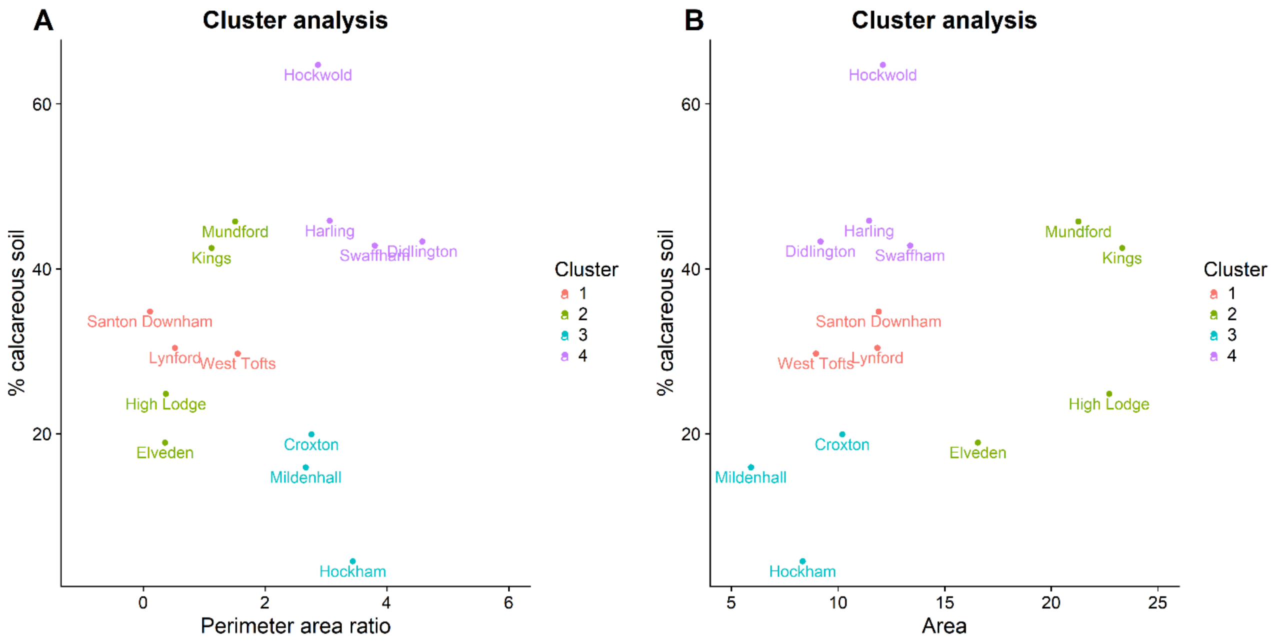


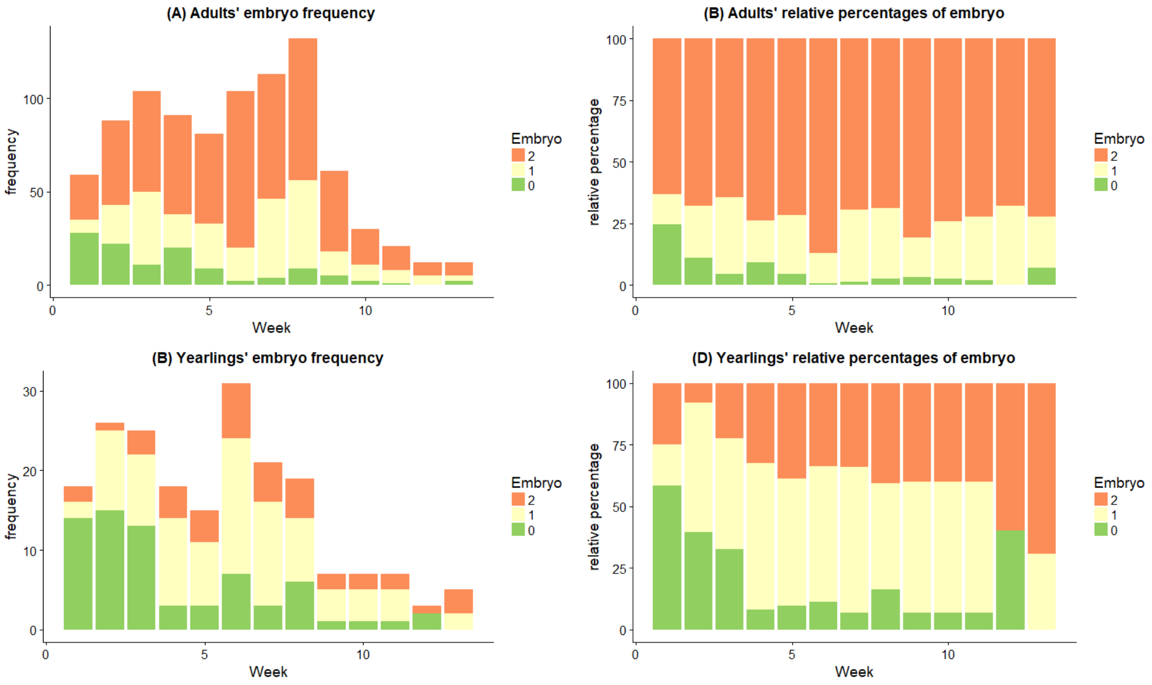
Fig A4.1: Cluster analysis. Cluster analysis, using hierarchical clustering and average agglomeration, of Thetford Forest subregions. The same colour was applied to forest subregions belonging to the same cluster.

Appendix B. Validation of the larder dataset

Carcass damage was recorded in the Forestry Commission data for 5.4 % of adults and 5.5 % of yearlings. Carcass damage is reported, together with other additional information, in a “remark” text field. However, some culled animals were not recorded as damaged although their recorded body mass was implausibly low (relative to expert opinion); I consider this likely to represent occasional errors in data entry, which those responsible for data capture report is more likely to result from failure to record the damage code rather than error in entry of body mass. I therefore imposed a threshold of 6 kg for a minimum yearling’s carcass body mass and 8 kg for an adult; further excluding 1% of yearling and 2% of adult individuals not coded as damaged.

I excluded all data for animals culled by non-FC rangers active in one forest subregion (Mundford) as I considered those data were not recorded accurately while I retained the data collected from FC rangers from the same forest subregion.

Appendix C. Effect of date on detectability of embryos


(A) Adults' embryo frequency

(B) Adults' relative percentages of embryo

(B) Yearlings' embryo frequency

(D) Yearlings' relative percentages of embryo

Fig A4.2: Apparent yearling and adult roe deer fecundity in relation to calendar week, showing total frequency (per calender week) and relative percentage (as % of the total for that calender week) of uterine records with no, one or two embryos. Weeks span from 01 of January to the last week of March.

I explored univariate models relating number of embryos to calendar week, coded as: continuous; continuous square rooted; categorical with one factor for each week; or as dummy categorical variables coded either with: 0=week 1, 1=weeks 2-12; or 0=weeks 1-2, 1=weeks 3-12; or 0=week 1-3, 1=week 4-12. The most parsimonious model was determined by comparing goodness of fit (model AIC) and model complexity (degrees of freedom). For adults the best-fitting model used 0=weeks 1-3, 1=weeks 4-12; for yearlings the best-fitting models used 0=weeks 1-2, 1=weeks 3-12.

Table A4.2: Model selection of week coding for adults and yearlings fecundity. For each model the difference in AIC value relative to the best supported model (ΔAIC) and the degrees of freedom (df) are shown.

Adults			
Variable	**Variabledf**	**ΔAIC**	**df**
Week dummy (0=weeks 1-3, 1=weeks 4-12)	1	0	906
Week dummy (0=weeks 1-2, 1=weeks 3-12)	1	4.3	906
Week square rooted	1	4.9	906
Week continuous	1	5.8	906
Week dummy (0=week 1, 1=weeks 2-12)	1	6.5	906
Week categorical	12	-1.6	895

Yearlings			
Variable	**Variable df**	**ΔAIC**	**df**
Week dummy (0=weeks 1-2, 1=weeks 3-12)	1	0	906
Week dummy (0=weeks 1-3, 1=weeks 4-12)	1	1.2	906
Week square rooted	1	3	906
Week continuous	1	4	906
Week dummy (0=week 1, 1=weeks 2-12)	1	6.2	906
Week categorical	12	8.4	895

Appendix D. Land cover and soil data

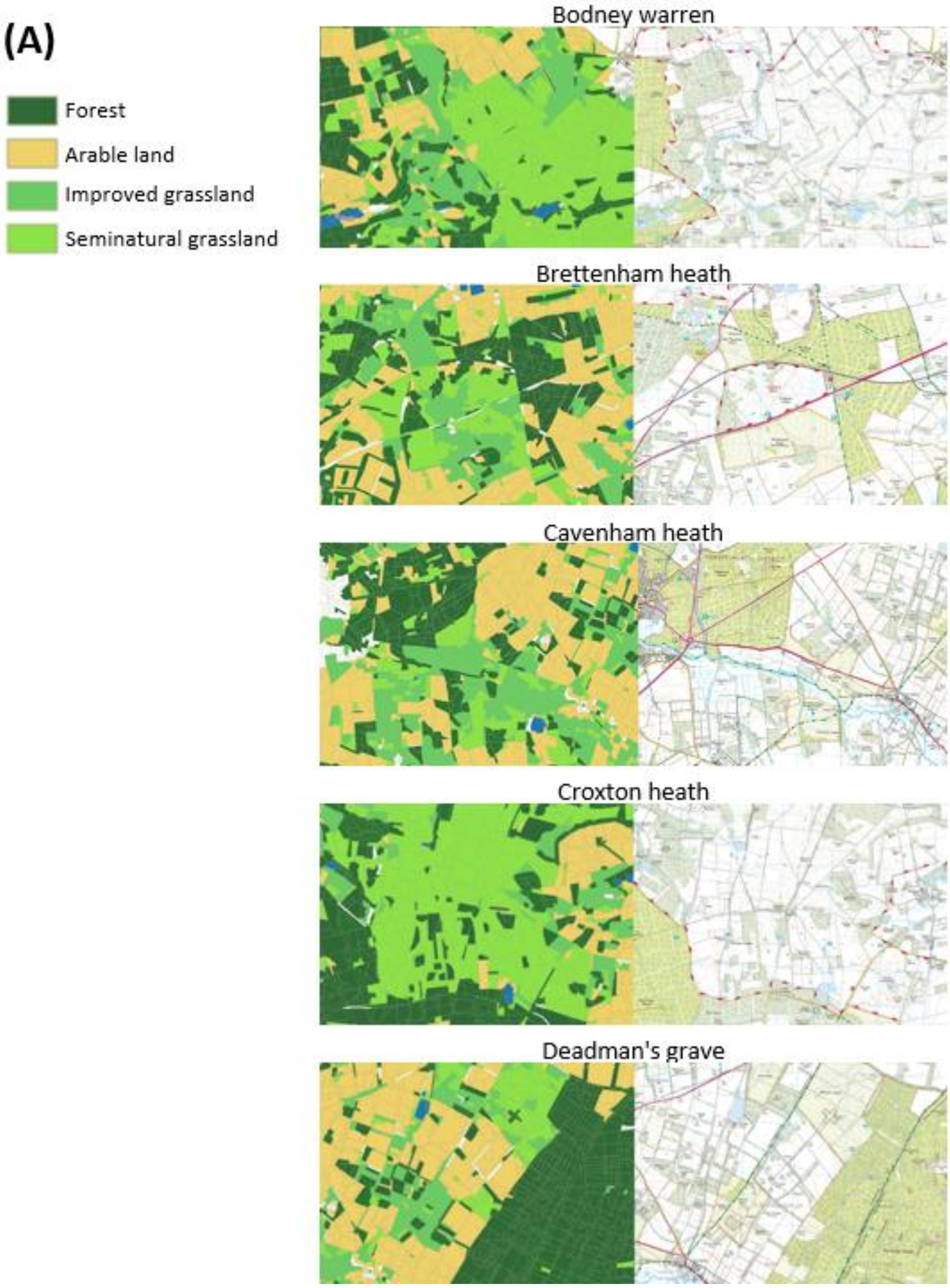
Surrounding landcover was obtained from the Land Cover Map 2007 (LCM 2007; Morton *et al.* 2014), that classifies 23 classes based on UK Biodiversity Action Plan (BAP) Broad Habitats (Jackson 2000) from composite summer-winter satellite images (pixel resolution 20-30 m), spatially referenced to the Ordnance Survey MasterMap digital topographic layer, with a minimum mapped resolution of 0.5 ha (smaller parcels, and linear features less than 20m, are dissolved into the surrounding landscape). Overall classification accuracy based on field validation is reported as 83% across all LCM 2007 classes, but is acknowledged to be poorer for some ecologically-similar land cover types (Morton *et al.* 2014). To explore reliability of CEH LCM 2007 data within the study area, areas were compared with a Google image cross-referenced by OS map data (Fig A4.3 A and B) for parts of the landscape well known to the researchers. This showed that improved grassland, different semi-natural grassland types, and mixed dwarf shrub and grassland, were not reliably separated, with frequent misclassification in LCM 2007 of seminatural grassland classes (either rough, neutral, or calcareous grassland, heather, and heather grassland) that were instead classified as improved grassland. Furthermore, within Breckland grass-heaths, calcareous grassland, acidophilous grassland and dwarf-shrub (heathland) assemblages can be intimately mixed over scales of a few meters (Dolman, Panter & Mossman 2012). Consequently, all CEH grassland types were merged and soil type was considered separately.

Two soil data layers were available and data were reconciled to a common classification. First, higher resolution (18 soil series, and their complexes, mapped to a minimum spatial resolution of 180 m) for the Thetford Forest were available from the Breckland forest soil map (Corbett 1973). Second, for the wider landscape, lower resolution data from Cranfield National Soil Map of England and Wales ((‘National Soil Map of England and Wales - NATMAP’), NATMAP) classify nine series mapped at 1:250,000 scale. These classifications were simplified to provide consistent classes of: acidic (including acidic complexes) and calcareous (including mixed calcareous/acid complexes) (Table A4.3, Fig.A4.4). They were validated by overlaying Breckland forest soil map and NATMAP data for those areas of Thetford Forest for which both were available (Fig. 4.4). Areas of wet soil types (gleys, peats) that comprised only a small proportion of the forest (5%) were excluded.

Soil was examined in terms of the proportionate extent of calcareous soil within the aggregate area of forest and grassland lying within each home-range buffer.

Table A4.3: Soil classification used in the study showing corresponding series and complexes from the Breckland Forest soil map and Cranfield NATMAP.

Aggregate classes	Breckland forest soil map	Cranfield NATMAP
Acidic soils	Acidic soils: bJ, bU, Fr, Ro, sN, Wk, Wt, Wt/Wt1, Wt/Wt2, Wt2; Acidic complexes: bJ/Fr, bJ/Fr/Ro, bU/Fr, bU/Fr/Ro, bU/Wt, r/Hh/Lx/rO, Fr/Ro, Fr/Ro/sN/Wt, Fr/Wt, Ro/Wt2, sN/Wt, sN/Wt1	0511g (Deep well drained sandy soils) 0554b (Deep well drained sandy soils in places very acid with subsurface pan)
Calcareous soils	Calcareous soils: Cr, Mo, Mw, Mw\Nf; Mixed complexes: cR/Fr, cR/Wt/Wt1 , Mo/Wt , Mw/Nf/Wt , Mw/Wt , Mw/Wt/Wt1 , Mw/Wt1 , Mw/Wt2 , Nf/Wt	0343f (Shallow well drained calcareous sandy and coarse loamy soils over chalk or chalk rubble) 0343g(Shallow well drained calcareous coarse loamy and sandy soils over chalk rubble) 0511e (Well drained calcareous coarse and fine loamy soils over chalk rubble) 0521(Well drained calcareous sandy soils)


(A)
Forest
Arable land
Improved grassland
Seminatural grassland
Bodney warren
Brettenham heath
Cavenham heath
Croxton heath
Deadman's grave

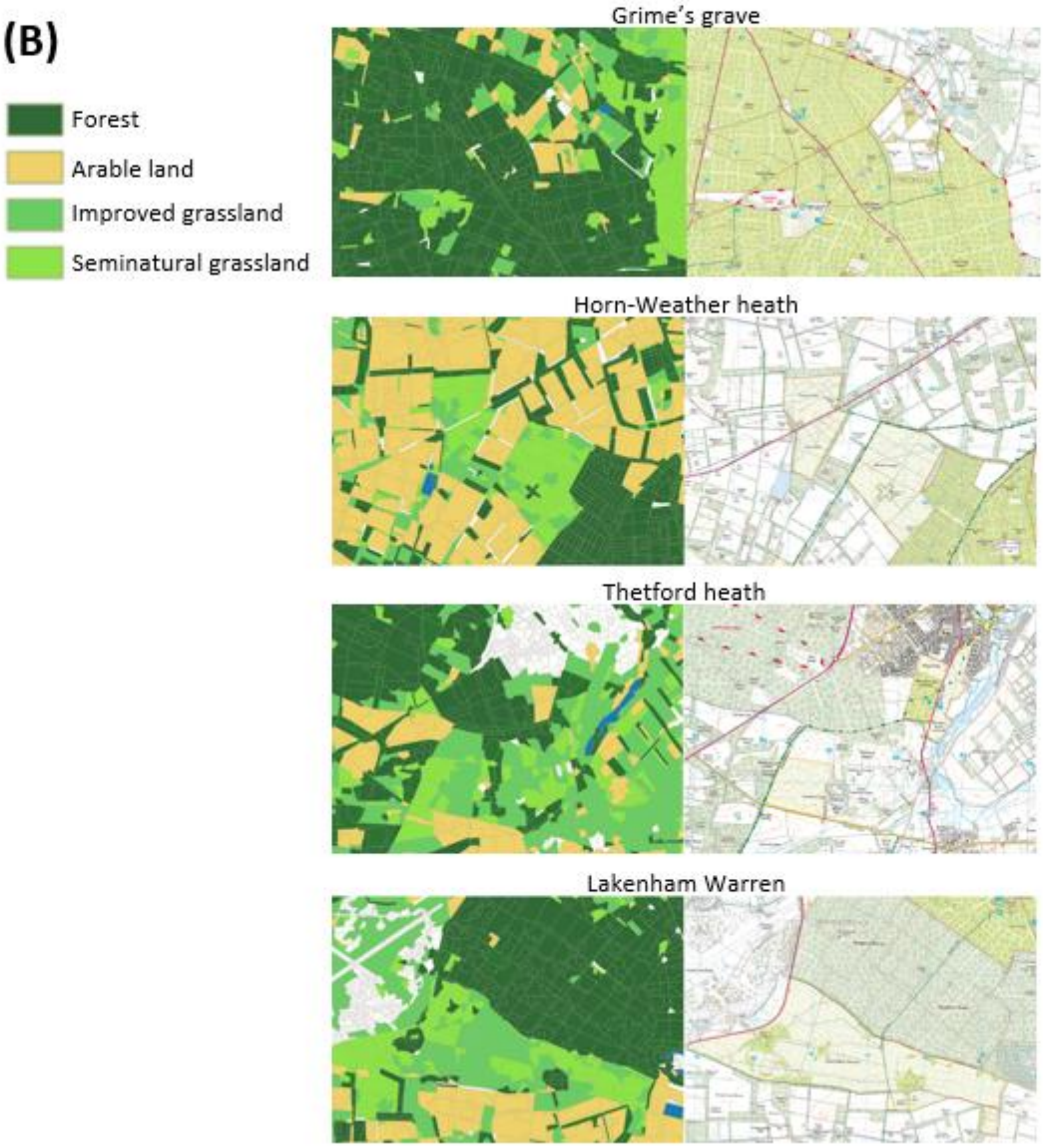


Fig A4.3 A and B: Grassland misclassification. Comparison of LCM 2007 land cover classification (left column) and Ordnance survey data (right column, contains OS data © *Crown copyright and database right* 2019) for a selection of areas surrounding Thetford forest.

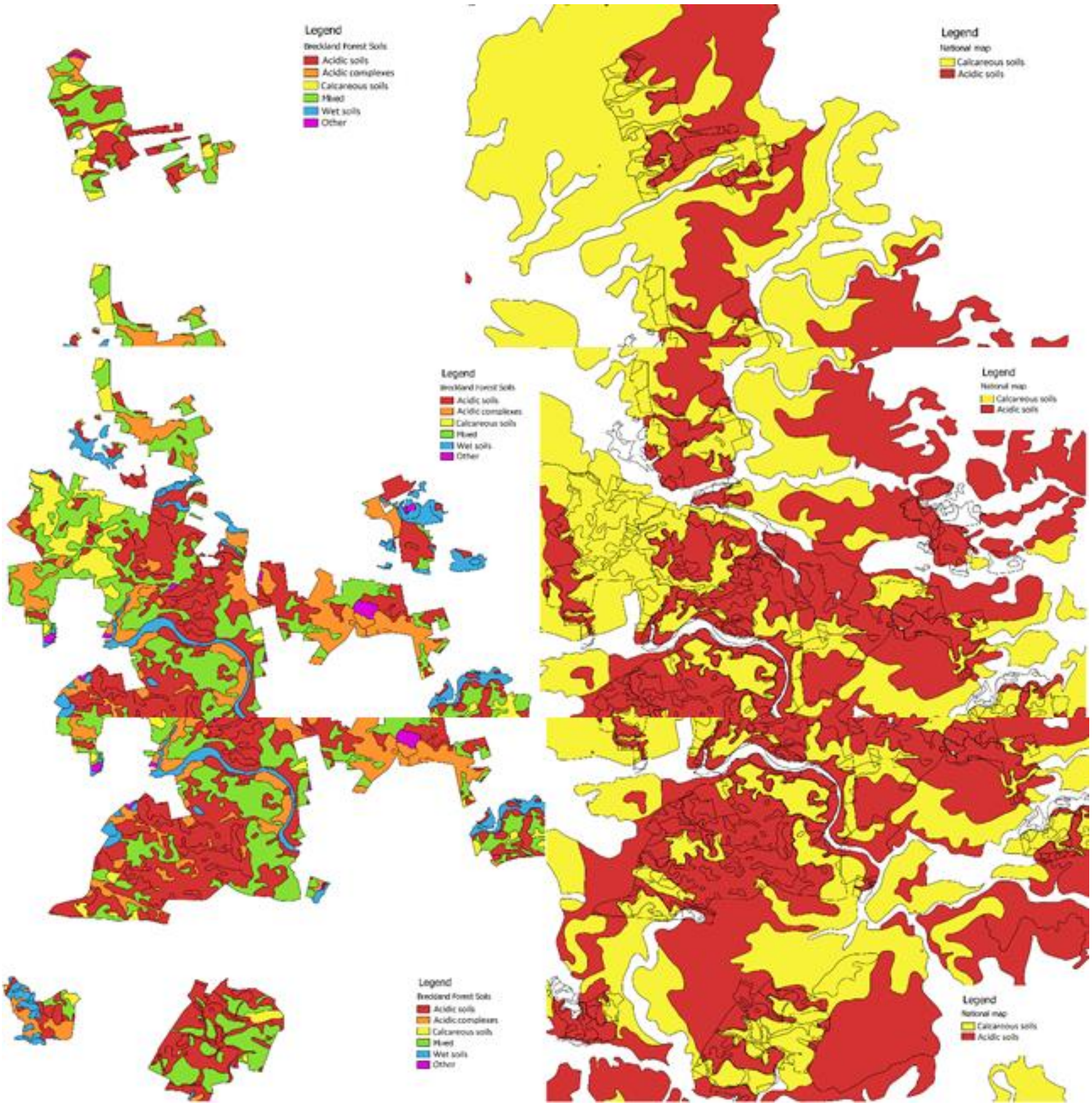


Fig A4.4: Soil map. Mapped examples, relating soil types classified from the Breckland forest soil map (left column) to those mapped by the Cranfield National soil map (right column), see Table A4.3 for definitions of soils and complexes.

References

Corbett, W.M. (1973) *Breckland Forest Soils Special Survey 7*. Harpenden, UK.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012) The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology*, **49**, 986–997.

Jackson, D.L. (2000) *Guidance on the Interpretation of the Biodiversity Broad Habitat Classification (Terrestrial and Freshwater Types): Definitions and the Relationship with Other Habitat Classifications (JNCC Report No. 307)*. Peterborough.

Morton, R.D., Rowland, C.S., Wood, C.M., Meek, L., Marston, C.G. & Smith, G.M. (2014) Land Cover Map 2007 (25m raster, GB) v1.2. *NERC Environmental Information Data Centre*.

National Soil Map of England and Wales - NATMAP. http://www.landis.org.uk/data/nmvector.cfm

R core Team. (2018) R: A Language and Environment for Statistical Computing.

Appendix E. Predicted fecundity per forest subregion

Table A4.4 Predicted fecundity per forest subregion. Predicted fecundity of adult roe deer calculated as an unweighted average across raster cells within each of 14 forest subregions from environmental fecundity models and coefficient of variation of forest subregion's predicted fecundity.

Forest subregion	**Adult fecundity (n˚embryo per female)**
Mundford	1.58
Elveden	1.52
Mundford West	1.61
Lynford	1.55
Croxton	1.51
Mildenhall	1.53
Harling	1.59
West Tofts	1.52
Didlington	1.54
Hockham	1.47
Kings	1.57
Santon Downham	1.60
Swaffham	1.52
High Lodge	1.51
CV	0.03

Chapter Five

Inter-specific competition and density-dependence in an ungulate assemblage modified by introduced species

Abstract

Inter-specific competition from introduced and naturally-colonising species is a potential threat to resident populations, but demographic consequences for vertebrates have rarely been tested. I tested hypotheses of inter-specific competition and intra-specific density-dependence for density, body mass and fertility of adult female roe deer *Capreolus capreolus* across a heterogeneous forest (195 km^2) landscape occupied by introduced Mediterranean fallow deer *Dama dama* and sub-tropical muntjac *Muntiacus reevesi*. Species-specific deer densities in buffers around culling locations of 492 adult female roe deer (sampled over seven years 2011-2017), were extracted from spatially-explicit Density Surface Models calibrated through extensive annual nocturnal thermal distance sampling. Roe fertility and body mass were related to local species-specific deer densities and local extent of arable (that provides nutritious food) using Structural Equation Models. Muntjac density (mean=15.1 individuals.km^{-2} SD=7.6) was lower at higher fallow deer densities (inter-quartile effect size, IQ =-2.4 individuals.km^{-2}), suggesting inter-specific avoidance or interference, but was greater when buffers included more arable (IQ=+1.01 individuals.km^{-2}). Roe deer body mass (13.7kg, SD=1.52) was marginally greater when buffers included more arable (IQ=0.32kg) and was independent of deer densities. However, roe deer fertility was unrelated to body mass, suggesting fertility benefits of condition exceeded an asymptotic threshold in this low-density population. Consistent with this, roe fertility was slightly greater (not reduced) in areas with greater local roe density (IQ=+0.9% probability of two instead of one or zero embryos), again indicating negligible density-dependence. In contrast, roe were less fertile in areas with greater muntjac densities (IQ=-14%), suggesting inter-specific competition exceeded density-dependence. I found no support for any effects of fallow deer density on roe density, body mass or fertility.

Complex networks of inter-specific competition operate in this deer assemblage. For muntjac, interspecific interference from fallow deer exceeded habitat effects. For native roe deer, inter-specific competition from introduced smaller sedentary muntjac reduced fertility, unlike density-dependence or potential competition with larger, more mobile, fallow deer. Mechanisms may include behavioural interference or stress; resource depletion is considered less likely as roe fertility was independent of body mass. Findings emphasise the importance of ensuring appropriate management strategies for controlling invasive species.

Introduction

A fundamental principle of species and community ecology is that species cannot stably coexist if the strength of inter-specific competition exceeds that of intra-specific competition (hereafter 'density-dependence', Armstrong & McGehee, 1980; Odum, 1971). Competitively subordinate species are predicted to experience niche-reduction, ecological displacement (Hardin 1960; Douglas, Marsh & Minckley 1994) or local extirpation if their fundamental niche lies within that of a co-occurring dominant species (Pulliam 2000). Inter-specific competition may arise from resource depletion (Dhondt 1977) or interference and agonistic behaviours (Ward & Sutherland 1997; Watts & Holekamp 2008). However, evidence of its effects remains elusive, as the signature is hard to detect in long-established assemblages, with coexisting species expected to have limited competition through resource partitioning (Hutchinson 1959); the 'ghost of competition past' (Connell 1980). Evidence of inter-specific competition is often indirect, inferred through density compensation (e.g. Peres & Dolman, 2000) or niche displacement (Herrmann, Stroud & Losos 2021), while demographic consequences are often unresolved (Latham 1999; Dolman & Wäber 2008). The need for greater understanding of the potential strength of inter-specific competition is amplified by concern at the potential disruption of species assemblages by arriving novel species that evolved in disjunct geographical regions (Mooney & Cleland 2001), with range shifts facilitated by global climatic change and introductions (Walther 2010; Bellard *et al.* 2012).

Despite frequent concern over the potential of naturally-colonising, introduced or invasive species to impact native species' populations (Mack *et al.* 2000; Davis 2009; Blackburn *et al.* 2011; Warren *et al.* 2016), evidence of inter-specific competition is incomplete in contrast to the well-demonstrated impacts of predation (Doherty *et al.* 2016), disease transmission (Rushton *et al.* 2006), and ecosystem modification (Hamann 1993; Reaser *et al.* 2007). Despite strong empirical evidence for inter-specific competition in invertebrates (see examples in Bengtsson, 1989; Human & Gordon, 1996; Schoener, 1983), for vertebrates few concrete examples quantify consequences of inter-specific competition for demographic parameters (Mishra *et al.* 2002; Belant *et al.* 2006; Richard *et al.* 2009). Competition resulting in habitat, resource (e.g. dietary), or spatial or temporal niche displacement, such as the dietary niche shift of the American mink *Mustela vison* coexisting with recovering native populations of the dominant Eurasian otter *Lutra lutra* (Bonesi, Chanin & Macdonald

2004), and shifts in temporal activity in foraging bats exposed to heterospecifics (Roeleke, Johannsen & Voigt 2018), can have consequences for individual condition, as in red deer *Cervus elaphus* (Richard *et al.* 2009). Understanding population consequences of such competition will be strengthened by quantifying demographic responses in relation to the relative densities of native and arriving species.

Ungulates are considered keystone species in many ecosystems, as they modify habitat structure and composition and ecosystem function (Jones, Lawton & Shachak 1994) with important effects on biodiversity (Crooks 2002; Wright & Jones 2004). Ungulate abundance has increased following predator removal across much of North America, Europe (Fuller & Gill 2001; VerCauteren 2003; Côté *et al.* 2004; Apollonio, Andersen & Putman 2010) and elsewhere (Iijima, Nagaike & Honda 2013). Globally, ungulate assemblages are often profoundly modified, with frequent introductions of Caprids and Cervids across multiple continents (Dolman & Wäber 2008; Genovesi *et al.* 2012). Density-dependent effects on condition, fertility and survival have been demonstrated for numerous deer species (Skogland 1985; Clutton-Brock, Major & Guinness 1985; Richard *et al.* 2009; Flajšman *et al.* 2018); but the relative strength of these versus inter-specific competition is poorly known. Potential interference and agonistic interactions may occur between deer species behaviour (Ferretti 2011; Ferretti et al., 2011), but demographic consequences are unknown. Co-occurring ungulate species may partition habitat or dietary niche-use (Murray & Brown 1993; Singer & Norland 1994; Hopcraft *et al.* 2012), but often show considerable dietary overlap within broad guilds of browsers or grazers (Storms *et al.* 2008; Obidziński *et al.* 2013) such that inter-specific exploitation competition has been predicted (Dolman & Wäber 2008).

I investigate competition effects for the complex sympatry of native roe deer *Capreolus capreolus*, and two introduced deer species, the larger fallow deer (*Dama dama*: originally Mediterranean, now widely introduced globally; Dolman & Wäber, 2008) and sub-tropical (SE Asia) muntjac (*Muntiacus reevesi*). Muntjac have been introduced to the UK France, and the Netherlands (Ferretti & Lovari 2014) and have spread rapidly in England where it reaches high densities (Wäber, Spencer & Dolman 2013), affects woodland structure and is considered invasive (Ferretti & Lovari 2014). In roe deer density-dependence affects reproductive rate (Vincent *et al.* 1995; Pettorelli *et al.* 2002), juvenile body mass (Vincent *et* *al.* 1995) and neonatal survival (Gaillard *et al.* 1997). Roe deer are considered potentially vulnerable also to inter-specific competition (Hemami, Watkinson & Dolman 2005; Dolman & Wäber 2008); with agonistic behaviour of fallow to roe (Ferretti 2011; Ferretti et al., 2011), spatial avoidance of roe by fallow (Ferretti et al., 2011), greater sensitivity of home range size to fallow density than to habitat (Focardi *et al.* 2006), and reduced bodyweight at greater fallow density (Focardi *et al.* 2006). Inter-specific competition of muntjac with roe has been proposed also, on the basis of dietary and habitat overlap (Dolman & Wäber, 2008), but not tested. Fertility consequences for ore of these potential inter-specific interactions are unknown, and the importance of inter-specific competition relative to density-dependence is poorly understood (Elofsson, Mensah & Kjellander 2017).

I tested a series of *a priori* hypotheses of intra-specific density-dependence and inter-specific competition (of fallow on muntjac density, fallow and muntjac on roe density, body mass and fertility, see Fig. 5.1), using a large cull sample of adult female roe body mass and fertility measures, over 7 years (2011-2017) across a heterogeneous extensive (195 km^2) forest landscape, across which fallow density varied along a north-south gradient, and muntjac density was manipulated quasi-experimentally between forest blocks. Measures were related to annual fine-scale densities of roe, muntjac and fallow deer, re-sampling species-specific density surfaces calibrated by intensive annual thermal imaging distance sampling.

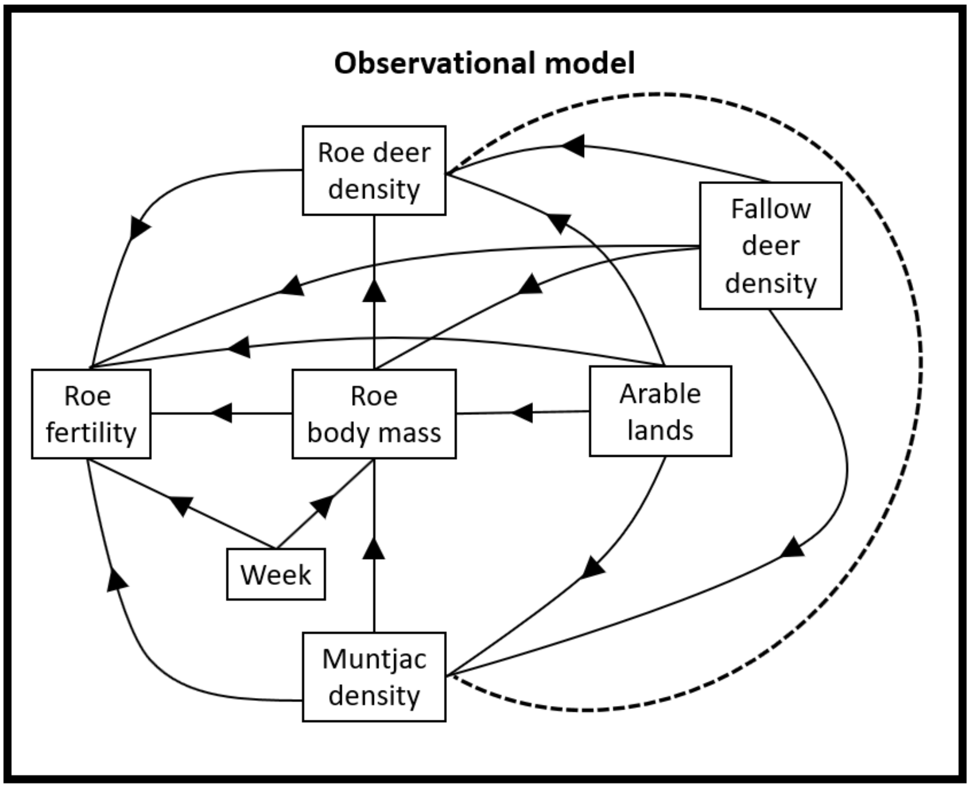


Figure 5.1. Observational model. Piecewise Structural Equation Models (SEMs) testing hypotheses of inter-specific competition among three deer species, and density-dependence of roe deer. Observational model representing all hypothesised directional causal effects (arrows) between variables (rectangular boxes, see Table 5.1 for details) that were tested by SEMs.

Table 5.1. Environmental and deer density variables tested in Structural Equation Models of roe deer density-dependence and inter-specific competition. For each, the coefficient of variation (CV: SD as a proportion of the mean) and range are reported, extracted at the mean Akaike-weighted buffer radius around all individual roe deer culling locations (pooling across years).

Variable	Description (units)	CV	Range	Mean
Arable	Extent of arable land in the buffer from LCM 2015 (%)	0.9	0-84%	20%
Roe deer density	Mean roe deer density across the buffer extracted from year-specific 100m resolution DSM raster (individual.km^{-2})	0.4	1-16	7.4
Muntjac density	Mean muntjac density across the buffer extracted from year-specific 100m resolution DSM raster (individual.km^{-2})	0.5	5-53	15.1
Fallow deer density	Mean of fallow deer density across the buffer extracted from three-year composite (sliding mean) 100m resolution DSM raster (individual.km^{-2})	2.3	0-198	1.2

Methods

Study system

Thetford Forest is a conifer-dominated plantation landscape, created in the 1930-1950s, and managed by clear-felling harvest and replanting, with much of the forest (62%) now in its second rotation. Across the heterogeneous forest landscape, multiple forest 'blocks' (*n*=14, mean area 1337 ha, SD=836) provided replication of forest configuration (contiguous core, or outliers with greater access to external arable and grassland), with block replicates across fallow density gradients and soil composition; within each block a finer-grained mosaic of age structure is formed by even-aged stands (mean area 8.3 ha, SD=5.4), ranging from clear-felled, restocked, pre-thicket, thicket, pole, and mature, to retained over-mature stands, including some earlier plantings up to 220 years old. A geographical gradient in fallow density, combined with variable roe and muntjac densities across the forest, allowed roe and muntjac performance to be related to fallow density while controlling for inter-annual variation in weather, and local forest composition.

Density dependence and inter-specific competition hypotheses (Fig. 5.1) were examined simultaneously using Piecewise Structural Equation Models (SEMs, Shipley 2016), that allow a quantitative analysis of complex conceptual models, whereby a variable can be both a predictor and a response (unlike in generalised linear models). Roe deer have a fixed annual fertility cycle (Raganella-Pelliccioni, Scremin & Toso 2007) and cull data were collected in late winter following embryo implantation; yearlings were reliably aged but were excluded from analysis due to low sample size. I *a priori* examined fertility and body mass responses of adult female roe deer, to roe density, species-specific densities of other deer and habitat availability (Fig. 5.1). In contrast to roe, I could not reliably model muntjac fertility as they are indeterminate aseasonal breeders (Chapman 1991) and cannot be reliably classified into age classes, confounding observations. However, I did *a priori* examined potential responses of local muntjac density to fallow density (Fig. 5.1).

Although SEMs allow multiple hypotheses to be tested simultaneously, reciprocal effects of muntjac density on roe density and *vice versa* could not be considered as the SEM would have been recursive; therefore I did not examine the potential response of muntjac to roe. I also did not examine the response of fallow to the other species, as fallow are invariant breeders that do not show density compensation (Putman *et al.* 1996) and are considered dominant over both roe deer and muntjac (Acevedo *et al.* 2010; Imperio *et al.* 2012). Potential effects of red deer were not examined as these were wide-ranging and pervasive across the entire study landscape, though at a low overall density (mean across the forest, across years=0.34 individuals.km^{-2}, SE=0.25).

Fertility and body mass data

Deer were managed by a professional ranger team. For each of 492 adult female roe deer (Zini, Wäber & Dolman 2021) culled, location (recorded using handheld GPS), date, sex, age (juvenile, yearling or adult, based on tooth eruption, Aitken 1975), reproductive status (number of corpora lutea, and embryos) and body mass (to the nearest 0.1 kg; after head, feet and viscera were removed and blood drained by hanging the carcass) were recorded as part of a long-term research collaboration between Forestry England and the University of East Anglia. Carcasses recorded as incomplete (damaged) or considered incomplete (with adult body mass <8 kg, following Zini, Wäber & Dolman 2019) were excluded from analyses.

Roe embryos are not clearly visible when opening the uterus before early January (Hewison 1996) due to embryonic diapause (Sempere, Mauget & Mauget 1998), therefore fertility analyses were restricted to data collected between 01 January and 31 March, and included a fixed categorical effect of week to account for embryo detectability (coded: 0=weeks 1-3; 1=weeks 4-12) following Zini et al. (2019). Fertility in adult roe deer was analysed as the probability of having one or zero *versus* two embryos, given the scarcity of non-pregnant females (9%) and high frequency of females carrying twin embryos (64%). As the roe population was heavily culled, senescence (with reduced fertility of females aged 8 years or older; Hewison & Gaillard 2001) was considered negligible. This was confirmed by a deterministic Leslie matrix model that incorporated study-site-specific measures of yearling fecundity, adult fecundity, neonatal survival from birth to autumn, yearling and adult mortality (estimated from road mortality and culling numbers relative to the estimated population; see Appendix A) run to a stable age distribution, at which females aged ≥ eight years comprised only 6% of the pre-birthing winter population.

Deer density mapping

In Thetford forest, densities of muntjac and roe deer vary at a fine-scale, with density-activity varying between stands (Hemami, Watkinson & Dolman 2004, 2005) and population density varying within and between blocks (Wäber, Spencer & Dolman 2013; Wäber & Dolman 2015). Culling intensity and pattern varied over the seven years of the study, including a deliberate effort to experimentally reduce muntjac numbers in two blocks. However, overall muntjac numbers increased while roe deer numbers fluctuated during the study; both varied in local distribution, further decoupling annual densities from local habitat. In contrast, fallow deer range more widely between resting-up and feeding areas and their density varied at a coarser scale (within and between blocks), and showed a marked density-gradient across the landscape (occurring at high abundance in three southern blocks but were absent or scarce in northern blocks; Fig. 5.2) that was stable throughout the study period (see Appendix B), reflecting earlier colonisation of the landscape from the south.

Annual species-specific deer densities for 2011-2017 were resampled from annual 100m resolution Density Surface Model (DSM) rasters, generated from distance sampling data obtained by nocturnal thermal imaging transects driven during January to March of each year (see Appendix C for year-specific survey coverage). Distance sampling procedures followed Wäber & Dolman, (2015), for more details see Appendix D. DSMs predicted the spatial variation of animal abundance by a two-step approach (Miller *et al.* 2013). First, species-specific detection functions were fitted to account for declining detectability with greater perpendicular distance (Buckland *et al.* 2001) that incorporated a covariate modelling differences in visibility class due to forest stand age, and when supported during initial model selection, a group size adjustment (see Appendix E). Then, for each survey-year the selected species-specific detection function (with visibility covariates) was used to estimate abundance per surveyed transect segment (minimum n= 587 in 2011, maximum n= 1239 in 2017, Appendix E). A Generalised Additive Model (GAM) modelled the relation between abundance per segment and complex polynomials of latitude and longitude using a penalised thin-plate regression spline. For more details on DSM methodology see Appendix E.

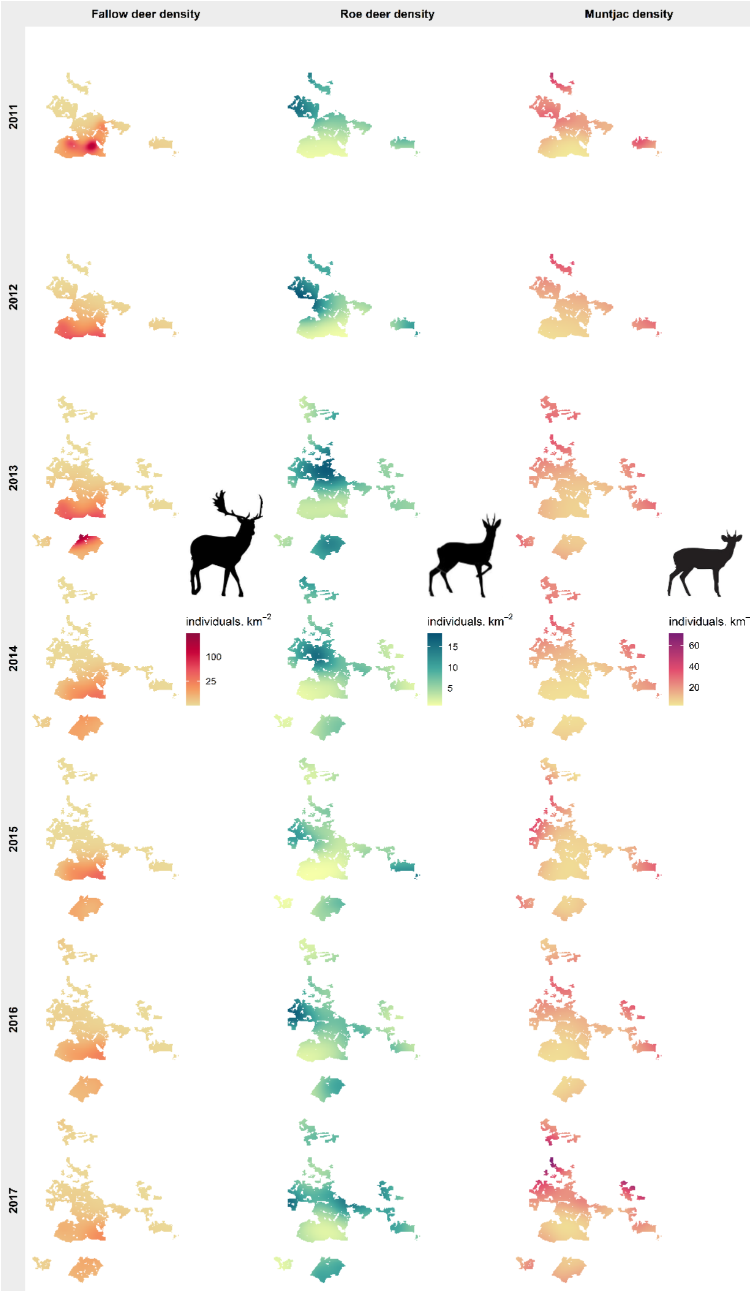


Figure 5.2. Annual densities of muntjac, roe and fallow deer across Thetford Forest (2011-2017), showing density surfaces (individuals.km^{-2}) interpolated at a 100x100m grid from annual density surface models (DSMs) including latitude and longitude. For fallow deer, surfaces show the three-year moving-average, due to lower encounter rate, larger group size and thus greater sampling variance.

Analyses

Variable selection and parameter estimation were performed using Multi-Model Inference (Burnham & Anderson 2002). SEMs consist of multiple dependent variables and a series of proposed direct and indirect (or mediated) cause-effect relations (Bollen 1989), that are written as a series of regressions (individual models) incorporated into a unique observational SEM (Fig. 5.1); reported coefficients partition the variance explained by each structural equation. Recently developed piecewise SEMs (Lefcheck 2016) allow for the inclusion of random effects and non-normal error distributions. Preliminary analysis of each individual model were conducted (across buffers) to select the best-fitting random effect structure. Through comparison of AICc of competing models (using the full fixed effect structure) with different random effect structures the best-fitting random effect structure was selected for subsequent SEM analysis. Analyses were performed using package “piecewiseSEM” (Lefcheck 2016) in R statistical software (R core Team 2018).

Roe deer are sedentary especially over the winter season (Bideau *et al.* 1993), and were hunted by stalking not drive-hunting, it was therefore assumed that the location in which the deer was shot lay within its home range. Individual roe deer fertility and body mass were related to environmental and species-specific density variables extracted from the area immediately surrounding it’s cull location. No telemetry data were available to support selecting the most appropriate buffer radius, therefore, following Zini et al. (2019), a series of SEMs was fitted, relating fertility and body mass to arable extent and species-specific deer densities extracted at increasing buffer radii from 400m to 600m (at 50m increments), corresponding to home-range sizes ranging from 50ha to 113ha — informed by the range of roe deer home ranges in comparable temperate study areas (northern Italy, France and Germany: monthly 90% fixed kernel home range, 59ha, Morellet *et al.* 2013; Thetford Forest, Minimum Convex Polygon 114ha, Chapman *et al.* 1993). Inference was then based on a model averaging approach (following Burnham & Anderson 2002) across this range of potential buffer radii.

For SEMs analysis, the same dataset needs to be used for each individual model; therefore buffer radii selected was solely based on roe deer home range, as roe deer fertility and body mass were the main focus of this analysis. When relating roe deer and muntjac density to fallow deer density and extent of arable lands the same series of buffer radii created around cull locations was used (with buffers measuring deer densities and arable overlapping), thus when muntjac density, that would vary at a smaller grain (as muntjac have smaller home ranges; Chapman *et al.* 1993) is analysed as the predictor, inference can be weaker.

Roe fertility was related to annual species-specific density of the three deer species (extracted from DSMs) and the individual's body mass using Generalised Linear Mixed Models (GLMM) with binomial error distribution. Models incorporated random effects of forest block (to control for unmeasured effects of human recreational use, forest management, and residual spatial autocorrelation) and cull year (to control for winter severity and weather effects on forage availability) and fixed effects of calendar period (0 or 1) on embryo detectability (see above), and the local extent of arable (that provide high quality forage). Previous analysis of roe cull data (spanning 2002-2015, Zini et al., 2019) showed body mass was higher but fertility was (counterintuitively) lower with greater extent of arable; no responses to other habitat variables (calcareous soil, grassland, young stands, mature stands measured as a percentage within the individual's home range) were found, therefore these were omitted from SEMS. The distribution of arable lands was obtained from the Land Cover Map 2015 (hereafter LCM 2015; Rowland et al. 2017) that maps 23 classes to 0.5 ha resolution, and was extracted from buffers around cull locations (see below) using R statistical software and the packages "sp" (Pebesma & Bivand 2005), "rgeos" and "rgdal" (Roger *et al.* 2017).

Roe body mass was related to annual species-specific deer densities, percentage of arable lands and calendar week (to control for variation in body mass across time) using GLMMs with normal error distribution, again including a random effect of forest block. Roe deer density and muntjac density were each related to fallow deer density and percentage of arable lands using GLMMs with normal error, again including random effects of forest block and cull year. As roe deer and muntjac have similar habitat requirements (Hemami, Watkinson & Dolman 2004), the positive relationship between the two densities (r=0.23 calculated using the SEM dataset) driven by habitat selection was controlled by introducing a correlated error structure between roe and muntjac density. In order to avoid leverage due to the high number of observations with low values fallow deer density was square rooted when included in the Structural Equation Model.

No strong intercorrelation (defined as r>0.78, Freckleton 2002), between predictor variables (arable extent and species-specific deer densities) was found at any buffer radii in any of the regressions contributing to the SEMs. For each radius all possible combinations of variables were built, following MMI procedures (Burnham & Anderson 2002) weighting resulting SEMs according to Akaike weights calculated across all models, and across all radii, using (package "qpcR", Spiess, 2018). This process was repeated 100 times to incorporate uncertainty in deer density estimates extracted from DSMs, resampling density from the 95% CI of density (mapped as the coefficient of variation of the density estimate). Model-averaged coefficients and CIs were averaged across these 100 iterations. Variables were considered to be supported if they were included in the 95% model confidence set (calculated across all models at all buffers) with a model-averaged parameter CI not spanning (i.e. differing from) zero. Consequences for roe deer fertility and body mass, of inter-specific competition and of density-dependence, were evaluated by predicting fertility from a model including supported variables measured at the Akaike-weighted mean buffer radius. In order to compare the relative strength of predictor variables, standardized (coefficients scaled by standard deviation) model coefficients are reported. Model performance was evaluated through individual R^2 of each regression with the supported variables extracted at the Akaike-weighted mean buffer radius.

Results

For adult female roe deer, mean body mass was 13.7kg (SD=1.52) and mean fertility (controlling for week) was 1.44 fetus per adult female (SD=0.05). Across the whole SEM, the Akaike-weighted mean buffer radius was 497m (SD=81m).

Muntjac density (at the Akaike-weighted mean buffer radius, individual model R^2= 0.78) was greater with greater extent of arable lands (inter-quartile IQ=+1.0 individual.km-^{2}) and lower (IQ=0.79 individual.km-^{2}) at higher local fallow deer density (Figs 5.2, 5.3D, 5.3E). The negative effect of fallow deer on muntjac density was stronger than the positive effect of arable (Welch’s t-test: t = 5.5285, df = 597.58, p-value = 4.83e-08). Roe deer density was unrelated to fallow deer density or arable extent (with no effects supported, Fig. 5.3).

Individual model of roe deer body mass explained a small proportion of variance (individual $R^2 = 0.17$), with adult female roe deer being heavier in localities with a greater extent of arable lands (IQ=+0.32kg; Figs 5.3, 5.4C). Roe body mass was not related to local roe density, or to the densities of either muntjac or fallow deer (Fig. 5.3).

Individual model of roe deer fertility explained a small proportion of variance (individual $R^2 = 0.10$) with lower fertility for individuals culled in buffers with a greater local density of muntjac (IQ=-14% probability of having two embryos instead of one or zero), while fertility was slightly greater in buffers with greater roe deer density (IQ =+9% probability of having two embryos instead of one or zero; Figs 5.3, 5.4A, 5.4B). No effects on roe fertility of the individual’s body mass, arable lands or fallow deer density were supported (Fig. 5.3).

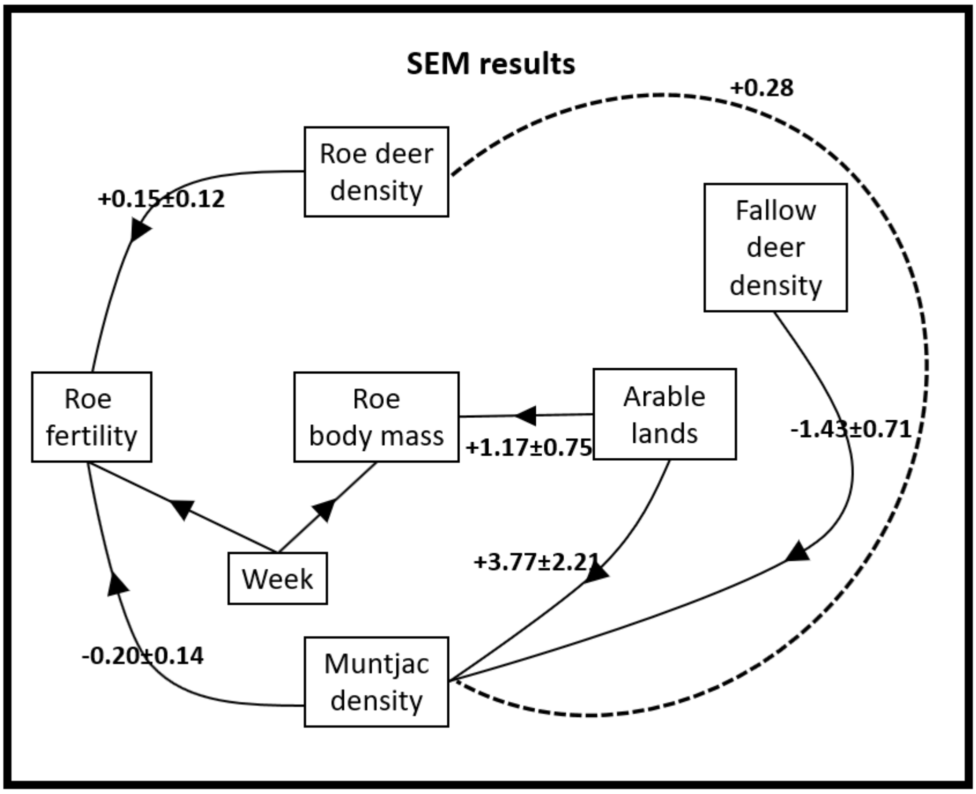


Figure 5.3. Results of Piecewise Structural Equation Models (SEMs) testing hypotheses of inter-specific competition among three deer species, and density-dependence of roe deer, showing supported causal effects (arrows) relating roe deer body mass and fertility to intra- and inter-specific deer densities and local extent of arable lands, showing model-averaged coefficients (across incremental buffer radii, 400m to 600m, corresponding to 59ha – 113ha) and their 95% Confidence Interval. Models incorporate random effects of cull year and forest block, dotted line represents the correlated error structure for which the correlation coefficient is also reported.

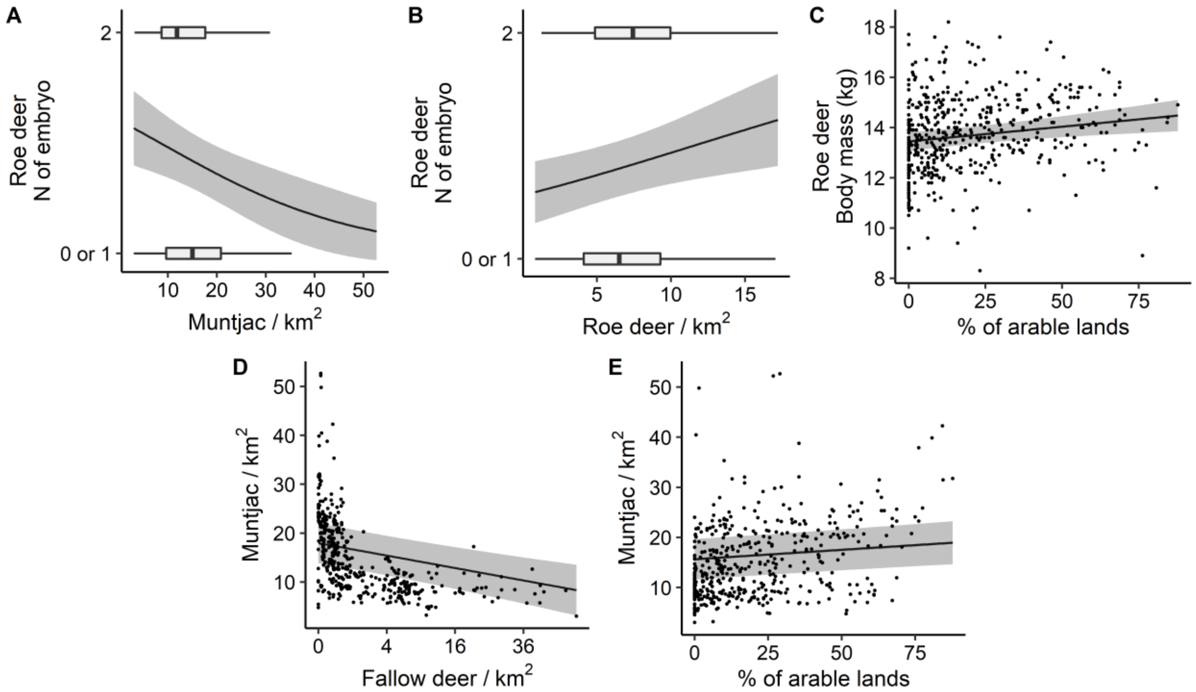


Figure 5.4. Relation of roe deer fertility (A, B), roe body mass (C), and muntjac density (D, E), to species-specific local deer densities (A, B, D) and local extent of arable (C, E), supported by model-averaging across piecewise Structural Equation Models (SEMs). Fertility, body mass and muntjac density were predicted from models including variables measured at the Akaike-weighted mean buffer radius (497m) following model-averaging of SEMs across incremental buffer radii (from 400m to 600m). For fertility, boxplots represent the distribution of individual roe deer with either two embryos *versus* zero or one embryos (combined reference level).

Discussion

This study utilised a large dataset, robust measures of deer densities, and a quasi-experimental approach (with landscape-scale replication that controlled for forest configuration and habitat quality) to investigate inter-specific competition between roe deer, muntjac and fallow deer. Although intra-specific density-dependence in roe has been widely documented elsewhere (e.g. Douhard et al. 2013; Gaillard et al. 1997; Pettorelli et al. 2002), no density-dependent effects on roe body mass, or of body mass on individual fertility were found, likely due to low overall densities. However complex patterns of inter-specific competition were found, with apparent displacement of muntjac but not roe by fallow, while roe deer were less fertile in areas with higher muntjac densities, suggesting inter-specific competition with muntjac outweighed density-dependence for roe in this system.

Competition between introduced fallow and muntjac has, to my knowledge, not been investigated previously. I found lower muntjac densities in localities with more fallow deer, with an effect size greater than the positive effect of arable lands. It is plausible that muntjac may be displaced by the larger, competitively dominant, fallow deer. Potential displacement may not be neutral in terms of their ecosystem functions, as Cervids can differ markedly in their patterns of seed dispersal (Eycott *et al.* 2007) and browsing impacts. In contrast, I found no evidence that high densities of fallow deer affected roe deer density, body mass, or fertility. This lack of inter-specific competition is notable, given that roe is subject to aggression by fallow (Ferretti 2011) that can displace roe from feeding areas (Ferretti, Sforzi & Lovari 2008, 2011); in central Italy roe deer densities are negatively related to those of fallow deer (Ferretti *et al.* 2011), similarly in the UK roe deer have been reported to be either absent or at low numbers where fallow deer occur in high numbers (Carne 1955). For enclosed populations (33.3 km^2) in central Italy, fallow deer decreased roe deer habitat quality (Focardi *et al.* 2006) and the roe deer population decreased while the fallow deer population was increasing, suggesting potential negative effects of fallow on the roe deer population (Imperio *et al.* 2012). It is possible that low overall roe density, combined with access to external farmland habitats, attenuated fallow impacts on roe in this study landscape.

In contrast to the lack of response to fallow, roe fertility was lower with higher local muntjac densities. While potential mechanisms underlying this effect include behavioural interference or exploitation competition through resource depletion, the lack of detectable intra-specific density-dependence in the roe population (see below) suggests forage depletion is unlikely. However, physiological and or endocrine stress (indicative of roe deer fitness; Escribano-Avila *et al.* 2013) from agonistic interactions with muntjac (interference competition) may have reduced implantation. Environmental challenges can increase glucocorticoid levels with consequences for decreased fitness (Sapolsky, Romero & Munck 2000; Gobush, Mutayoba & Wasser 2008; Bonier *et al.* 2009), and in roe deer glucocorticoids have been shown to vary in relation to habitat quality (Escribano-Avila *et al.* 2013). Inter-specific agonistic encounters may also cause physiological stress; Australian lace monitors *Varanus varanus* had higher corticosteroid levels when exposed to higher red fox *Vulpes vulpes* densities (Jessop *et al.* 2015). Such a proximal effect of muntjac acting on roe fertility can explain an earlier counter-intuitive finding of apparent lower fertility of Thetford Forest roe deer in areas with greater arable (Zini, Wäber & Dolman 2019); in the current study inclusion of both muntjac density and arable extent simultaneously within the SEM showed a response to local muntjac abundance but no effect of arable lands, that may have acted as a proxy for muntjac in the earlier study (that did not incorporate species-specific deer densities). That roe appeared to be susceptible to competition with muntjac, but not fallow, is curious. One possibility is that the mobile nature of fallow herds and their habit of commuting between diurnal resting-up and nocturnal feeding areas, allowed roe to avoid them in space and time, in contrast the highly sedentary nature of local muntjac home ranges may make them a constant and unavoidable presence within a roe home range.

The apparent lack of detectable intra-specific density-dependent effects on roe deer body mass or fertility is not unexpected, given low recent overall densities. Annual thermal imaging distance surveys show that roe deer abundance in Thetford Forest reduced from 6 to 34 individual.km^{-2} per forest block in 2009 (Wäber 2010), to 4 individual.km^{-2} in 2017 (Appendix E), lower than reported elsewhere in southern England (e.g. 34-71 individuals.km^{-2}; Gill, Johnson, Francis, Hiscocks, & Peace, 1996). Previous long-term data from this roe population showed decrease and subsequent partial recovery of body mass and fertility, attributable to initial population growth (1960's to 1990) and subsequent suppression by culling (2001 to 2009) (Wäber 2010), consistent with density-dependence. Elsewhere in Europe, adult female roe body mass increased by 20% after density decreased by 60% (Pettorelli *et al.* 2002), and roe litter size is density-dependent (Flajšman *et al.* 2018) but with effects more likely to be detected at high population densities (Gaillard *et al.* 2000). The maximum number of embryos in roe deer is determined by body weight below an asymptotic threshold, after which further body mass increments cease to affect fertility (Flajšman, Jerina & Pokorny 2017). In the current study, the relatively high average adult female body mass (13.7kg, SD=1.52; compared to 11.8 kg SD=2.4, in 1989-1990 when roe were more abundant, Wäber 2010) and lack of detectable effects of roe density on body mass, are consistent with low overall roe numbers. Counter-intuitively, roe deer fertility appeared to be positively (though weakly) related to local roe density, again implying an absence of density-dependence. It is plausible that unmeasured habitat features (i.e. low levels of human recreational pressure, composition of ground flora) favoured both local aggregation and greater fertility.

The results reported here, show roe experienced inter-specific competition from muntjac, and muntjac appeared to be displaced by fallow deer, while intra-specific competition (density-dependence) was negligible at the roe deer densities investigated. The competitive exclusion principle (Armstrong & McGehee 1980) implies that roe, muntjac and fallow deer may not stably coexist, with roe deer potentially excluded to spatial refugia. With numbers and range increasing for both fallow and muntjac (Noble, Aebischer, Newson, Ewald, & Dadam, 2012), competition might be of growing concern for the native roe; however, the effects of competition found in this study were subtle and considered a low density roe population. If control measures reduced sufficiently for the roe population to increase to higher abundance, then intraspecific density dependence may assume greater importance relative to inter-specific effects. This study shows the complex nature of competitive interactions within a vertebrate guild enhanced by introductions.

References

Acevedo, P., Ward, A.I., Real, R. & Smith, G.C. (2010) Assessing biogeographical relationships of ecologically related species using favourability functions: a case study on British deer. *Diversity and Distributions*, **16**, 515–528.

Aitken, R.J. (1975) Cementum layers and tooth wear as criteria for ageing roe deer (*Capreolus capreolus*). *Journal of Zoology*, **175**, 15–28.

Apollonio, M., Andersen, R. & Putman, R. (2010) *European Ungulates and Their Management in the 21st Century.* Cambridge University Press, Cambridge, UK.

Armstrong & McGehee. (1980) Competitive exclusion. *The American Naturalist*, **115**.

Belant, J.L., Kielland, K., Follmann, E.H. & Adams, L.G. (2006) Interspecific resource partitioning in sympatric ursids. *Ecological Applications*, **16**, 2333–2343.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Bengtsson, J. (1989) Interspecific competition increases local extinction rate in a metapopulation system. *Nature*, **340**, 713–715.

Bideau, E., Gerard, J.F., Vincent, J.P. & Maublanc, M.L. (1993) Effects of age and sex on space occupation by European roe deer. *Journal of Mammalogy*, **74**, 745–751.

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U. & Richardson, D.M. (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, **26**, 333–339.

Bollen, K.A. (1989) *Structural Equations with Latent Variables*. John Wiley & Sons, Inc., Hoboken, NJ, USA.

Bonesi, L., Chanin, P. & Macdonald, D.W. (2004) Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift. *Oikos*, **106**, 19–26.

Bonier, F., Martin, P.R., Moore, I.T. & Wingfield, J.C. (2009) Do baseline glucocorticoids predict fitness? *Trends in Ecology & Evolution*, **24**, 634–642.

Buckland, S.T., Anderson, D.R., Thomas, L., Burnham, K.P., Laake, J.L. & Borchers, D.L. (2001) Line transects. *Introduction To Distance Sampling: Estimating Abundance of Biological Populations*, pp. 104–14. Oxford University Press, Oxford.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multi-Model Inference. A Practical Information—Theoretic Approach*, 2nd ed (ed Springer Verlag). New York.

Carne, P.H. (1955) Roe deer and fallow. *Oryx*, **3**, 104.

Chapman, N.G. (1991) Chinese muntjac Muntiacus reevesi. *The Handbook of British Mammals* (eds G.B. Corbet & S. Harris), pp. 526–532. Blackwell scientific publications, Oxford.

Chapman, N.G., Claydon, K., Claydon, M., Forde, P.G. & Harris, S. (1993) Sympatric populations of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*): a comparative analysis of their ranging behaviour, social organization and activity. *Journal of Zoology*, **229**, 623–640.

Clutton-Brock, T.H., Major, M. & Guinness, F.E. (1985) Population regulation in male and female red deer. *The Journal of Animal Ecology*, **54**, 831.

Connell, J.H. (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, **35**, 131.

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.

Crooks, J.A. (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, **97**, 153–166.

Davis, M.A. (2009) *Invasion Biology*. Oxford University Press.

Dhondt, A.A. (1977) Interspecific competition between great and blue tit. *Nature*, **268**, 521–523.

Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G. & Dickman, C.R. (2016) Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 11261–11265.

Dolman, P.M. & Wäber, K. (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research*, **35**, 202.

Douglas, M.E., Marsh, P.C. & Minckley, W.L. (1994) Indigenous fishes of western North America and the hypothesis of competitive displacement: *Meda fulgida* (Cyprinidae) as a case study. *Copeia*, **1994**, 9.

Douhard, M., Gaillard, J.-M., Delorme, D., Capron, G., Duncan, P., Klein, F. & Bonenfant, C. (2013) Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females. *Ecology*, **94**, 1805–14.

Elofsson, K., Mensah, J.T. & Kjellander, P. (2017) Optimal management of two ecologically interacting deer species-reality matters, beliefs don’t. *Natural Resource Modeling*, **30**, e12137.

Escribano-Avila, G., Pettorelli, N., Virgos, E., Lara-Romero, C., Lozano, J., Barja, I., Cuadra, F.S. & Puerta, M. (2013) Testing Cort-Fitness and Cort-Adaptation hypotheses in a habitat suitability gradient for roe deer. *Acta Oecologica*, **53**, 38–48.

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**, 107–118.

Ferretti, F. (2011) Interspecific aggression between fallow and roe deer. *Ethology Ecology and Evolution*, **23**, 179–186.

Ferretti, F., Bertoldi, G., Sforzi, A. & Fattorini, L. (2011) Roe and fallow deer: are they compatible neighbours? *European Journal of Wildlife Research*, **57**, 775–783.

Ferretti, F. & Lovari, S. (2014) Introducing aliens: problems associated with invasive exotics. *Behaviour and management of European ungulates*, 78–109.

Ferretti, F., Sforzi, A. & Lovari, S. (2008) Intolerance amongst deer species at feeding: roe deer are uneasy banqueters. *Behavioural Processes*, **78**, 487–491.

Ferretti, F., Sforzi, A. & Lovari, S. (2011) Behavioural interference between ungulate species: roe are not on velvet with fallow deer. *Behavioral Ecology and Sociobiology*, **65**, 875–887.

Flajšman, K., Borowik, T., Pokorny, B. & Jędrzejewska, B. (2018) Effects of population density and female body mass on litter size in European roe deer at a continental scale. *Mammal Research*, **63**, 91–98.

Flajšman, K., Jerina, K. & Pokorny, B. (2017) Age-related effects of body mass on fertility and litter size in roe deer. *PLOS ONE*, **12**, e0175579.

Focardi, S., Aragno, P., Montanaro, P. & Riga, F. (2006) Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. *Ecography*, **29**, 407–417.

Freckleton, R.P. (2002) On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *Journal of Animal Ecology*, **71**, 542–545.

Fuller, R.J. & Gill, R.M.A. (2001) Ecological impacts of increasing numbers of deer in British woodland. *Forestry*, **74**, 193–199.

Gaillard, J.M., Boutin, J.M., Delorme, D., Van Laere, G., Duncan, P. & Lebreton, J.D. (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, **112**, 502–513.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toïgo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Genovesi, P., Carnevali, L., Alonzi, A. & Scalera, R. (2012) Alien mammals in Europe: updated numbers and trends, and assessment of the effects on biodiversity. *Integrative Zoology*, **7**, 247–253.

Gill, R.M.A., Johnson, A.L., Francis, A., Hiscocks, K. & Peace, A.J. (1996) Changes in roe deer

(*Capreolus capreolus L.*) population density in response to forest habitat succession. *Forest Ecology and Management*, **88**, 31–41.

Gobush, K.S., Mutayoba, B.M. & Wasser, S.K. (2008) Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female African elephants. *Conservation Biology*, **22**, 1590–1599.

Hamann, O. (1993) On vegetation recovery, goats and giant tortoises on Pinta Island, Galápagos, Ecuador. *Biodiversity and Conservation*, **2**, 138–151.

Hardin, G. (1960) The competitive exclusion principle. *Science*, **131**, 1292–1297.

Hemami, M.R., Watkinson, A.R. & Dolman, P.M. (2004) Habitat selection by sympatric muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a lowland commercial pine forest. *Forest Ecology and Management*, **194**, 49–60.

Hemami, M.R., Watkinson, A.R. & Dolman, P.M. (2005) Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* in a lowland pine forest. *Forest Ecology and Management*, **215**, 224–238.

Herrmann, N.C., Stroud, J.T. & Losos, J.B. (2021) The evolution of 'Ecological Release' into the 21st Century. *Trends in Ecology & Evolution*, **36**, 206–215.

Hewison, A.J.M. (1996) Variation in the fecundity of roe deer in Britain: effects of age and body weight. *Acta Theriologica*, **41**, 187–198.

Hewison, A.J.M. & Gaillard, J.M. (2001) Phenotypic quality and senescence affect different components of reproductive output in roe deer. *Journal of Animal Ecology*, **70**, 600–608.

Hopcraft, J.G.C., Anderson, T.M., Pérez-Vila, S., Mayemba, E. & Olff, H. (2012) Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology*, **81**, 201–213.

Human, K.G. & Gordon, D.M. (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia*, **105**, 405–412.

Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, **93**, 145–159.

Iijima, H., Nagaike, T. & Honda, T. (2013) Estimation of deer population dynamics using a bayesian state-space model with multiple abundance indices. *The Journal of Wildlife Management*, **77**, 1038–1047.

Imperio, S., Focardi, S., Santini, G. & Provenzale, A. (2012) Population dynamics in a guild of four Mediterranean ungulates: density-dependence, environmental effects and inter-specific interactions. *Oikos*, **121**, 1613–1626.

Jessop, T.S., Anson, J.R., Narayan, E. & Lockwood, T. (2015) An introduced competitor elevates corticosterone responses of a native lizard (*Varanus varius*). *Physiological and Biochemical Zoology*, **88**, 237–245.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373.

Latham, J. (1999) Interspecific interactions of ungulates in European forests: an overview. *Forest Ecology and Management*, **120**, 13–21.

Lefcheck, J.S. (2016) piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, **7**, 573–579.

Mack, R., Simberloff, D., Lonsdale, M.W., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications*, 689–710.

Miller, D.L., Burt, M.L., Rexstad, E.A. & Thomas, L. (2013) Spatial models for distance sampling data: recent developments and future directions. *Methods in Ecology and Evolution*, **4**, 1001–1010.

Mishra, C., Wieren, S.E., Heitkönig, I.M.A. & Prins, H.H.T. (2002) A theoretical analysis of competitive exclusion in a Trans-Himalayan large-herbivore assemblage. *Animal*

Conservation, **5**, 251–258.

Mooney, H.A. & Cleland, E.E. (2001) The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 5446–5451.

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J.D.C., Nicoloso, S., Sustr, P., Urbano, F. & Mysterud, A. (2013) Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, **82**, 1326–1339.

Murray, M.G. & Brown, D. (1993) Niche separation of grazing ungulates in the Serengeti: an experimental test. *The Journal of Animal Ecology*, **62**, 380.

Noble, D.G., Aebischer, N.J., Newson, S.E., Ewald, J.A. & Dadam, D. (2012) A comparison of trends and geographical variation in mammal abundance in the breeding bird survey and the national gamebag census. *JNCC Report*, **468**, 2012.

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. *Open Life Sciences*, **8**, 8–17.

Odum, E.P. (1971) *Fundamentals of Ecology* (ed S.W. Saunders). Philadelphia.

Pebesma, E.J. & Bivand, R.S. (2005) Classes and methods for spatial data in R. *R News 5*, **2**, 9–13.

Peres, C.A. & Dolman, P.M. (2000) Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia*, **122**, 175–189.

Pettorelli, N., Gaillard, J.-M., Van Laere, G., Duncan, P., Kjellander, P., Liberg, O., Delorme, D. & Maillard, D. (2002) Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **269**, 747–753.

PTES. (2017) Living with mammals update 2017. *British Wildlife*.

PTES. (2018) Living with mammals update 2018. *British Wildlife*.

Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.

Putman, R.J., Langbein, J., Hewison, A.J.M. & Sharma, S.K. (1996) Relative roles of density-dependent and density-independent factors in population dynamics of British deer. *Mammal Review*, **26**, 81–101.

R core Team. (2018) R: A Language and Environment for Statistical Computing.

Raganella-Pelliccioni, E., Scremin, M. & Toso, S. (2007) Phenology and synchrony of roe deer breeding in northern Italy. *Acta Theriologica*, **52**, 95–100.

Reaser, J.K., Meyerson, L.A., Cronk, Q., De Poorter, M., Eldrege, L.G., Green, E., Kairo, M., Latasi, P., Mack, R.N., Mauremootoo, J., O'Dowd, D., Orapa, W., Sastroutomo, S., Saunders, A., Shine, C., Thrainsson, S. & Vaiutu, L. (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environmental Conservation*, **34**, 98–111.

Richard, E., Gaillard, J.M., Saïd, S., Hamann, J.L. & Klein, F. (2009) High red deer density depresses body mass of roe deer fawns. *Oecologia*, **163**, 91–97.

Roeleke, M., Johannsen, L. & Voigt, C.C. (2018) How bats escape the competitive exclusion principle-seasonal shift from intraspecific to interspecific competition drives space use in a bat ensemble. *Frontiers in Ecology and Evolution*, **6**, 1–11.

Roger, A., Rowlingson, B., Sumner, M., Hijmans, R. & Rouault, E. (2017) Package ' rgdal '.

Rowland, C.S., Morton, R.D., Carrasco, L., McShane, G., O'Neil, A.W. & Wood, C.M. (2017) Land Cover Map 2015 (vector, GB).

Rushton, S.P., Lurz, P.W.W., Gurnell, J., Nettleton, P., Bruemmer, C., Shirley, M.D.F. & Sainsbury, A.W. (2006) Disease threats posed by alien species: the role of a poxvirus in the decline of the native red squirrel in Britain. *Epidemiology and Infection*, **134**, 521–533.

Sapolsky, R.M., Romero, L.M. & Munck, A.U. (2000) How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews*, **21**, 55–89.

Schoener, T.W. (1983) Field experiments on interspecific competition. *The American Naturalist*, **122**, 240–285.

Sempere, A.J., Mauget, R. & Mauget, C. (1998) Reproductive physiology of roe deer. *The European Roe Deer: The Biology of Success*, pp. 161–188. Scandinavian University Press, Oslo.

Shipley, B. (2016) *Cause and Correlation in Biology*. Cambridge University Press, Cambridge.

Singer, F.J. & Norland, J.E. (1994) Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. *Canadian Journal of Zoology*, **72**, 1383–1394.

Skogland, T. (1985) The effects of density-dependent resource limitations on the demography of wild reindeer. *The Journal of Animal Ecology*, **54**, 359.

Spiess, A.-N. (2018) qpcR: Modelling and Analysis of Real-Time PCR Data.

Storms, D., Aubry, P., Hamann, J.-L., Saïd, S., Fritz, H., Saint-Andrieux, C. & Klein, F. (2008) Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. *Wildlife Biology*, **14**, 237–250.

Tennessen, J.B., Parks, S.E., Tennessen, T.P. & Langkilde, T. (2016) Raising a racket: invasive species compete acoustically with native treefrogs. *Animal Behaviour*, **114**, 53–61.

VerCauteren, K.C. (2003) The deer boom: discussions on population growth andrange expansion of the white-tailed deer. *Bowhunting Records of North AmericaWhitetail Deer* (eds G. Hisey & K. Hisey), pp. 15–20. Pope and Young Club, Chatfield, MN.

Vincent, J.P., Bideau, E., Hewison, A.J.M. & Angibault, J.M. (1995) The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). *Journal of Zoology*, **236**, 371–382.

Wäber, K. (2010) *Landscape Scale Deer Management. PhD Thesis*. University of East Anglia.

Wäber, K. & Dolman, P.M. (2015) Deer abundance estimation at landscape-scales in heterogeneous forests. *Basic and Applied Ecology*, **16**, 610–620.

Wäber, K., Spencer, J. & Dolman, P.M. (2013) Achieving landscape-scale deer management for biodiversity conservation: the need to consider sources and sinks. *Journal of Wildlife Management*, **77**, 726–736.

Walther, G.-R. (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2019–2024.

Ward, P. & Sutherland, W.J. (1997) From Individual Behaviour to Population Ecology. *The Journal of Animal Ecology*, **66**, 605.

Warren, R.J., Chick, L.D., DeMarco, B., McMillan, A., De Stefano, V., Gibson, R. & Pinzone, P. (2016) Climate-driven range shift prompts species replacement. *Insectes Sociaux*, **63**, 593–601.

Watts, H.E. & Holekamp, K.E. (2008) Interspecific competition influences reproduction in spotted hyenas. *Journal of Zoology*, **276**, 402–410.

Wright, J.P. & Jones, C.G. (2004) Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology*, **85**, 2071–2081.

Zini, V., Wäber, K. & Dolman, P.M. (2019) Habitat quality, configuration and context effects on roe deer fecundity across a forested landscape mosaic. *PLOS ONE*, **14**, e0226666.

Zini, V., Wäber, K. & Dolman, P.M. (2021) Roe deer competition dataset.

Appendices

Appendix A. Senescence of adult roe deer

If the roe deer population contained a substantial proportion of older females then reproductive senescence (Hewison & Gaillard, 2001) could cause additional unexplained variation in observed fertility, lessening the statistical power of environmental models. As the age (in years) of individual adult roe was not known, the potential age structure of the female population was explored using a structured demographic model. Age-class composition of culled pre-birthing (late-winter) females from larder data was: 19% kids, 8% yearlings and 73% adults (shooting is random with respect to age). As embryos can be missed shortly after implantation (Ratcliffe & Mayle, 1992), mean fertility (from data collected from 2006-2009) was calculated considering females culled after week 6 of each calendar year. Mean yearling fertility was 0.86 (SD=0.73) embryos per female per year and for adults 1.44 (SD=0.50) embryos per female per year. For 2008-2010, the mean annual mortality rate (assumed to be age-independent), calculated as the proportion of the population (estimated through distance sampling thermal imaging, see Wäber & Dolman, (2015) dying from culling plus recorded road-traffic (RTA) mortality, was estimated at 25% of the population per year (Wäber, Spencer, & Dolman, 2013). Culling is the overwhelming primary cause of mortality, with recorded RTAs forming only a small (5%) proportion of recorded deaths. Although total mortality may be slightly under-estimated due to further unreported RTAs, any bias would result in the proportion of the population comprising older females to be over-estimated. Annual adult survival was calculated considering mortality rate due to culling and RTA (25%). Following Wäber, Spencer, & Dolman (2013) neonatal survival from birth to first winter was calculated by relating the autumn kid-adult female ratio (from field observations in October–November 2007–2009: 83% ± 0.04, 95% CI), to average adult fertility from larder data (of January–February 2006–2009). Annual kid survival from birth to the next spring was then calculated considering neonatal mortality (17%) and mortality due to overwinter culling, resulting in a 63% survival probability. A deterministic Leslie matrix was created with a starting population distributed according to the observed age class proportions of kid: yearling: adult, initially assuming all adults were 2 years-old. A stable age composition was reached after 14 years at which point the percentage of senescent individuals (defined as 8 years or older, following (Hewison & Gaillard, 2001) comprised only 6% of the female pre-birthing adult winter numbers. I therefore consider that senescence will have only a minor effect on observed adult fertility. Furthermore, as culling is pervasive across the forest, age structure was considered spatially non-confounding.

References

Hewison, A. J. M., & Gaillard, J. M. (2001). Phenotypic quality and senescence affect different components of reproductive output in roe deer. *Journal of Animal Ecology*, *70*(4), 600–608. doi: 10.1046/j.1365-2656.2001.00528.x

Ratcliffe, P. R., & Mayle, B. A. (1992). Roe deer biology and management. *Forestry Commission Bulletin*, *105*, 1–28.

Wäber, K., & Dolman, P. M. (2015). Deer abundance estimation at landscape-scales in heterogeneous forests. *Basic and Applied Ecology*, *16*(7), 610–620. doi: 10.1016/j.baae.2015.06.005

Wäber, K., Spencer, J., & Dolman, P. M. (2013). Achieving landscape-scale deer management for biodiversity conservation: the need to consider sources and sinks. *Journal of Wildlife Management*, *77*(4), 726–736. doi: 10.1002/jwmg.530

Appendix B. Forest-wide density of fallow deer

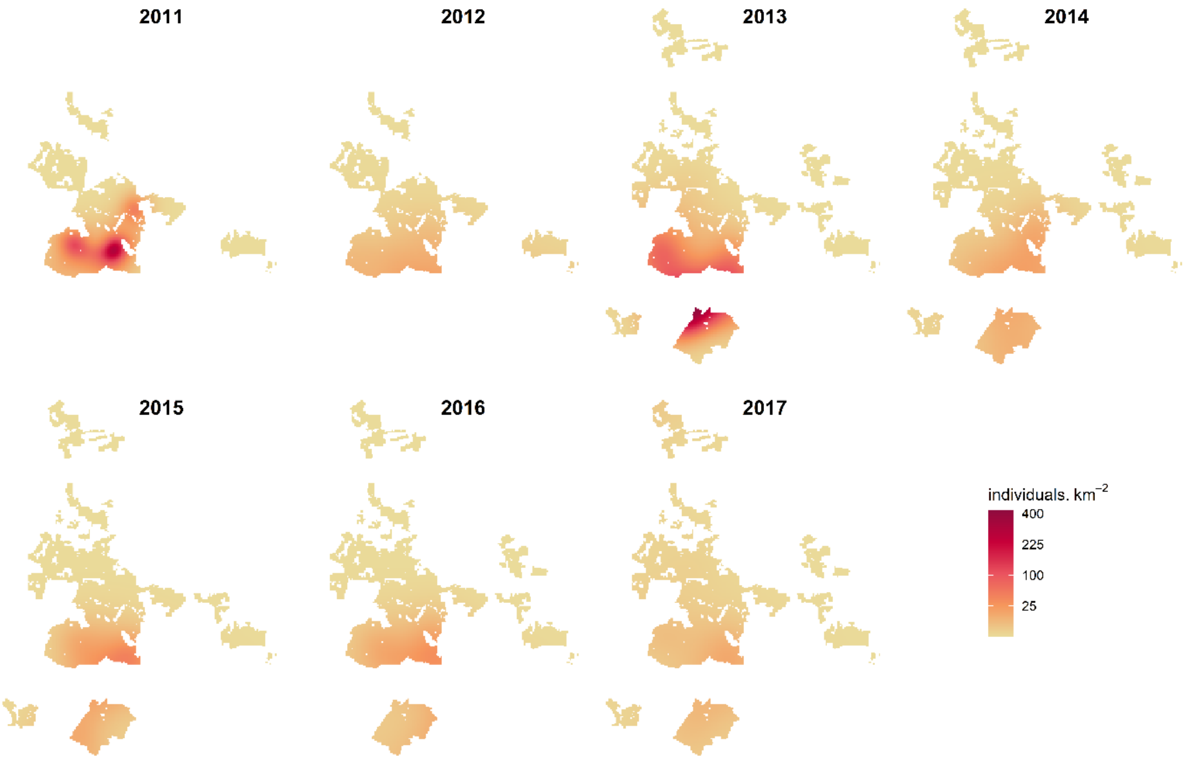
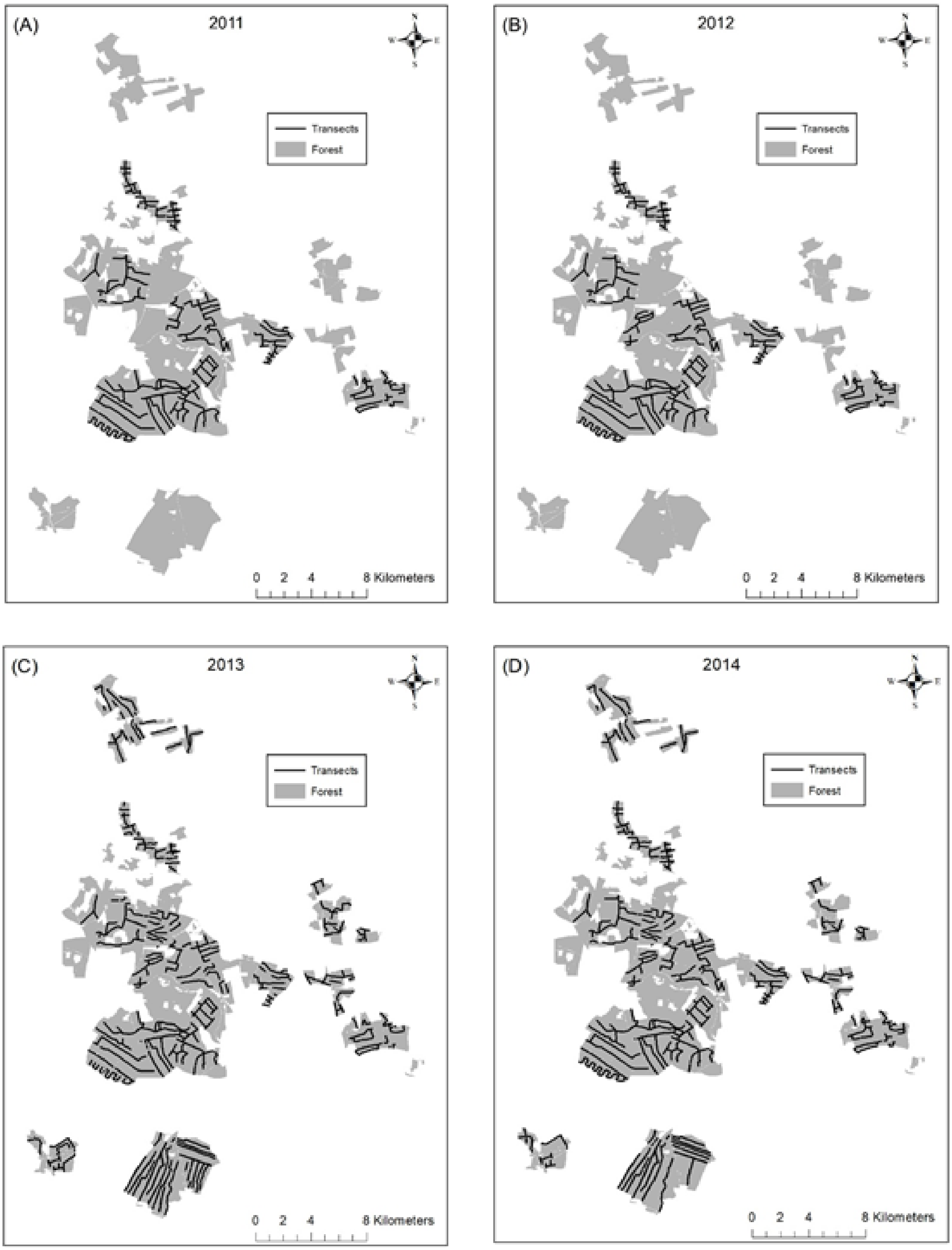


Figure A5.1: Annual fallow deer density across Thetford Forest 2011-2017. Shown are density surfaces (individuals/km^2) predicted at a 100x100m resolution from density surface models including latitude and longitude.

Appendix C. Annual extent of deer sampling by distance sampling transects



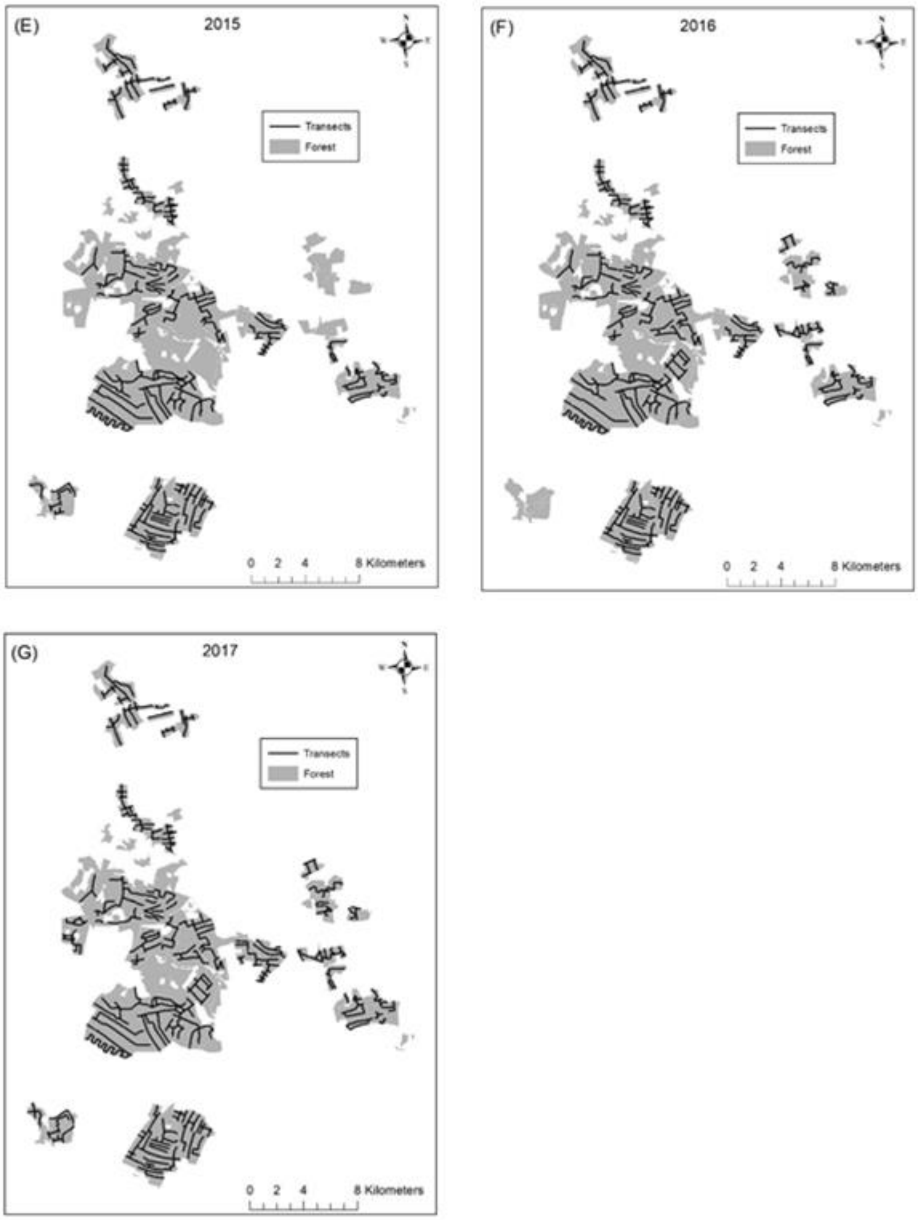


Figure A5.1: Annual thermal imaging distance sampling transects in Thetford Forest from 2011 to 2017. In each year, between 7 and 14 discrete forest blocks were surveyed and density was only estimated for the surveyed forest blocks. For details of transect length and segments, see Table A5.1.

Appendix D: Distance sampling thermal imaging surveys.

Distance sampling data were collected at night during the late winter as died-back vegetation allowed better detectability of animals and lower temperatures increase thermal contrast. One-sided transects were conducted from the front passenger seat of a 4-wheel drive a vehicle, driven at a maximum speed of 16 km/h with headlights off. The distance to each individual (or when a group was observed, the distance to the centre of the group) was measured using a Leica Laser Range Finder ‘LRF 800’ that was rigidly mounted on a night vision ‘Maxi-Kite Mk 4’ (THALES optics, St. Asaph, UK) with an infrared illuminator. An angle board was used to estimate (to 5°) the angle of the animal to the transect line to allow subsequent calculation of perpendicular distance.

Appendix E. Density surface models methodological detail

Density surface models (DSMs) predict the spatial variation of animal abundance by a two-step approach following (Miller et al., 2013); first, species-specific detection functions to account for declining detectability with greater perpendicular distance (Buckland et al., 2001) were fitted in order to select the key detection function, also incorporating a detectability class covariate (three levels: open, dense and mature) modelling differences in visibility class due to forest stand age and whether or not the stand had been thinned (see below for details on detectability class covariate). Separately for each survey year, the selected species-specific detection function and covariate were fitted, giving estimated abundance per surveyed transect segment (Table A5.1). Then, a Generalised Additive Model (GAM) modelled the relation between abundance per segment and latitude and longitude as a smoothing parameter using a penalised thin plate regression spline.

Table A5.1: Annual thermal imaging distance sampling transects in Thetford Forest from 2011 to 2017, showing for each year: the numbers of forest blocks surveyed, numbers of distance transect segments used in the density surface model, mean survey effort (transect distance relative to total block area) across surveyed blocks, and total length of transects driven .

Year	Number of blocks surveyed	Number of segments	Transect driven (km)	Mean effort (km/km^2)
2011	7	587	145.7	1.11
2012	7	604	150.5	1.14
2013	13	1075	264.8	1.41
2014	13	1078	264.0	1.41
2015	12	1013	245.2	1.47
2016	12	1075	264.5	1.45
2017	14	1239	299.8	1.60

Detectability class covariate and criteria for combining sections

As deer detectability during nocturnal thermal imaging distance sampling differs between forest growth stages (Hemami et al., 2007; Wäber and Dolman, 2015), I included a categorical variable in the detection function to model differences in detectability due to the tree crop age of the forest stand sampled by each transect section. Following (Hemami, 2003), detectability classes were classified *a priori* between three categories according to growth stage and management, as: ‘open’ (comprising permanent open areas, clear-felled unplanted stands, and recently restocked stands 0-3 years since planting); ‘dense’ (comprising restocked stands 4-5 years old, pre-thicket stands 6-10 years old and thicket stands 11-20 years old, and those pole stage stands, between 21-40 years old, that had not yet received a first thinning cut, when one in four tree rows are removed) and ‘mature’ (comprising those pole stage stands 21-40 years old that had received at least one thinning cut and all mature stands >40 years old).

The single-sided driven transects sequentially surveyed individual forest stands that differed in growth stage and potentially in visibility class, generating a series of short (n=2414, mean length 225 m, SD=128) transect ‘sections’ (with the start and end defined by each individual forest stand). Large numbers of sections with zero observations caused zero-inflation in the density surface model (DSM) and also inflated values of local density in those sections with one or more deer recorded. Therefore, to improve model precision and avoid zero-inflation, sections were combined into fewer, longer, composite ‘segments’ that were constrained to have a consistent visibility class. In a few instances (n=29) where longer individual sections (max length=944m, mean =700 m, SD=102) ran through or alongside a single large stand (of uniform visibility class), these were retained in their entirety. Remaining segments were created by running an algorithm structured such that the full extent of the combined segment was no greater than 600 m between the most distal points (combined start and end). As long as the constraints of overall length ≤600 m and common visibility class were met, a composite segment could comprise contiguous (end-to-end) sections, and/or non-contiguous sections interrupted by other sections differing in detectability class (that were kept unique, or combined in a different segment), with sections lying on the same or on alternative sides of the transect centre-line. Figure A5.1 shows three examples of this process, whereby the initial 2414 sections were merged and reduced to 1162 composite segments (mean length=462 m, SD=297).

Nearby or overlapping segments allowed models to control for detectability when estimating local density estimates that were then used to calibrate the density surface map.

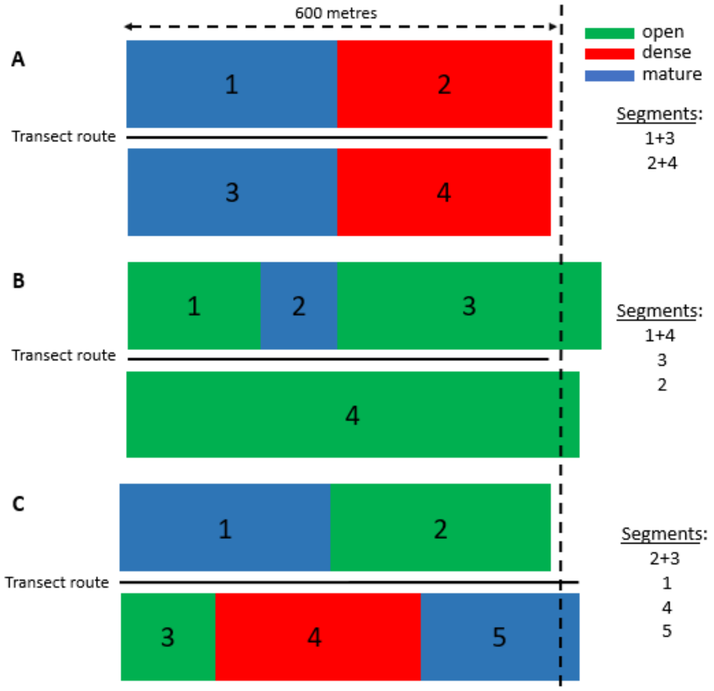


Figure A5.1: Schematic illustrating showing how nearby distance transect sections were combined into fewer longer segments of common detectability class (denoted by colours). In A: one segment comprised two single-sided sections that each sampled mature stands (1 and 3) on opposite sides of the transect centre-line, a second segment comprised two sections that each sampled dense stands (2 and 4). In B: one long section (4) exceeded 600 m but was not subdivided (as it sampled a single stand), this was combined with a short section (1) on the opposite side of the transect centre-line, that also sampled a stand of the same visibility class (open). Although the remaining section also sampled a stand of this visibility class (open), this section was not combined in the same segment as it projected further beyond section (4); section (2) sampled a different visibility class (mature) and was not combined with either of these segments (though would be a candidate for combination with other nearby section(s) further along the centre line if they also sampled a mature stand and lay within 600 m). In C: I combined two sections (2 and 3) on opposite sides of the transect centre-line as both sampled stands of the same visibility class (open) and lay within 600 m, while two sections (1 and 5) that sampled mature stands were not combined as they exceeded 600 m from start to finish, section (4) sampled a different visibility class (dense) and was therefore not combined with any of these segments; again sections 1, 5, 4 would be candidates for combination with other nearby sections lying within 600 m along the transect centre-line if these sampled the same visibility class.

Detection function, covariate and adjustments selection.

Analyses were conducted separately for each species, using data pooled across 2011 to 2017. I evaluated alternative detection function models fitting each of the available key detection functions: half-normal and hazard-rate with adjustments (cosine, hermite, polynomial), with and without a term relating group size to perpendicular distance (to account for potentially lower detectability of distant smaller groups) and with or without the categorical detectability class covariate. Following (Buckland et al., 2001) the 5% most distal observations were excluded. The model with the lowest value of Akaike's information criterion (AIC) was selected for each species, unless alternative models differed by less than 2 units when the most parsimonious model was also considered. Analyses were performed in R (R core Team, 2018) using package "Distance" (Miller, 2016).

For muntjac and roe deer, a hazard-rate detection function with detectability class and group size covariates were superior to alternative formulations (Table A5.2, Fig A5.2). For fallow deer, I selected the best fitting model (lower AIC value): a half-normal detection function with detectability class covariate and no support for group size covariate (Table A5.2, Fig A5.2), rejecting a more parsimonious model with similar degree of support (based on AIC) but that lacked the detectability class covariate that was considered necessary, as extensive fieldwork experience confirmed age class profoundly affects the ability to detect even large deer.

Table A5.2: Detection function, covariate and adjustment selection of muntjac, roe, fallow deer distance sampling data. For each model AIC and the difference in AIC value relative to the best supported model (ΔAIC) are shown

<table>
<tr><th colspan="4">Muntjac</th></tr>
<tr><th>Key function</th><th>Formula</th><th>AIC</th><th>ΔAIC</th></tr>
<tr><td>Hazard-rate</td><td>~detectability class + group size</td><td>21157.96</td><td>0</td></tr>
<tr><td>Hazard-rate</td><td>~detectability class</td><td>21162.81</td><td>4.852733</td></tr>
<tr><td>Hazard-rate</td><td>~hermite</td><td>21185.44</td><td>27.47821</td></tr>
<tr><td>Hazard-rate</td><td>~cosine</td><td>21185.44</td><td>27.47821</td></tr>
<tr><td>Hazard-rate</td><td>~polynomial</td><td>21185.44</td><td>27.47821</td></tr>
<tr><td>Hazard-rate</td><td>~1</td><td>21185.44</td><td>27.47821</td></tr>
<tr><td>Half-normal</td><td>~cosine</td><td>21193.64</td><td>35.67672</td></tr>
<tr><td>Half-normal</td><td>~polynomial</td><td>21237.64</td><td>79.68529</td></tr>
<tr><td>Half-normal</td><td>~detectability class + group size</td><td>21240.26</td><td>82.29678</td></tr>
<tr><td>Half-normal</td><td>~hermite</td><td>21242.98</td><td>85.01553</td></tr>
<tr><td>Half-normal</td><td>~detectability class</td><td>21243.19</td><td>85.22783</td></tr>
<tr><td>Half-normal</td><td>~1</td><td>21266.43</td><td>108.4673</td></tr>
<tr><th colspan="4">Roe deer</th></tr>
<tr><th>Key function</th><th>Formula</th><th>AIC</th><th>ΔAIC</th></tr>
<tr><td>Hazard-rate</td><td>~detectability class + group size</td><td>9688.111</td><td>0</td></tr>
<tr><td>Hazard-rate</td><td>~detectability class</td><td>9692.245</td><td>4.133737</td></tr>
<tr><td>Hazard-rate</td><td>~hermite</td><td>9718.419</td><td>30.3086</td></tr>
<tr><td>Hazard-rate</td><td>~cosine</td><td>9718.419</td><td>30.3086</td></tr>
<tr><td>Hazard-rate</td><td>~polynomial</td><td>9718.419</td><td>30.3086</td></tr>
<tr><td>Hazard-rate</td><td>~1</td><td>9718.419</td><td>30.3086</td></tr>
<tr><td>Half-normal</td><td>~detectability class + group size</td><td>9737.106</td><td>48.99535</td></tr>
<tr><td>Half-normal</td><td>~detectability class</td><td>9737.294</td><td>49.18303</td></tr>
<tr><td>Half-normal</td><td>~cosine</td><td>9738.816</td><td>50.70492</td></tr>
<tr><td>Half-normal</td><td>~hermite</td><td>9744.298</td><td>56.18685</td></tr>
<tr><td>Half-normal</td><td>~polynomial</td><td>9761.627</td><td>73.51579</td></tr>
<tr><td>Half-normal</td><td>~1</td><td>9761.627</td><td>73.51579</td></tr>
</table>

Fallow deer			
Key function	**Formula**	**AIC**	**ΔAIC**
Half-normal	~detectability class	3197.52	0
Hazard-rate	~hermite	3197.575	0.054453
Hazard-rate	~cosine	3197.575	0.054453
Hazard-rate	~polynomial	3197.575	0.054453
Hazard-rate	~1	3197.575	0.054453
Hazard-rate	~detectability class	3198.036	0.515737
Half-normal	~hermite	3198.068	0.547442
Half-normal	~cosine	3198.068	0.547442
Half-normal	~polynomial	3198.068	0.547442
Half-normal	~1	3198.068	0.547442
Half-normal	~detectability class + group size	3199.128	1.607455
Hazard-rate	~detectability class + group size	3200.034	2.5136

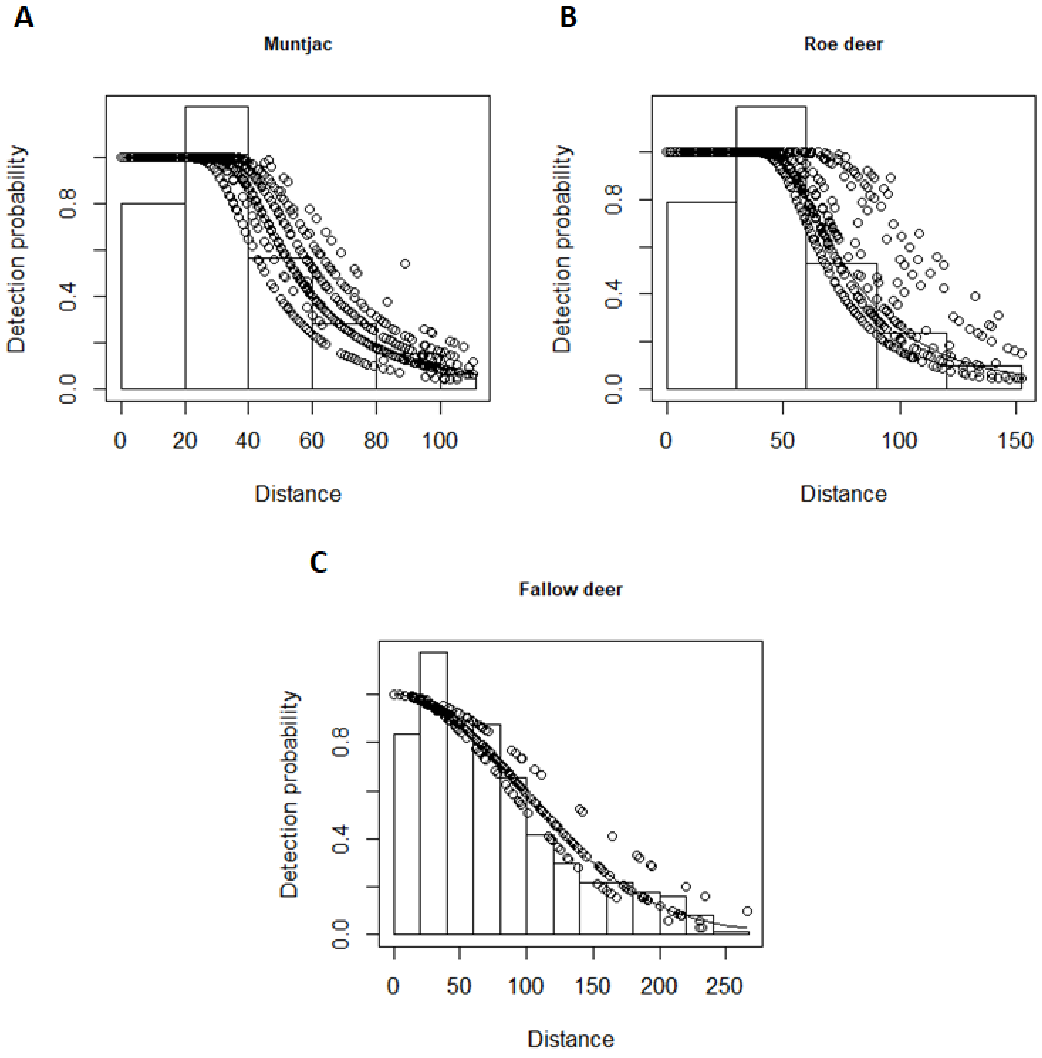


Figure A5.2: Species-specific detection functions. Selected species-specific detection functions of muntjac (A), roe deer (B) and fallow deer (C) of distance sampling data pooled across 2011 to 2017. Continuous lines represent the average detection function, while hollow points represent observations along the categories of the covariate adjustments: for muntjac and roe deer these consider detectability class and group size covariates; for fallow, detectability class.

Density surface models year-specific parameters

Separately for each deer species, the selected detection functions and adjustments were used to predict the density in each transect segment. Pooling the detection function across years would not allow fitting of species-specific annual DSMs, therefore, separate detection functions were fitted each year using a consistent detection function formulation based on the exploration of pooled data (see above). The number of observations differed annually (Table A5.3), as a result of changes in deer densities and also sampling effort (Table A5.1), but were sufficient to allow fitting of robust annual species-specific detection functions allowing annual species-specific Density Surface Models to be generated (Table A5.3).

Table A5.3. Annual species-specific number of observation and Effective Strip Width and average species-specific density. For each year number of group observations, Effective Strip Width (ESW) and average species specific density of deer across the surveyed blocks for each species muntjac, roe and fallow deer are reported.

Year	**Muntjac**			**Roe deer**			**Fallow deer**		
	N. obs	**ESW**	**Deer /km^{-2}**	**N. obs**	**ESW**	**Deer /km^{-2}**	**N. obs**	**ESW**	**Deer /km^{-2}**
2011	231	57	12.6	95	94	3.7	42	23	6.3
2012	205	54	11.1	93	86	3.6	30	142	0.6
2013	440	61	12.2	182	76	4.2	55	24	3.6
2014	295	54	9.3	149	83	3.3	47	114	0.8
2015	273	55	9.3	129	97	2.4	47	90	1.2
2016	397	60	11.4	163	77	3.9	53	120	0.9
2017	662	70	15.2	260	83	4.8	45	142	0.5

Table A5.4: Species-specific Coefficients of Variation (CV) of detection functions, GAM and total CV.

	CV Detection function	CV from GAM	Total CV
Roe 2011	0.12	0.32	0.34
Roe 2012	0.09	0.21	0.23
Roe 2013	0.06	0.1	0.11
Roe 2014	0.06	0.09	0.11
Roe 2015	0.05	0.12	0.14
Roe 2016	0.08	0.1	0.13
Roe 2017	0.04	0.07	0.08
Muntjac 2011	0.05	0.32	0.33
Muntjac 2012	0.06	0.15	0.16
Muntjac 2013	0.04	0.06	0.07
Muntjac 2014	0.04	0.07	0.08
Muntjac 2015	0.05	0.07	0.09
Muntjac 2016	0.04	0.06	0.08
Muntjac 2017	0.03	0.04	0.05
Fallow deer 2011	0.66	0.34	0.74
Fallow deer 2012	0.1	1.62	1.62
Fallow deer 2013	0.63	0.27	0.69
Fallow deer 2014	0.12	0.19	0.23
Fallow deer 2015	0.25	0.2	0.33
Fallow deer 2016	0.08	0.19	0.21
Fallow deer 2017	0.33	0.19	0.38

Fallow deer annual observations were lower compared to the observations collected for the other species and detection function less robust (Table A5.4). Fallow deer are herding animals (average group size across years =5.0, SD =3.4), with much wider home ranges (average across winter and spring home ranges = 219ha, Borkowski & Pudełko 2007) while muntjac and roe are relatively sedentary (average across winter and spring home ranges =19.4ha and 73.9ha, Chapman *et al.* 1993) and occur only singly or in small groups (average group size across years: muntjac = 1.2, SD 0.4; roe deer = 1.7, SD 0.8). Consequently, when collecting distance sampling thermal imaging data for fallow detecting (or missing) a single herd introduces greater sampling error than for the two smaller species. Annual density surfaces were generated for fallow deer as a running mean across the focal and adjacent years (for 2011: mean of 2011-12; for all other years 2012-2017: the running average of three years centred on the focal year as data from 2018 were also available). For the two smaller species robust annual density surfaces were generated, owing partly to their greater overall frequency.

References

Borkowski, J., Pudełko, M., 2007. Forest habitat use and home-range size in radio-collared fallow deer. Ann. Zool. Fennici 44, 107–114.

Buckland, S.T., Anderson, D.R., Thomas, L., Burnham, K.P., Laake, J.L., Borchers, D.L., 2001. Line transects, in: Introduction To Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, pp. 104–14.

Chapman, N.G., Claydon, K., Claydon, M., Forde, P.G., Harris, S., 1993. Sympatric populations of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*): a comparative analysis of their ranging behaviour, social organization and activity. J. Zool. 229, 623–640. https://doi.org/10.1111/j.1469-7998.1993.tb02660.x

Hemami, M.R., 2003. The ecology of roe deer (Capreolus capreolus) and muntjac (Muntiacus reevesi) in a forested landscape in eastern England. University of East Anglia.

Hemami, M.R., Watkinson, A.R., Gill, R.M.A., Dolman, P.M., 2007. Estimating abundance of introduced chinese muntjac Muntiacus reevesi and native roe deer Capreolus capreolus using portable thermal imaging equipment. Mamm. Rev. 37, 246–254. https://doi.org/10.1111/j.1365-2907.2007.00110.x

Miller, D.L., 2016. Package ‘Distance.’

Miller, D.L., Burt, M.L., Rexstad, E.A., Thomas, L., 2013. Spatial models for distance sampling data: recent developments and future directions. Methods Ecol. Evol. 4, 1001–1010. https://doi.org/10.1111/2041-210X.12105

R core Team, 2018. R: A Language and Environment for Statistical Computing.

Wäber, K., Dolman, P.M., 2015. Deer abundance estimation at landscape-scales in heterogeneous forests. Basic Appl. Ecol. 16, 610–620. https://doi.org/10.1016/j.baae.2015.06.005

Chapter Six

Conclusion

Conclusion

In this thesis I examined the diverse deer assemblage in Thetford Forest to explore aspects of deer ecology related to their densities, fertility, inter- and intra-specific competition, and impacts on commercial forestry. I examined how local deer density responds to local habitat or landscape context, in order to evaluate the usefulness of forest management as a tool in creating higher and lower deer densities to focus cull efforts. Another aim of the study was to identify which of the four species were mainly responsible for the impacts on tree crops and quantify a deer density threshold required for forest establishment. This thesis also comprises one of the first studies examining consequences of habitat and inter-specific competition on fertility and body mass in this complex species assemblage.

Local habitat effects on deer densities

Local deer density reduction is often needed to ensure woodland and forest regeneration (Gill 1992b; Côté *et al.* 2004). However, reduction of deer numbers may not be immediately achievable across a landscape because of inadequate resources. As forest management dramatically changes the habitat, that in turn, affects how suitable the forest is for the deer (Reimoser 2003), I explored to what extent knowledge of drivers of deer densities could be used as a tool to mitigate impacts. My results show that, although local habitat management affected roe and muntjac densities, the magnitude of the change was small for both species. This suggests the opportunity to place vulnerable crops in areas attracting fewer roe or muntjac, or shielding vulnerable crops by managing recreational access, may not be effective as a tool for mitigating impacts by these smaller deer. Furthermore, in this system damage to pine crops was primarily caused by larger deer (discussed further below); these species are wide-ranging and thus less susceptible to local habitat structure or manipulation of recreation. Roe deer preference for young stands (or young growth forest) is well known and has been attributed to the high settling stimuli of restocked stands within forests with visual separation of biotopes (Reimoser & Ellenberg 1999). Muntjac densities, on the other hand, were higher in mature stands and calcareous soil. Based on their body size, roe deer and muntjac are both concentrate selectors (Bodmer 1990); however, as muntjac body mass is even smaller than roe and adapted to tropical climates, differences in habitat selection are to be expected. Restocked stands offer more food (Smolko, Veselovská & Kropil 2018) than mature stands, but little cover for thermal protection. This lack of cover might be a limiting factor for muntjac that instead, selects better food patches on calcareous soils within the mature stands. These habitat preferences were consistent with a study in Thetford using pellet counts (Hemami, Watkinson & Dolman 2004). Abundance of both species was lower closer to grasslands, likely due to competition with fallow (see Chapter 5) and red deer (to a lesser extent since their densities are much lower in Thetford forest) grazing in grasslands (Thirgood 1995; Trdan & Vidrih 2008).

The most interesting outcome of this analysis was the response of deer to recreationists with roe deer densities being lower in areas of high recreation, while the reverse was true for muntjac. However, the magnitude of the effect of recreation on deer densities was also small, limiting the potential application for management. Nevertheless, these results emphasise important aspects of the ecology of roe and muntjac, showing the greater potential of the muntjac to adapt to highly disturbed environments. This is consistent with the widely reported, increased occurrence of this species in urban environments (perhaps because of their small size and solitary nature) more so than the occurrence of roe (PTES 2017, 2018). Despite their disadvantage in urban areas, roe deer have successfully increased in the UK countryside; data from National Gamebag Census and Breeding Bird Survey (BBS) document the roe deer increase in number from 1995 to 2009 (Noble *et al.* 2012), while the 2017 BBS report shows roe deer have increased in rural areas by 81% from 2006 to 2017 (Harris *et al.* 2018). Roe deer avoidance of human disturbance and muntjac tolerance of it should be further investigated as they can affect the effectiveness of their population control (see practical applications to deer and forest management).

Impacts on tree crops

Fallow deer were apparently responsible for most of the herbivory impacts on commercial crops in Thetford Forest. To reduce browsing damage to an acceptable level (20% Prien & Müller 2010) densities of fallow deer need to be reduced to 0.06 individuals/km^2. Managing fallow deer down to such low numbers is impractical as it requires investing a lot of resources in staff culling deer. The same 20% damage can be achieved by focusing cull efforts on both large deer and reducing their densities to 2.3 individuals/km^2. This may also require a concerted effort from all the adjacent landowners, to cull fallow and red deer at a wide scale and avoid source-sink movements (Wäber, Spencer & Dolman 2013). Other studies report higher, more easily achievable thresholds. For Scots pine regeneration in Scotland semi-natural woodland (where other food such as heather is also accessible in the close by heather-moorland) a density of 3.5 red deer/km^2 was indicated (Rao 2017) and other studies on pine regeneration indicated similar densities ranging from 3-5 individuals/km^2 (Holloway 1967; Beaumont *et al.* 1995; Staines, Balharry & Welch 1995; Scott *et al.* 2000). Scots pine is a less preferred tree species than most broadleaves (Gill 1992a) and for establishment of broadleaved woodlands, an even lower deer density may be required, as highlighted in Spake et al., (2020), however tree establishment is also influenced by resilience to browsing and loss of value due to browsing. This contrasts with the relatively high sustainable density required for natural regeneration (which is less prone to damage than a forest managed by clear-felling and replanting) such as 10 deer/km^2 predicted for English coniferous and deciduous lowland woodlands (Gill & Morgan 2010) or the 7-9 deer/km^2 in deciduous forests in northwestern Pennsylvania (Horsley, Stout & De Calesta 2003). Contrasting density thresholds for regeneration are partly attributable to differences in the availability of alternative food in the study areas examined, some are due to the management system. Plantations consist of a few thousands seedlings per hectare, while natural regeneration can offer several hundred thousand seedlings per hectare (Reimoser & Gossow 1996) and thus have greater inherent redundancy and resilience. Second, solitary seedlings (as placed in planted forests) are more likely to be browsed (Reimoser & Gossow 1996), and lastly restocked areas are more attractive to deer. An experiment in western Poland shows all ungulate species present (European bison *Bison bonasus*, red deer, roe deer, moose *Alces alces* and wild boar *Sus scrofa*) visited clear-felled areas twice as much compared to closed forest stands (Kuijper *et al.* 2009); this means that the economically sustainable density (related to the losses due to deer damage) of a clear-cut management regime is much lower than the habitat-related density when settling stimuli are high, but productivity is low (Reimoser & Gossow 1996). It is thus expected that restocking more palatable species such as broadleaves will be even more challenging than restocking pines (Pépin *et al.* 2006; Spake *et al.* 2020), as I can the threshold for large deer (already very low) will be even lower for broadleaves. In addition, roe deer and muntjac, while being unlikely to impact on pine crops (Chapter 3) are known to browse on deciduous species (Kay 1993; Cooke & Lakhani 1996; Cooke 2001), compounding the impact of larger species.

Roe deer fertility

The analysis of the long-term dataset (2002-2016, Chapter 4) showed roe deer fertility and body mass were only affected by arable lands, with roe deer being heavier in arable and at the same time, being less fertile. At current, low roe deer density, this implies that the forest habitat overall is highly suitable for this species as the forest management regimes creates a mosaic of growth stages where deer have easy access to cover and food. A previous study in Thetford Forest showed similar results, with roe that had greater access to arable being heavier, but with fertility not being affected by access to farmlands (Wäber 2010). Fragmented woodland, with close access to farmlands are thought to be among the causes for the increase in deer densities in the northern hemisphere – according to the 'fragmentation nutrition hypothesis' (Sinclair 1997). However, despite roe being heavier when closer to arable, their fertility was lower, contradicting this hypothesis. Further analysis (Chapter 5) revealed that this counter-intuitive effect may have arisen as a proxy for the detrimental effect of high muntjac densities (that are greater near arable lands) on roe deer fertility. In Thetford Forest, muntjac outnumber roe deer two- to three-fold, and my findings show this to affect roe deer fertility; the mechanism through which this happens is however unclear. Roe deer could reduce the number of embryo's carried because of increased stress resulting from high number of muntjac, or as a result of depletion of important forage resources. The concept that fertility is linked to levels of glucocorticoids (cort-fitness hypothesis; Bonier *et al.* 2009) has been explored and received support in roe deer (Escribano-Avila *et al.* 2013), but this test referred to habitat features and season, rather than the presence of other deer species. In a heavily hunted population such as the one analysed in this thesis, source-sink population dynamics are driven by the cull targets placed by landowners. As roe deer are currently managed well below any carrying capacity, the effect of muntjac on roe deer fertility is therefore slight, but combined with the displacement by fallow deer widely reported in the literature, inter-specific competition from these two species is likely to have some effects on roe deer demography and source-sink dynamics. Previous literature shows fallow deer being aggressive towards roe (Ferretti 2011b), and roe deer densities being negatively related to fallow deer densities (Carne 1954, 1955; Ferretti *et al.* 2011). This was not confirmed by my results, likely due to the overall low roe density in the study area. A negative relation between muntjac and fallow deer instead was highlighted by the analysis and this has never been reported for muntjac before. As muntjac are smaller in size the same interspecific aggression observed for the roe deer is to be expected.

Practical applications to deer and forest management

Culling is expensive but necessary for successful natural tree regeneration, particularly as other tree protection methods currently available – such as deer fencing - are costly (Gill 2003) at around 7.2 pounds per metre. Using bigger fences, would reduce the cost per m^2 of crop protected. In underplanted areas the advantage of big fences comes at the cost of increased time spent by staff culling deer that are sometimes left inside underplanted forest stands when trying to exclude them from such a big area. Fences have additional associated costs, for example, the cost of monitoring fence integrity, as they can be damaged by falling trees, the public, or deer and dogs breaking into them (pers. Comm.). When the fence is structurally intact its effectiveness is still not entirely guaranteed as large deer are able to jump into the fenced areas (pers. Comm.) currently used in Thetford (fence height = 1.8m). To reduce the pressure on deer to break or jump in the fenced areas (nullifying crop protection efforts) densities outside the fence still need to be kept low. An abrupt increase in fenced areas, would artificially increase densities of deer, requiring more culling efforts outside of fences. Culling, however, would be more difficult as both deer and recreationists would have access to a smaller area of the forest for their activities. This is exemplified in Kings Forest (one of the southern blocks of Thetford Forest) where recreational activity is high and fenced area has increased from 4 to 8% from 2018 to 2019 and the impact on the crop in the block is among the highest (60% on average). Managers concerned with the effects of deer on forest ecosystems should focus on deer impact as well as deer density in making management decisions. Ideally, managers would use sustainable density targets to trade-off the cost of ranger time with the cost of the damage on the forest crop caused by a given deer density. To do this, monitoring of deer populations is required, as well as a landscape-scale approach to deer management, to coordinate efforts across large areas. In Thetford Forest, where the deer density target is not achievable short-term, postponing clear-felling (and thus replanting) is an alternative solution, provided the minimum area of open ground within the forest required for Breckland invertebrates as well as woodlark (*Lullula arborea*) and nightjar (*Caprimulgus Europaeus*) is already met.

Evidence suggests that muntjac, fallow and red deer populations are more difficult to manage than roe deer. Muntjac can use areas with high human disturbance more than roe, giving them an advantage in highly urbanised Britain; culling is more difficult in urban areas where proximity to roads and houses makes it almost impossible to cull safely. Fallow and red deer on the other hand, are wider-ranging and their management is more difficult as it requires a landscape-scale approach with neighbouring landowners sharing the same strategy. As fallow and red are more difficult to manage and have been shown to have greater impacts on forestry than roe, when tree establishment is concerned these should be the species on which to focus management resources. When biodiversity is concerned, efforts should also include muntjac and roe. Muntjac however, have been classed as non-native, invasive species (DEFRA 2018); this combined with the evidence for inter-specific competition with the native roe (Chapter 5) supports the idea that muntjac should be preferentially targeted over roe.

Provision of opportunities of outdoor recreation has been identified as an important ecosystem service for humans economy and well-being (Chan *et al.* 2006) and nature-based activities have become more popular (Flather & Cordell 1995). Fallow and red deer have been shown to be affected by recreation (Boer *et al.* 2004; Sibbald *et al.* 2011; Westekemper *et al.* 2018). In south-western Germany a spatial zonation of hunting, recreational access, forestry and red deer habitat management was implemented. Analysis of red deer GPS data reveal that individual pattern of habitat use was determined by recreational access so that areas where low or no recreational access was allowed were used significantly less than quieter zones where also a higher level of impact to the forest was expected and accepted by managers (Coppes *et al.* 2017). Red deer are known for being more susceptible to disturbance (Jiang, Zhang & Ma 2008) than roe and occur at low densities in the forest (presumably as a consequence of the high recreational disturbance within the forest) while being in higher numbers in the neighbouring Stanford training area (unpublished). Similarly, fallow deer have been reported to be in higher numbers in the shooting ranges within the forest where no recreationists are allowed (unpublished). My results (Chapter 2) show roe deer are slightly, though significantly, negatively affected by recreation; in Thetford, however, recreational access is pervasive across the whole forest with overall little variance between areas of high and low recreational disturbance and stronger effects could be achieved if a level of zonation as described in Coppes et al., (2017) was implemented for safer culling and impact mitigation. While outdoor recreation can be used for deer impact mitigation, (Coppes *et al.* 2017) its numerous negative effects (Marzano & Dandy 2012) need to be accounted for when planning forest access to visitors.

Further research

Thetford Forest rely on a clear-felling management regime to create open areas within the forest that are important for Breckland invertebrates and bird species such as woodlark and nightjar (Wright *et al.* 2007; Lin, James & Dolman 2007). Clear-cuts make forest establishment more challenging for mitigating deer damage (Reimoser & Gossow 1996) and across the UK deer currently pose one of the main threat to forest establishment. This is why it is important to identify an economically viable tree species that is less palatable or more resilient to browsing to ensure forest resilience. Some studies have attempted a comparison of effects of browsing in different tree species and the economic implications of the damage, showing species such as larch (*Larix spp.*) and sycamore (*Acer pseudoplatanus*) to be resilient to repeated browsing (Perks, Smith & McEvoy 2005; Hein *et al.* 2009), but more research is needed regarding species-specific resilience to browsing and palatability. More research examining underplanting (planted trees benefitting from older trees shelter), as an alternative for some sites to either open restocks or natural regeneration is needed, as well as alternative protection methods.

Recreation affects disturbance-sensitive species such as some ground-nesting birds including *woodlark Lullula arborea*, nightjar and stone curlew *Burhinus oedicnemus* (Mallord *et al.* 2006; Liley & Sutherland 2007) and birds of prey (Martínez-Abraín *et al.* 2010) while other indirect impacts arise, for example, from tramping on vegetation (Littlemore & Barker 2001; Cole 2004), or from soil compaction leading to reduced microbial activity (Kissling *et al.* 2009). A more comprehensive research approach is needed on the management of recreation under different systems, for example, comparing a zonation system (with access to recreationists restricted to some areas such as the one described in Coppes et al., 2017), with access of recreationists permitted across the whole area (such as Thetford Forest). Quantifying the trade-offs associated with deer impact mitigation (derived from deer densities being lower in areas if high recreational activity) and impacts on disturbance-sensitive species under these scenarios is needed to explore potential application of managing recreation without having detrimental effects on biodiversity.

This thesis showed that large deer were responsible for most of the impacts on forestry in this pine-dominated system and studies show both species also have impacts on biodiversity (e.g. Baines, Sage & Baines 1994; Holt, Fuller & Dolman 2010). A substantial body of literature, however, shows smaller roe and muntjac deer to also have impacts on flora and more widely understorey vegetation (Kay 1993; Massey & Welch 1993; Cooke 1997, 2001; Sage *et al.* 2004; Joys, Fuller & Dolman 2004), suggesting thresholds for biodiversity would need to account for large deer as well as smaller deer species. It is then crucial for conservation to establish its own species-specific deer densities (Mitchell & Kirby 1990).

As the roe deer is subject to inter-specific competition from both muntjac and fallow (Chapter 5, Ferretti, 2011; Focardi et al., 2006), as well as red deer (Richard *et al.* 2009) it is important to understand how the ecosystem services provided by roe deer would differ if replaced by muntjac or any of the other deer species. Firstly, the increased abundance of a non-native invasive species over the native or even the loss of the native species altogether, would decrease naturalness of this ecosystem (Siipi 2004). This may have repercussions on the public enjoyment of nature as wild animals are objects of aesthetic appreciation (Parson 2007), but whether the wider public appreciates the difference in naturalness is unknown. More importantly, even if roe and muntjac have similar diets and body size, social and ranging behaviour, the role in the ecosystem of roe deer may not be replaced by muntjac in its entirety. For example, it has been shown that muntjac has lower endo-zoochorous seed dispersal rate than muntjac (Eycott *et al.* 2007), but other ecosystem services might be affected as well. For example, muntjac browsing preferences can be different as this species is native to south-east Asia and might have evolved different responses to plant defences than the roe deer, thus being able to browse on different plant species, than the roe. The different, less thick coat of the muntjac can also make it more prone to tick infestation than that of the roe deer (pers. Comm.), affecting the ability to spread tick borne diseases.

More research is needed to understand ecosystem dynamics and impacts of modified ungulate assemblages across the world.

References

Baines, D., Sage, R.B. & Baines, M.M. (1994) The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *The Journal of Applied Ecology*, **31**, 776.

Beaumont, D., Dugan, D., Evans, G. & Taylor, S. (1995) Deer management and tree regeneration in the RSPB Reserve at Abernethy forest. *Our Pinewood Heritage* (ed J.R. Aldous), pp. 186–195. Forestry Commission, RSPB, SNH.

Bodmer, R.E. (1990) Ungulate frugivores and the browser-grazer continuum. *Oikos*, **57**, 319.

Boer, H.Y. de, Breukelen, L. van, Hootsmans, M.J.M. & Wieren, S.E. van. (2004) Flight distance in roe deer, *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. *Wildlife Biology*, **10**, 35–41.

Bonier, F., Martin, P.R., Moore, I.T. & Wingfield, J.C. (2009) Do baseline glucocorticoids predict fitness? *Trends in Ecology & Evolution*, **24**, 634–642.

Carne, P.H. (1954) Roe deer, fallow and sika. *Oryx*, **2**, 388–391.

Carne, P.H. (1955) Roe deer and fallow. *Oryx*, **3**, 104.

Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C. & Daily, G.C. (2006) Conservation planning for ecosystem services. *PLoS Biology*, **4**, e379.

Cole, D. (2004) Impacts of hiking and camping on soils and vegetation: a review. *Environmental Impacts of Ecotourism* (ed R. Buckley), pp. 41–60. CABI, New York.

Cooke, A.S. (1997) Effects of grazing by muntjac (*Muntiacus reevesi*) on bluebells (*Hyucinthoides non-scripta*) and a field technique for assessing feeding activity. *Journal of Zoology*, **242**, 365–369.

Cooke, A.S. (2001) Impact of muntjac deer (*Muntiacus reevesi*) at Monks Wood National Nature Reserve, Cambridgeshire, eastern England. *Forestry*, **74**, 241–250.

Cooke, A.S. & Lakhani, K.H. (1996) Damage to coppice regrowth by muntjac deer *Muntiacus* *reevesi* and protection with electric fencing. *Biological Conservation*, **75**, 231–238.

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**, e0175134.

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.

DEFRA. (2018) *Tackling Invasive Non-Native Species: A New Enforcement Regime*.

Escribano-Avila, G., Pettorelli, N., Virgos, E., Lara-Romero, C., Lozano, J., Barja, I., Cuadra, F.S. & Puerta, M. (2013) Testing Cort-Fitness and Cort-Adaptation hypotheses in a habitat suitability gradient for roe deer. *Acta Oecologica*, **53**, 38–48.

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**, 107–118.

Ferretti, F. (2011a) Interspecific aggression between fallow and roe deer. *Ethology Ecology and Evolution*, **23**, 179–186.

Ferretti, F. (2011b) Interspecific aggression between fallow and roe deer. *Ethology Ecology & Evolution*, **23**, 179–186.

Ferretti, F., Bertoldi, G., Sforzi, A. & Fattorini, L. (2011) Roe and fallow deer: are they compatible neighbours? *European Journal of Wildlife Research*, **57**, 775–783.

Flather, C. & Cordell, C. (1995) Outdoor recreation: historical and anticipated trends. *Wildlife and Recreationists: Coexistence Through Management* (eds R. Knight & K. Gutzwil- ler), p. Island Press, Washington DC, USA.

Focardi, S., Aragno, P., Montanaro, P. & Riga, F. (2006) Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. *Ecography*, **29**, 407–417.

Gill, R.M.A. (1992a) A review of damage by mammals in north temperate forests: 1. Deer.

Forestry, **65**, 145–169.

Gill, R.M.A. (1992b) A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. *Forestry*, **65**, 363–388.

Gill, R.M.A. (2003) The economic implications of deer damage in forests and woodlands. *Proceedings of the Future for Deer Conference*, p. English Nature Research Report No. 548.

Gill, R.M.A. & Morgan, G. (2010) The effects of varying deer density on natural regeneration in woodlands in lowland Britain. *Forestry*, **83**, 53–63.

Harris, S.J., Massimino, D., Gillings, S., Eaton, M.A., Noble, D.G., Balmer, D.E., Procter, D. & Pearce-Higgins, J.W., Woodcock, P. (2018) *The 2017 BBS Report*.

Hein, S., Collet, C., Ammer, C., Goff, N. Le, Skovsgaard, J.P. & Savill, P. (2009) A review of growth and stand dynamics of *Acer pseudoplatanus L.* in Europe: implications for silviculture. *Forestry*, **82**, 361–385.

Hemami, M.R., Watkinson, A.R. & Dolman, P.M. (2004) Habitat selection by sympatric muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a lowland commercial pine forest. *Forest Ecology and Management*, **194**, 49–60.

Holloway, C.W. (1967) *The Effect of Red Deer and Other Animals on Naturally Regenerated Scots Pine. Ph.D. Thesis.* University of Aberdeen.

Holt, C.A., Fuller, R.J. & Dolman, P.M. (2010) Experimental evidence that deer browsing reduces habitat suitability for breeding common nightingales *Luscinia megarhynchos*. *Ibis*, **152**, 335–346.

Horsley, S.B., Stout, S.L. & De Calesta, D.S. (2003) White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications*, **13**, 98–118.

Jiang, G., Zhang, M. & Ma, J. (2008) Habitat use and separation between red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus pygargus bedfordi* in relation to human disturbance in the Wandashan Mountains, northeastern China. *Wildlife Biology*, **14**, 92–

100.

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**, 23–37.

Kay, S. (1993) Factors affecting severity of deer browsing damage within coppiced woodlands in the south of England. *Biological Conservation*, **63**, 217–222.

Kissling, M., Hegetschweiler, K.T., Rusterholz, H.P. & Baur, B. (2009) Short-term and long-term effects of human trampling on above-ground vegetation, soil density, soil organic matter and soil microbial processes in suburban beech forests. *Applied Soil Ecology*, **42**, 303–314.

Kuijper, D.P.J., Cromsigt, J.P.G.M., Churski, M., Adam, B., Jędrzejewska, B. & Jędrzejewski, W. (2009) Do ungulates preferentially feed in forest gaps in European temperate forest? *Forest Ecology and Management*, **258**, 1528–1535.

Liley, D. & Sutherland, W.J. (2007) Predicting the population consequences of human disturbance for ringed plovers Charadrius hiaticula: a game theory approach. *Ibis*, **149**, 82–94.

Lin, Y.-C., James, R. & Dolman, P.M. (2007) Conservation of heathland ground beetles (Coleoptera, Carabidae): the value of lowland coniferous pantations. *Biodiversity and Conservation*, **16**, 1337–1358.

Littlemore, J. & Barker, S. (2001) The ecological response of forest ground flora and soils to experimental trampling in British urban woodlands. *Urban Ecosystems*, **5**, 257–276.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2006) Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology*, **44**, 185–195.

Martínez-Abraín, A., Oro, D., Jiménez, J., Stewart, G. & Pullin, A. (2010) A systematic review of the effects of recreational activities on nesting birds of prey. *Basic and Applied Ecology*, **11**, 312–319.

Marzano, M. & Dandy, N. (2012) Recreationist behaviour in forests and the disturbance of wildlife. *Biodiversity and Conservation*, **21**, 2967–2986.

Massey, M.E. & Welch, R.C. (1993) *Monks Wood - The Experience of 40 Years 1953-93*.

Mitchell, F.J.G. & Kirby, K.J. (1990) The impact of large herbivores on the conservation of semi-natural woods in the british uplands. *Forestry*, **63**, 333–353.

Noble, D.G., Aebischer, N.J., Newson, S.E., Ewald, J.A. & Dadam, D. (2012) A comparison of trends and geographical variation in mammal abundance in the breeding bird survey and the national gamebag census. *JNCC Report*, **468**, 2012.

Parson, G. (2007) The aesthetic value of animals. *Environmental Ethics*, **29**, 151–169.

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**, 302–313.

Perks, M., Smith, S. & McEvoy, C. (2005) Development of multiple leaders in sitka spruce and Japanese larch following outplanting. *Information note - Forestry Commission, Edinburgh*, 1–6.

Prien, S. & Müller, M. (2010) *Wildschäden Im Wald. Ökologische Grundlagen Und Integrierte Schutzmaßnahmen*. Neumann-Newdamm.

PTES. (2017) Living with mammals update 2017. *British Wildlife*.

PTES. (2018) Living with mammals update 2018. *British Wildlife*.

Rao, S.J. (2017) Effect of reducing red deer *Cervus elaphus* density on browsing impact and growth of Scots pine *Pinus sylvestris* seedlings in semi-natural woodland in the Cairngorms, UK. *Conservation Evidence*, **14**, 22–26.

Reimoser, F. (2003) Steering the impacts of ungulates on temperate forests. *Journal for Nature Conservation*, **10**, 243–252.

Reimoser, F. & Ellenberg, H. (1999) Forest management systems as a component of ungulate-game pest management with special reference to roe deer and edge effects. *Advances in Vertebrate Pest Management*, pp. 219–238.

Reimoser, F. & Gossow, H. (1996) Impact of ungulates on forest vegetation and its dependence on the silvicultural system. *Forest Ecology and Management*, **88**, 107–119.

Richard, E., Gaillard, J.M., Saïd, S., Hamann, J.L. & Klein, F. (2009) High red deer density depresses body mass of roe deer fawns. *Oecologia*, **163**, 91–97.

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**, 115–120.

Scott, D., Welch, D., Thurlow, M. & Elston, D.A. (2000) Regeneration of *Pinus sylvestris* in a natural pinewood in NE Scotland following reduction in grazing by *Cervus elaphus*. *Forest Ecology and Management*, **130**, 199–211.

Sibbald, A.M., Hooper, R.J., McLeod, J.E. & Gordon, I.J. (2011) Responses of red deer (*Cervus elaphus*) to regular disturbance by hill walkers. *European Journal of Wildlife Research*, **57**, 817–825.

Siipi, H. (2004) Naturalness in biological conservation. *Journal of Agricultural and Environmental Ethics*, **17**, 457–477.

Sinclair, A.R.E. (1997) Carrying capacity and the overabundance of deer. *The Science of Overabundance: Deer Ecology and Population Management*, pp. 380–394. Smithsonian Institution, Washington.

Smolko, P., Veselovská, A. & Kropil, R. (2018) Seasonal dynamics of forage for red deer in temperate forests: importance of the habitat properties, stand development stage and overstorey dynamics. *Wildlife Biology*, **2018**, wlb.00366.

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 ed J. Bennett. *Journal of Applied Ecology*, **57**, 1376–

1390.

Staines, B.W., Balharry, R. & Welch, D. (1995) The impact of red deer and their management on the natural heritage in the uplands. *Heaths and Moorland: Cultural Landscapes* (eds D.B.A. Thompson, A.J. Hester, & M.B. Usher), pp. 294–308. HMSO, Edinburgh.

Thirgood, S.J. (1995) The effects of sex, season and habitat availability on patterns of habitat use by fallow deer (*Dama dama*). *Journal of Zoology*, **235**, 645–659.

Trdan, S. & Vidrih, M. (2008) Quantifying the damage of red deer (*Cervus elaphus*) grazing on grassland production in southeastern Slovenia. *European Journal of Wildlife Research*, **54**, 138–141.

Wäber, K. (2010) *Landscape Scale Deer Management. PhD Thesis*. University of East Anglia.

Wäber, K., Spencer, J. & Dolman, P.M. (2013) Achieving landscape-scale deer management for biodiversity conservation: the need to consider sources and sinks. *Journal of Wildlife Management*, **77**, 726–736.

Westekemper, K., Reinecke, H., Signer, J., Meißner, M., Herzog, S. & Balkenhol, N. (2018) Stay on trails – effects of human recreation on the spatiotemporal behavior of red deer *Cervus elaphus* in a German national park. *Wildlife Biology*, **2018**.

Wright, L.J., Hoblyn, R.A., Sutherland, W.J. & Dolman, P.M. (2007) Reproductive success of woodlarks *Lullula arborea* in traditional and recently colonized habitats. *Bird Study*, **54**, 315–323.